

Phylogenetic Systematics of the Potamanthidae (Ephemeroptera)

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ABSTRACT

A comprehensive comparative morphological and distributional study of mayflies of the family Potamantidae (superfamily Ephemeroidea) resulted in the recognition of 23 included species. An analysis of cladistic relationships among them was based on 36 larval and adult characters. A phylogenetic classification, incorporating sequencing, was devised from a highly parsimonious cladogram. It entailed the following revision: Genus *Rhoenanthus* Eaton [= *Potamanthindus* Lestage, *Neopotamanthodes* Hsu, and *Neopotamanthus* Wu & You, new synonyms] (subgenus *Rhoenanthus* s.s.) includes *R. distafurcus*, new species and *R. speciosus* Eaton. *Rhoenanthus* (subgenus *Potamanthindus*, new status) includes *R. magnificus* Ulmer [= *R. vitalisi* Navás, *R. ferrugineus* Navás, and *Neopotamanthodes lanchi* Hsu, new synonyms]; *R. obscurus* Navás [= *Potamanthindus auratus* Lestage, new synonym]; *R. coreanus* (Yoon & Bae), new combination [= *R. rohdendorfi* Tshernova, new synonym]; and *R. youi* (Wu & You), new combination. Genus *Anthopotamus* McCafferty & Bae includes *A. distinctus* (Traver); *A. myops* (Walsh) [= *A. inequalis* (Needham) and *A. rufous* (Argo), new synonyms]; *A. verticis* (Say) [= *A. diaphanus* (Needham) and *A. walkeri* (Ide), new synonyms]; *A. neglectus neglectus* (Traver), new status; and *A. neglectus disjunctus*, new subspecies. *Potamanthus* Pictet [= *Potamanthodes* Ulmer and *Stygifloris* Bae, McCafferty & Edmunds, new synonyms] (subgenus *Potamanthus* s.s.) includes *P. huoshanensis* Wu; *P. luteus luteus* (Linnaeus), new status [= *P. ferreri* Pictet, new synonym]; and *P. luteus oriens*, new subspecies. *Potamanthus* (subgenus *Stygifloris*, new status) includes *P. sabahensis* (Bae, McCafferty & Edmunds), new combination. *Potamanthus* (subgenus *Potamanthodes*, new status) includes *P. macrophthalmus* (You), new combination; *P. yooni*, new species; *P. formosus* Eaton, combination revalidated [= *P. iyonis* Matsumura, new synonym]; *P. idiocerus*, new species; *P. kwangsiensis* (Hsu), new combination [= *Potamanthodes fujianensis* You, Wu, Gui & Hsu, new synonym]; *P. longitibius*, new species; *P. sangangensis* (You), new combination; and *P. yunnanensis* (You, Wu, Gui & Hsu), new combination. The latter six species are considered *sedis mutabilis* because exact branching sequences among them cannot be deciphered until certain life stages become known. *Potamanthus nanchangi* (Hsu), new combination, and *Potamanthus subcostalis* Navás, although appearing valid, are considered *incertae sedis* in that they cannot yet be placed to subgenus due to insufficient data. *Rhoenanthus shima* Matsumura is a *nomen dubium* excluded from Potamantidae.

The family is redefined; genera, subgenera, species, and subspecies are described, illustrated (half-tone habitus, line drawings, and SEM's), and keyed. Nomenclatural histories of all taxa are given; taxon distributions are plotted; and all materials examined are cited. Character polarities and distributions as well as the linear classification are tabulated; cladograms and phylograms are figured. Three major lineages involve *Rhoenanthus*, representing one of the initial branches (defined by six synapomorphies), and the opposite initial branch (defined by six synapomorphies) leading to the most recent hypothetical ancestor of *Anthopotamus* (defined by three synapomorphies) and *Potamanthus* (defined by four synapomorphies). The phylogeny and thus generic classification is highly reflective of considerable

previously unstudied larval characterization. The family demonstrates a Laurasian (Nearctic, Palearctic, and Oriental) distributional pattern. Area cladograms were generated to hypothesize historical biogeography of genera and subgenera, which is highlighted by a major East-West Hemispheric vicariance between North American *Anthopotamus* and Eurasian *Potamanthus*. A Wagner groundplan-divergence phylogram shows relative degree of evolutionary change among genera and subgenera. *Potamanthus* has reduced tusks and other apomorphies possibly related to differences in feeding or burrowing. All genera have filter-feeding larvae, however, based on correlations of ultrastructure and function, *Anthopotamus* is the most specialized.

INTRODUCTION

The family Potamanthidae is a well-established, distinct monophyletic lineage of the superfamily Ephemeroidea, or burrowing mayflies (McCafferty 1979, 1991b, McCafferty & Edmunds 1979, Landa & Soldán, 1985). Phylogenetic relationships within the family, however, have not been studied (McCafferty 1975a, Edmunds et al. 1976). The potamanthids, or hacklegills (McCafferty 1981), consist of only 23 species (herein), but as a group are widely distributed throughout the Holarctic and Oriental regions, including the Indian subcontinent (Fig. 1). The majority of the species are distributed in eastern and southeastern Asia.

The larvae of Potamanthidae (Fig. 11-17) are distinguished by somewhat dorsoventrally flattened bodies; small to large, somewhat convergent mandibular tusks projecting in front of the head; outspread legs; and posterolaterally oriented, fringed, and bilobed gills on abdominal segments 2-7. A distinct frontal process on the head and modifications of the legs, which are associated with burrowing in other ephemeroids (e.g., see Keltner & McCafferty 1986), are not present in potamanthids. The adults and subimagos of Potamanthidae are distinguished primarily by wing characters (Fig. 82-117). Besides a strongly arched MP_2 and CuA of the forewings, which is typical of all ephemeroids, the A_1 is distinctly forked, and the hindwings each have an acute costal projection. Depending on the species, adults and subimagos can have three well-developed caudal filaments, or the median terminal filament may be partially developed or rudimentary.

Based on species that have been studied, potamanthid larvae are generally found in medium-sized streams to large rivers where the current is moderately erosional (McCafferty 1975a, Bartholomae & Meier 1977, Munn & King 1987b, Watanabe 1988, Bae et al. 1990). The general morphological features of potamanthid larvae, especially the dorsoventrally flattened bodies and outspread, slender legs, has led to a historical conventional wisdom that they are "sprawlers" rather than "burrowers," which typically have cylindrical bodies and fossorial legs (e.g., McCafferty 1975a, Bartholomae & Meier 1977, Cummins et al. 1984). However, in a recent ecological study of *Anthopotamus* larvae, Bae & McCafferty (unpublished) demonstrated that they do burrow in mixed substrates (sand to cobble) and commonly reside in interstitial microhabitats or crevices, although they do not form or maintain well-defined tube-burrows as do most other burrowing mayflies. They are occasionally taken on the substrate surface and may be collected with devices commonly used for benthic macroinvertebrates; e.g., kickscreens or Surber samplers (see McCafferty 1981, Merritt et al. 1984).

In temperate regions, species of Potamanthidae are univoltine, overwinter as larvae, and have an emergence period from spring through summer (Ide 1935, Landa 1968, McCafferty 1975a, Bartholomae & Meier 1977, Macan 1979, Elliott & Humpesch 1983, Munn & King 1987a, Watanabe 1988). Based on collection records cited herein, emergence appears to

occur throughout the year in tropical or subtropical regions. The emergence of subimagos takes place at the water surface and may occur for several hours after dusk (Schoenemund 1930, Verrier 1956, Kite 1962, Munn & King 1987a, Watanabe 1989). Swarming and oviposition behavior has seldom been observed, suggesting that these activities may be nocturnal (Munn & King 1987a). We have commonly taken subimagos and adults at light at night near streams, but the capture of adults some 11 Km from the nearest larval habitat suggests that they fly considerable distances (Verrier 1956). Biological information is limited to observations of a few temperate species; most species have not been studied, and certain details of behavior and life history are lacking even for common species.

When Pictet (1843) formally established the name *Potamanthus* for the first known of these mayflies, the taxonomic concept of *Potamanthus* was still vague, and, in fact, certain mayflies from other families (Leptophlebiidae, Ephemerellidae) were lumped with them. Eaton (1868, 1871) refined the concept of *Potamanthus* (type species: *Ephemera lutea* Linnaeus 1767), and in so doing generally defined the family concept we use today. The forked A_1 of the forewings was the primary basis of this concept, and as a result, some workers (e.g., Lestage 1930, Ulmer 1939, Demoulin 1958) included some unrelated mayflies (Neophemeridae) with the Potamanthidae because their adults possess a similar A_1 . Eaton (1883-88) firmly established a concept of *Potamanthus* by adding larval characterization for the first time, later supplemented by Lestage (1930).

Albarda (1888) gained authorship for the family level grouping with the name Potamanthines, but his concept of the group was less restricted than that of Eaton. Jacobson & Bianchi (1905), however, recognized Eaton's (1868, 1871, 1883-88) concept at the subfamily category, and Klapálek (1909) was the first to recognize the taxon as a bona fide family. Since then, some workers conservatively recognized the taxon as a subfamily (e.g., Traver 1935, Burks 1953) or tribe (e.g., Lameere 1917, Handlirsch 1925) of Ephemeridae. However, ever since the mayfly classification given by Ulmer (1920a), European ephemeropterists have generally used the familial designation, and ever since the reclassification of mayflies by Edmunds & Traver (1954), the family categorization has been consistently used in all major works dealing with Ephemeroptera classification, including Demoulin (1958), Edmunds (1962), Tshernova (1970), Edmunds et al. (1976), McCafferty & Edmunds (1979), Landa & Soldán (1985), and McCafferty (1991b). Ulmer (1932-33) and Edmunds et al. (1963) provided world keys to families for adult and larval stages, respectively, although Ulmer included certain neophemerids in his Potamanthidae.

Eaton (1871) had a rather broad concept of *Potamanthus* but later (Eaton 1881) established *Rhoenanthus*, and Ulmer (1920b) established *Potamanthodes*. Lestage (1930) attempted to revise the family, adding four more genera. Of these, his *Potamanthellus*, *Rhoenanthodes*, and *Leucorhoenanthus* have all proven to be neophemerids (see Ulmer 1932, Edmunds 1961, Demoulin 1962, and Taxonomy, herein). Ulmer (1932) established *Rhoenanthopsis* and later (Ulmer 1939) established *Neophemeropsis*, which proved to be a neophemerid (Burks 1953). Hsu (1937-38b) described *Neopotamanthodes*, and Wu & You (1986) described *Neopotamanthus* (see Taxonomy, below). More recently, Bae et al. (1990) described *Stygifloris*, and McCafferty & Bae (1990) established *Anthopotamus*.

The genera and subgenera, as they are herein revised, appeared in the phylogenetic classificatory list (list 2) of the Ephemeroidea presented by McCafferty (1991b). Because of an inadvertent type setting error, however, *Potamanthus* was listed as "subgenus" rather than "genus." It was then correctly followed by "subgenus *Potamanthus*," "subgenus *Stygifloris*," and "subgenus *Potamanthodes*." Because the incorrect listing of "subgenus *Potamanthus*" followed "genus *Anthopotamus*," it could erroneously appear that *Potamanthus* and its subgenera are all subgenera of *Anthopotamus*. *Potamanthus*, obviously, could never be

regarded as a subgenus of *Anthopotamus*, under any circumstances, because of the priority of the name *Potamanthus*.

With respect to species, the single potamanthid species in Europe, *Potamanthus luteus*, has been reported from almost all European countries since Linnaeus listed the species as *Ephemera lutea* in 1767 in the 12th edition of his *Systema Naturae*. In the late 19th and early 20th Centuries, the potamanthid fauna of Southeast Asia and India was investigated by European workers who had access to material from that region. Eaton (1881, 1892) described two species from Sumatra and Tenasserim Valley in Burma, Ulmer (1920b), Navás (1922, 1930), and Lestage (1930) described new species from Tonkin (Vietnam), and Navás (1931) described a new species from northern India (see *Rhoenanthus* and *Potamanthus*, below). More recently, Bae et al. (1990) described a new species from northern Borneo. Hsu (1935-36, 1937-38a, 1937-38b) was the first to describe species from China, but recently, additional species have been described by You et al. (1980, 1982), You (1984), Wu & You (1986), and Wu (1987b) (see *Rhoenanthus* and *Potamanthodes*, below). In Far East Asia, Matsumura (1931) and Imanishi (1940) described species from Japan, Imanishi (1940) reported a larva of *Potamanthus* from Manchuria, Yoon & Bae (1985) described a species from Korea, and Tshernova (1985) described the same species from the far eastern USSR (see *Rhoenanthus* and *Potamanthus*, below).

The North American potamanthids, which are limited to the eastern half of the continent (Northeastern and Southeastern geographic regions of McCafferty & Waltz 1990), were recently placed in the genus *Anthopotamus* by McCafferty & Bae (1990). Say (1839) had described the first North American potamanthid species (from Indiana) under the name of *Baetis verticis* (see McCafferty & Bae 1991). Subsequently, Walsh (1863) described a second species under the name *Ephemera*, and additional species were described by Needham (1907, 1908), Banks (1908), Morgan (1913), Argo (1927), Traver (1935), and Ide (1935). Many of these species, however, have proven to be synonyms of each other (see *Anthopotamus*, below). Studies aimed at reviewing or revising the North American potamanthids have been conducted by Needham (1920), Argo (1927), McDunnough (1926), Traver (1935), Burks (1953), and McCafferty (1975a).

Historically, studies of Potamanthidae have been based on adult characterization. The larvae of Potamanthidae, including morphological and ecological characters of systematic importance, have not been previously studied to any extent. Only by a comprehensive study of comparative larval morphology has the present revision of genera and species been possible.

The specific objectives of this study have been 1) to delineate and describe each species of the Potamanthidae; 2) to determine the most likely relationships of these species based on cladistic methodology; 3) to revise the supraspecific classification within the family so that it is consistent with the phylogeny and excludes any paraphyletic as well as polyphyletic groupings; 4) to apply phylogenetic findings to interpreting historical biogeography; and 5) to present inferences regarding evolutionary adaptations in and among the Potamanthidae, as much as the current state of ecological, behavioral, and functional morphology knowledge will allow.

The data resulting from this work are given under Taxonomy, Phylogeny and Phylogenetic Classification, Historical Biogeography, and Evolution sections. Cladistic methodology employed herein, deduced character state polarities, and methods for hypothesizing historical events or transitions associated with phylogeny are given in those pertinent sections. Our generic, subgeneric, and specific classification is derived from the results of our phylogenetic analysis. It is also herein ordered linearly in a strict phylogenetic sense rather than alphabetically; however, the use of the Table of Contents will allow any particular taxa to be located quickly without presuming a knowledge of phylogeny.

CHARACTERS AND MATERIALS

Larval Characters

Size. Length of body is given as the dorsal distance from the anterior margin of the clypeus to the posterior margin of tergum 10, and thus excludes mandibular tusks and caudal filaments.

Coloration. Although color patterns may vary within species or even within populations, patterns can be sometimes useful in DIAGNOSIS.— In general, two basic types of patterns are found in potamanthid larvae. A *Potamanthus*-type pattern (Fig. 15) is typified by a brown to dark brown ground color with various light markings on the head, thorax, and abdomen, including a pair of C-shaped markings in the medioposterior region of the pronotum, as well as median and paired submedian longitudinal stripes on abdominal terga 1-10. A *Rhoenanthus*-type pattern (Fig. 13) is typified by a brown to purplish brown ground color with various dorsal light markings on the head and thorax, but never with a pair of C-shaped medioposterior markings on the pronotum. The abdominal terga often have two pairs of submedian spots (a pair of teardrop-shaped markings and a pair of tiny round spots).

Armature. Setae of the mouthparts and forelegs that are functionally related to feeding and burrowing habits in mayfly larvae (Strenger 1953, 1973, 1975, 1977, 1979, Froehlich 1964, Soldán 1979, Wallace & Merritt 1980, Keltner & McCafferty 1986, McShaffrey & McCafferty 1986, 1988, 1990) were found to be important taxonomic characters in the Potamanthidae. The terminology and classification of setae are modified from those from Farmer (1974) as follows.

Simple Setae. These have a smooth surface, lack setules, and are not divided; they include simple-stout setae (Fig. 38-47), which have a relatively small length/width ratio and are found, e.g., on tusks and legs. They often appear as small socketed spines and are also technically referred to as spurs. Simple setae also include simple-hairlike setae, which are pointed apically, have relatively large length/width ratios, and are found along the lateral margins of caudal filaments.

Pectinate Setae. These bear a row or rows of setules arising along their shaft (such setules may be in single row as in Fig. 66-69, or multiple rows as in Fig. 48, 65, but are most often double rowed, or bipectinate). They include bipectinate-stout setae, which are short and stout, with weak and often rudimentary setules (they are often the early stage of bipectinate-hairlike setae); bipectinate-lanceolate setae (Fig. 61, 74-75), which are short to medium sized, blade-like, often flattened apically, and have pointed setules; and bipectinate-hairlike setae (Fig. 48-59, 65-69), which are long, often with hooked tips, and have pointed or peglike setules that are even or uneven in length (most common on mouthparts and forelegs of potamanthid larvae).

Pilose Setae (Fig. 60). These are hairlike setae bearing numerous small setules arising randomly over the surface.

The shape of the setule can sometimes be important; i.e., hairlike (Fig. 49), hooklike (Fig. 66), peglike (Fig. 69), or bladelike (Fig. 61). The evenness of the setules can be important and sometimes longer setules alternate with 3-4 shorter setules (Fig. 68). Palmate, pinnate, and furcate setae are not found in Potamanthidae.

Large apical spines on the mandibular tusks (Fig. 26, 28) or on the apices of foretibiae (Fig. 34) as well as humplike processes on the dorsal surface of the mandibular tusks (Fig. 40) are also important characters.

Compound Eyes. Relative size of compound eyes of mature larvae is an important character because it reflects the important diagnostic eye-size characteristics of the adults. Relative size of compound eyes of mature larvae was measured by the formula $ES = B / D$

(where ES: compound eye size, B: shortest distance between compound eyes, D: longest dorsal diameter of a compound eye) as in adult compound eyes. We apply relative size terms for eyes of mature larvae as follows: full-sized (ES = 0.5-2.0, Fig. 11-13, 15-16, 142) and minute (ES = 2.1-4.0, Fig. 14, 17, 143).

Clypeus. Only setation characteristics were found to be taxonomically useful.

Mandibles. The mandibular base and the broad nonconstricted base of the tusks are referred to as the body of the mandible; the narrow apical portion is referred to as the tusks, proper. Armature, relative length, degree of apical constriction, angle, and curvature are all important. Armature is noted by presence or absence of an apical spine and the abundance and distribution of simple-stout and bipectinate-hairlike setae on the dorsal and lateral surfaces. Length is measured along a direct line of the longitudinal plane from the base of the medial margin to the apex of the tusk. The angle is that between the direct line of length and the line in the longitudinal plane along the outer margin of the incisors. The curvature is measured by the angle between the direct line of length of tusk and the direct line from base of the medial margin to midlength of the tusk. Curvature was not applicable to short-tusked larvae.

Maxillae. In most Potamanthidae species, the crown of the galealaciniae is slightly to moderately angled from the lateral margin and bears well-developed bipectinate-hairlike setae (Fig. 58-59) on 2/3 to 3/4 of the apical surface. But in one species, the crown of the galealaciniae is clearly demarcated from the lateral margin, appearing truncate, and bears longer, well-developed bipectinate-hairlike setae on the entire margin (Fig. 19). Setation of the maxillary palpi (measured by abundance, relative length, or arrangement of bipectinate-hairlike setae), relative length of the terminal segment of the palpi compared to segment 2, and slenderness of the terminal segment of the palpi are important at the supraspecific level.

Hypopharynx. Setation (measured by abundance and relative length of setules) (Fig. 63-64) and degree of lateral expansion of the superlinguae are useful in differentiating certain species.

Labium. Setation (measured by distribution and abundance of bipectinate-hairlike setae) of the paraglossae, degree of lateral expansion of the paraglossae, setation of the palpi (measured by abundance and relative size of simple-stout setae along their medial margin and distribution and abundance of bipectinate-hairlike setae), degree of medial expansion of the terminal segment of the palpi (Fig. 44-47), and relative length of the terminal segment of the palpi compared to segment 2 are useful at either the specific or supraspecific levels.

Pronotum. Variation in the relative expansion of the lateral margins of the pronotum is of some taxonomic importance, as is the degree of development of the anterolateral corners, which appear as spine-like processes in some.

Forelegs. Dorsal setation of the forefemora (measured by abundance and distribution of simple-stout setae or bipectinate-hairlike setae) is important in supraspecific and certain specific classifications. The presence of a dorsal row of simple-stout setae (Fig. 72) on the forefemora is an especially important character in distinguishing the subgenera *Stygifloris* and *Potamanthodes*. Setation of the foretibiae and foretarsi (measured by relative length, abundance, distribution, and arrangement of bipectinate-hairlike setae and relative length, abundance, and arrangement of setules on bipectinate-hairlike setae) is important at supraspecific or specific levels. The relative length of the foretibiae to the forefemora or foretarsi varies among taxa, and the presence of a ventral tuft of bipectinate-hairlike setae subapically on the foretibiae (Fig. 73) distinguishes *Stygifloris* and *Potamanthodes*.

Gills. The orientation, segmentation, and setation of gills 1 distinguish the family, and the arrangement (either single-rowed or multiple-rowed basally) of fibrillae of gills 2-7 are important at the supraspecific level.

Adult Characters

Size. Body length, compound eye diameter, distance between compound eyes, antennae length, forewings length and width, hindwings length and width, foreleg segments length, genital forceps length, penes length, cerci length, and median terminal filament length were measured. The length of the body was taken as the distance between the frons and the posterior margin of abdominal segment 10. Compound eye measurements are discussed below. Foreleg length was measured from the base of the forefemora to the apex of the tarsal segment 5. Penes length was measured from the posterior margin of the subgenital plate to the apex of the penal lobe.

Coloration. In general, most adults of the Potamanthidae have white to yellowish brown or light brown ground coloration with various brown to dark brown, sometimes purplish brown markings. Conspicuous differences among taxa include the presence or absence of markings as follows: median and pair of lateral stripes on the head and thorax; stripes and triangularly arranged dark spots on the forewings; U-shaped marking, pairs of teardrop-shaped and of tiny round markings, and pair of dark lateral spots on the abdominal terga; and dark bands on the caudal filaments.

Compound Eyes. Relative size of compound eyes of male and female adults was measured by the formula $ES = B / D$ (where ES: compound eye size, B: shortest distance between compound eyes, D: longest dorsal diameter of a compound eye). The relative eye sizes encountered among potamanthids are shown graphically in Fig. 146-150. We apply relative size terms, in order of decreasing size, as follows: large (ES = 0.0-0.2, Fig. 146), medium-sized (ES = 0.3-0.5, Fig. 147), small (ES = 0.6-0.9, Fig. 148), very small (ES = 0.9-1.6, Fig. 149), and tiny (ES = 1.7-3.0, Fig. 150).

Forewings. Venation and pigmentation of the forewings are important taxonomic characters. The distal branch of the forked A_1 may be slightly (Fig. 83) to greatly (Fig. 94) pronounced. In one species, A_1 appears to be forked twice (Fig. 82). The MA sector is subequal to, or shorter than MA_1 in all Potamanthidae except in the subgenus *Potamanthus*, where the relative length of MAs varies among individuals. Although CuA and MP_2 are always arched basally, some species have MP_2 basally connected to CuA (Fig. 82-83, 96-99). The numbers of crossveins between Sc and R_1 or between R_1 and R_2 are of importance in distinguishing certain species, and the concentration of 3-5 crossveins near the bullae is of importance in distinguishing certain species of the subgenus *Potamanthindus*. The number of basal crossveins between MP_1 and MP_2 is sometimes of importance. The pigmentation of veins, infuscation of crossveins, and presence of stained markings and their patterns are important. Infuscation is the dark shading that can border crossveins laterally, and sometimes appear convex (e.g., Fig. 82-90, 93-94, 96-99). Species of the subgenus *Potamanthodes* tend to have heavy infuscation developed into irregular blotches within the costal region of the forewings. Sexual dimorphism with regard to infuscation and membrane staining is present in certain species.

Hindwings. The costal projection is basally oriented in Potamanthidae, but the shape of the costal projection, although acute in most species, is rounded in a few species. The development of the basal arch of R_1 (Fig. 115-117), as measured by the angle between the short diagonal base and the long horizontal line of R_1 , is an important character that distinguishes the subgenus *Potamanthodes*, whereas relative length of R_s to R_2 and MP_s (MP sector) to MP_1 , although used in previous treatments of Potamanthidae, were found to vary individually (0.6-2.1, 0.2-1.0, respectively). In *Rhoenanthus*, MP_2 is basally connected to CuA , and together with the base of MP_1 and crossveins MP_1 -IMP and IMP- MP_2 , form a MP-cell (Fig. 100-106). Infuscation and other staining of the wing membrane are sometimes useful at either supraspecific or specific levels.

Forelegs. Color patterns and relative length of foretibiae to forefemora or foretarsi vary among certain species.

Genitalia. The shape of the subgenital plate [e.g., concave (Fig. 118-123) vs convex (Fig. 124-133)] varies among genera. The shape of the terminal segment of the genital forceps [e.g., rounded (Fig. 129) vs notched apically (Fig. 131), and presence (Fig. 122) vs absence (Fig. 124) of medial expansion] varies among certain species. The shape of the penal lobe [e.g., flattened (Fig. 134) vs cylindrical (Fig. 141)], shape of apex [e.g., pointed (Fig. 129), rounded (Fig. 118), or notched (Fig. 133)], lateral expansions, and point of furcation are important at either supraspecific or specific levels. Penes that are described as Y-shaped (Fig. 129-130) are cylindrical, apically divergent and pointed penes without any lateral expansions or lobes.

Caudal Filaments. The length of the terminal filament compared to that of the cerci is an important generic level character. In some species, the terminal filament is developed in females but rudimentary in males. Relationship of the length of the cerci and body varies among some species.

Egg Characters

Eggs of exemplar species of each genus (*Rhoenanthus obscurus*, *R. coreanus*, *Anthopotamus distinctus*, *A. myops*, *A. verticis*, *Potamanthus luteus luteus*, *P. sabahensis*, *P. yooni*, and *P. formosus*) were examined. Terminology is based on Koss (1968, 1970) and Koss & Edmunds (1974). Number and shape of polar caps (Fig. 76-78) and shape of micropyle (Fig. 80-81) are important in distinguishing the family. Although relative size and abundance of tubercles on the chorion (Fig. 76-81) are somewhat larger and sparser in *Potamanthus* compared with *Rhoenanthus* and *Anthopotamus*, the character is too subtle to be of practical use for diagnosing genera (Koss & Edmunds 1974). Differences that were consistent and of practical use could not be found in egg structure.

Internal Anatomical Characters

Data on internal anatomy are mainly taken from Landa (1948, 1969), Soldán (1981), and Landa & Soldán (1985) that were based on materials of *Rhoenanthopsis* sp. [= *Rhoenanthus obscurus*], *Potamanthus* sp. [= *Anthopotamus myops* or *A. verticis*], *Potamanthus luteus* [= *Potamanthus luteus luteus*], and *Potamanthodes* sp. [= *Potamanthus formosus*]. We additionally examined *Rhoenanthus coreanus* and *Anthopotamus verticis*.

Materials

The material examined for this study included over 3,200 adult and subimaginal specimens, both pinned and fluid preserved, and over 2,300 larval specimens. Numerous collections from throughout the world were used (see e.g., the acronym list, below). Reared associations of life stages were especially valuable. Type specimens (34 primary types and 295 secondary types) were loaned to us in most instances, but the Museum of Comparative Zoology at Harvard University was visited for examination of the many types held there.

For each species or subspecies treated, "Type Material Examined" is noted, as is "Other Material Examined." For each type, the stage (larva, adult, or subimago), sex, preservation method (larvae may be assumed to be preserved in alcohol unless otherwise indicated), institutional type designation number (if any), our own specimen identification number, locality, date, collector(s), collecting method, and institution of deposition are provided when such data are available. For other material examined, the most pertinent information is noted but preservation methods, collectors, and collecting methods are not given to conserve space, unless very important. The order of listing of material is alphabetical by nation, state or

province, and county or other geographical subunit. Any additional important information about specimens is provided within brackets.

The following abbreviations are used for the sex and stage of specimens:

L	larva	Ms	male subimago
M	male adult	Fs	female subimago
F	female adult		

Abbreviations of frequently used locale words are as follows:

Prov	Province		
Co	County	S	South
R	River	E	East
Cr	Creek	W	West
Mt	Mountain	km	kilometer
Nat	National	mi	mile
St	State	fk	fork
Pk	Park	jct	junction
Hwy	Highway	nr	near
Br	Bridge		
N	North		

Prepositions and articles are generally omitted to conserve space.

Collections and their Acronyms

BAR	(Museum of Barcelona) Ajuntament de Barcelona, Museu de Zoologia, Apartat de Correus 593, Parc de la Ciutadella, 08003 Barcelona, Spain.
BER	(Berlin Museum) Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Invalidenstr. 43, 1040 Berlin, Germany.
BM	(British Museum of Natural History) Entomology Department, British Museum of Natural History, Cromwell Rd., London SW7 5BD, England.
CU	(Cornell University) Dept. of Entomology, Cornell University, Ithaca, New York 14853.
CSU	(Colorado State University) Dept. of Entomology, Colorado State University, Fort Collins, Colorado 80523.
FAMU	(Florida A & M University) Dept. of Entomology & Structural Pest Control, Florida A & M University, Tallahassee, Florida 32307.
FEM	(Frost Entomological Museum) Dept. of Entomology, Pennsylvania State University, University Park, Pennsylvania 16802.
FIC	(Freshwater Institute of Canada) 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada.
HAM	(Hamburg Museum) Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin Luther King Platz #3, D-2000 Hamburg 13, Germany.
INHS	(Illinois Natural History Survey) Natural Resources Bldg., 607 East Peabody Dr., Champaign, Illinois 61820.
KAGU	(Kagawa University) Environmental Science Lab., Kagawa University, Takamatsu, Kagawa 760, Japan.
KBS	(Kansas Biological Survey) State Biological Survey of Kansas, 2045 Ave. A. Campus West, Lawrence, Kansas 66044.

- KEI (Korean Entomological Institute) Korean Entomological Institute, Korea University, 1 Anam-dong, Songbuk-ku, Seoul 136-701, Korea.
- KYOU (Ohtsu Hydrobiological Station) Ohtsu Hydrobiological Station, Kyoto University, Kyoto 606, Japan.
- LENU (Leningrad University) Dept. of Entomology, Leningrad University, Leningrad 199034, USSR.
- MARU (Marshall University) Dept. of Biological Science, Marshall University, Huntington, West Virginia 25701.
- MCZ (Museum of Comparative Zoology) Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138.
- NNU (Nanjing Normal University) Dept. of Biology, Nanjing Normal University, 122 Ning Hai Road, Nanjing, The People's Republic of China.
- NYSM (New York State Museum) New York State Museum, Collection Management, Albany, New York 12230.
- PERC (Purdue Entomological Research Coll.) Dept. of Entomology, Purdue University, West Lafayette, Indiana 47907.
- PM (Paris Museum) Muséum National de'Histoire Naturelle, Laboratoire d'Entomologie, 45 Rue de Buffon, F-75005 Paris, France.
- ROM (Royal Ontario Museum) Royal Ontario Museum of Zoology, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada.
- UFL (University of Florida) Dept. of Zoology, University of Florida, Gainesville, Florida 32611.
- UGRA (University of Granada) Departamento de Biología, Universidad de Granada, 18071 Granada, Spain.
- UME (University of Maine) Dept. of Entomology, Univ. of Maine, Orono, Maine 04469.
- UMN (University of Minnesota) Dept. of Entomology, Univ. of Minnesota, St. Paul, Minnesota 55108.
- UMOS (University of Moscow) Department of Entomology, University of Moscow, Moscow, USSR.
- USNM (U. S. National Museum of Natural History) National Museum of Natural History - Smithsonian Institution, Washington, D.C. 20560.
- UU (University of Utah) Dept. of Biology, University of Utah, Salt Lake City, Utah 84112.
- UWI (University of Wisconsin) Dept. of Entomology, Univ. of Wisconsin, Madison, Wisconsin 53706.
- WIEN (Vienna Museum) Naturhistorisches Museum Wien, Zweite Zoologische Abteilung - Insekten, Burgring 7, A-1014 Wien, Austria.

DESCRIPTIONS OF TAXA

Family Potamanthidae

LARVA.— *General Form*: Length of last instar body 7.5-30.0 mm, caudal filaments 4.5-16.0 mm. Body somewhat flattened; dorsum either bare or with scattered pilose setae (Fig. 36-37, 60); sternum without setae; legs and gills laterally oriented (Fig. 11-17). *Head*: Compound eyes of mature male larvae minute to full-sized ($ES=0.73-3.67$). Frons not produced into distinct frontal process. Vertex without processes dorsal to antennae. Anterior margin of clypeus convex. Mandibles (Fig. 11-17, 26-43) extending as tusks anteriorly from head, 0.1-2.3x length of head; body of mandibles with numerous simple-stout setae mixed with variable number of bipectinate-hairlike setae (setules weakly to moderately developed as in

Fig. 48-51) on at least lateral margin; tusks narrow, convergent apically, slightly upcurved when fully developed, round in cross section, attenuated, and with or without some simple-stout setae laterally. Maxillae (Fig. 18-25) with more-or-less distinct galealacinal crown bearing bipectinate-hairlike setae (setules well developed as in Fig. 58-59); palpi distinctly 3-segmented, never twice or more length of galealacinae; terminal segment of maxillary palpi 1.0-4.0x length of segment 2, with scattered bipectinate-hairlike setae (setules well-developed as in Fig. 52-57) variously developed in apical half and along medial margin. Labial palpi (Fig. 18-25) 3-segmented and laterally oriented; terminal segment of labial palpi (Fig. 44-47) falcate to symmetrically pointed, 0.8-2.7x length of segment 2, with weak to well-developed scattered bipectinate-hairlike setae, and with rows of 10-30 simple-stout setae on medial margin. *Thorax*: Convex lateral margin of pronotum (Fig. 11-17) moderately to strongly pronounced. Coxae with acute dorsal process (Fig. 12). Forefemora (Fig. 26, 70, 72) dorsally with scattered simple-stout setae sometimes intermixed with well-developed bipectinate-hairlike setae. Foretibiae (Fig. 26, 30-31, 33-34, 70-71) cylindrical, not greatly expanded, with long bipectinate-hairlike setae. Hindfemora and hindtibiae with well-developed bipectinate-lanceolate or pinnate setae on anterior margin (Fig. 61, 74-75); hindtibiae without terminal tibial process. *Abdomen*: Gills (Fig. 11-17) 1 single, 2-segmented, and anterolaterally oriented; each lamella of gills 2-7 with 20-70 lateral marginal fibrillae.

ADULT.—*Head*: Compound eyes of male tiny to large (0.28-1.60 mm dorsal diameter), nearly contiguous to widely separated ($ES = 0.02-2.89$) and narrowly developed ventrally as seen in facial view (ventrally developed portion often darker). *Thorax*: Wings hyaline, heavily stained in some species, sometimes only in females (Fig. 86, 105). Forewings (Fig. 82-85, 87-92, 94-95, 97-99) with MAs 0.6-1.3x length of MA₁; MP₂ very strongly arched basally (apex of arch juxtaposed or directly connected to CuA and appearing derived from CuA); 2-5 cubital intercalaries present (1-4 of them forked); A₁ forked, without attaching veinlets; angle between A₁ and R₁ greater than 80°. Hindwings (Fig. 100-104, 106-110, 112-113, 115-117) with costal projections well-developed and basally oriented. All legs of both sexes functional and fully developed. *Abdomen*: Male genitalia (Fig. 118-141) with 3-segmented forceps; basal segment longest (segment 2 and 3 together 0.19-0.61x length of basal segment). Female subanal plate variously notched. Male median terminal filament 0.02-0.97x length of cerci; female terminal filament 0.05-1.00x length of cerci.

INTERNAL ANATOMY.—*Nervous System*: Ganglia present in prothorax, mesothorax, metathorax, and abdominal segments 2-7; abdominal ganglia 1 missing; abdominal ganglia 7 and 8 fused in abdominal segment 7 [Fig. I, 6 in Landa & Soldán (1985)]. *Tracheal System*: Tracheal anastomosis in abdominal segments 3-9 [as in Fig. VI, 31 in Landa & Soldán (1985)]. Visceral tracheae in metathorax and abdominal segments 4-8 [as in Fig. IX, 41 in Landa & Soldán (1985)]. *Alimentary System*: Stomodaeum not distinguishable from mesenteron; mesenteron and posterior oesophagus subequal in width. Colon in abdominal segment 7 or extended to segment 8. Malpighian tubules coiled [Tab. 13, Fig. 1 in Landa (1948)]; 6 trunks branched outwardly; one long trunk on either side, and two short trunks on dorsal and ventral side [as in Fig. XVI, 75 in Landa & Soldán (1985)]. *Reproductive Organs*: Testes lateral in metathorax and abdominal segments 1-6 [Fig. 7 in Soldán (1981)], cylindrical, moderately flattened, bluntly pointed or rounded in thorax [Fig. 219-220 in Soldán (1981)]; testicular follicles equal in length and size, arranged into regular longitudinal rows, perpendicular to vas deferens; seminal vesicle formed by suddenly expanded vas deferens in abdominal segments 8-9. Ovaries lateral in mesothorax, metathorax, and abdominal segments 1-6 [Fig. 12 in Soldán (1981)], tongue-shaped, bilaterally flattened, pointed or bluntly pointed in thorax [Fig. 223 in Soldán (1981)]; ovarioles well developed, slightly or moderately oblique to oviductus lateralis [Fig. 227, 229 in Soldán (1981)].

EGG.— *Size and Coloration*: Long axis (excluding polar caps) 123-150 mm; short axis 85-116 mm. Color pale yellow to yellow in nature, white in alcohol (polar caps white in nature and in alcohol). *Chorionic Sculpturing*: Egg surface with numerous scattered tubercles (Fig. 76-81); basal diameter of tubercle 0.1-1.5 mm. *Chorionic Structure*: Eight-12 knob-terminated coiled threads present (Fig. 76-79), nearly evenly distributed at each pole, with diameters 10-14 mm (0.06-0.10x long axis of egg). Two large polar caps (Fig. 76-78) present, shape hemispheric to conical, with basal diameter 48-68 mm (0.49-0.60x short axis of egg) and height 29-35 mm (0.26-0.35x long axis of egg). Micropyle (Fig. 76-78, 80-81) single, tageniform; micropylar opening and micropylar canal located at midlength between polar caps and vertical to long axis of egg. Sperm guide circular to somewhat ovoid; diameter 10-16 mm (0.08-0.13x long axis of egg).

DIAGNOSIS.— The larvae of Potamanthidae (Fig. 11-17) are distinguished from those of Ephemeridae and Polymitarciidae (with the exception of Euthyplociinae and Exeuthyplociinae) by their somewhat flattened body, absence of distinct frontal process, outspread legs, cylindrical foretibiae, lateral gills 2-7, and anterolaterally oriented, 2-segmented, and setaceous gills 1; they are distinguished from Euthyplociinae and Exeuthyplociinae by their shorter mandibles (less than 2.3x length of head), lack of long hairlike setae on the tusks, relatively short maxillary palpi (less than 2.0x length of galealaciniae), and anterolaterally oriented, 2-segmented, and setaceous gills 1. The adults of Potamanthidae are distinguished from those of Ephemeridae and Polymitarciidae by their distinctly forked A_1 of forewings and the absence of attaching veinlets in this region (Fig. 82-99). Eggs of Potamanthidae (Fig. 76-81) are distinguished from those of Ephemeridae and Polymitarciidae by their two large polar caps and tageniform micropyle. Internal anatomy is generally similar to other Ephemeroidea, but the lateral orientation of gonads of Potamanthidae is somewhat different from that of Ephemeridae and Polymitarciidae, which possess gonads ventrolaterally (Soldán 1981, Landa & Soldán 1985).

DISTRIBUTION.— Fig. 1: Palearctic (reported herein or elsewhere from USSR, Korea, Japan, Mongolia, China, Turkey, Syria, European nations, northern Morocco, northern Algeria); Oriental (southern China, Taiwan, Vietnam, Laos, Cambodia, Thailand, Burma, Malaysia, Indonesia, India); Nearctic (eastern USA, southeastern Canada).

Genus RHOENANTHUS

Rhoenanthus Eaton, 1881. Entomol. Month. Mag. 17: 192 [Type species: *Rhoenanthus speciosus* Eaton, 1881, by monotypy].

Potamanthindus Lestage, 1930. Mem. Soc. Entomol. Belg. 23: 123 [Type species: *Potamanthindus auratus* Lestage, 1930, by monotypy], NEW SYNONYM, previously synonymized with *Potamanthodes* Ulmer, 1920b, by Tshernova (1985).

Rhoenanthopsis Ulmer, 1932. Stett. Entomol. Zeit. 93: 212 [Type species: *Rhoenanthus magnificus* Ulmer, 1920b, by monotypy], synonymized by Tshernova (1985).

Neopotamanthodes Hsu, 1937-38b. Peking Nat. Hist. Bull. 12: 221 [Type species: *Neopotamanthodes lanchi* Hsu, 1937-38b, by original designation], NEW SYNONYM, previously synonymized with *Potamanthodes* Ulmer, 1920b, by Tshernova (1985).

Neopotamanthus Wu & You, 1986. Acta Zootaxon. Sin. 11: 401 [Type species: *Neopotamanthus youi* Wu & You, 1986, by monotypy], NEW SYNONYM.

MATURE LARVA.— *Dimensions* (mm): Length of body 12.5-30.0, mandibles 1.2-4.6, caudal filaments 7.0-16.0. *Head*: Compound eyes of mature male larvae full-sized (ES =

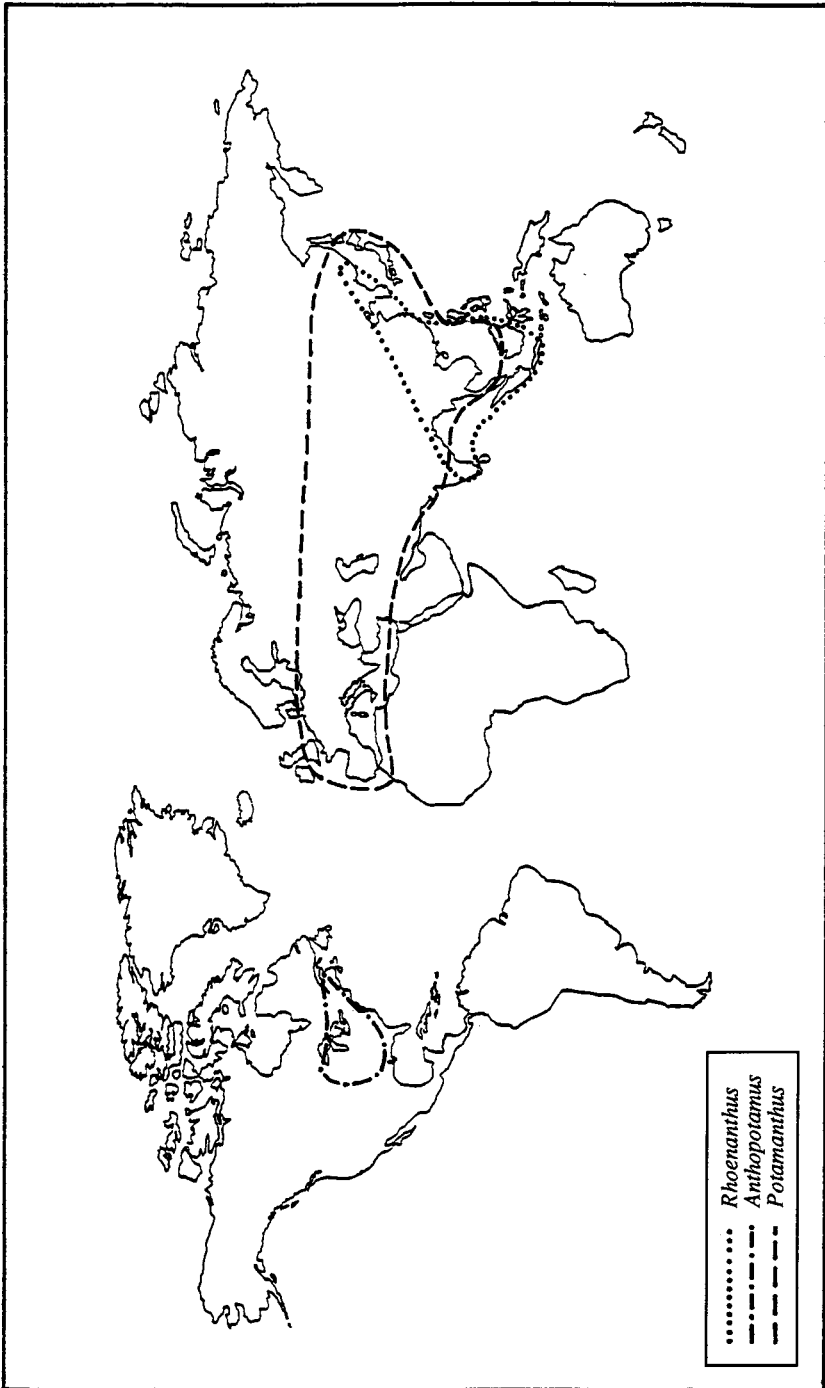
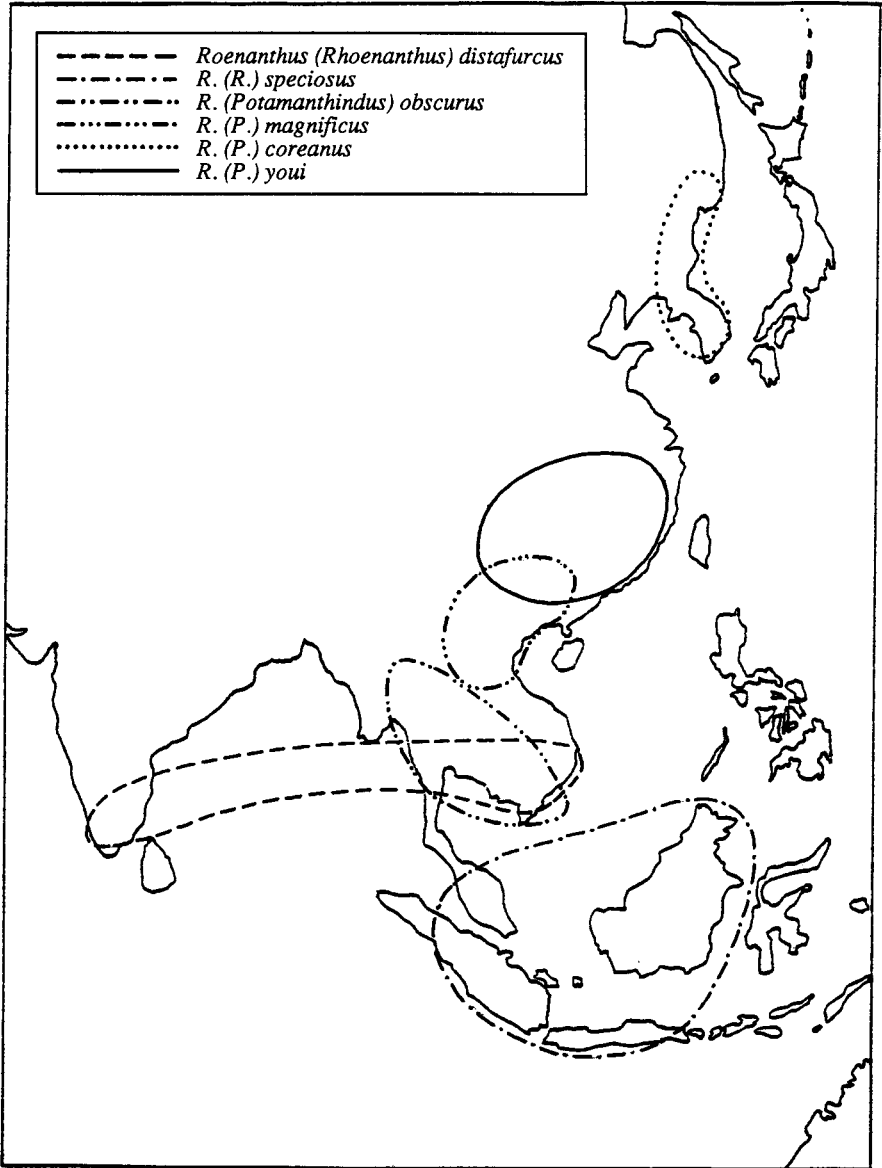


FIGURE 1. Distribution of Potamantidae.

1.12-2.13) (Fig. 11-13). Clypeus (Fig. 26-29) with both simple-stout and bipectinate-hairlike setae (setules on bipectinate-hairlike setae weakly developed as in Fig. 65) on dorsal surface. Mandibles (Fig. 11-13, 26-29) developed into long tusks, 0.9-2.3x length of head, moderately to strongly arched inward (15-28°); body of mandibles (Fig. 38-39) dorsally bare, but with 20-55 simple-stout setae mixed with 4-20 bipectinate-hairlike setae (setules weakly to moderately developed as in Fig. 48) on lateral surface; tusks with 0-8 simple-stout lateral setae, and with or without large, lateral, subapical spine (when large spine present, tusks may appear forked terminally as in Fig. 26). Terminal segment of maxillary palpi 1.7-4.0x length of segment 2, with rows of bipectinate-hairlike setae (setules well developed as in Fig. 52-55) along medial margin. Hypopharynx moderately to greatly expanded laterally. Labium with paraglossae (Fig. 18-20) greatly expanded laterally, without ventral bipectinate-hairlike setae; terminal segment of labial palpi (Fig. 18-20) falcate, 1.3-1.9x length of segment 2; medial margin of terminal segment (Fig. 44) with 2-3 rows of 15-30 large simple-stout setae, and without bipectinate-hairlike setae. *Thorax*: Pronotum (Fig. 11-13, 26-27) greatly produced laterally; anterolateral corners each produced into acute spinelike process. Forefemora (Fig. 11-13, 26-27) dorsally with well-developed bipectinate-hairlike setae (setules weakly developed as in Fig. 62) intermixing with relatively sparse simple-stout setae along anterior and posterior margins, with band of cuticle devoid of setae running lengthwise near posterior border. Foretibiae (Fig. 11-13, 26) 1.2-1.5x length of forefemora, 2.3-2.8x length of foretarsi, with long bipectinate-hairlike setae (setules weakly to moderately developed as in Fig. 66) irregularly distributed on both anterior margin and dorsal surface, and without ventral, subapical tuft of bipectinate-hairlike setae. *Abdomen*: Terga 1-10 (Fig. 11-13) often with pair of light, submedian, teardrop-shaped spots and pair of tiny round spots within dark, broad, midlongitudinal stripe (Fig. 11-13). Gills (Fig. 11-13) 2-7 with 20-70 marginal fibrillae arranged in double rows basally and in single row apically.

MALE ADULT.—*Dimensions (mm) & Coloration*: Length of body 12.0-18.0, forewings 9.5-15.0, hindwings 3.7-6.3, forelegs 7.8-14.4, genital forceps 1.02-1.76, cerci 21.4-50.0, median terminal filament 0.8-7.0; width of forewings 4.1-6.7, hindwings 2.6-4.7. Body ground color pale yellow or light brown; with purplish brown markings. *Head*: Compound eyes large (1.00-1.60 mm dorsal diameter) (ES=0.03-0.21). *Thorax*: Pronotum width 2.84-3.50x length. Forewings (Fig. 82-85, 87-88) with purplish brown to dark brown markings; MAs shorter than MA₁ (MAs/MA₁=0.60-0.97); MP₂ originating at base of either MP₁ (Fig. 84-85, 87-88) or CuA (Fig. 82-83); 3-5 cubital intercalaries present, with 2-4 of them forked. Hindwings (Fig. 100-104, 106) with purplish brown to dark brown markings; base of R₁ slightly (130-150°) to moderately (103-108°) arched toward SC; MP₂ not directly connected to MPs, appearing connected to CuA and forming MP-cell (Fig. 100-104, 106). Foretibiae 1.24-1.71x length of forefemora, 1.02-1.71x length of foretarsi. *Abdomen*: Terga 1-10 each with U-shaped dark marking encompassing most of tergum, and/or with midlongitudinal stripe containing pair of light, submedian, teardrop-shaped spots and pair of tiny round markings as in mature larvae. Genitalia (Fig. 118-123) with subgenital plate convex; genital forceps with segment 2 and 3 together 0.19-0.34x length of basal segment; penes furcated below midlength. Median terminal filament rudimentary, 0.02-0.19x length of cerci.

FEMALE ADULT.—*Dimensions (mm)*: Length of body 14.0-21.5, forewings 13.5-18.5, hindwings 4.4-8.0, forelegs 7.3-11.6, cerci 19.7-31.0, median terminal filament 1.0-14.8; width of forewings 5.5-7.5, hindwings 2.2-5.0. Body color and markings generally similar to male (exceptionally different in wing color pattern in two species). *Body*: Similar to male except wings more heavily stained in some (Fig. 86, 105); foretibiae 1.00-1.41x length of forefemora, 1.92-3.21x length of foretarsi; and median terminal filament 0.02-0.71x length of cerci.

FIGURE 2. Distribution of *Rhoenanthus*.

DIAGNOSIS.— *Rhoenanthus* larvae (Fig. 11-13) may be told from *Potamanthus* larvae by their long mandibular tusks and setaceous mouthparts (Fig. 18-20). *Rhoenanthus* larvae are easily distinguished from those of *Anthopotamus*, which also possess well-developed tusks, by their relatively long foretibiae and the presence of bipectinate-hairlike setae of the dorsal and lateral foretibiae. Adults of *Rhoenanthus* are not as easily distinguished from those of *Anthopotamus* and *Potamanthus*. For Old World adults, various color markings of wings (Fig. 82-88), the basal attachment of MP_2 in hindwings, and other characters presented in the key to adults, above, should be consulted.

DISTRIBUTION.— Fig. 1-2: Eastern Palearctic (eastern USSR, Korea, China); Oriental (Vietnam, Thailand, Malaysia, Indonesia, India).

DISCUSSION.— Eaton (1881) established his genus *Rhoenanthus* for potamanthids whose adults possess a reduced median terminal filament that distinguished them from his notion of *Potamanthus* at that time. There are a number of Asian species that are phylogenetically closely related to the type species of *Rhoenanthus*, *R. speciosus* Eaton. Together, these constitute a monophyletic grouping, substantiated by a number of adult and larval synapomorphies, that we recognize as the genus *Rhoenanthus* (see Phylogeny and Phylogenetic Classification section, below). These species have variously been considered under a number of genus-group names that are thus junior synonyms. They include *Potamanthindus* Lestage, *Rhoenanthopsis* Ulmer, *Neopotamanthodes* Hsu, and *Neopotamanthus* Wu & You.

As for the taxonomic history of potamanthids in general, *Rhoenanthus* and other associated names were based on adult phenetics that has resulted in considerable confusion regarding generic limits. Our study of adult morphology, including that of types, consideration of associated larval comparative morphology, and cladistic analysis has allowed a resolution of this problem. In the case of *Neopotamanthodes*, the one male subimago and one female adult known of the type species *Rhoenanthus lanchi* (Hsu) are lost (You, personal communication). However, enough evidence is available from Hsu's (1937-38b) description to warrant its inclusion in *Rhoenanthus* at this time. Although Hsu considered MP_2 of the forewings to originate from CuA, his figure clearly indicates that MP_2 is forked with MP_1 but coalesces with CuA for a short distance near the base. All these characteristics are in agreement with *Rhoenanthus* characterization.

Tshernova (1985) synonymized *Rhoenanthopsis* with *Rhoenanthus* but placed *Neopotamanthodes* under the name *Potamanthodes* [= *Potamanthus* (*Potamanthodes*), herein]. Given the fact that *Rhoenanthus* and *Potamanthodes* are at the opposite ends of different clades, there is no justification for the latter synonymy. The broad differentiation of the two is perhaps best typified by their very different larvae.

One specific name, *Rhoenanthus shima* Matsumura, 1931, does not appear in the formal listings or synonymies of Potamanthidae, herein, because the name cannot be authenticated. No Matsumura's types of *Rhoenanthus shima* exist at Hokkaido University (S. Takagi, personal communication), and based on the description, it cannot even be placed to family. We therefore consider it a *nomen dubium*.

***Rhoenanthus* (subgenus *Rhoenanthus*), NEW STATUS**

Rhoenanthus Eaton, 1881. Entomol. Month. Mag. 17: 192 [Type species: *Rhoenanthus speciosus* Eaton, 1881, by monotypy].

MATURE LARVA.— *Dimensions* (mm): Length of body 17.0-19.0, mandibles 2.9-4.6, caudal filaments 9.0-12.0. *Head*: Compound eyes of mature male larvae full-sized (ES =

1.12). Mandibles (Fig. 11, 26) very long, 1.7-2.3x length of head, moderately arched inward (15°); body of mandibles with 28-46 simple-stout setae and 4-5 bipectinate-hairlike setae laterally, and without setae on medial margin; tusks with large, subapical spine (Fig. 11, 26). Terminal segment of maxillary palpi (Fig. 18) slender, with moderately developed bipectinate-hairlike setae along medial margin. *Thorax*: Foretibiae (Fig. 11, 26) 2.72-2.82x length of foretarsi.

ADULT.— *Thorax*: Forewings (Fig. 82-83) with dark stained markings variously at base of forks of veins; MP_2 originating at base of CuA; 38-42 crossveins between Sc and R_1 , no crossveins concentrated near bulla. Foretibiae of male 1.02-1.05x length of foretarsi. *Abdomen*: Male genitalia (Fig. 118-119, 134-135) with penes basally furcated (V-shaped), flattened, and somewhat rounded apically. Median terminal filament of female rudimentary, 0.02-0.05x length of cerci.

DIAGNOSIS.— Larvae of *Rhoenanthus* s.s. (Fig. 11) are distinguished from those of subgenus *Potamanthindus* (Fig. 12-13) by their terminally spined mandibular tusks that appear forked (Fig. 11, 26) and slender maxillary palpi (Fig. 18). Adults are distinguished by MP_2 of forewings being basally connected to CuA (Fig. 82-83) and by their dorsoventrally flattened, deeply furcated, and apically rounded penes (Fig. 118-119, 134-135).

DISTRIBUTION.— Fig. 2: Oriental (Vietnam, Thailand, Malaysia, Indonesia, India).

DISCUSSION.— The genus *Rhoenanthus* s.s. comprises a distinct phylogenetic lineage within *Rhoenanthus* (see Phylogeny and Phylogenetic Classification section, below). The subgenus represents the more traditional concept of *Rhoenanthus*. The larval description may require modification when the larval stage of *Rhoenanthus distafurcus* is discovered.

***Rhoenanthus distafurcus*, NEW SPECIES**

Morphology Fig. 82, 100, 118, 134

Distribution Fig. 2

LARVA.— Unknown.

MALE ADULT.— *Dimensions* (mm): Length of body 15.5, forewings 15.0, hindwings 5.7, forelegs (foretarsi 3-5 missing) > 12.0 ; forceps (terminal segment missing) > 1.38 ; cerci 50.0; median terminal filament 1.1; width of forewings 6.3, hindwings 3.5; dorsal diameter of compound eyes 1.40; distance between compound eyes 0.20. *Head*: Color yellowish brown. Compound eyes black in alcohol, large, nearly contiguous ($ES = 0.14$). *Thorax*: Color yellowish brown to brown; nota somewhat lighter than pleura and sterna. Forewings (Fig. 82) transparent, with light brown to brown stained marks variously developed at base of forks; longitudinal veins light brown to brown; costal crossveins purplish brown and infuscated, other crossveins dark brown and infuscated, numbering 39 between SC and R_1 and 22 between R_1 and R_2 ; MAs 0.60x length of MA_1 ; cubital region with 5 intercalaries (4 forked); A_1 forked twice. Hindwings (Fig. 100) transparent, with brown stained marks variously at base of forks; longitudinal veins colorless; crossveins dark brown and infuscated in central area; costal projections acute ($< 90^\circ$); base of R_1 slightly arched (ca. 130°) toward Sc. Forelegs yellowish brown; middle region of foretibiae and foretarsal segment 2 white; midlegs and hindlegs pale yellow; claws light brown. *Abdomen*: Terga 1-10 each yellow, with dark brown, broad, midlongitudinal stripe containing 2 pairs of light, teardrop-shaped spots, with pair of dark brown, broad, diagonal stripes running from anterolateral corner to median posterior margin, and with 2-4 narrow, elongated, spots arranged on lateral margin. Sterna 1-10 each yellow, with 2 pairs of dark, submedian spots (anterior pair larger and more

widely separated) and pair of narrow, longitudinal, lateral stripes. Genital forceps pale yellow, with segment 20.17x length of basal segment; penes (Fig. 118, 134) with ventral surface pale yellow, dorsal surface light brown, dorsoventrally flattened, furcated at level of subgenital plate, and rounded apically. Cerci pale yellow, relatively long (3.23x length of body), with purplish brown band at each suture; median terminal filament rudimentary, 0.02x length of cerci, pale yellow with dark brown band at each suture.

FEMALE ADULT.—*Dimensions* (mm): Length of body 15.0, forewings 13.5, hindwings 4.4, forelegs 7.3, cerci 19.7, median terminal filament 1.0; width of forewings 5.5, hindwings 2.2; dorsal diameter of compound eyes 0.58; distance between compound eyes 0.85. *Head*: Compound eyes small, black in alcohol, widely separated (ES = 1.47). *Thorax*: Prothorax with purplish brown, midlongitudinal and lateral stripes on notum and pleura extending to mesonotum and mesopleura, respectively. Forewings with dark brown, infuscated crossveins, and with 4 cubital intercalaries (3 forked); other venation as in male. Hindwings with acute costal projections (< 90°). Forelegs purplish brown, with pale yellow band at midlength of foretibiae and on foretarsal segments 2-4; foretibiae 1.25x length of forefemora, 1.92x length of foretarsi. *Abdomen*: Color pattern as in male. Cerci pale yellow, with dark band at each suture; median terminal filament black, rudimentary, 0.05x length of cerci.

DIAGNOSIS.— This species is distinguished from other *Rhoenanthus* s.s. and other potamanthids by the double forked A₁ in their forewings (Fig. 82) and their unique male genitalia (Fig. 118, 134).

ETYMOLOGY.— The trivial name *distafurcus* is Latin, masculine, from *disto* (different, unusual), and *furca* (fork), an allusion to the unusual extra fork of A₁ in the forewings.

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (alcohol, BAE-7), THAILAND: Khao-Yai Nat. Pk., 750 m, VII-26-1962, E.S. Ross, D.Q. Cavagnaro, deposited in PERC.

OTHER MATERIAL EXAMINED.— INDIA: 1 F (pinned, BAE-88), Malabar, Nadungayan, 200 m, IX-16-22-1938, B.M.-C.M. Expdn S India, Sept-Oct, 1938 (BM). VIETNAM: 1 Ms, 1 Fs, 14 km W Phan Rang, 60 m, VI-22-1960 (UU).

DISCUSSION.— One female adult (BAE-88) from Malabar, southern India, although taken a considerable distance from Indochina, where other materials are known, suggests a broad Oriental or disjunct Oriental distribution pattern. Such patterns have been noted for species of *Ephemera* and *Afromera* in the Ephemeridae (McCafferty & Edmunds 1973, McCafferty & Gillies 1979).

Rhoenanthus speciosus Eaton

Morphology Fig. 11, 18, 26, 52, 83, 101, 119, 135

Distribution Fig. 2

Rhoenanthus speciosus Eaton, 1881. Entomol. Month. Mag. 17: 192 [Material: M (Holotype), F & Subimago (sex unknown); Holotype locality: Indonesia (Sumatra); Holotype deposition: Leiden Museum (lost: Kimmins 1960); Neotype (designated herein) locality: East Malaysia (Sabah); Neotype deposition: PERC]; Ulmer, 1939. Arch. Hydrobiol. Suppl. 16: 602 (first L description).

MATURE LARVA.— *Dimensions* (mm): Length of body 17.0-19.0, antennae 5.0-6.5, mandibles 2.9-4.6, caudal filaments 9.0-12.0; dorsal diameter of male compound eyes 0.9-1.1, female compound eyes 0.5-0.6. *Head*: Vertex (Fig. 11) light brown with irregular light markings. Compound eyes black; male compound eyes (Fig. 11) full-sized (ES = 1.12). Antennae 2.8-3.3x length of head. Mandibles (Fig. 11, 26) light brown, 1.7-2.3x length of head, with tusks moderately arched inward (15°), and with large lateral, subapical spine; body

of mandibles with 28-46 simple-stout setae and 4-5 bipectinate-hairlike setae laterally, without medial setae; tusks bare and relatively slender (2.0-3.2x length and 0.5-0.6x width of body of mandibles). Maxillae (Fig. 18) with bipectinate-hairlike setae on apical 3/4 of galealacinal crown; terminal segment of maxillary palpi 2.8-2.9x length of segment 2, with moderately developed row of bipectinate-hairlike setae (setules well developed as in Fig. 52) along medial margin. *Thorax*: Ground color brown with irregular light markings dorsally, and with white stripe in lateral margin of pronotum. Legs pale yellow, without clearly defined markings or patterns. Foretibiae 1.20-1.23x length of forefemora, 2.72-2.82x length of foretarsi. *Abdomen*: Ground color light brown with marking of terga often not clearly defined; some individuals with terga 1-10 each with 2 pairs of dark, submedian stripes and with 2 pairs of teardrop-shaped spots (anterior pair larger than posterior pair) within stripes (Fig. 11). Gills (Fig. 11) 2-7 white to light brown with darker tracheae, sometimes pink tinged; gills 3 each with 43-46 marginal fibrillae along each lateral margin of dorsal lamellae, and 30-36 on ventral lamellae. Caudal filaments without whorls of simple-stout setae.

MALE ADULT.—*Dimensions* (mm): Length of body 13.0-15.2, forewings 11.0-11.6, hindwings 4.3, forelegs 10.9-11.5, forceps 1.26, cerci 32.0-32.5, median terminal filament 0.8; width of forewings 5.5, hindwings 2.9; dorsal diameter of compound eyes 1.53-1.54; distance between compound eyes 0.05. *Head*: Compound eyes large, nearly contiguous (ES = 0.03), gray in alcohol, darker gray ventrally. *Thorax*: Color dark brown. Forewings (Fig. 83) with dark brown stained marks variously at base of forks of longitudinal veins; crossveins somewhat infuscated in central area, numbering 33-42 between SC and R₁ and 19-22 between R₁ and R₂; MAs 0.97x length of MA₁; cubital region with 3 intercalaries (2 forked); A₁ forked once, with distal branch somewhat more divergent than basal branch. Hindwings (Fig. 101) transparent, with dark brown stained marks variously at forks of longitudinal veins and with infuscated crossveins in central area; costal projection acute (<90°); base of R₁ slightly arched (ca. 150°) toward Sc. Forelegs pale yellow with dark band at apex of tibiae and at each tarsal joint; foretibiae 1.33-1.39x length of forefemora, 1.02-1.05x length of foretarsi. Midlegs and hindlegs pale yellow. *Abdomen*: Terga 1-10 each light brown, with dark brown, broad, midlongitudinal, stripe, and with 2 pairs of teardrop-shaped light spots within stripe. Sterna of abdomen pale yellow, with black spot at anterolateral corners. Genital forceps (Fig. 119) white, with purplish brown band at apex of segment 1; terminal segment apically rounded, with medial expansion, subequal to, or slightly shorter than, segment 2 (segment 3/segment 2 = 0.87-1.17); segment 2 and 3 together 0.29-0.34x length of basal segment. Penes (Fig. 119, 135) white, V-shaped (basally furcated), leaf-shaped and dorsoventrally flattened, and somewhat rounded apically. Caudal filaments pale yellow with dark brown band on every other suture; median terminal filament rudimentary, 0.02x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 14.0-16.8, forewings 15.2-15.5, hindwings 4.6-4.8, forelegs 10.3-10.9, cerci 20.0-21.5, median terminal filament 1.1-1.2; width of forewings 6.1-6.5, hindwings 2.6-2.7; dorsal diameter of compound eyes 0.72-0.75; distance between compound eyes 0.90-0.15. *Head*: Compound eyes small, black in alcohol, widely separated (ES = 1.20-1.60). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male. Prothorax with notal and pleural stripes extending to metathorax. Forewings with 3 cubital intercalaries (2 forked). Foretibiae 1.28-1.30x length of forefemora, 2.67-2.83x length of foretarsi. *Abdomen*: Color pattern similar to male. Cerci pale yellow, with dark band at each suture; median terminal filament rudimentary, 0.06x length of cerci, basally dark brown, and with dark band at each suture.

DIAGNOSIS.— Larvae of this species (Fig. 11) can be easily distinguished from other *Rhoenanthus* by their mandibular tusks, which appear forked. Adults are distinguished from other *Rhoenanthus* s.s. by the single forked A₁ in their forewings (Fig. 83) and by the male

genitalia (Fig. 119, 135).

TYPE MATERIAL EXAMINED.— NEOTYPE: M (alcohol, BAE-108), MALAYSIA (East), Sabah, Sungai Moyog, 3 mi E Penampang, IX-27-1978, G. F. & C. H. Edmunds, 26°C, deposited in PERC.

OTHER MATERIAL EXAMINED.— INDONESIA: 1 M, Sumatra (BER); 1 F, Borneo, Nanga Serawei, XI-12-18-1924, Sammelreise (HAM); 1 Fs, West Java, Djampungs Omg. Soekanegara, 700-1000 m, XII-23-28-1931 (FAMU). MALAYSIA (East): 2 M, Borneo (Sabah), Sandakan (BM); 75 L, 2 M, 5 F, 11 Ms, 5 Fs, Sabah, Sungai Moyog, 3, 8 & 11 mi E Penampang, IX-27-X-2-1978 (UU, PERC); 24 L, Sabah, Sungai, Tuaran, Tamparuli, X-3-1989 (UU, PERC); 3 F, Sabah, Ranau, Liwagu R at Br, 335 m, VIII-11-16-1972 (FAMU); 13 L, 1 Ms, Sabah, Mansuncun R, NE Kota, Kinabalu, ca 300 km, VIII-18-1972 (UU, FAMU). MALAYSIA (West): 1 M, Pahang, King George V Nat Pk, Traham R, XI-4-1959 (PERC).

DISCUSSION.— We designate herein the neotype of *Rhoenanthus speciosus* from material recently collected by G. F. & C. H. Edmunds because Eaton's type material is lost (Kimmins 1960).

Rhoenanthus (subgenus **Potamanthindus**), NEW STATUS

Potamanthindus Lestage, 1930. Mem. Soc. Entomol. Belg. 23: 123 [Type species: *Potamanthindus auratus* Lestage, 1930 (= *Rhoenanthus obscurus* Navás, 1922), by monotypy], previously synonymized with *Potamanthodes* Ulmer, 1920b, by Tshernova (1985).

Rhoenanthopsis Ulmer, 1932. Stett. Entomol. Zeit. 93: 212 [Type species: *Rhoenanthus magnificus* Ulmer, 1920b, by monotypy], NEW SYNONYM.

Neopotamanthodes Hsu, 1937-38b. Peking Nat. Hist. Bull. 12: 221 [Type species: *Neopotamanthodes lanchi* Hsu, 1938, by original designation], NEW SYNONYM, previously synonymized with *Potamanthodes* Ulmer, 1920b, by Tshernova (1985).

Neopotamanthus Wu & You, 1986. Acta Zootaxon. Sin. 11: 401 [Type species: *Neopotamanthus youi* Wu & You, 1986, by monotypy], NEW SYNONYM.

MATURE LARVA.— *Dimensions* (mm): Length of body 12.5-30.0, mandibles 1.2-4.5, caudal filaments 7.0-16.0. *Head*: Compound eyes of mature male larvae full-sized (ES = 1.37-2.13). Mandibles (Fig. 12-13, 27-29) very long, 0.9-1.6x length of head, strongly arched inward (25-28o); body of mandibles (Fig. 38-39) with 20-55 simple-stout setae and 5-20 bipectinate-hairlike setae laterally, and with 10-20 simple stout setae on medial margin; tusks without large, subapical spine. Terminal segment of maxillary palpi (Fig. 19-20) thick, with well-developed rows of bipectinate-hairlike setae along medial margin. *Thorax*: Foretibiae 2.26-2.69x length of foretarsi.

ADULT.— *Thorax*: Forewings (Fig. 84-88) with purplish brown markings variously throughout wing; MP₂ originating at base of MP₁; 19-35 crossveins between Sc and R₁, 3-4 crossveins concentrated near bulla. Foretibiae of male 1.13-1.71x length of foretarsi. *Abdomen*: Male genitalia (Fig. 120-123, 136-137) with penes basally cylindrical, furcated at midlength (Y-shaped), and apically notched. Median terminal filament of female 0.10-0.71x length of cerci.

DIAGNOSIS.— Larvae of *Potamanthindus* (Fig. 12-13) are easily distinguished from those of *Rhoenanthus* s.s. (Fig. 11) by the absence of a large, subapical, lateral spine on mandibular tusks (when a spine or seta is present, it is very small as in Fig. 13, 28-29). They also possess relatively thick maxillary palpi (Fig. 19-20). Adults are distinguished by MP₂

of forewings being basally connected to MP_1 (Fig. 84-88) and by their basally somewhat cylindrical, Y-shaped, and apically notched penes (Fig. 120-123, 136-137).

DISTRIBUTION.— Fig. 2: Eastern Palearctic (far eastern USSR, Korea, China); Oriental (Vietnam, Thailand).

DISCUSSION.— To adhere to a strict phylogenetic classification, and to gain some consistency with subgeneric usage in the family (see subgenera under *Potamanthus*), we have chosen to recognize the two initial branches within *Rhoenanthus*, as subgenera. The distinctiveness of *Rhoenanthus* s.s. and *Potamanthindus* makes it easy to differentiate them.

In determining the appropriate name for this subgenus, one of the several synonyms of *Rhoenanthus* (see above) had to be used since all of their type species are included in this monophyletic grouping (see Phylogeny and Phylogenetic Classification section, below). *Potamanthindus* Lestage (1930) has chronological priority. Since we show the single species of placed under that name, *Potamanthindus auratus* Lestage (1930), to be a junior synonym of *Rhoenanthus obscurus* Navás (1922) (see below), *Rhoenanthus obscurus* becomes the type of the subgenus.

***Rhoenanthus magnificus* Ulmer**

Morphology Fig. 84, 102, 120

Distribution Fig. 2

Rhoenanthus magnificus Ulmer, 1920b. Arch. Nat. 85: 11 [Material: M (Holotype), F (misidentification) & Subimago (sex ?); Holotype locality: Vietnam; Holotype deposition: WIEN].

Rhoenanthus vitalisi Navás, 1922. Bolet. Soc. Entomol. Esp. 1922: 59 [Material: M (Holotype); Holotype locality: Vietnam; Holotype deposition: BAR], NEW SYNONYM.

Rhoenanthus ferrugineus Navás, 1930. Broteria. Ser. Zool. 24: 15 [Material: F (Holotype); Holotype locality: Vietnam; Holotype deposition: PM], NEW SYNONYM.

Rhoenanthopsis magnificus (Ulmer): Ulmer, 1932. Stett. Entomol. Zeit. 93: 212.

Neopotamanthodes lanchi Hsu, 1937-38b. Peking Nat. Hist. Bull. 12: 221 [Material: Ms (Holotype), F & Fs; Holotype locality: China (Zhejiang Prov); Holotype deposition: Y. C. Hsu's collection (destroyed)], NEW SYNONYM.

LARVA.— Unknown.

MALE ADULT.—*Dimensions* (mm): Length of body 13.2-13.7, forewings 12.7-13.0, hindwings 5.1-5.2, forelegs 11.1-12.4, genital forceps 1.42, cerci 30.1, median terminal filament 1.2; width of forewings 5.7-6.1, hindwings 3.3-3.6; dorsal diameter of compound eyes 1.03; distance between compound eyes 0.13. *Head*: Color purplish brown. Compound eyes dark brown, large, nearly contiguous (ES = 0.13). *Thorax*: Color dark purplish brown; nota somewhat lighter than pleura and sterna. Forewings (Fig. 84) with purplish brown stained marks variously throughout membrane; veins dark brown; crossveins infuscated, numbering 34-35 between SC and R_1 and 20-24 between R_1 and R_2 , with single crossvein connecting IR_2 and R_3 basally, and 0-2 crossveins between MP_1 and MP_2 basally; MAs 0.82-0.92x length of MA_1 ; cubital region with 5 intercalaries (4-5 forked). Hindwings (Fig. 102) purplish brown stained throughout; veins dark brown; costal projections acute ($< 90^\circ$); base of R_1 slightly arched (ca. 130°) toward Sc; Rs 0.96x length of R_2 . Forelegs purplish brown; foretarsal segments 2-4 pale yellow; foretibiae 1.43-1.48x length of forefemora, 1.13-1.16x length of foretarsi; foretarsal segment 2 1.19-1.22x length of segment 3; midlegs and hindlegs pale yellow; claws dark brown. *Abdomen*: Terga 1-10 each with dark purplish brown, broad, midlongitudinal stripe containing pair of light, teardrop-shaped spots anteriorly and pair of

tiny round spots posteriorly, and with pair of dark purplish brown, broad, diagonal stripes running from anterolateral corner to median posterior margin. Genital forceps (Fig. 120) purplish brown, with terminal segment 1.13x length of segment 2, and with segment 2 and 3 together 0.29x length of basal segment. Penes (Fig. 120) purplish brown, basally cylindrical, Y-shaped (furcated at midlength), slightly notched apically, and without lateral expansions. Cerci purplish brown basally, with 2 purplish brown segments alternating with 3 white segments in apical portion, and with dark band at each suture; median terminal filament rudimentary, 0.04x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 15.5-16.0, forewings 14.3-16.5, hindwings 5.7-6.5, forelegs 9.8, cerci 20.7, median terminal filament 9.2; width of forewings 6.2-6.9, hindwings 3.4-3.8; dorsal diameter of compound eyes 0.60; distance between compound eyes 1.15. *Head*: Compound eyes small, black in alcohol, widely separated (ES = 1.92). *Thorax*: Color purplish brown. Forewings purplish brown stained throughout, with slightly lighter areas in central and apical regions, and with dark purplish brown veins; crossveins infuscated, numbering 35-37 between Sc and R₁, 27-28 between R₁ and R₂, 2-3 between IR₂ and R₃ basally, and 0-2 between MP₁ and MP₂ basally; MAs 0.58-0.59x length of MA₁; cubital region with 4-5 cubital intercalaries (4-5 forked). Hindwings as per male. Forelegs purplish brown, with foretarsal segments 2-4 pale yellow; foretibiae 1.41x length of forefemora, 3.00x length of foretarsi. *Abdomen*: Color pattern similar to male, but less intense. Cerci purplish brown basally, with white segment alternating with 3 purplish brown segments in apical portion; median terminal filament similar color pattern to cerci, 0.44x length of cerci.

DIAGNOSIS.— Male adults of this species are distinguished from those of other *Potamanthindus* by the presence of variously stained markings throughout the forewing (Fig. 84) and the shape of genitalia (Fig. 120). Female adults are distinguished from those of other *Potamanthindus* by a combination of their fully stained forewings (as in Fig. 86) and slightly arched R₁ in the hindwings (as in Fig. 102).

TYPE MATERIAL EXAMINED.— HOLOTYPE (*Rhoenanthus magnificus* Ulmer, 1920b): M (pinned, with Ulmer's type label, BAE-192), Central-Tonkin (VIETNAM), Chiem-Hoa, Aug Sept, H. Fruhstorfer (WIEN). PARATYPE (*Rhoenanthus magnificus* Ulmer, 1920b): M (pinned, BAE-193), same data and deposition as Holotype. HOLOTYPE (*Rhoenanthus vitalisi* Navás, 1922): M (pinned, det Navás, BAE-190), VIETNAM, Ban Nam Coum, 10 III 17 (BAR). HOLOTYPE (*Rhoenanthus ferrugineus* Navás, 1930): F (pinned, right wing under cellophane, parts of wings, legs, and abdomen missing, det Navás, BAE-195), Tonkin (VIETNAM), reg de Hoa-Binh, A. de Cooman, 1928 (PM).

OTHER MATERIAL EXAMINED.— VIETNAM: 1 Ms, 2 F, Sonla Prov, Song Ma, V-1986 (LENU).

DISCUSSION.— Based on comparative examinations of the holotypes of *Rhoenanthus magnificus*, *R. vitalisi*, and *R. ferrugineus*, the latter two names should be considered junior synonyms of *R. magnificus*. The forewings of the male holotype of *R. vitalisi* have slightly more staining and 1-2 more crossveins basally between IR₂ and R₃ than do the forewings of the male holotype of *R. magnificus*, but these are commonly individually variable and all other characters are in complete agreement. The female holotype of *R. ferrugineus*, although badly damaged, is similar to the female of *R. magnificus* in color pattern, wing venation, and extrapolated body size. In addition, although all material of Hsu's *Neopotamanthodes lanchi* were destroyed during the Sino-Japanese War (You, personal communication) his descriptions (1937-38b) agree with *R. magnificus*, including that of the holotype male subimago. We therefore also synonymize Hsu's *N. lanchi* with *R. magnificus*.

Ulmer's (1920b) female paratype (BAE-196) of *R. magnificus* from San Chouen,

southern China, was misidentified and is actually *R. youi*. It possesses a medial transverse stripe in the forewings rather than the almost completely stained forewings of *R. magnificus* (see also discussions of *R. youi*). Our description of the female adult of *R. magnificus* and synonymy of *R. ferrugineus* are based on two well-preserved female adults from Vietnam that were collected together with a male subimago of *R. magnificus* by N. Ju. Kluge (LENU) near the type locality of *R. magnificus*.

***Rhoenanthus obscurus* Navás**

Morphology Fig. 12, 19, 27, 38, 48, 53, 62, 64-65, 85-86, 104-105, 121, 136;

Distribution Fig. 2

Rhoenanthus obscurus Navás, 1922. Bolet. Soc. Entomol. Esp. 1922: 58 [Material: M (Holotype), F; Holotype locality: Vietnam; Holotype deposition: BAR]. *Potamanthindus auratus* Lestage, 1930. Mem. Soc. Entomol. Belg. 23: 123 [Material: F (Holotype); Holotype locality: Vietnam; Holotype deposition: PM (missing)], NEW SYNONYM.

Potamanthus sp. TPA: Gose, 1969. Nat. Life SW Asia, Japan. 6: 125 (first L description).

MATURE LARVA.— *Dimensions* (mm): Length of body 12.5-16.7, antennae 3.5-4.7, mandibles 1.2-1.6, caudal filaments 7.0-7.5; dorsal diameter of male compound eyes 0.75-0.83, female compound eyes 0.56-0.58. *Head*: Vertex (Fig. 12) brown or purplish brown with irregular light markings. Compound eyes black; male compound eyes (Fig. 12) full-sized (ES = 1.37-2.13). Antennae 2.50x length of head. Mandibles (Fig. 12, 27) 0.86-0.88x length of head, with tusks strongly arched inward (28°); body of mandibles (Fig. 38) light brown, relatively broad, with 10-15 simple-stout setae intermixed with 3-4 bipectinate-hairlike setae medially, with 20-28 relatively large simple-stout setae intermixed with 15-20 bipectinate-hairlike setae (setules moderately developed as in Fig. 48) laterally; tusks dark brown, bare, 1.65-2.26x length and 0.32-0.35x width of body of mandibles. Galealacinal crown (Fig. 19) of maxillae straight, not rounding, at right-angle to lateral margin, and with well-developed rows of bipectinate-hairlike setae (setules well developed) on entire crown; terminal segment of maxillary palpi 3.7-4.0x length of segment 2. Hypopharynx (Fig. 19) greatly expanded laterally, with row of well-developed bipectinate-hairlike setae (setules well developed as in Fig. 64) along medial margin. *Thorax*: Ground color generally brown or purplish brown, with markings often not clearly defined, sometimes with light irregular markings dorsally and white stripes laterally on pronotum. Legs pale yellow, without clearly defined markings. Foretibiae 1.32-1.47x length of forefemora, 2.55-2.69x length of foretarsi. *Abdomen*: Ground color generally brown to purplish brown, with markings of terga often not clearly defined; some individuals with slightly darker, broad midlongitudinal stripe on terga 1-10, and with 2 pairs of light submedian teardrop-shaped spots (anterior pair larger than posterior pair) on each tergum (Fig. 12). Gills (Fig. 12) 2-7 relatively short, white with darker tracheae; gills 3 each with 35-45 marginal fibrillae along each lateral margin of dorsal lamellae, and 20-25 on ventral lamellae. Caudal filaments (Fig. 12) 0.5-0.6x length of body, without whorls of simple-stout setae.

MALE ADULT.— *Dimensions* (mm): Length of body 12.0-13.0, forewings 9.5-10.0, hindwings 3.7-4.1, forelegs 7.8-8.5, forceps 1.02-1.05, cerci 21.4-24.0, median terminal filament 1.0-1.1; width of forewings 4.1-4.4, hindwings 2.6-2.8; dorsal diameter of compound eyes 1.00; distance between compound eyes 1.05-1.20. *Head*: Compound eyes large, nearly contiguous (ES = 0.20), yellowish brown in alcohol (ventrally darker gray than rest of eyes). *Thorax*: Color light brown; mesothorax and metathorax brown to purplish brown. Forewings

(Fig. 85) with narrow, transverse, light brown stained stripe and infuscated crossveins at approximately midlength of forewings, and with additional light brown stain at base of IMP; 19-28 crossveins between SC and R_1 and 16-20 between R_1 and R_2 ; MAs 0.62-0.67x length of MA_1 ; cubital region with 4 intercalaries (3 forked). Hindwings (Fig. 104) stained light brown; costal projections rounded ($> ca. 110^\circ$); base of R_1 moderately arched ($ca. 108^\circ$) toward Sc; crossveins slightly infuscated in central area. Forelegs light brown; midlegs and hindlegs pale yellow; foretibiae 1.48-1.71x length of forefemora, 1.61-1.71x length of foretarsi. *Abdomen*: Terga 1-10 each light brown, with midlongitudinal stripe and submedian spots as described for mature larvae, and with purplish brown, broad, U-shaped mark encompassing most of each tergum. Sterna 1-10 each light brown, with 2 pairs of purplish brown, lateral stripes. Genital forceps (Fig. 121) white, with apex of segment 1 somewhat dark; terminal segment rounded, slightly shorter than segment 2 (segment 3/segment 2 = 0.92) and together with segment 2 0.24x length of basal segment. Penes (Fig. 121, 136) light brown, furcated at midlength beyond subgenital plate (Y-shaped), basally cylindrical, and apically notched. Cerci light brown, with white segment alternating with every 3 darker segments; terminal filament dark brown, rudimentary, 0.04-0.05x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 15.5-17.0, forewings 14.0-14.2, hindwings 5.8-5.9, forelegs 9.2-9.6, cerci 20.3-20.8, median terminal filament 12.7-14.8, width of forewings 6.0-6.3, hindwings 3.1-3.4; dorsal diameter of compound eyes 0.55-0.70; distance between compound eyes 0.83-1.10. *Head*: Compound eyes black in alcohol, very small and widely separated (ES = 1.50-1.57). *Thorax*: Color patterns of body and legs generally similar to those of male but less intense. Forewings (Fig. 86) lightly tinged with purple-brown over entire membrane; crossveins brown, slightly infuscated in central area, with 34-35 crossveins between SC and R_1 , 23-28 between R_1 and R_2 , and with 4-5 cubital intercalaries (4 forked). Hindwings (Fig. 105) lightly tinged with purple-brown over entire membrane, with apical half darker; otherwise as per male. Foretibiae 1.35-1.36x length of forefemora, 2.89-3.21x length of foretarsi; foretarsal segments 2-4 white. *Abdomen*: Color pattern similar to male but often not clearly defined. Cerci color pattern as per male; median terminal filament slender, 0.63-0.71x length of cerci, with white stripe on every 4th segment.

DIAGNOSIS.— Larvae of this species are distinguished from those of other *Potamanthindus* by the strongly arched mandibular tusks (Fig. 12, 27), highly setaceous mouthparts and truncated galealacinal crown (Fig. 19). Male adults of this species are distinguished from those of other *Potamanthindus* by their moderately arched R_1 and greatly rounded costal projections in the hindwings (Fig. 104) and by their genitalia (Fig. 121, 136); female adults are distinguished by the combined characters of fully stained forewings (Fig. 86) and hindwings (Fig. 105) and moderately arched R_1 in the hindwings (Fig. 105).

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (pinned, parts of hindwings, legs, and cerci missing, det Navás, BAE-191), VIETNAM, Don Khoua, 17-XI-18 (BAR).

OTHER MATERIAL EXAMINED.— THAILAND: 238 L, 5 M (reared), 3 F, Chiangmai Prov, E fk Mae Ping, 56 Km N Chiangmai, 1300 m, XI-21, 24-1964 (UU, FAMU, PERC); 79 L, 2 M (reared), 2 F, Chiangmai Prov, E fk Mae Ping at junc, 59 km N Chiangmai, 1350 m, XI-30-1964 (UU, PERC); 3 L, Chiangmai Prov, Mae Ping, Chiangmai, 1000 m, XI-17-1964 (UU); 6 L, Chiangmai Prov, Nam Chai R ab hydro st intake at Fang Holt St, 550 m, XI-15-1985 (UU).

DISCUSSION.— The male holotype is damaged in part, but venation and markings of the forewings as well as body size were helpful in confirming the species concept. Descriptions of all stages and sexes of this species were established with the aid of numerous larvae and reared adult material recently collected from Thailand by W. L. and J. G. Peters.

According to J. Legrand (personal communication), the type of *Potamanthindus auratus*

Lestage can not be located at the Paris Museum. Nevertheless, from the description (Lestage 1930), especially wing venation, it is quite clearly equivalent to *R. obscurus*.

***Rhoenanthus coreanus* (Yoon & Bae), NEW COMB.**

Morphology Fig. 13, 20, 28-29, 39, 44, 54-55, 66, 76, 80, 88, 103, 122

Distribution Fig. 2

Potamanthus nb: Imanishi, 1940. Rep. Limnobiol. Surv. Kwant. Manch. 1940: 182 (first L description).

Potamanthus coreanus Yoon & Bae, 1985. Entomol. Res. Bull., Korean Entomol. Inst., Seoul. 11: 95 [Material: M (Holotype), F, Ms, Fs & L; Holotype locality: Korea (South); Holotype deposition: KEI].

Rhoenanthus rohdendorfi Tshernova, 1985. Taxon. Ecol. Arthropods Far East. 1985: 15 [Material: M (Holotype); Holotype locality: USSR (Far East; Maritime Terr.); Holotype deposition: UAMOS], NEW SYNONYM.

MATURE LARVA.— *Dimensions* (mm): Length of body 17.0-28.0, antennae 4.5-10.0; mandibles 2.4-4.5, caudal filaments 9.0-12.0; dorsal diameter of male compound eyes 0.7-1.0, female compound eyes 0.4-0.7. *Head*: Vertex (Fig. 13) brown or purplish brown with irregular, light markings. Compound eyes black; male compound eyes (Fig. 13) full-sized (ES = 1.47). Antennae 2.2-2.3x length of head. Mandibles (Fig. 13, 28-29) 1.1-1.6x length of head, with tusks strongly arched inward (25°); body of mandibles (Fig. 39) light brown, with 10-20 simple-stout setae medially, and with 37-47 simple-stout setae and 5-10 bipectinate-hairlike setae laterally; tusks dark brown, 2.0-3.2x length and 0.5-0.6x width of body of mandibles, bare, with 0-3 simple-stout lateral setae, and sometimes with rudimentary lateral subapical spine (Fig. 13, 28-29). Maxillae (Fig. 20) with bipectinate-hairlike setae on apical 3/4 of galealacinal crown; terminal segment of maxillary palpi (Fig. 20) 2.1-2.2x length of segment 2, with relatively well-developed row of bipectinate-hairlike setae (setules well developed as in Fig. 54-55) along medial margin. Terminal segment of labial palpi (Fig. 44) with row of 30-50 simple-stout setae along medial margin. *Thorax*: Ground color brown to purplish brown; pronotum (Fig. 13) with white lateral margins, sometimes with 6-8 irregular, light, somewhat round markings; mesonotum and metanotum together with 6-10 irregular, light markings. Legs (Fig. 13) light brown to pale yellow, with dorsal white band sometimes evident near posterior margin of femora. Foretibiae 1.20-1.23x length of forefemora, 2.26-2.61x length of foretarsi. *Abdomen*: Ground color generally brown to purplish brown; terga (Fig. 13) 1-10 each with pair of light submedian teardrop-shaped spots followed by pair of tiny round spots, and with pair of light marginal markings posteriorly. Gills (Fig. 13) 2-7 white to light brown with darker tracheae, sometimes pink tinged; gills 3 with 45-60 marginal fibrillae along each lateral margin of dorsal lamellae, and 35-50 on ventral lamellae. Caudal filaments (Fig. 13) 0.4-0.5x length of body, without whorls of simple-stout setae.

MALE ADULT.— *Dimensions* (mm): Length of body 14.5-18.0, forewings 12.5-15.0, hindwings 4.7-6.3, forelegs 11.4-14.4, forceps 1.25-1.68, cerci 36.5-45.0, median terminal filament 3.8-5.0; width of forewings 5.5-6.7, hindwings 3.5-4.7; dorsal diameter of compound eyes 1.38-1.60; distance between compound eyes 0.13-0.22. *Head*: Compound eyes large, nearly contiguous (ES = 0.08-0.22), gray in alcohol, darker gray ventrally. *Thorax*: Color dark brown. Forewings (Fig. 88) with narrow, transverse, purplish brown stained stripe and infuscated crossveins at approximately midlength, and with purplish brown stain at base of IMP; 28-35 crossveins between SC and R₁ and 17-20 between R₁ and R₂, and with 4 cubital intercalaries (3 forked). Hindwings (Fig. 103) stained purplish brown in apical half; costal projections acute (< 90°); base of R₁ slightly arched (ca. 150°) toward Sc; crossveins slightly

infuscated in central area. Forelegs dark brown; midlegs and hindlegs pale yellow; claws light brown; foretibiae 1.32x length of forefemora, 1.38x length of foretarsi. *Abdomen*: Terga 1-10 each light brown to pale yellow, with purplish brown, broad, U-shaped mark encompassing most of each tergum. Sterna of abdomen pale yellow, with pair of anterolateral spots. Genital forceps (Fig. 122) white; terminal segment of genital forceps rounded, expanded laterally, slightly shorter than segment 2 (segment 3/segment 2 = 0.71-0.90) and together with segment 2 0.24x length of basal segment. Penes (Fig. 122) purplish brown, somewhat cylindrical, not elongated, furcated beyond subgenital plate and not divergent apically, and slightly notched apically. Cerci purplish brown, with white band on every 2nd segment in basal portion and every 3rd segment in distal portion; median terminal filament slender, 0.1x length of cerci, purplish brown, with white band on every 3rd segment in basal portion and every 4th segment in distal portion.

FEMALE ADULT.—*Dimensions* (mm): Length of body 16.5-18.0, forewings 15.0-16.0, hindwings 5.8-6.0, forelegs 10.1-10.2, cerci 27.3-27.8, median terminal filament 12.0-12.5; width of forewings 6.5-6.8, hindwings 3.7-3.8; dorsal diameter of compound eyes 0.7-0.8; distance between compound eyes 0.9-1.0. *Head*: Compound eyes black in alcohol, very small and widely separated (ES = 1.25-1.29). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male but lighter in intensity. Prothorax with midlongitudinal and lateral stripes extending to mesonotum and mesopleura, respectively. Forewings with 32-34 crossveins between SC and R₁, 20-21 crossveins between R₁ and R₂, and with 4 cubital intercalaries (3 forked). Foretibiae 1.13-1.18x length of forefemora, 2.32-2.50x length of foretarsi; foretarsal segment 1-4 white. *Abdomen*: Color pattern similar to male but lighter. Cerci purplish brown at base, with pair of white segments alternating with pair of purplish brown segments; median terminal filament slender, 0.43-0.46x length of cerci, with every 4th segment white.

DIAGNOSIS.— Larvae of this species (Fig. 13) are distinguished from others of the subgenus *Potamanthindus* by their very long and moderately arched mandibular tusks (sometimes small, subapical, lateral spine is present as in Fig. 28-29), the absence of whorl of simple-stout setae on the caudal filaments, and the presence of marginal markings restricted to the posterior region of each abdominal tergum. Male adults of this species are distinguished from others of the subgenus *Potamanthindus* by the shape of their genitalia (Fig. 122); female adults are distinguished by the combined presence of a central transverse stripe in the forewings as in males (Fig. 88) and their Far East Asian distribution.

TYPE MATERIAL EXAMINED.— **HOLOTYPE** (*Potamanthus coreanus* Yoon & Bae, 1985): M (alcohol, BAE-150), KOREA (SOUTH), Kyonggi-do, Kapyong, Chojong R at Chongpyong, IX-5-1985, Y. J. Bae (KEI). **PARATYPES** (*Potamanthus coreanus* Yoon & Bae, 1985) [all from Korea (South)]: 23 M (4 reared), 29 F, 10 Ms (2 reared), 6 Fs (1 reared), same data as Holotype (KEI, PERC, USNM, FAMU); 1 F (alcohol, reared), Kyonggi-do, Namyangju, Wangsukchon, V-20-1984, Y. J. Bae (PERC); 18 L (1 L on SEM stage), same locale as Holotype, VI-12-1983, Y. J. Bae (KEI, PERC); 10 L Namyangju, Paldang, S Han R, V-23-1982, J. U. Byun (KEI); 21 L, Kyonggi-do, Namyangju, Kwangnung, II-21-1983, Y. J. Bae (KEI); 2 L, Kangwon-do, Omi-ri, VI-19-1983, I. B. Yoon (KEI); 8 L, Kangwon-do, Inje, Tutayon, III-15-1968, I. B. Yoon (KEI); 14 L, Chungchongbuk-do, Okchon, Sodaesan (=Mt Sodae), IV-9-1972, X-14-1972, I. B. Yoon, IX-25-1982, J. U. Byun (KEI).

OTHER MATERIAL EXAMINED.—KOREA (NORTH): 2 Ms, 2 Fs, Pyongannam-do, Pyongyang, Daedong R, VII-4-5, 16-1988. KOREA (SOUTH): 8 Ms, Kyonggi-do, Yonsan, VI-18-1954 (UU); 9 Ms, Seoul, Ttuksom, VI-28-1959, VII-1-1959, VII-10-1959 (UU); 5 Ms, Seoul, Mojin-dong, VIII-31-1959 (PERC); 4 L, Kyonggi-do, S Han R & Trib N Han R, N Expressway, IV-23-1969 (PERC); 30 L, same locale as Holotype, VII-26-1989, XII-28-

1989 (KEI, PERC); 12 L, Kangwon-do, Kapyong, Odae R nr Odae Mt Nat Pk, VIII-16-1978 (UU). USSR (Far East): 2 L, Sinelnikovo, R Razdolnaya, nr Ussuriysk, N Vladivostok, VII-25-1985 (LENU); 1 L, 1 M, Primor'ye, R Razdolnaya, VII-20-22-1987 (FAMU).

DISCUSSION.— The larva of this species was first studied by Imanishi (1940) from Kyonggi-do, Korea. It was referred to as *Potamanthus* nb (arbitrary name). Yoon & Bae (1985) reared this species and described it as *Potamanthus coreanus*. In the meantime, Tshernova (1985) described the same species, based on a male adult, as *Rhoenanthus rohdendorfi* from far eastern USSR near the Korea-USSR border. Soviet material was recently reared by T. M. Tiunova (Kluge, personal communication). Our examination of reared adults from both Korea and the USSR (see Material Examined, above) showed them to be conspecific, although some intraspecific variations among larvae were evident. The small subapical spine of the mandibular tusks is not distinct in some individuals, being replaced by several lateral simple-stout setae. All adults were consistently identical.

Although both *Potamanthus coreanus* and *Rhoenanthus rohdendorfi* were published in 1985, *R. coreanus* has nomenclatural priority by one day because the issue of the Entomological Research Bulletin of the Korean Entomological Institute, where *R. coreanus* was published, is dated December 30, 1985. Since the issue of Taxonomy and Ecology of the Arthropods of the Far East, where *R. rohdendorfi* was published, gives no month and day of issuance, it must be considered to be the last day of the year, December 31, 1985 (ICZN, 1985: Chapter V, Article 21, c, ii).

***Rhoenanthus youi* (Wu & You), NEW COMB.**

Morphology Fig. 87, 106, 123, 137

Distribution Fig. 2

Neopotamanthus youi Wu & You, 1986. Acta Zootaxon. Sin. 11: 401 [Material: M (Holotype), F, Ms, Fs, L; Holotype locality: China (Anhui Prov); Holotype locality: NNU].

MATURE LARVA.— *Dimensions* (mm): Length of body 30.0, antennae 7.0, mandibles 3.6, caudal filaments 16.0; dorsal diameter of female compound eyes 0.9. *Head*: Vertex brown with large, pale yellow, submedian markings. Compound eyes black. Antennae 2.5x length of head, without setae on the surface. Mandibles 1.3x length of head, with tusks strongly arched inward (25°); base of mandibles light brown, with 18 simple-stout setae medially and 55 simple-stout setae and 5 bipectinate-hairlike setae laterally; tusks dark brown, 1.8x length and 0.5x width of body of mandibles, with 8 simple-stout setae laterally. Maxillae with bipectinate-hairlike setae on apical 3/4 of galealacinal crown; terminal segment of maxillary palpi 1.73x length of segment 2. *Thorax*: Ground color generally brown; pronotum with white lateral margins, and with 6-8 irregular light markings; mesonotum and metanotum together with 6-8 irregular light markings laterally. Legs pale yellow, with broad, brown, subapical and medial bands on femora dorsally; tibiae with broad dark band at midlength; foretarsi dark brown. Foretibiae 1.21x length of forefemora, 2.52x length of foretarsi, with simple-stout setae more concentrated along anterior and posterior margins. *Abdomen*: Ground color of terga generally brown, sterna light brown; terga 1-10 each with pair of light submedian teardrop-shaped spots followed by pair of small round spots, and with pair of light posterior marginal markings extending to submedian spots (appearing as paired submedian stripes). Gills 2-7 white, somewhat pink tinged, gills 3 each with 70 marginal fibrillae along each lateral margin of dorsal lamellae, and 55 on ventral lamellae. Caudal filaments with whorls of rudimentary simple-stout setae on posterior margin of each segment.

MALE ADULT.—*Dimensions* (mm): Length of body 15.5-17.7, forewings 12.8-14.5,

hindwings 5.0-5.7, forelegs 11.8-12.1, forceps 1.40-1.76, cerci 33.6-37.8, median terminal filament 6.3-7.0; width of forewings 5.8-6.3, hindwings 3.4-3.9; dorsal diameter of compound eyes 1.36-1.50; distance between compound eyes 0.28. *Head*: Compound eyes large, nearly contiguous (ES=0.18-0.21), gray in alcohol, darker gray ventrally. *Thorax*: Color dark brown. Forewings (Fig. 87) with narrow, transverse, purplish brown stripe and infuscated crossveins at approximately midlength, and with purplish brown stain at base of IMP; 26-33 crossveins between SC and R_1 and 15-17 between R_1 and R_2 ; MA_s 0.64-0.73x length of MA_1 ; cubital region with 4 intercalaries (3 forked). Hindwings (Fig. 106) stained purplish brown in apical half; crossveins somewhat infuscated in central area; costal projections acute ($< 90^\circ$); base of R_1 slightly arched (ca. 135°) toward Sc. Forefemora, foretibiae, foretarsal segment 1, and apical half of foretarsal segment 5 dark brown; remainder of forelegs, midlegs, and hindlegs pale yellow; claws light brown; foretibiae 1.24-1.36x length of forefemora, 1.13x length of foretarsi. *Abdomen*: Terga 1-10 each light brown, with dark brown, broad, U-shaped mark and submedian stripes. Sterna of abdomen pale yellow. Genital forceps (Fig. 123) white, with segment 2 and 3 dark; terminal segment rounded, slightly shorter than segment 2 (segment 3/segment 2 = 0.67-0.77) and together with segment 2 0.19-0.22x length of basal segment. Penes (Fig. 123, 137) white, elongated, cylindrical basally, furcated beyond subgenital plate at midlength (Y-shaped), and apically notched. Caudal filaments purplish brown at base, with purplish brown segment alternating with 3 white segments apically; median terminal filament slender, 0.17-0.19x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 20.0-21.5, forewings 17.0-18.5, hindwings 7.0-8.0, forelegs 11.6, cerci 31.0, median terminal filament 9.0; width of forewings 7.0-7.5, hindwings 4.0-5.0; dorsal diameter of compound eyes 0.8-1.0; distance between compound eyes 1.0-1.2. *Head*: Compound eyes black in alcohol, very small, widely separated (ES = 1.20-1.25). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male but less intense. Prothorax with dorsal midlongitudinal and lateral stripes extending to mesonotum and mesopleura, respectively. Forewings with 4 cubital intercalaries (3 forked). Foretibiae subequal to forefemora, 2.14x length of foretarsi; foretarsal segments 1-4 white. *Abdomen*: Color pattern similar to male. Cerci purplish brown, with white segment alternating with 3 purplish brown segments in basal portion and 4 purplish brown segments in apical portion; median terminal filament slender, 0.29x length of cerci, purplish brown at base, white elsewhere, with dark band at each suture.

DIAGNOSIS.— Larvae of this species are distinguished from others of the subgenus *Potamanthindus* by the presence of very long and moderately arched mandibular tusks having several lateral simple-stout setae, whorl of simple-stout setae on the caudal filaments, and the anteriorly extended light marginal markings on each posterior abdominal tergum that appearing as midlongitudinal submedian stripes. Male adults of this species are distinguished from others of the subgenus *Potamanthindus* by the the shape of their genitalia (Fig. 123, 137), whereas female adults are distinguished by a combination of the central transverse pigmentation in the forewings as per the male (Fig. 87) and the species' distribution in China.

TYPE MATERIAL EXAMINED.— **PARATYPES** (*Neopotamanthus youi*, Wu & You, 1986): 2 L (BAE-155), 1 F (BAE-156), CHINA, Anhui Prov, Huoshan County, Zhufuan (31 18'N, 116 18'E), VI-1984, X. Wu (NNU).

OTHER MATERIAL EXAMINED.— CHINA: 6 M, 1 F (labeled as paratype of *Neopotamanthus hunanensis* Zhang, 1987 (manuscript name only), BAE-32, 160), Hunan Prov, Hongjiang Shi, VI-15-1986, J. Zhang (NNU); 1 Ms, 1 Fs, Sichuan Prov, Shinkaisi, Mt Omei [= Emei Shan], 4400 ft, VII-10-15-1934 (USNM); 1 F (pinned, labeled as type [female paratype] of *Rhoenanthus magnificus* Ulmer, 1920b, BAE-196), San Chouen, 1913, (PM).

DISCUSSION.— Among the material of Potamanthidae that we borrowed from Nanjing

Normal University in Nanjing, China, we discovered male and female adults labeled as types of a manuscript species *Neopotamanthus hunanensis*, collected from Hunan Province. This material is structurally identical to *R. youi*. Males, however, had basally darker forelegs than are typical of *R. youi*, but the females were identical. This material, therefore, does not represent a new, separate species.

The female adult specimen designated as a paratype of *Rhoenanthus magnificus* (BAE-196) was misidentified by Ulmer (1920b) and is actually *R. youi*. These two species are easily differentiated.

Genus ANTHOPOTAMUS

Potamanthus Pictet (in part): Needham, 1920. Bull. Bur. Fish. 36: 287.

Potamanthus Pictet (as *Especies nearctiques*): Lestage, 1930. Mem. Soc. Entomol. Belgique. 23: 114.

Anthopotamus McCafferty & Bae, 1990. Entomol. News 101: 201 [Type species: *Baetis verticis* Say, 1839, by original designation].

MATURE LARVA.—*Dimensions* (mm): Length of body 10.0-17.5, mandibles 1.2-2.5, caudal filaments 4.0-8.3. *Head*: Compound eyes of mature male larvae minute (ES = 2.00-3.47). Clypeus (Fig. 30-35) without simple-stout or bipectinate-hairlike setae on dorsal surface. Mandibles (Fig. 14, 30-31, 34-35) developed into long tusks, 0.9-1.3x length of head, weakly to moderately arched inward (8-17°); body of mandibles (Fig. 40) with 50-100 simple-stout setae mixed with 10-15 bipectinate-hairlike setae (setules weakly to moderately developed as in Fig. 49) evenly distributed on dorsal and lateral surface; tusks with 0-10 lateral and/or dorsal simple-stout setae, without subapical spine. Terminal segment of maxillary palpi (Fig. 21) 2.1-4.0x length of segment 2, with rows of bipectinate-hairlike setae along medial margin. Hypopharynx moderately expanded laterally. Labium (Fig. 21) with paraglossae weakly to moderately expanded laterally, with few ventral bipectinate-hairlike setae; terminal segment of labial palpi (Fig. 21, 45) falcate, 1.1-2.7x length of segment 2; medial margin of terminal segment with 15-30 relatively small simple-stout setae, and with bipectinate-hairlike setae. *Thorax*: Pronotum (Fig. 14, 30-31, 33) greatly produced laterally; anterolateral corners each produced into more-or-less acute spine. Forefemora dorsally with sparse simple-stout setae, with or without dorsal bipectinate-hairlike setae. Foretibiae 0.8-1.2x length of forefemora, 1.2-1.9x length of foretarsi, with long bipectinate-hairlike setae (setules well developed as in Fig. 68) distributed only along anterior margin, without dorsal bipectinate-hairlike setae, and without ventral, subapical tuft of bipectinate-hairlike setae. *Abdomen*: Terga 1-10 each with light midlongitudinal stripe and paired submedian longitudinal stripes as in Figure 14. Gills 2-7 (Fig. 14) with 20-45 marginal fibrillae arranged in single row.

MALE ADULT.—*Dimensions* (mm) & *Coloration*: Length of body 7.2-14.5, forewings 7.4-12.5, hindwings 3.0-5.1, forelegs 5.3-11.3, genital forceps 0.70-1.20, cerci 17.5-29.0, median terminal filament 12.5-21.3; width of forewings 3.4-6.1, hindwings 1.7-3.3. Body white to pale yellow with light brown to dark brown markings. *Head*: Compound eyes small to tiny (0.23-0.65 mm dorsal diameter) (ES = 0.68-2.89). *Thorax*: Pronotum width 1.6-2.0x length. Forewings (Fig. 89-92) without markings; MAs shorter than, or subequal to, MA₁ (MAs/MA₁ = 0.65-1.00); MP₂ originating from base of MP₁; 3-4 cubital intercalaries present (2-3 forked). Hindwings (Fig. 107-110) without markings; base of R₁ slightly arched (148-158°) toward Sc; MP₂ directly connected to MPs, forming more-or-less symmetrical fork with MP₁ (Fig. 107-110), in some coalesced with CuA for short distance near base (Fig. 109).

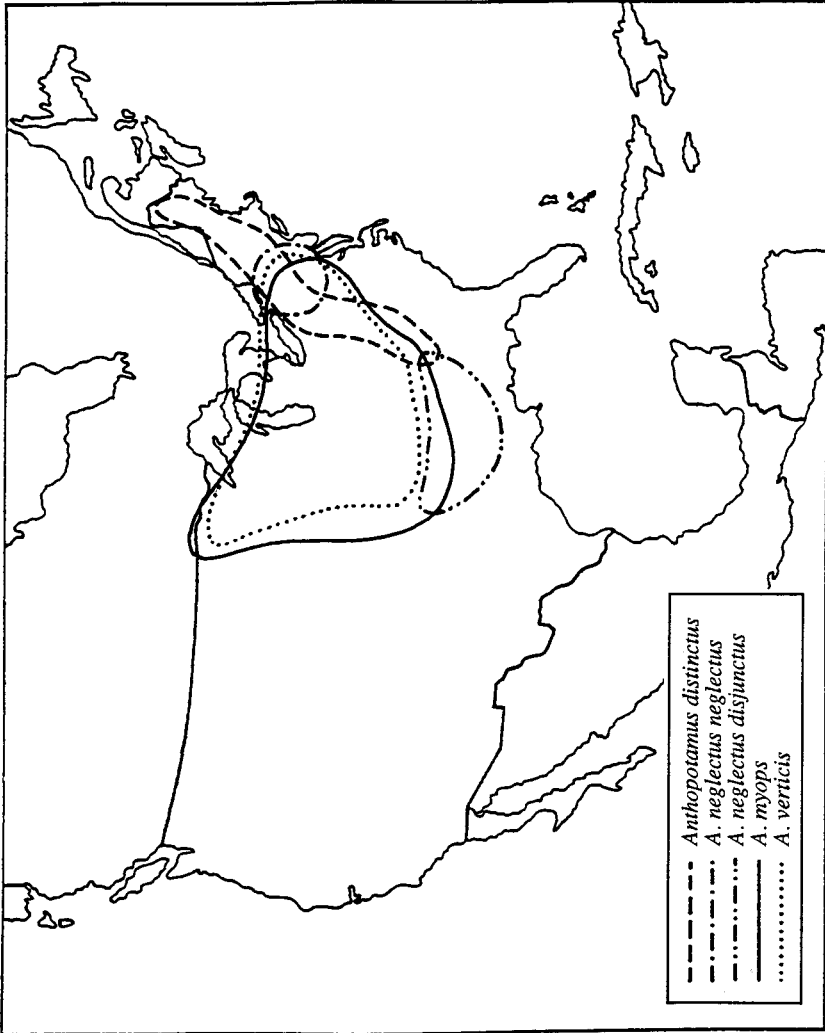


FIGURE 3. Distribution of *Anthopotamus*.

Foretibiae 1.29-1.63x length of forefemora, 0.73-1.29x length of foretarsi. *Abdomen*: Terga 1-10 each with pair of large dark round sublateral markings, in some markings less intensive. Genitalia (Fig. 124, 138) with subgenital plate concave; genital forceps with segments 2 and 3 together 0.48-0.60x length of basal segment; penes subapically furcated. Median terminal filament fully developed, 0.59-0.97x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 7.0-14.0, forewings 8.8-14.6, hindwings 2.5-6.1, forelegs 4.2-8.2, cerci 10.0-20.0, median terminal filament 9.0-20.0; width of forewings 3.4-6.1, hindwings 1.5-3.3. Body color and markings similar to male. *Body*: Similar to male except foretibiae 1.00-1.25x length of forefemora, 1.50-1.84x length of foretarsi and median terminal filament 0.93-1.00x length of cerci.

DIAGNOSIS.— Larvae of *Anthopotamus* (Fig. 14) are easily distinguished from those of *Rhoenanthus* by their well-developed bipectinate-hairlike setal field along anterior margin of the foretibiae (Fig. 70-71), and from those of *Potamanthus* by their relatively long mandibles (Fig. 30-31, 34). Male adults of *Anthopotamus* are distinguished from those of *Rhoenanthus* by their relatively small compound eyes and three fully developed caudal filaments, from those of *Potamanthus* (*Potamanthus*) by their relatively small compound eyes, and from those of *Potamanthus* (*Stygifloris*) and *Potamanthus* (*Potamanthodes*) by the fact that MP_2 of their forewings is connected to MP_1 basally (Fig. 89-92). For female differences, consult the key.

DISTRIBUTION.— Fig. 1, 3: Eastern North America.

DISCUSSION.— Needham (1920) first classified North American potamanthids as *Potamanthus* (see history of the North American group in McCafferty 1975a). Recently, McCafferty & Bae (1990) established the genus *Anthopotamus* for the North American fauna, the larvae of which are very distinct from those of *Potamanthus* s.s. The results of cladistic analysis, presented below, fully support the generic classification.

***Anthopotamus distinctus* (Traver)**

Morphology Fig. 14, 30, 67, 70, 89, 107, 124, 138, 149

Distribution Fig. 3

Potamanthus distinctus Traver, 1935. Comstock Publ. Co., Ithaca, NY. p. 280. [Material: M (Holotype), F; Holotype locality: USA (Ohio); Holotype deposition: CU]; Traver, 1937. J. Elisha Mitchell Sci. Soc. 53: 32 (first L description).

Anthopotamus distinctus (Traver): McCafferty & Bae, 1990. Entomol. News 101: 201.

MATURE LARVA.— *Dimensions* (mm): Length of body 13.5-17.5, antennae 3.0-3.3, mandibles 1.6-1.9, caudal filaments 7.0-8.0; dorsal diameter of male compound eyes 0.6-0.7, female compound eyes 0.6-0.7. *Head*: Vertex (Fig. 14) brown or purplish brown with irregular, light markings. Compound eyes of male minute ($ES = 2.13-2.34$). Antennae 2.5-2.8x length of head. Mandibles (Fig. 14, 30) 1.0-1.1x length of head, with tusks gradually narrowed from body of mandibles and moderately arched inward (10°); body of mandibles with 80-100 simple-stout setae mixed with 10-15 bipectinate-hairlike setae; tusks 1.2-2.4x length and 0.3-0.5x width of body of mandibles, with 5-10 simple-stout setae dorsally and laterally. Terminal segment of maxillary palpi 2.1-2.4x length of segment 2. Paraglossae weakly developed laterally; terminal segment of labial palpi 1.1-1.2x length of segment 2. *Thorax*: Nota brown to purplish brown; pronotum (Fig. 14) with 8-12 irregular, light, somewhat round markings, with pair of conspicuous C-shaped markings, with lateral expansions white and strongly developed, but with anterolateral corners not produced into spinelike processes (Fig.

14); mesonotum and metanotum together with 6-10 irregular, light markings. Wingpads (Fig. 14) with tiny black spots along rudimentary longitudinal veins, reflective of infuscated crossveins of adult forewings. Legs pale yellow, with broad, brown to purplish brown band at subbasal and subapical regions of femora, midlength of tibiae, and base and apex of tarsi. Forefemora (Fig. 70) with moderately developed bipectinate-hairlike setae (setules weakly developed) dorsally. Foretibiae (Fig. 70) 0.8-0.9x length of forefemora, 1.2-1.5x length of foretarsi; bipectinate-hairlike setae along anterior margin (setules moderately developed as in Fig. 67) moderately developed and not arranged in distinct rows; apical spine absent. *Abdomen*: Color brown to purplish brown; terga (Fig. 14) 1-10 each with light, median marking at posterior margin (sometimes somewhat extended anteriorly) as well as pair of light, submedian markings posteriorly and anteriorly. Gills (Fig. 14) 2-7 white with dark tracheae; gills 3 with 35-45 marginal fibrillae along each lateral margin of dorsal lamellae, and 35-40 on ventral lamellae. Caudal filaments 0.4-0.6x length of body.

MALE ADULT.—*Dimensions* (mm): Length of body 10.4-14.5, antennae 1.45, forewings 10.6-12.1, hindwings 4.1-4.5, forelegs 10.2-11.3, forceps 1.20, cerci 22.0-25.0, median terminal filament 19.0-21.3; width of forewings 4.5-5.3, hindwings 2.4-2.5; dorsal diameter of compound eyes 0.45-0.65; distance between compound eyes 0.50-0.63. *Head*: Compound eyes very small ($ES = 0.92-1.25$) (Fig. 149). *Thorax*: Color yellowish brown; pronotum with median purplish brown stripe extending to mesonotum. Forewings (Fig. 89) without markings, but with crossveins strongly infuscated; 26-28 crossveins between SC and R_1 , 19-21 between R_1 and R_2 , and not concentrated near bulla; MAs 0.77-0.83x length of MA₁; cubital region with 4 intercalaries (3 forked). Hindwings (Fig. 107) without markings, but with crossveins strongly infuscated in central area; Rs 0.74-0.85x length of R_2 ; MP₁ 0.26-0.29x length of MP₁; MP₂ symmetrically forked with MP₁ (some individuals with MP₂ connected to CuA and forming MP-cell). Mid-region of forefemora, apex of foretibiae and each foretarsal segment dark; midlegs and hindlegs white; claws dark; foretibiae 1.33-1.63x length of forefemora, 0.73-0.81x length of foretarsi. *Abdomen*: Terga 1-10 each white, with pair of dark round lateral markings; sterna white, without markings. Genitalia as in Fig. 124 and 138. Cerci and median terminal filament white, with dark band at each suture; median terminal filament 0.76-0.97x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 10.5-14.0, forewings 11.4-14.6, hindwings 3.5-5.7, forelegs 6.0-8.0, cerci 16.0-20.0, median terminal filament 15.7-20.0; width of forewings 4.5-6.0, hindwings 1.8-3.3; dorsal diameter of compound eyes 0.50-0.58; distance between compound eyes 0.75-0.88. *Head*: Compound eyes very small, widely separated ($ES = 1.50-1.52$) as in Fig. 149. *Thorax*: Color pale yellow, patterned as in male. Forewings as in male, except 25-30 crossveins between SC and R_1 , 15-18 between R_1 and R_2 ; MAs 0.65-0.90x length of MA₁. Hindwings generally as in male. Legs patterned as in male; foretibiae 1.00-1.07x length of forefemora, 1.52-1.78x length of foretarsi. Midlegs and hindlegs white. *Abdomen*: Terga and caudal filaments patterned as in male; median terminal filament 0.98-1.00x length of cerci.

DIAGNOSIS.— Larvae of *A. distinctus* (Fig. 14) can be distinguished from those of all other species of *Anthopotamus* by the presence of hairlike setae on the forefemora (Fig. 14, 70), the anterolateral corners of pronotum which are not produced into spine-like processes (Fig. 30), the relatively short terminal segment of the maxillary palpi (< 2.5x length of segment 2) and labial palpi (< 1.3x length of segment 2). The larvae of *A. distinctus* additionally can be told from those of *A. verticis* and *A. neglectus* by their evenly attenuated mandibles (Fig. 30), the randomly arranged bipectinate-hairlike setae along the anterior margin of the foretibiae (Fig. 70), and the absence of foretibial apical spine. Fully mature larvae of *A. distinctus* are additionally distinguished from those of *A. myops* by the presence

of dark spots in the wingpads (Fig. 14).

Male adults of *A. distinctus* can be distinguished from those of *A. myops* and *A. verticis* by their very small compound eyes (ES = 0.92-1.25), intermediate between *A. verticis* (larger) and *A. myops* (smaller), and the strongly infuscated crossveins in the forewings (Fig. 89) and hindwings (Fig. 107). They are distinguished from males of *A. neglectus* by their larger compound eyes and bodies (10.4-14.5 mm long). Female adults of *A. distinctus* can be told from those of *A. myops* and *A. verticis* by their strongly infuscated crossveins in the forewings and hindwings, and are distinguished from those of *A. neglectus* by their larger bodies (10.5-14.0 mm long).

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (dried under cellophane, CU type 1348-1, BAE-31-1), USA (Ohio), Willoughby, VII-1-1934, J. R. Traver (CU). PARATYPES: 1 F (dried under cellophane, labeled "Allotype", CU type 1348-2, BAE-31-2); USA (Ohio), Willoughby, at store window light, VIII-9-1934, J. R. Traver (CU); 2 F (alcohol, CU type 1348.3-4), USA (New York), Little Falls, E Canada Cr, VII-24-1934, H. K. Townes (CU).

OTHER MATERIAL EXAMINED.— GEORGIA: 5 L, Chattooga Co, Chattahoochee Nat For ca 5 mi N Armuchee, Hwy 156 Br, V-26-1990 (PERC); 4 M, 5 F, Chattahoochee R, 2 mi S Helen, VII-19-1945 (INHS); 1 M, Trion, VI-22-1940 (INHS); 1 M, 3 F, Chestatee R, 1.2 mi N Cleveland, VII-31-1945 (INHS). MAINE: 2 L (exuviae), 2 M (reared), Aroostook Co, Aroostook R at Washburn, VI-28, VII-6, 8-1987 (UME); 3 M, 2 F, Ashland, VII (MCZ). MASSACHUSETTS: 1 M, Chester, VIII-3 (MCZ). NEW YORK: 1 F, Kast Bridge, W Canada Cr, VII-10-1934 (UMN). NORTH CAROLINA: 4 L, 2 Fs (reared), Davidson R, Pisgah For, VI-20, 26-28-1936 (CU); 15 L, McDowall Co, (UFL); 1 L, McDowell Co, nr Old Fort, VIII-18-1961 (UFL); 1 F, Penrose, VII-19-1930 (CU); 1 Fs, Swannanoa R, N Fk, VI-30-1930 (CU); 1 F, Watauga Co, Beech Cr nr Boone, VII-24-1948 (UFL); 2 Fs, Watauga Co, Shull's Mill, VII-28-1948 (UFL); 1 L, Watauga Co, Blowing Rock, II-28-1956 (UFL). OHIO: 2 M (labeled as c.w.t. "Holotype" by B. D. Burks, BAE-221), Chagrin Falls, VI-20-1941 (INHS). PENNSYLVANIA: 1 M, 1 F, Crawford Co, Saegertown, VII-24-1973 (PERC); 1 Ms, Potter Co, Kettle Cr, nr Cross Fk, June 1939 (INHS). TENNESSEE: 1 M, Gatlinburg, VI-14-1940 (INHS); 12 M, Sevier Co, Pigeon Forge, VII-24-1957 (UFL); 1 L, Union Co (UFL). VIRGINIA: 8 L, S Fk Holster R, 2 mi NW Damascus, Hwy 58 Br, VI-25-1965 (UU); 8 L, Wythe Co, Wythewill, Reed Cr, V-22-1985 (ROM); 1 M, Pennington, Mouth Fork R (MCZ). VERMONT: 9 L, 1 M, 6 F (reared), Windhams Co, N Brook Wedge Wilmington, VI-20-1976 (PERC); 1 M, Dummerston, VII-14 (MCZ). WEST VIRGINIA: 1 F, Justice, VII-12-1930 (CU); 2 L, Smoke Hole, VIII-7-1930 (CU); 3 M, 2 F, Indian Cr (MARU).

DISCUSSION.— *Anthopotamus distinctus* is apparently restricted to the Appalachians Mountains area, from Maine to northern Georgia. Reports of adults of *A. distinctus* from Arkansas appear in unpublished documents as well as in Peters and Warren (1966) and McCafferty & Provonsha (1978). However, we restudied Arkansas material and determined that they are actually assignable to *A. neglectus disjunctus* (see below). This would have been a common misidentification based on characteristics previously thought to be associated with the species. Occasionally, *A. myops* adults have also been misidentified as *A. distinctus*.

***Anthopotamus myops* (Walsh)**

Morphology Fig. 21, 31, 40, 45, 49, 56, 58, 68, 91, 109

Distribution Fig. 3

Ephemera myops Walsh, 1863. Proc. Entomol. Soc. Phil. 2: 207 [Material: M (Holotype); Holotype locality: USA (Illinois); Holotype deposition: Chicago Academy of Science (destroyed); Neotype (designated herein) locality: USA (Illinois); Neotype deposition: MCZ].

- Potamanthus medius* Banks, 1908. Trans. Am. Entomol. Soc. 34: 259 [Material: F (Syntypes); Type locality: USA (Kansas); Type deposition: MCZ], synonymized by Burks (1953).
- Potamanthus inequalis* Needham, 1909. In: Needham 1908. Rep. St. Entomol., N. Y. St. Mus. 134: 74 [Material: M (Syntypes); Type locality: USA (New York); Type deposition: NYSM], NEW SYNONYM.
- Potamanthus myops* (Walsh): McDunnough, 1926. Can. Entomol. 58: 186; McCafferty, 1975a. Trans. Am. Entomol. Soc. 101: 455 (L description).
- Potamanthus rufous* Argo, 1927. J. N. Y. Entomol. Soc. 35: 323 [Material: M & F (Syntypes); Type locality: USA (New York); Type deposition: CU], NEW SYNONYM; Ide, 1935. Can. Entomol. 67: 121 (first L description).
- Anthopotamus inequalis* (Needham): McCafferty & Bae, 1990. Entomol. News 101: 201, NEW SYNONYM.
- Anthopotamus myops* (Walsh): McCafferty & Bae, 1990. Entomol. News 101: 201.
- Anthopotamus rufous* (Argo): McCafferty & Bae, 1990. Entomol. News 101: 201, NEW SYNONYM.

MATURE LARVA.— *Dimensions* (mm): Length of body 13.5-17.0, antennae 3.0-3.5, mandibles 1.6-2.5, caudal filaments 7.5-8.3; dorsal diameter of male compound eyes 0.4-0.5, female compound eyes 0.4-0.5. *Head*: Vertex light brown to dark brown with irregular, light markings. Compound eyes of male minute (ES = 3.00-3.47). Antennae 2.5-3.0x length of head. Mandibles (Fig. 31) 1.1-1.3x length of head, with tusks gradually narrowed from body of mandibles and moderately arched inward (17°); body of mandibles (Fig. 40) with 80-100 simple-stout setae mixed with 10-15 bipectinate-hairlike setae (setules moderately developed as in Fig. 49); tusks 1.9-2.9x length, and 0.3-0.4x width, of body of mandibles, with 1-5 simple-stout setae laterally. Terminal segment of maxillary palpi (Fig. 21, 56) 2.7-4.0x length of segment 2. Paraglossae of labium (Fig. 21) moderately developed laterally; terminal segment of labial palpi (Fig. 21, 45) 2.3-2.7x length of segment 2. *Thorax*: Notal light brown to dark brown; pronotum with 8-12 irregular, light, somewhat round markings, with pair of conspicuous C-shaped markings, with lateral expansions (Fig. 31) white and strongly developed, and with anterolateral corners each produced into spinelike process; mesonotum and metanotum together with 10-15 irregular, light markings. Legs pale yellow, with broad, light to dark brown band at subbasal and subapical regions of femora, at midlength of tibiae, and at base and apex of tarsi. Forefemora without simple-hairlike setae dorsally. Foretibiae 0.9-1.1x length of forefemora, 1.5-1.9x length of foretarsi, with strongly developed bipectinate-hairlike setae (setules well developed and with longer setule alternating with 3-4 shorter setules as in Fig. 68) along anterior margin but not arranged in well-defined rows; apical spine moderately developed. *Abdomen*: Color light to dark brown; terga 1-10 each with light midlongitudinal stripe, and with light, submedian, somewhat longitudinally elongated markings posteriorly and anteriorly. Gills 2-7 white with slightly darker tracheae; gills 3 with 33-45 marginal fibrillae along each lateral margin of dorsal lamellae, and 30-40 on ventral lamellae. Caudal filaments 0.5-0.6x length of body.

MALE ADULT.— *Dimensions* (mm): Length of body 11.3-13.0, antennae 1.0-1.2, forewings 10.7-12.5, hindwings 4.8-5.1, forelegs 9.0-9.5, forceps 0.85-0.88, cerci 25.0-29.0, median terminal filament 16.8-19.0; width of forewings 5.3-6.1, hindwings 3.1-3.3; dorsal diameter of compound eyes 0.33-0.46; distance between compound eyes 0.83-0.93. *Head*: Compound eyes tiny (ES = 1.91-2.71). *Thorax*: Color pale yellow, slightly darker than head and abdomen; prothorax with notal and pair of lateral, longitudinal, purplish brown stripes extending to mesonotum and mesopleura, respectively. Forewings (Fig. 91) without markings or crossvein infuscation; 27-38 crossveins between SC and R_1 , 16-20 between R_1 and R_2 and not concentrated near bulla; MAs 0.74-0.98x length of MA_1 ; cubital region with

4 intercalaries (3 forked). Hindwings (Fig. 109) without markings or crossvein infuscation; R_s 0.63-1.25x length of R_2 ; MP_s 0.29-0.39x length of MP_1 ; MP_2 symmetrically forked with MP_1 (few individuals with MP_2 connected to CuA). Forefemora and apex of foretibiae and each foretarsal segment slightly darker than remainder of forelegs; midlegs and hindlegs white; claws dark; foretibiae 1.29-1.52x length of forefemora, 0.86-1.18x length of foretarsi. *Abdomen*: Terga 1-10 white, without markings, sometimes each tergum with pair of slightly darker round lateral markings. Cerci and median terminal filament white, with dark band at each suture; median terminal filament 0.59-0.70x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 12.0-12.8, forewings 11.8-13.5, hindwings 4.8-4.9, forelegs 6.9-8.2, cerci 15.5-16.0, median terminal filament 14.5-16.0; width of forewings 5.4-6.1, hindwings 2.9-3.0; dorsal diameter of compound eyes 0.45-0.50; distance between compound eyes 0.98-1.10. *Head*: Color similar to male. Compound eyes tiny ($ES = 2.18-2.20$). *Thorax*: Colored and patterned as in male. Forewing membrane and veins unmarked as in male; 34 crossveins between SC and R_1 , 21-27 crossveins between R_1 and R_2 and not concentrated near bulla; MA_s 0.70-0.79x length of MA_1 ; 4 cubital intercalaries (3 forked). Hindwings generally as in male. Legs patterned as in male; foretibiae 1.17-1.25x length of forefemora, 1.65-1.84x length of foretarsi. *Abdomen*: Terga 1-10 each white, without markings. Caudal filaments patterned as in male; median terminal filament 0.94-1.00x length of cerci.

DIAGNOSIS.— Larvae of *A. myops* can be distinguished from those of *A. distinctus* by the absence of hairlike setae on the forefemora, the anterolateral spine-like processes of the pronotum (Fig. 31), the relatively long terminal segment of the maxillary palpi ($> 2.7x$ length of segment 2) (Fig. 21) and labial palpi ($> 2.3x$ length of segment 2) (Fig. 21). Later instar larvae of *A. myops* can also be distinguished from those of *A. distinctus* by the absence of dark wingpad spots. The larvae of *A. myops* can be told from those of *A. verticis* and *A. neglectus* by their evenly attenuated mandibles (Fig. 31), the randomly arranged bipectinate-hairlike setae along anterior margin of foretibiae, and the absence of a foretibial apical spine.

Male adults of *A. myops* can be distinguished from those of all other species of *Anthopotamus* by the combination of the tiny compound eyes ($ES = 1.91-2.71$) and the absence of crossvein infuscation in the forewings (Fig. 91) and hindwings (Fig. 109). Female adults of *A. myops* can also be distinguished from those of all other *Anthopotamus* by the absence of crossvein infuscation in the forewings and hindwings.

TYPE MATERIAL EXAMINED.— NEOTYPE (*Ephemera myops* Walsh, 1863): M (pinned, MCZ type 11202, Walsh 42, BAE-90), USA (Illinois), Rock Island, 1864, deposited in MCZ. SYNTYPES (*Potamanthus medius* Banks, 1908): 2 F (pinned, MCZ type 11422, BAE-93, 94), USA (Kansas), Douglas Co., July [1908], Collection N. Banks, Taken at Electronic Light (MCZ). SYNTYPES (*Potamanthus inequalis* Needham, 1909): 3 M (pinned, BAE-222-224), USA (New York), Schenectady, N. Y., Je. 29, 1909, N. Y. S. Coll. (NYSM). SYNTYPES (*Potamanthus rufous* Argo, 1927): M (alcohol, genitalia dissected and missing, wings damaged in part, BAE-60), USA (New York), Tompkins Co., McLean Res., Mud Pond, 12 Jy 24 (CU); 2 M, 2 F (alcohol, seriously damaged, BAE-59), Corning, New York, (At window), 7/8/26 (CU).

OTHER MATERIAL EXAMINED.— USA: ALABAMA: 7 L, 1 M, 4 F (reared), Jackson Co, Paint Rock R ca 2 mi N Princeton (private farm), V-27-1990 (PERC). ARKANSAS: 2 M, Boone Co, Tucker Hollow Rec Area, V-28-1974 (PERC); 1 M, Fulton Co, 8 mi S Mammoth Springs on Hwy 63 then 2.5 mi SW, VII-2-1985 (ROM); 2 M, 8 F, Izard Co, Strawberry R St Hwy 289 ca 4 mi S Horseshoe bend, VII-3-1981 (PERC); 1 F, Montgomery Co, Little Missouri R, Albert Pike Rec Area, V-30-1974 (PERC); 10 M, 17 F, Montgomery Co, Ouachita R, Rocky Shoals Boat Camp, VI-1-1974 (PERC); 1 M, Pike Co, Antoine R, City

of Antoine, IX-30-1980 (PERC); 14 M, 5 F, Pike Co, Caddo R, Glenwood, V-23-1984 (UFL); 26 M, Polk Co, Mt Folk R, Hwy 246, VI-15-1979 (PERC); 18 M, 12 F, Polk Co, Cossatot R, Hwy 246, 7 mi E Vandervoort, VI-27-1980 (PERC); 20 M, 12 F, Saline Co, Saline R N Fk, 7 mi NW Benton, VIII-15-1980 (PERC); 30 M, 30 F, Saline Co, Middle Fk Saline R, 1 mi NW Owensville, VII-10-1981 (PERC); 21 M, 6 F, Yell Co, Fourche la Fave R at Nimrod Lake, V-24-1981 (PERC). GEORGIA: 3 M, 3 F, Ringgold, VI-14-1939 (UFL, INHS). ILLINOIS: 6 L, Belvidere, Kishwaukee Cr, VI-18-1938 (INHS); 1 L, nr Castle Rock, Rock R, X-15-1939 (INHS); 4 L, Cleveland, Rock R, V-9-1954 (UU); 4 L, Culps, Rock R, VI-23-1925 (INHS); 3 L, Danville, Middle Fk R, VIII-27-1936 (INHS); 1 L, Good Field, Mackinaw R, VI-16-1931 (INHS); 1 L, Greenup, Embarass Cr, IV-16-1935 (INHS); 2 F, Hardin, Illinois R, VII-1-1937 (INHS); 15 L, Homer, Salt Fk, nr Falls, VI-30-1925 (INHS); 12 M, 3 F, Kankakee, VIII-2,3-1938, VI-29-1939 (INHS); 3 L, Kankakee Co, Kankakee R, 3.6 mi SW Mومence, IX-12-1979 (INHS); 1 M, 7 F, Mahomet, VIII-3-1937 (INHS); 2 M, 2 F, McHenry, VI-30-1937 (INHS); 2 L, Milan, Rock R, VI-4-1940 (INHS); 1 L, Moultrie Co, Sullivan, Kaskaskia R (INHS); 4 M, 2 F, Muncie, VI-27-1932 (INHS); 5 L, 1 M, 1 F (reared), Oakwood, Salt Fk R, VI-16-1927, VI-29-1929, VII-6-1936, V-22-1938, VII-1-1940, III-21-1947 (INHS); 26 F, 6 Ms, 1 Fs, Oregon, VII-9-1925, VII-18-1927 (INHS); 6 M, 3 F, Rockford, VI-10-15-1931, VI-12,29-1938 (CU, INHS); 1 L, Roscoe, VII-30-1926 (INHS); 37 L, Serena, Indian Cr, V-12-1938 (UU); 1 L, 1 Ms (reared), Spring Grove, VI-18-25-1938 (INHS); 18 L, Spring Gr, Nippersink Cr, VI-4,8-1938 (INHS); 1 F, Urbana, VI-15-1938 (INHS); 14 L, Vermilion Co, Middle Fk R at Kickapoo St Pk, VI-30-1977 (KBS); 3 L, Vermilion Co, Salt Fk R, riffle, 2.7 mi W & 1.75 mi S Oakwood, VI-15-1983 (KBS); 1 L, White Pines Pk, V-30-1936 (INHS); 7 L, Woodford Co, Mackinaw R at 4 Km WSW Kappa, V-13-1985 (INHS). INDIANA: 3 L, Benton Co, Sugar Cr at St line Rd ca 3 mi NW Freeland Pk, V-25-1976 (PERC); 5 M, 5 F, Carroll Co, Rodger's Farm, VII-16-1974 (PERC); 1 L, Cass Co, Dear Cr 2 mi E city of Dear Creek, VII-19-1974 (PERC); 19 M, 20 F, Cass Co, Wabash R at Logansport, VII-16-1973 (PERC); 6 M, Elkhart Co, Elkhart, VI-18-1901 (CU); 1 L, Elkhart Co, Elkhart R at 1 mi SE Millersburg, V-25-1973 (PERC); 1 L, Elkhart Co, Elkhart Rd at Hwy 33, VI-11-1974 (PERC); 3 L, Grant Co, Mississinewa R at Marion, IV-18-1974 (PERC); 1 L, Harrison Co, Blue R at White Cloud, X-13-1973 (PERC); 1 M, 2 F, Huntington Co, 1 mi W Markle, VI-21-1976 (PERC); 3 L, Johnson Co, dam on Big Blue R at Edinburg, VI-15-1978 (PERC); 3 L, Johnson Co, Sugar Cr at Furnas Mill, VI-15-1978 (PERC); 1 M, Marion Co, Fall Cr at Keystone Ave, Indianapolis, VIII-22-1975 (PERC); 3 M, 2 F, Martin Co, E Fk White R at shoals, VII-2-1974 (PERC); 1 L, LaGrange Co, Pigeon R, Rt 5, Scott, V-20-1972 (PERC); 1 L, Montgomery Co, Sugar Cr at Deers Mill, VI-1-1973 (PERC); 28 L, 3 M, 33 F, Pulaski Co, Tippecanoe R at 1.5 mi S Tippecanoe St Pk, VII-14,30-1976, V-31, VI-30-1978 (PERC); 1 M, Ripley Co, Friendship, V-28-1959 (PERC); 5 L, Shelby Co, Flat Rock R at Hwy 252, VI-15-1978 (PERC); 19 M, 10 F, 1 Ms, Tippecanoe Co, W Lafayette, VI-18,25,VII-8,12,31-1974 (PERC); 25 L, 16 M, 22 F, Tippecanoe Co, Wabash R at W Lafayette, VII-5,13-1973, VII-18-1974, VII-29-1975, V-9-1985 (PERC); 1 L, Warren Co, Mud Pine Cr, 1.5 mi W Rainsville, V-31-1973 (PERC); 2 F, Wells Co, Wabash R at Bluffton, VII-16-1974 (PERC); 13 L, 4 M, 33 F, White Co, Tippecanoe R at Hwy 18 Br, VII-25-1973, VII-19-1974, VI-14,VII-6-1988, VI-22-1989 (PERC). IOWA: 2 L, Boone Co, Des Moines R nr High Br at Boone, X-7-1966 (KBS); 19 L, Cerro Gordo Co, Winnebago R, Lime Cr, Cons Area, N Mason City, VI-23-1989 (CSU); 2 L, Fayette Co, Turkey Run, 1.4 mi S Clermont, 0.3 mi E IA 172 Hwy Br, III-24-1976 (KBS); 10 L, Hardin Co, Iowa R 0.6 mi below Iowa Falls, low water dam, III-26-1976 (KBS); 3 L, Story Co, Skunk R 0.1 mi N US 30 Hwy Br by AMES, III-27-1976 (KBS); 1 L, Vista Co, Sioux R at Buena, VII-6-1931 (CU). KANSAS: 1 M, 3 F, Chase Co, St Lake W end, VIII-31-1977 (KBS); 15 L, Chase Co,

Cottonwood R 3.0 mi S & 1.0 mi W Elmdale, IV-16-1982 (KBS); 2 M, 1 F, Chautaugua Co, Caney R at riffle nr K 99 Br, Cedar Vale, VI-15-1977 (KBS); 1 L, 1 Ms (reared), Chautaugua Co, Big Caney R 0.6 mi E Cedar Vale, US Hwy 116, IV-22-1976 (KBS); 8 L, Chautaugua Co, Big Caney R 1.0 mi E Cedar Vale, N US 116 Br, VI-6-1980 (KBS); 8 L, Cherokee Co, Spring R at K-96 Hwy, E Crestline, V-17-1979, I-20-1981 (KBS); 1 M, 6 F, Coffey Co, Neosho R at Burlington, VI-15-1976 (KBS); 3 L, Elk Co, 1.5 mi W Howard, V-28-1980 (KBS); 10 L, Franklin Co, Marais Des Cyges R at Ottawa City Pk, V-29-1979 (KBS); 6 L, Geary Co, Lyon Cr, K-77 Br, VI-2-1976 (KBS); 5 L, Geary Co, Lyon Cr 2 mi NW St Lake, V-11-1977 (KBS); 1 L, Greenwood Co, Verdigrin R 2.0 mi N Hill Top, XII-28-1976 (KBS); 25 L, Labette Co, Neosho R at Chetopa, IX-16-1976, XI-6-1980 (KBS); 8 L, Lyon Co, Neosho R 2.7 mi W Americus, V-3-1978 (KBS); 12 L, Montgomery Co, Verdigris R 1.2 mi N & 3.1 mi W Liberty, VI-5-1980 (KBS); 3 M, 20 F, Montgomery Co, Montgomery Co St. Lake, flow area, VI-24-1976 (KBS); 10 F, Montgomery Co, Elk R, Oak Ridge Campground at Elk City Res, VII-25-1978 (KBS); 3 L, 1 F (reared), Morris Co, Neosho R 0.5 mi W Dunlap, VI-14-1978 (KBS); 3 M, 3 F, Neosho Co, Neosho Co St Lake, N End Lake, VII-18-1977 (KBS); 7 L, Neosho Co, Neosho R at 0.4 mi S & 2.3 mi W St Paul, XII-17-1982 (KBS); 1 F, Riley Co, Manhattan, X-1933 (CU); 1 L, Wabaunsee Co, Kansas R 2.1 mi E & 3.0 mi N Wabaunsee, VI-14-1978 (KBS); 2 L, Wamego, Kansas R, at K-99 Hwy Br, V-14-1980 (KBS); 36 L, Wilson Co, Fall R 0.4 mi S & 0.8 mi E Fredonia, VI-4-1980 (KBS). KENTUCKY: 1 F, Bell Co, Pineville, VI-24-1938 (INHS); 1 F, Crail Hope, VI-6-1946 (UU); 3 L, Nelson Co, Beech Fk 10.8 km downstream from Bluegrass Parkway, S Bellwood, VIII-2, XI-2-1983 (PERC). MANITOBA: 2 M, 2 F, 2 Ms, 2 Fs, Roseau R, VI-13, 25, VII-12, VIII-8, 10, 26, IX-7, 13-1976 (FIC). MARYLAND: 1 M, 1 F, Frederick Co, ca 7.5 mi NE Frederick, VII-8-1971 (PERC); 1 L, Montgomery Co, Potomac R, 4 mi below mouth Monocacy R, VIII-26-1965 (UU); 1 L, Montgomery Co, Potomac R, 2 mi below Jct Monocacy R, VIII-23-1966 (UU); 1 M, 5 F, 1 Ms, Washington Co, Conococheague Cr nr Hagerstown, VII-22-1926 (CU); 2 M, 5 F, Washington Co, Conococheague Pk, VI-3-1925 (CU). MICHIGAN: 2 L, Shiawassee Co, Barcroft Shiawassee R, I-21-1967 (PERC); 1 M, 2 F, Ag Coll Mich, VI-10-1899 (MCZ). MINNESOTA: 4 L, 3 M, 6 F, 1 Ms (reared), Anoka Co, Fridley, Mississippi R, VI-23-26, VII-6-13-1937 (UMN); 6 F, Anoka Co, Anoka, Run R, VI-26-1937 (UMN); 1 F, Benton Co, Rice, Little Rock Lake, VIII-4-1961 (UU); 1 F (reared), Blue Earth Co, VIII-13-1938 (UMN); 15 L, Blue Earth Co, Blue Earth R at Rapidan, X-11-1937 (INHS); 7 L, Blue Earth Co, Blue Earth R above dam, VI-23-1942 (INHS); 21 L, 1 M, Blue Earth Co, Minnesota R at mi 106.5, 108 & 112, VII-11-12-1979 (UMN); 2 F (reared), Brown Co, Minnesota R at Kettner's Landing along Co Rd 10, VIII-15-1980 (PERC); 3 L, Coodhue Co, Cannon R at St Hwy 20, V-21-1978 (UMN); 3 M, 5 F (reared), Fillmore Co, Root R at Chatfield, V-9-1939 (UMN); 1 L, Fillmore Co, Root R at Rushford, IV-12-1938 (UMN); 1 F, Hennepin Co, Lake Minnetonka, VI-26-1932 (UMN); 9 M, 10 F, Minneapolis, VIII-3, 13, 18, 31-1938, VII-29-1939 (UMN); 1 M, 1 F, Morrison Co, VII-10-1938 (UMN); 1 M, 1 F, Morrison Co, Mississippi R at Little Falls, VII-15-1940 (INHS); 8 L, 1 M, 4 F (reared), Ottertail Co, Ottertail R, Mi 40 below Orwell dam at Hwy 15 Br, IX-20-1979, VIII-18-19-1982 (UMN); 8 M, 4 F, Pine Co, Pine City, VIII-15-1938 (UMN); 63 L, 2 Ms, Pine Co, Snake R, VI-12, 25, 29-1977 (UMN); 1 L, Polk Co, Red Lake R at Crookston, VIII-16-1936 (UMN); 6 F, Polk Co, Crookston, VII-27-1937 (UMN); 1 M, 17 F, Polk Co, Crookston, VIII-25-1956 (UU); 3 L, Polk Co, Red Lake R at Climax, VIII-14-1977 (UMN); 2 M, 1 F, Ramsey Co, St Paul, VII-7-1937 (UMN); 60 L, Sherburne Co, Mississippi R at Elk River, II-9, 21-1978 (UMN); 1 M, Washington Co, VII-17-1938 (UMN); 1 M, 2 F (reared), Yellow Medicine Co, Minnesota R, VIII-10-11-1981 (UMN); 2 F, VII-6-1938 (UMN). MISSOURI: 2 F, Cole Co, Jefferson, VI-25-1989 (CSU); 2 F, Palmyra, VI-8-1939 (INHS); 8 L, St Clair Co, Sac R at

US 54 Hwy Br, VIII-19-1977 (KBS); 5 M, 21 F, 7 mi E Sullivan, VI-13-1959 (UU); 5 L, Taylor, V-17-1940 (INHS); 10 M, 10 F, Texas Co, Big Piney R 0.5 mi downstream confluence Arthur Cr, VII-15-1978 (KBS); 1 L, Texas Co, Big Piney R 1.0 mi downstream old MO 32 Hwy Br, VII-17-1978 (KBS). NEW YORK: 1 Ms (labeled "Ephemera inequalis," BAE-225) Menands, VII-10-1899 (NYSM); 7 M, 6 F, Tompkins Co, Ithaca, VII-13-1931, VII-2-1932 (CU); 3 M, 13 F, Susquehanna R at Oneonta, VII-5-1935 (UMN). NORTH DAKOTA: 3 L, Grand Forks Co, 1st Str S county line on Rt 18, 45 mi NW Grand Forks, VII-9-1981 (ROM). OHIO: 1 L, Ashland Co, Clear Fork R, Clear Fork St Pk, IX-26-27-1967 (ROM); 5 M, 14 F, Sidney, Miami R at Hwy 47, VI-26-1953 (PERC); 2 L, Miami R, Taylorsville Dam, VIII-27-1952 (UU); 7 M, 6 F, Morrow, Little Miami R, VI-28-1953 (PERC). ONTARIO: 1 F, Burlington, VIII-15-1956 (UU); 1 M, 7 F, Erindale, VII-9,21-1934 (ROM). PENNSYLVANIA: 1 Fs, Harrisburg, VI-1912, (MCZ); 2 M, Lock Haven, VII-28-1952 (FEM); 10 F, 1 Ms, Crawford Co, Saegertown, VII-24-1973 (PERC); 4 L, Snyder Co, Penn's Cr, III-13,VI-25,26-1979 (FEM). TENNESSEE: 1 F, Davidson Co, VI-28-1954 (UFL); 11 M, 2 F, Sevierville, VI-12-1940 (INHS). VIRGINIA: 2 F, Loudoun Co, Dulles Airport, VI-23-1964 (UU). WEST VIRGINIA: 3 L, 1 F, Indian Cr (MARU). WISCONSIN: 27 L, Dane Co, Sugar R, VII-30-1969, V-30-1978, V-16-1979, VI-29-1984, VI-16, VII-9-1985 (UWI); 1 L, Dunn Co, Chippewa R, IX-21-1971 (UWI); 1 F, Eau Clair, VII-15-1940 (INHS); 7 L, Grant Co, Grant R, X-30-1980 (UWI); 2 L, Grant Co, Little Platle R, V-10-1979 (UWI); 4 L, Lafayette Co, Pecatonica R W Br, III-29-1969, VI-22-1972, VII-3-1973 (UWI); 1 L, Lafayette Co, Galena R, IV-26-1979 (UWI); 13 L, Milwaukee Co, Milwaukee R, X-13-1980 (UWI); 28 L, Ozaukee Co, Milwaukee R, V-12, X-17-1980 (UWI); 14 L, Racine Co, Honey Cr, V-22-1979 (UWI); 30 L, Rock Co, Yahara R, VI-26-1975, VI-27-1977 (UWI); 1 L, Rock Co, X-10-1980 (UWI); 3 L, Sauk Co, Honey Cr, III-27-1971 (UWI); 2 L, Shawano Co, Embarrass R, X-29-1980 (UWI); 10 L, Sheboygan Co, Onion R, X-31-1979 (UWI); 3 L, St Croix Falls, Apple R on US Hwy 8, VII-4-1933 (INHS); 4 L, Turtle Co, V-5-1980 (UWI); 10 L, Walworth Co, Sugar Cr, V-23-1979 (UWI); 2 L, Washington Co, Milwaukee R, V-28-1980 (UWI).

DISCUSSION.— This is the most widespread species of *Anthopotamus*, occurring throughout most of eastern North America (Fig. 3). It is also arguably the most commonly collected species of the genus, although *A. verticis* is also very commonly taken in the Midwest.

Ephemera myops is one of the Walsh species originally described from Rock Island, Illinois, but whose types were destroyed in the Great Chicago Fire of 1871. Duplicate specimens of most of those species are fortunately located at the MCZ. Those with the same date as the Holotype are available for lectotype designation if necessary, but those collected subsequently are not (see Burks, 1953). No possible lectotype is available of *E. myops*, and we have thus selected a neotype from Walsh's subsequently collected material at the MCZ as designated above.

Our examination of the type material of *A. rufous* and *A. inequalis* clearly show these to be junior synonyms of *A. myops*. We also discovered that the collection date Argo (1927) published for two male and two female adults (BAE-59) from Corning, New York is July 8, 1924; however, the date accompanying the specimens reads "7/8/26."

Needham collected material and described *Potamanthus inequalis* in 1909 and added it to the publication (Rep. St. Entomol., N. Y. St. Mus.), which was in press at the time (see Needham 1908) and was later published with a 1908 journal date. *P. inequalis*, therefore, should be dated 1909, not 1908.

The first larval description of *A. myops* was given by Ide (1935) under the name *Potamanthus rufous*. The first comprehensive larval description, however, was given by McCafferty

(1975a), under *Potamanthus myops*. Lord & Meier (1977) reported some intraspecific variation of the larvae of this species.

***Anthopotamus verticis* (Say)**

Morphology Fig. 32-35, 71, 74-75, 81, 92-93, 110-111, 148

Distribution Fig. 3

Baetis verticis Say, 1839. J. Acad. Nat. Sci. Phil. 8: 42 [Material: F (?) (lost); Type locality: USA (Indiana); Neotype (designated by McCafferty & Bae 1991) locality: USA (Indiana); Neotype deposition: PERC].

Ephemera flaveola Walsh, 1862. Proc. Acad. Nat. Sci. Phil. 1862: 377 [Material: M (Holotype), F; Holotype locality: USA (Illinois); Holotype deposition: Chicago Academy of Science (destroyed); Lectotype (designated by McCafferty & Bae 1991) locality: USA (Illinois); Lectotype deposition: MCZ], synonymized by McDunnough (1926).

Polymitarcys albus (Say): Howard, 1905. Bull. N. Y. St. Mus. 86: 60 (first L description), misidentification; Needham, 1920. Bull. Bur. Fish. 36: 285, figs. 39-45 (L figure), misidentification.

Potamanthus diaphanus Needham, 1907. Rep. St. Entomol., N. Y. St. Mus. 124: 193 [Material: M (Holotype), L; Holotype locality: USA (New York); Holotype deposition: CU], NEW SYNONYM.

Potamanthus bettini Morgan, 1913. Ann. Entomol. Soc. Am. 6: 412, figs. 7, 23, 24 [L figure; Type information: unknown], synonymized by McCafferty (1975b). *Potamanthus flaveola* (Walsh): Needham, 1920. Bull. Bur. Fish. 36: 287, figs. 52-56, synonymized by McDunnough (1926).

Potamanthus verticis (Say): McDunnough, 1926. Can. Entomol. 58: 185.

Potamanthus walkeri Ide, 1935. Can. Entomol. 67: 119 [Material: M (Holotype), F, L; Holotype locality: CANADA (Ontario); Holotype deposition: ROM], NEW SYNONYM.

Anthopotamus diaphanus (Needham): McCafferty & Bae, 1990. Entomol. News 101: 201, NEW SYNONYM.

Anthopotamus verticis (Say): McCafferty & Bae, 1990. Entomol. News 101: 201.

Anthopotamus walkeri (Ide): McCafferty & Bae, 1990. Entomol. News 101: 201, NEW SYNONYM.

MATURE LARVA.— *Dimensions* (mm): Length of body 10.0-11.0, antennae 2.0-2.5, mandibles 1.2-1.5, caudal filaments 4.0-5.0; dorsal diameter of male compound eyes 0.5, female compound eyes 0.4. *Head*: Vertex brown to dark brown, without light markings. Compound eyes of male minute (ES = 2.00-2.15). Antennae 1.7-2.1x length of head. Mandibles (Fig. 34-35) 0.9-1.3x length of head, with tusks abruptly narrowed from body of mandibles and slightly arched inward (8o); body of mandibles with 50-70 simple-stout setae mixed with 10-15 bipectinate-hairlike setae; tusks 2.7-3.0x length and 0.4-0.5x width of body of mandibles, and without simple-stout setae laterally. Terminal segment of maxillary palpi 2.7-2.8x length of segment 2. Paraglossae moderately developed laterally; terminal segment of labial palpi 2.0-2.3x length of segment 2. *Thorax*: Nota brown to dark brown, often with no light markings or with 10-12 relatively small, light, somewhat round markings on pronotum (C-shaped markings not clearly defined), and with 12-16 relatively small, irregular, light markings together on mesonotum and metanotum in some. Pronotum (Fig. 33) with lateral expansions white and strongly developed; anterolateral corners each produced into spinelike process. Legs pale yellow, with broad, brown to dark brown band at subbasal and subapical regions of femora, midlength of tibiae and tarsi, but foretarsi often dark throughout. Forefemora without simple-hairlike setae dorsally. Foretibiae 1.1-1.2x length of forefemora, 1.4-1.5x length of foretarsi; bipectinate-hairlike setae (setules well developed, with 1 long setule alternating with 3-4 shorter setules as in Fig. 68) along anterior margin strongly developed in 3 rows (Fig. 71); apical spine present (Fig. 34), 0.4x length of foretarsi.

Abdomen: Color brown to dark brown; terga 1-10 each with light midlongitudinal stripe and light submedian spots, but light markings sometimes missing. Gills 2-7 white with slightly darker tracheae; gills 3 with 30-35 marginal fibrillae along each lateral margin of dorsal lamellae, and 25-30 on ventral lamellae. Caudal filaments 0.4-0.5x length of body.

MALE ADULT.—*Dimensions* (mm): Length of body 7.8-10.5, antennae 1.0-1.2, forewings 9.0-9.8, hindwings 3.4-3.5, forelegs 6.5-8.3, forceps 0.76, cerci 19.8-23.0; median terminal filament 14.3-15.3; width of forewings 4.0-4.6, hindwings 1.7-2.2; dorsal diameter of compound eyes 0.50-0.55; distance between compound eyes 0.38-0.50. *Head*: Compound eyes small (ES = 0.68-0.94) (Fig. 148). *Thorax*: Color pale yellow, slightly darker than head or abdomen; pronotum with median purplish brown stripe extending to mesonotum. Forewings (Fig. 92) membrane and veins without markings; 24-27 crossveins between SC and R_1 and 17-20 between R_1 and R_2 , not concentrated near bulla; MAs 0.74-1.00x length of MA_1 ; cubital region with 3-4 intercalaries (2-3 forked). Hindwings (Fig. 110) membrane and veins without markings; Rs 0.91-1.08x length of R_2 ; MPs 0.38-0.44x length of MP_1 ; MP_2 symmetrically forked with MP_1 (not connected to CuA). Forefemora and apex of foretibiae and each foretarsal segment slightly darker than remainder of foreleg; midlegs and hindlegs white; claws dark; foretibiae 1.55-1.59x length of forefemora, 0.88-1.29x length of foretarsi. *Abdomen*: Terga 1-10 each white, with pair of dark round lateral markings; sterna white, without markings. Caudal filaments white, with dark band at each suture; median terminal filament 0.62-0.77x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 9.5-10.2, forewings 10.6-10.7, hindwings 3.4-3.6, forelegs 5.4-6.0, cerci 10.2-11.2, median terminal filament 9.6-10.4; width of forewings 4.2-4.6, hindwings 2.1-2.3; dorsal diameter of compound eyes 0.38-0.48; distance between compound eyes 0.63-0.68. *Head*: Compound eyes very small (ES = 1.42-1.66). *Thorax*: Patterned as in male. Forewings (Fig. 93) similar to male, except with crossveins slightly infuscated in central region; 29-31 crossveins between SC and R_1 , 20-21 between R_1 and R_2 ; MAs 0.68-0.71x length of MA_1 . Hindwings (Fig. 111) generally as in male. Legs patterned as in male. Foretibiae 1.11-1.25x length of forefemora, 1.50-1.67x length of foretarsi. *Abdomen*: Terga and caudal filaments patterned as in male. Median terminal filament 0.93-0.94x length of cerci.

DIAGNOSIS.— Larvae of *A. verticis* can be distinguished from those of *A. distinctus* and *A. myops* by the abrupt constriction at the base of the mandibles (Fig. 34), the presence of 3 rows of bipectinate-hairlike setae along the anterior margin of foretibiae (Fig. 71), and the presence of a foretibial apical spine (Fig. 34). Fully mature larvae of *A. verticis* can also be distinguished from those of *A. neglectus* by their uniformly dark color pattern (as in Fig. 39 in Needham 1920), their slightly longer mandibular tusks (0.9-1.3x length of head), and their slightly larger male compound eyes (ES = 2.00-2.15).

Male adults of *A. verticis* can be distinguished from those of all other species of *Anthopotamus* by the combination of small compound eyes (ES = 0.68-0.94) and the absence of crossvein infuscation in the forewings (Fig. 92). Female adults of *A. verticis* can be told from those of all other species of *Anthopotamus* by the combination of the slightly infuscated crossveins in the forewings (Fig. 93) and their medium-sized bodies (9.5-10.2 mm long).

TYPE MATERIAL EXAMINED.— **NEOTYPE** (*Baetis verticis* Say, 1839): M (alcohol, BAE-218), USA (Indiana), Tippecanoe Co., W. Lafayette, at light, VI-25-1974, A. V. Provonsha (PERC). **LECTOTYPE** (*Ephemera flaveola* Walsh, 1862): M (pinned, MCZ type 11210, BAE-91), USA (Illinois), Rock Island, 1860, Walsh (MCZ). **PARALECTOTYPES** (*Ephemera flaveola* Walsh, 1862): 3 M, 3 F (pinned, 1 F labeled as MCZ type 11210, BAE-92), same data and deposition as Lectotype. **HOLOTYPE** (*Potamanthus diaphanus* Needham, 1907): M (pinned, wings and abdomen missing, BAE-228), USA (New York), Buffalo, N.

Y., July 24, 1906, N. Y. S. Coll. (CU). HOLOTYPE (*Potamanthus walkeri* Ide, 1935): M (pinned, BAE-28), CANADA (Ontario), Erindale, VI-27-1934, F. P. Ide (ROM). PARATYPE (*Potamanthus walkeri* Ide, 1935): F (pinned, labeled "allotype," BAE-197), Ontario, Erindale, VI-11-1934, F. P. Ide (ROM).

OTHER MATERIAL EXAMINED.—ILLINOIS: 8 F, Antioch, VII-1-1931 (INHS); 17 L, Culps, Rock R, VI-23-1925 (INHS); 1 M, Elgin, Rainbow Springs, VI-6-1939 (INHS); 1 M, nr Foster, Mississippi R, VII-11-1939 (INHS); 2 F, Hardin, Illinois R, VII-1-1937 (INHS); 1 M, N Havana, NHS Lab, VI-9-1940 (INHS); 1 F, 1 Ms, Kankakee, VIII-2,16-1938 (INHS); 34 L, Keithsburg, Summer 1932 (INHS); 3 F, Moline, VI-26-1954 (PERC); 6 M, 9 F, Momence, VI-22,24-1939 (INHS); 17 F, 2 Ms, 2 Fs, Oregon, VII-9-1925, VII-18-1927 (INHS); 1 L, Prophetstown, VII-24-1947 (INHS); 1 Fs, Quincy, Mississippi R, VII-6-1939 (INHS); 1 M, Richmond, VI-5-1938 (INHS); 21 M, 2 F, Rockford, VII-2-1931, VI-12,29-1938 (INHS); 4 M, Rock Island, VI-17-1948 (INHS); 7 M, 5 F, Rockton, VII-2-1935 (INHS); 7 L, Roscoe, VII-30-1926 (INHS); 31 M, 2 F, S Beloit, VII-2-1931 (INHS); 3 M, 1 F, 2 Fs, Sterling, VI-7-1939 (INHS); 5 F, Wilmington, VIII-3-1937 (INHS); 2 F, Yorkville, VI-25-1936 (INHS). INDIANA: 1 M, Cass Co, Eel R at Logansport, VII-16-1973 (PERC); 1 F, Elkhart Co, Elkhart R at Elkhart R Pres, Benton, VII-2-1977 (PERC); 3 L, Gibson Co, White R at Cunningham's Ferry, 5 mi NW Patoka, VII-11-1973 (PERC); 26 L, 14 M, 65 F, Martin Co, E Fk White R at Hindostan Falls, VI-20,21,VIII-13-1974, VII-17-1975, VI-8-1978, VII-15-1982 (PERC); 1 M, Martin Co, White R at shoals, VII-2-1979 (PERC); 3 L, Tippecanoe Co, Wabash R at Fort Ouiatenon, VII-16-1976 (PERC); 14 L, Tippecanoe Co, Wabash R at W Lafayette, VII-18-1974, VII-29-1975, VII-6-1977, V-9-1985 (PERC); 8 M, 3 F (alcohol, BAE-219), same locale and data as Neotype of *Baetis verticis* Say (PERC); 2 L, 13 M, 2 F, 1 Ms, Tippecanoe Co, W Lafayette, VII-8,12,31-1974 (PERC); 47 L, 15 M, 302 F, 11 Ms, 11 Fs (some reared), White Co, Tippecanoe R at Hwy 18 Br, VII-2-1973, VI-17,VII-19-1974, V-23,VI-14,VII-6-1988, VI-6,14,22,VII-8,VIII-1-1989, VII-11-1990 (PERC). IOWA: 4 L, 6 M, 3 F, 7 Ms, Muscatine Co, Fairport, Biol Lab, VI-8-1921, VII-1-1931 (CU); 1 M, Polk Co (?), VII-7-1939 (INHS). MARYLAND: 2 L, Frederick Co, Potomac R at Brunswick, VI-19-1926 (CU); 3 M, 6 F, Frederick Co, ca 7.5 mi NE Frederick, Rt 15, VII-8-1971 (PERC); 31 L, Frederick Co, Potomac R nr Frederick, IX-2-4-1964, VIII-24-1965 (UU); 28 L, Frederick Co, 1 mi ab Rt 15, point of rocks (UU); 1 L, Montgomery Co, Potomac R Dickerson, III-14-1973 (PERC); 32 L, Montgomery Co, Potomac R at 2-4 mi below mouth Monocacy R, VIII-26-28-1965, VIII-23-1966 (UU); 1 M, Washington Co, Conococheague Pk, VII-22-1926 (CU). MICHIGAN: 1 M, Ingham Co, E Lansing, VII-3-1936 (INHS). MINNESOTA: 1 M, 1 F, Anoka Co, Anoka, VI-26-1937, VII-9-1939 (UMN); 12 L, 6 M, 39 F, 1 Fs (some reared), Anoka Co, Fridley, Mississippi R, V-6-1931, V-18-1933, VI-6,26-1937, VI-28,VII-1-1939 (UMN); 1 M, Carlton Co, VII-14-1938 (UMN); 1 L, 1 F (reared), Mississippi R at Coon Rapids, VII-21-1939, VI-11-1966 (UMN); 3 L, Mahnomen Co, Wild Rice R, VIII-8-1977 (UMN); 4 L, 30 M, 19 F, Minneapolis, VII-13-21,VIII-3-1938, VI-29,VII-1,13-1939 (UMN); 3 F, Morrison Co, Little Falls, VII-10-1938 (UMN); 1 M, 2 F, Pine Co, Pine City, VII-6-,VIII-15-1938 (UMN); 7 L, Pine Co, Snake R, II-23,V-14-1977 (UMN); 2 F, Ramsey Co, St Paul, VII-10,VIII-5-1938 (UMN); 40 L, Sherburne Co, Elk R, II-9,21-1978 (UMN); 22 L, 10 M, 1 F, St Croix R, Taylors Falls, VII-6-1928, X-11,18-1938 (UMN); 1 M, Washington Co, VII-17-1938 (UMN); 2 M, Winona, VII-5-1937 (UMN). MISSOURI: 17 F, Hollister, VII-11,14-1938 (INHS); 16 L, McDonald Co, Elk R at MO 43 Hwy Br, 5 mi N & 6 mi W Noel, V-20-1981 (KBS); 3 L, McDonald Co, Indian Cr at MO 76 Hwy Br, E Anderson, V-20-1981 (KBS). NEW YORK: 1 M, 8 F, Buffalo, VII-31-1906 (CU); 8 M, 35 F, Ithaca, VII,VIII-1931, VII-2-1932, VII-4-5-1935, VI-19-1936 (CU); 1 M (labeled "Ephemera diaphanus", BAE-226), 1 F, Schenectady, VI-29-1909 (NYSM). ONTARIO: 2

M, 23 F, Erindale, VII-9,16,21,23-1934 (ROM). PENNSYLVANIA: 6 M, 10 F, 2 Fs, Harrisburg, July 10-13 (MCZ); 1 L, Lycoming Co, Little Pine Cr, Waterville, IX-17-1988 (FEM); 3 L, Lycoming Co, Pine Cr, 1 mi N Cammal, IX-17-1988 (FEM); 1 L, Luzerne Co, Susquehanna R, Harding, old power plant, X-8-1988 (FEM); 67 L, Wyoming Co, Susquehanna R, 0.75 mi NW Tunkhannoch, IX-1965 (UU); 45 L, Wyoming Co, Susquehanna R, 1.5 mi SE Mehoppny, IX-1965 (UU). TENNESSEE: 1 F, Cheatham Co, VII-2-1954 (UFL); 1 F, Davidson Co, VI-28-1954 (UFL); 1 M, 7 F, Knoxville, Tennessee R at Island Home Pk, VI-20-1931 (CU); 2 M, Knoxville, Univ Tennessee campus, VI-22-1931 (CU). VIRGINIA: 3 L, Berryville, Shenandoah R, V-12-1938 (PERC); 1 M, Great Falls, June 18 (MCZ). WISCONSIN: 6 L, Barron Co, Red Cedar R, V-12-1979 (UWI); 5 L, Burnett Co, St Croix R, Little Soderbeck, Land, VIII-29-1985 (UWI); 3 L, Douglas Co, St Croix R, V-16-1979 (UWI); 4 L, Langlade Co, Wolf R, X-17-1980 (UWI); 2 L, Lincoln Co, Wisconsin R, VI-7-1966 (UWI); 9 M, 3 F, Merrill, VII-24-1937 (INHS); 3 L, Rusk Co, Big Jump R, V-12-1979 (UWI).

DISCUSSION.— *Anthopotamus verticis* is another common species of Potamanthidae, found primarily in midwestern North America as far north as Ontario and as far south as Tennessee and also in the eastern United States as far south as Virginia (Fig. 3). The Mississippi record given by McCafferty (1975a) is applicable to *A. neglectus disjunctus* (see below).

The species has a rather confused nomenclatural history that was clarified by McCafferty & Bae (1991). The concept of the species was solidified by naming a neotype of *Baetis verticis* Say, and *Ephemera flaveola* Walsh was confirmed to be a junior synonym. Moreover, Eaton's (1871, 1883-88) references to *Heptagenia flaveola* and *Ecdyurus verticis* represent a misidentification of *Stenonema terminatum* (Walsh) and are not referable to Potamanthidae (see McCafferty & Bae 1991).

Our study of the type material of *P. diaphanus* Needham and *P. walkeri* Ide indicated that they should be considered junior synonyms of *A. verticis*. The holotype of *P. diaphanus* is badly damaged, but eye size and crossvein infuscation indicate the synonymy. Argo's (1927) reference to *P. verticis* is applicable to *A. neglectus neglectus*. The first larval description of *A. verticis* was given by Howard (1905) under the name *Polymitarcys albus* (Say), a misidentification.

***Anthopotamus neglectus* (Traver)**

Morphology Fig. 90, 108

Distribution Fig. 3

Potamanthus verticis (Say): Argo, 1927. J. N. Y. Entomol. Soc. 35: 322, misidentification.

Potamanthus neglectus Traver, 1935. Comstock Publ. Co., Ithaca, NY. p. 282 [Material: M (Holotype),

F; Holotype locality: USA (New York); Holotype deposition: CU].

Anthopotamus neglectus (Traver): McCafferty & Bae, 1990. Entomol. News 101: 201.

MATURE LARVA.— *Dimensions* (mm): Length of body 10.3-10.7, antennae 2.3-2.5, mandibles 0.8-0.9, caudal filaments 4.5-5.0; dorsal diameter of male compound eyes 0.38, female compound eyes 0.38. *Head*: Vertex brown or purplish brown with irregular, light markings. Compound eyes of male minute (ES = 2.53). Antennae 2.0-2.5x length of head. Mandibles (as in Fig. 34-35) 0.7-0.8x length of head, with tusks abruptly narrowed from body of mandibles and slightly arched inward (8°); body of mandibles with ca. 50 simple-stout setae mixed with ca. 10 bipectinate-hairlike setae; tusks 1.6-2.1x length and 0.3x width of body of mandibles, without simple-stout setae dorsally and laterally. Terminal segment of maxillary palpi 2.8-3.0x length of segment 2. Paraglossae moderately developed laterally;

terminal segment of labial palpi 1.9-2.1x length of segment 2. *Thorax*: Nota brown to purplish brown; pronotum with 8-12 irregular, light, somewhat round markings, with pair of conspicuous C-shaped markings, with lateral expansions white and strongly developed, and with anterolateral corners each produced into spinelike process; mesonotum and metanotum together with 6-10 irregular, light markings. Wingpads of female with tiny black spots along longitudinal veins, reflective of infuscated crossveins of adult forewings (as in Fig. 14). Legs pale yellow, with broad, brown to purplish brown band at subbasal and subapical regions of femora, midlength of tibiae, and base and apex of tarsi. Forefemora with few bipectinate-hairlike setae dorsally. Foretibiae 1.02-1.14x length of forefemora, 1.36-1.55x length of foretarsi; bipectinate-hairlike setae along anterior margin strongly developed and arranged in 3 rows; apical spine present, 0.36-0.44x length of foretarsi. *Abdomen*: Color brown to purplish brown; terga 1-10 each with light, median marking at posterior margin (sometimes somewhat extended anteriorly) as well as pair of light, submedian markings posteriorly and anteriorly (as in Fig. 14). Gills 2-7 white with dark tracheae; gills 3 with 28-30 marginal fibrillae along each lateral margin of dorsal lamellae, and 28-30 on ventral lamellae. Caudal filaments 0.5x length of body.

MALE ADULT.—*Dimensions* (mm): Length of body 7.2-9.2, antennae 0.9-1.0, forewings 7.4-8.8, hindwings 3.0-3.5, forelegs 5.3-6.6, forceps 0.67-0.76, cerci 17.5-20.5, median terminal filament 12.5-14.0; width of forewings 3.4-4.2, hindwings 1.8-2.3; dorsal diameter of compound eyes 0.23-0.30; distance between compound eyes 0.63-0.65. *Head*: Compound eyes tiny (ES = 2.08-2.89). *Thorax*: Color pale yellow, slightly darker than head and abdomen; pronotum with median purplish brown stripe extending to mesonotum. Forewings (Fig. 90) without markings, but with crossveins infuscated in central region; 23-30 crossveins between SC and R_1 , 14-18 between R_1 and R_2 , not concentrated near bulla; MAs 0.86-0.89x length of MA_1 ; cubital region with 3-4 intercalaries (2-3 forked). Hindwings (Fig. 108) without markings, but crossveins infuscated in central region; Rs 0.64-1.81x length of R_2 ; MPs 0.27-0.36x length of MP_1 ; MP_2 symmetrically forked with MP_1 (in some individuals MP_2 connected to CuA and forming MP-cell). Apex of foretibiae and each foretarsal segment slightly darker than remainder of forelegs; midlegs and hindlegs white; claws white; foretibiae 1.31-1.48x length of forefemora, 0.94-1.04x length of foretarsi. *Abdomen*: Terga and sterna white, without markings or sometimes with pair of slightly darker round lateral markings. Genitalia similar to Fig. 124 and 138; terminal segment of genital forceps subequal to segment 2, segment 2 and 3 together 0.52-0.59x length of basal segment. Caudal filaments white, with dark band at each suture; median terminal filament 0.65-0.71x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 8.5-9.2, forewings 8.8-9.2, hindwings 2.5-3.1, forelegs 4.2-4.9, cerci 9.2-11.2, median terminal filament 8.0-11.2; width of forewings 3.4-4.0, hindwings 1.5-1.8; dorsal diameter of compound eyes 0.28-0.33; distance between compound eyes 0.65-0.75. *Head*: Color white; vertex purplish brown. Compound eyes tiny (ES = 2.27-2.61). *Thorax*: Patterned as in male. Forewings similar to male, except 21-24 crossveins between SC and R_1 , 12-17 crossveins between R_1 and R_2 ; MAs 0.70-0.89x length of MA_1 . Hindwings as in male. Legs similar to male except foretibiae 0.94-1.25x length of forefemora, 1.42-1.60x length of foretarsi. *Abdomen*: Similar to male, except median terminal filament 0.87-1.00x length of cerci.

DIAGNOSIS.— Larvae of *A. neglectus* are similar to those of *A. verticis* in mouthpart and foreleg structure, but are similar to *A. distinctus* and *A. myops* in color pattern. They can be distinguished from larvae of *A. distinctus* and *A. myops* by their abruptly narrowed mandibles (as in Fig. 33-34), the presence of 3 rows of bipectinate-hairlike setae along anterior margin of foretibiae (as in Fig. 71), and the presence of a foretibial apical spine (as in Fig. 34). Fully mature larvae of *A. neglectus* are distinguished from those of *A. verticis* by their distinct color

pattern (as in Fig. 14), their slightly shorter mandibular tusks (0.7-0.8x length of head), and their slightly smaller compound eyes in the male (ES = 2.53).

Male adults of *A. neglectus* can be distinguished from those of *A. distinctus* and *A. verticis* by their tiny compound eyes (ES = 2.08-2.89). They are distinguished from those of *A. myops* by their infuscated forewing and hindwing crossvenation (Fig. 90, 108). Male and female adults of *A. neglectus* can also be told from those of all other species of *Anthopotamus* by their smaller bodies (7.2-9.2 mm long).

DISCUSSION.— This has been a poorly known species because adult characterization was dubious, few specimens were confirmed, and the larvae have been unknown. Actually, the adults are very distinct, but we have found two disjunct geographic populations that we treat as subspecies (see below). The nominal subspecies occurs in northeastern North America, and the new subspecies occurs in the southern and south-central United States (Fig. 3). Some minor morphological variation tends to parallel geographic differences (see Diagnoses under subspecies treatments, below).

McCafferty (1975a) and McCafferty & Provonsha (1978) tentatively identified mature larvae (BAE-67) taken from Benton County, Arkansas as *A. neglectus* because they were unlike any other *Anthopotamus* larvae, although their tusks were similar to those of *A. verticis*. Furthermore, adults (BAE-66) of *A. neglectus* were known from the same locality and same time of year. These included adults from Benton County, Arkansas recorded as either *A. neglectus* or *A. distinctus*. In light of our detailed analysis of *Anthopotamus*, the above association, although not based on actual rearing, is sufficient for making a tentative determination of these larvae as *A. neglectus*. Obviously, direct rearings will be necessary for verification.

***Anthopotamus neglectus neglectus* (Traver), NEW STATUS**

Distribution Fig. 3

DIAGNOSIS.— Most adults of *A. neglectus neglectus* possess strongly infuscated crossveins in both their forewings and hindwings, and MP_1 in the hindwings is symmetrically forked with MP_2 . Markings on abdominal terga of this subspecies are often not distinctly defined. The larval stage is unknown.

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (alcohol, CU type 1349-1, BAE-30-1), USA (NEW YORK), Ithaca, July 2, 1932, C. N. Hardy (CU). PARATYPES: 1 F (dried under cellophane, labeled "Allotype", CU type 1349-2, BAE-30-2): New York, Ithaca, Aug. 2, 1934, A. M. French (CU); 4 M, 9 F (alcohol, CU type 1849-11-25), MARYLAND, Hagerstown, July 22, 1926, V. Argo (CU); 10 F (alcohol), Maryland, Conococheague Cr near Hagerstown, July 22, 1926, V. Argo (CU); 9 F (alcohol), New York, Ithaca, July 2, 1932, C. N. Hardy (CU).

OTHER MATERIAL EXAMINED.— NEW YORK: 1 F, Etica, VII-5-1935 (CU).

***Anthopotamus neglectus disjunctus*, NEW SUBSPECIES**

Morphology Fig. 90, 108

Distribution Fig. 3

DIAGNOSIS.— Adults of *A. neglectus disjunctus*, particularly from populations from Mississippi, demonstrate some variation not found in *A. neglectus neglectus*. The MP_1 in the hindwings is more frequently connected to CuA, forming a MP-cell as in *Rhoenanthus*, and the pair of round lateral markings on each abdominal tergum are often distinctly defined as in *A. verticis*. Crossveins of forewings and hindwings are, however, slightly to strongly infuscated.

ETYMOLOGY.— The subspecific name *disjunctus* is masculine, from the Latin *disjunctus* (disjunct, disunited), alluding to the disjunct geographical distribution of the subspecies in southeastern North America from that of *A. neglectus neglectus* in northeastern North America.

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (alcohol, BAE-187) USA (MISSISSIPPI), Pike Co., Cat. No. 8-1954-3, L. Berner No. 3647.3, deposited in UFL. PARATYPES: 2 F (alcohol, BAE-229) same data and deposition as Holotype; 1 M, 5 F (alcohol, BAE-230), same locale as Holotype, Cat. No. 8-1854-4, L. Berner No. 3645.6, deposited in PERC.

OTHER MATERIAL EXAMINED.— USA: ARKANSAS: 4 L (BAE-67), 2 M (BAE-66), 20 F, 2 Ms, Benton Co, VI-3,24-1963 (PERC); 3 M, IZARD Co, Strawberry R at St. Hwy 289, ca 4 mi S Horseshoe bend, VII-3-1981 (PERC); 11 M, 10 F, Little River Co, Little R at Little River Country Club, S Horatio, VI-26-1980 (PERC); 2 M, 22 F, Nevada Co, Little Missouri R, NE Aescott, VI-15-1980 (PERC); 94 M, 80 F, Ouachita Co, Conf Little Missouri R & Ouachita R, VII-9, VIII-9-1980 (PERC). GEORGIA: 2 F, Calhoun, VI-15-1980 (PERC). MISSISSIPPI: 3 M, 4 F, Lowndes Co, Columbus, VI-21-1947 (UFL). OKLAHOMA: 1 L, Delaware Co, Flint Cr, Flint, VI-6-1973 (UU). TENNESSEE: 4 M, 17 F, 1 Fs, Hamilton Co (UFL); 1 M, Lincoln Co (UFL).

Genus POTAMANTHUS

Ephemera Linnaeus (in part), 1767. Syst. Nat., 12th Ed., Pt. 2, Nos. 1-11: 906.

Potamanthus Pictet, 1843. Histoire naturelle générale et particulière des Insectes Névroptères. Famille des Éphémérines. Genève. 1843: 111 [Type species: *Ephemera lutea* Linnaeus, 1767, by subsequent designation by Eaton (1868)]; Eaton, 1868. Entomol. Month. Mag. 5: 86, restricted.

Eucharidis Joly & Joly, 1876. Rev. Sc. Nat. Mont. 5:314 [Type species: *Eucharidis reaumurii* Joly & Joly, by monotypy] (first L description), synonymized by Eaton (1883).

Potamanthodes Ulmer, 1920b. Arch. Nat. 85: 11 [Type species: *Potamanthus formosus* Eaton, 1892, by original designation], NEW SYNONYM.

Stygifloris Bae, McCafferty & Edmunds, 1990. Ann. Entomol. Soc. Am. 83: 887 [Type species: *Stygifloris sabahensis* Bae, McCafferty & Edmunds, 1990, by original designation], NEW SYNONYM.

MATURE LARVA.— *Dimensions* (mm): Length of body 7.5-15.9, mandibles 0.13-0.63, caudal filaments 4.5-8.0. *Head*: Compound eyes of mature male larvae full-sized to minute (ES = 0.61-3.67). Clypeus (Fig. 36-37) without simple-stout or bipectinate-hairlike setae on dorsal surface. Mandibles (Fig. 15-17, 36-37, 41-43) developed into short tusks, 0.10-0.47x length of head, slightly arched inward; body of mandibles with 20-80 simple-stout setae mixed with 10-50 bipectinate-hairlike setae (setules weakly developed as in Fig. 50-51) evenly distributed on dorsal and lateral surface; tusks without subapical spine. Terminal segment of maxillary palpi (Fig. 22-25), 0.96-1.50x length of segment 2, without distinct rows of bipectinate-hairlike setae along medial margin. Hypopharynx weakly to moderately expanded laterally. Labium with paraglossae (Fig. 22-25) weakly expanded laterally, with or without ventral bipectinate-hairlike setae; terminal segment of labial palpi either falcate (Fig. 23) or symmetrically pointed (Fig. 22, 24-25, 46-47), 0.83-1.36x length of segment 2; medial margin of terminal segment with 10-30 relatively large, simple-stout setae, without bipectinate-hairlike setae. *Thorax*: Pronotum (Fig. 15-17) moderately produced laterally; anterolateral corners not produced into acute spine. Forefemora (Fig. 15-17) dorsally with sparse simple-stout setae intermixed with only few bipectinate-hairlike setae or without bipectinate-hairlike setae. Foretibiae (Fig. 15-17) 0.63-0.99x length of forefemora, 0.95-

2.20x length of foretarsi, with relatively sparse and short bipectinate-hairlike setae (setules weakly developed as in Fig. 69) irregularly distributed only along anterior margin, without dorsal bipectinate-hairlike setae. *Abdomen*: Gills 2-7 (Fig. 15-17) with 20-40 marginal fibrillae arranged in single row on each lamellae.

MALE ADULT.—*Dimensions (mm) & Coloration*: Length of body 8.0-14.0, forewings 7.7-14.5, hindwings 3.0-4.5, forelegs 6.2-11.7, forceps 0.60-1.15, cerci 18.2-25.8, median terminal filament 0.5-20.4; width of forewings 3.7-6.0, hindwings 1.8-3.0. Body white to pale yellow with light brown to dark brown markings. *Head*: Compound eyes tiny to large (0.28-1.15 mm dorsal diameter) (ES=0.02-2.62). *Thorax*: Pronotum width 1.53-2.80x length. Forewings without markings (Fig. 94-95) or with only marginal markings (Fig. 97-99) or 3 small spots (Fig. 96); MAs either shorter or longer than MA_1 ($MA_s/MA_1 = 0.68-1.32$); MP_2 originating from base of either MP_1 or CuA; 2-4 cubital intercalaries present (1-3 forked). Hindwings (Fig. 112-117) with base of R_1 either slightly arched ($130-155^\circ$) or strongly arched ($90-100^\circ$) toward Sc; MP_s 0.24-0.46x length of MP_1 ; MP_2 basally connected to MP_s , forming symmetrical fork with MP_1 . Foretibiae 1.25-2.71x length of forefemora, 0.65-1.71x length of foretarsi. *Abdomen*: Color pattern variable. Genitalia (Fig. 125-133, 139-141) with subgenital plate concave; genital forceps with segments 2 and 3 together 0.31-0.61x length of basal segment; penes furcated basally to subapically. Median terminal filament fully developed, 0.62-0.97x length of cerci, or rudimentary, 0.02x length of cerci.

FEMALE ADULT.—*Dimensions (mm)*: Length of body 7.4-15.8, forewings 7.1-15.2, hindwings 2.3-5.0, forelegs 3.9-7.6, cerci 9.5-18.8, median terminal filament 9.5-17.8; width of forewings 3.0-6.5, hindwings 1.2-3.0. *Body*: Similar to male except foretibiae 0.98-1.17x length of forefemora, 1.20-1.52x length of foretarsi, and median terminal filament 0.80-1.00x length of cerci.

DIAGNOSIS.— Larvae of *Potamanthus* (Fig. 15-17) are easily distinguished from those of *Rhoenanthus* or *Anthopotamus* by their short tusks, weakly setaceous mouthparts (Fig. 22-25), and weakly developed bipectinate-hairlike setae along anterior margin of foretibiae. Adults of *Potamanthus* are distinguished from those of *Rhoenanthus* by their regular (symmetrical) fork of MP_1 and MP_2 in the hindwings (Fig. 112-117) and their fully developed median terminal filament. They differ from *Anthopotamus* in that in most of them MP_2 of the forewings originates basally from CuA (Fig. 96-99), R_1 of the hindwings is strongly arched (Fig. 115-117), and for those with MP_2 of forewings originating from MP_1 , the compound eyes of the male are large.

DISTRIBUTION.— Fig. 1, 4-5: Palearctic (USSR, Korea, Mongolia, China, Turkey, Syria, Poland, Czechoslovakia, Austria, Hungary, Germany, Switzerland, Italy, England, France, Spain, northern Morocco, northern Algeria); Oriental (Borneo, southern China, Taiwan, Vietnam, Laos, Cambodia, Thailand, Burma, Malaysia, India).

DISCUSSION.— Our expanded concept of *Potamanthus* is based primarily on phylogenetic results discussed below. As such, the genus comprises all short-tusked larval potamanthids, including previous Old World *Potamanthus* as well as the Asiatic *Potamanthodes* and *Stygifloris*, all of which we treat as separate subgenera.

Navás (1931) described *Potamanthus subcostalis* from India, and Hsu (1937-38b) described *Potamanthodes nanchangi* from China. We are unable to place these two species precisely in any subgenera of *Potamanthus* at this time because of lack of morphological evidence, although we are confident that they belong to the genus *Potamanthus* (see further discussions, below).

Potamanthus (subgenus **Potamanthus**), NEW STATUS

Ephemera Linnaeus (in part), 1767. Syst. Nat., 12th Ed., Pt. 2, Nos. 1-11: 906.

Eucharidis Joly & Joly, 1876. Rev. Sc. Nat. Mont. 5:314 [Type species: *Eucharidis reaumurii* Joly & Joly, by monotypy](first L description), synonymized by Eaton (1883).

Potamanthus Pictet, 1843. Histoire naturelle générale et particulière des Insectes Névroptères. Famille des Éphémérides. Genève. 1843: 111 [Type species: *Ephemera lutea* Linnaeus, 1767, by subsequent designation by Eaton (1868)]; Eaton, 1868. Entomol. Month. Mag. 5: 86, restricted.

MATURE LARVA.— *Head*: Compound eyes of male full-sized (ES = 0.61-0.73). Mandibles (Fig. 15, 22, 36, 41) 0.10-0.22x length of head. Paraglossae (Fig. 22) with ventral bipectinate-hairlike setae. Terminal segment of labial palpi (Fig. 22, 46) symmetrically pointed, 0.83-1.17x length of segment 2; medial margin of terminal segment with relatively large 15-30 simple-stout setae. *Thorax*: Forefemora without well-developed dorsal transverse row of simple-stout setae [only weakly developed with small simple-stout setae in some individuals (Fig. 15)]. Foretibiae (Fig. 15) 0.63-0.80x length of forefemora, 0.95-1.31x length of foretarsi, without ventral subapical tuft of bipectinate-hairlike setae. *Abdomen*: Terga 1-10 with median longitudinal stripe and 2 pairs of submedian longitudinal stripes as in Fig. 15. Gills 2-7 (Fig. 15) with 30-40 marginal fibrillae arranged in single row.

ADULT. *Head*: Compound eyes of male large as in Fig. 146 (0.67-1.15 mm dorsal diameter) (ES = 0.08-0.25). *Thorax*: Prothorax and metathorax without longitudinal stripes on notum and pleura. Forewings (Fig. 94-95) without markings; MAs subequal to, or longer than, MA₁ (MA₂/MA₁ = 0.95-1.32); MP₂ originating from base of MP₁; MP with 1-2 crossveins between MP₁ and MP₂ basally in at least one wing; distal branch of A₁ fork more divergent than basal branch. Hindwings (Fig. 112-113) with costal projections acute (< 90°); base of R₁ slightly arched toward Sc (150-155°). Foretibiae of male 1.38-1.68x length of forefemora, 0.81-1.03x length of foretarsi. Foretibiae of female 1.00-1.17x length of forefemora, 1.28-1.38x length of foretarsi. *Abdomen*: Terga 1-10 each with dark, broad, midlongitudinal stripe containing 2 pairs of light spots. Male genitalia (Fig. 125-126, 139) with penes basally somewhat cylindrical, furcated subapically; each penis lobe laterally pronounced and apically pointed. Median terminal filament of male fully developed, 0.93-0.97x length of cerci. Median terminal filament of female fully developed, 0.90-0.98x length of cerci.

DIAGNOSIS.— Larvae of the subgenus *Potamanthus* are distinguished from those of the subgenera *Stygifloris* and *Potamanthodes* by the lack of a distinct transverse row of well-developed simple-stout setae dorsally on the forefemora and the lack of a ventral, subapical tuft of hairlike setae on the foretibiae. Adults of the subgenus *Potamanthus* are distinguished from those of *Stygifloris* and *Potamanthodes* in that MP₂ of forewings is directly connected to MP₁.

DISTRIBUTION.— Fig. 4: Palearctic (USSR, Korea, Mongolia, China, Turkey, Syria, Poland, Czechoslovakia, Austria, Hungary, Germany, Switzerland, Italy, England, France, Spain, northern Morocco, northern Algeria).

DISCUSSION.— The subgenus *Potamanthus* is equivalent to Eaton's (1868, 1871, 1883-88) restricted concept of *Potamanthus*.

Potamanthus huoshanensis Wu

Morphology Fig. 15, 95, 113, 126, 139

Distribution Fig. 4

Potamanthus huoshanensis Wu, 1987b. Acta Zootaxon. Sin. 12: 421 [Material: M (Holotype), F, L; Holotype locality: China (Anhui Prov); Holotype deposition: NNU].

MATURE LARVA.— *Dimensions* (mm): Length of body 11.6-12.2, antennae 1.7-1.8, mandibles 0.20-0.25, caudal filaments 4.7-5.2; dorsal diameter of male compound eyes 0.80, female compound eyes 0.53-0.58. *Head*: Vertex (Fig. 15) light brown to brown with irregular, light markings. Compound eyes of male full-sized (ES = 0.61-0.75); compound eyes of female full-sized (ES = 1.70-1.72). Antennae 1.2-1.4x length of head. Mandibles (Fig. 15) 0.16-0.17x length of head; body of mandibles with 20-25 simple-stout setae mixed with 15-20 bipectinate-hairlike setae; tusks 0.25-0.33x length, and 0.13-0.20x width of body of mandibles. Terminal segment of maxillary palpi 1.17-1.32x length of segment 2. Terminal segment of labial palpi 0.83-1.00x length of segment 2. *Thorax*: Nota (Fig. 15) light brown to brown; pronotum with 3-4 pairs of irregular, light, somewhat round markings, and with paired, C-shaped markings in medioposterior region; mesonotum and metanotum with irregular, poorly defined light markings. Lateral expansions of pronotum white, moderately developed, with anterolateral corners not produced into spine-like processes (Fig. 15). Legs (Fig. 15) pale yellow, with broad, light brown to brown band at subbasal and subapical region of femora, and at midlength of tibiae and tarsi. Forefemora with scattered dorsal simple-stout setae, appearing rowed at midlength in some, without simple-hairlike setae dorsally. Foretibiae 0.7-0.8x length of forefemora, 1.0-1.2x length of foretarsi. *Abdomen*: Color light brown to brown; terga 1-10 (Fig. 15) each with light midlongitudinal stripe and pairs of light submedian and sublateral stripes. Gills (Fig. 15) 2-7 white with slightly darker tracheae; gills 3 with 33-38 marginal fibrillae along each lateral margin of dorsal lamellae, and 30-32 on ventral lamellae. Caudal filaments 0.4-0.5x length of body.

MALE ADULT.— *Dimensions* (mm): Length of body 14.0, antennae 0.75, forewings 11.2, hindwings 4.0, forelegs 9.4, forceps > 1.08; cerci 25.0; median terminal filament > 17.0 (tip broken); width of forewings 5.3, hindwings 2.8; dorsal diameter of compound eyes 0.67; distance between compound eyes 0.05. *Head*: Vertex light brown. Compound eyes dorsally yellowish brown and dark gray in ventrally extended region, large (ES = 0.08). *Thorax*: Color light brown; pronotum with slightly darker broad midlongitudinal stripe. Forewings (Fig. 95) without markings; veins not pigmented; crossveins not infuscated, numbering 38 between SC and R₁ and 25 between R₁ and R₂; radial region with 1 single crossvein connecting IR₂ and R₃ basally; MAs 1.18x length of MA₁; cubital region with 4 intercalaries (3 forked). Hindwings (Fig. 113) without markings; veins not pigmented; crossveins not infuscated; Rs 0.77x length of R₂; MP₁ 0.35x length of MP₁. Forelegs pale yellow, with reddish brown band at apex of foretibiae and foretarsi segment 1; foretibiae 1.43x length of forefemora, 1.03x length of foretarsi. Midlegs and hindlegs white. Claws light brown. *Abdomen*: Terga 1-10 each pale yellow, with slightly dark, broad, midlongitudinal stripe containing pair of light, submedian, teardrop-shaped spots anteriorly and pair of round, tiny spots posteriorly, without pair of dark lateral spots; sterna white, without markings. Terminal segment of forceps (Fig. 126) rounded, not expanded laterally, 0.83x length of segment 2; segment 2 and 3 together 0.44x length of basal segment; penes (Fig. 126, 139) dorsally light brown, ventrally white; lateral lobes relatively large. Caudal filaments basally reddish brown, apically white, with dark band at each suture; median terminal filament greater than 0.68x length of cerci.

FEMALE ADULT.— *Dimensions* (mm): Length of body 13.6-14.4, antennae 0.60-0.63,

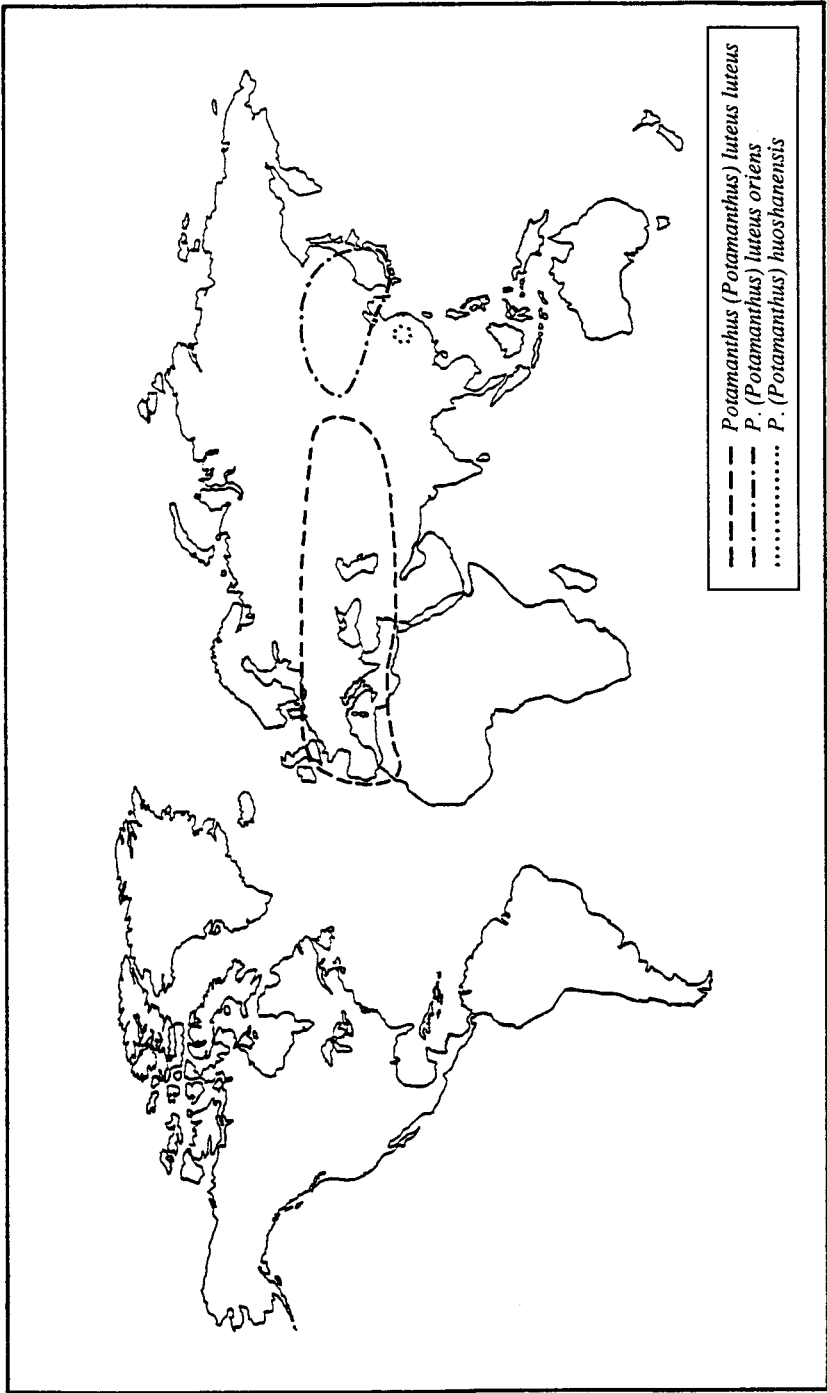


FIGURE 4. Distribution of *Potamanthus* (*Potamanthus*).

forewings 12.0-12.3, hindwings 3.6-3.8, forelegs 6.1-6.2, cerci 15.6-16.5, median terminal filament 14.0-15.5; width of forewings 5.0, hindwings 2.0-2.3; dorsal diameter of compound eyes 0.65-0.70; distance between compound eyes 0.60-0.63. *Head*: Vertex pale yellow; compound eyes purplish dark brown in alcohol, small (ES=0.89-0.92). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male but lighter in intensity, and forewings with 38 crossveins between SC and R₁, 24 crossveins between R₁ and R₂. Foretibiae 1.00-1.05x length of forefemora, 1.28-1.35x length of foretarsi. *Abdomen*: Color pattern similar to male but lighter. caudal filaments pale yellow, with dark band at each suture; median terminal filament 0.90-0.94x length of cerci.

DIAGNOSIS.— Larvae of *P. huoshanensis* (Fig. 15) cannot unequivocally be distinguished from *P. luteus* morphologically. Adults of *P. huoshanensis*, however, are easily distinguished from those of *P. luteus* by the nonpigmented veins and noninfuscated crossveins in their forewings (Fig. 95), more extensive crossvenation (ca. 38) between Sc and R₁ in forewings, and the lack of pairs of dark lateral spots on each abdominal tergum.

TYPE MATERIAL EXAMINED.— PARATYPES (*Potamanthus huoshanensis* Wu, 1987b): 3 L (BAE-159), 1 M (BAE-33), 2 F (BAE-157) (alcohol), CHINA, Anhui Prov, Huoshan County, Zhufuan (31 18'N, 116 18'E), VI-11-1983, VI-11-1984, X. Wu (NNU).

Potamanthus luteus (Linnaeus)

Morphology Fig. 22, 36, 41, 46, 50, 59-60, 63, 69, 79, 94, 112, 125

Distribution Fig. 4

Ephemera sp., Geoffroy, 1764. Hist. Ab. Ins. Paris. ii. 1764: 238, synonymized by Eaton (1871).

Ephemera lutea Linnaeus, 1767. Syst. Nat., 12th Ed., Pt. 2, Nos. 1-11: 906 [Material: Alate; Type information: unknown; Neotype (designated herein) locality: England (Surry); Neotype deposition: BM].

Ephemera marginata Müller, 1776. Zool. Dan. Prod. 1776: 142 [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Ephemera reticulata Fourcroy, 1785. Ent. Paris. ii. 1785: 350 [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Ephemera hyalina Panzer, 1804. Explic. Schaeff. Ic. xliiii [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Baetis mellea Curtis, 1834. Phil. Mag. ser. 3. 1834: 121 [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Baetis marginalis Burmeister, 1839. Handb. Ent. Bd. ii. Abth. ii. 1839: 801 [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Ephemera flavicans Rambur, 1842. Nevropt. 1842: 296 [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Ephemera chlorotica Rambur, 1842. Nevropt. 1842: 296 [Material: Alate; Type information: unknown], synonymized by Eaton (1871).

Potamanthus luteus (Linnaeus): Pictet, 1843-45. Histoire naturelle générale et particulière des Insectes Névroptères. Famille des Éphémérides. Genève. 1843: 208; Eaton, 1883-88. Trans. Linn. Soc., 2nd Ser. Zool., 3: 79 (M & L figured).

Potamanthus ferreri Pictet, 1843-45. Histoire naturelle générale et particulière des Insectes Névroptères. Famille des Éphémérides. Genève. 1843: 203 [Material: M (Holotype); Holotype locality: Italy (Turin); Holotype deposition: Geneva Museum (lost: Eaton 1883-88)], NEW SYNONYM.

Eucharidis reaumurii Joly & Joly, 1876. Rev. d. Sc. Nat. Montpellier. v. 1876: 314 [Material: L; Type information: unknown] (first L description), synonymized by Eaton (1883-88).

MATURE LARVA.—*Dimensions* (mm): Length of body 10.8-15.9, antennae 2.0-2.2, mandibles 0.15-0.40, caudal filaments 5.2-8.0; dorsal diameter of male compound eyes 0.78-0.88, female compound eyes 0.50-0.63. *Head*: Vertex light brown to brown with irregular, light markings. Compound eyes of male full-sized ($ES = 0.70-1.00$); female compound eyes full-sized ($ES = 1.25-2.00$). Antennae 1.2-1.4x length of head. Mandibles (Fig. 36, 41) 0.10-0.23x length of head; body of mandibles with 40-50 simple-stout setae mixed with 30-50 bipectinate-hairlike setae (setules weakly developed as in Fig. 50); tusks 0.29-0.30x length and 0.13-0.15x width of body of tusks. Terminal segment of maxillary palpi (Fig. 22) 1.07-1.34x length of segment 2. Terminal segment of labial palpi (Fig. 22, 46) 0.92-1.17x length of segment 2. *Thorax*: Nota light brown to brown; pronotum with 3-4 pairs of irregular, light, somewhat round markings, and with paired, C-shaped markings in medioposterior region as in Fig. 15; mesonotum and metanotum with irregular, light markings. Lateral expansions of pronotum white and moderately developed, with anterolateral corners not developed into spine-like processes. Legs pale yellow, with broad, light brown to brown band at subbasal and subapical regions of femora, and at midlength of tibiae and tarsi. Forefemora with scattered simple-stout setae and few hairlike setae dorsally. Foretibiae 0.63-0.80x length of forefemora, 0.95-1.31x length of foretarsi. *Abdomen*: Color light brown to brown; terga 1-10 each with light, midlongitudinal stripe, and with pair of light submedian and sublateral stripes as in Fig. 15. Gills 2-7 white with slightly darker tracheae; gills 3 with 30-40 marginal fibrillae along each lateral margin of dorsal lamellae, and 30-40 on ventral lamellae. Caudal filaments 0.41-0.53x length of body.

MALE ADULT.—*Dimensions* (mm): Length of body 9.5-13.3, antennae 0.65-0.70, forewings 10.4-12.0, hindwings 3.5-4.3, forelegs 8.6-11.4, forceps 0.97-1.13, cerci 18.2-22.5, median terminal filament 17.3-19.5; width of forewings 4.2-5.4, hindwings 2.1-2.8; dorsal diameter of compound eyes 1.00-1.15; distance between compound eyes 0.13-0.25. *Head*: Color pale yellow. Compound eyes dorsally dark brown and black in ventrally extended region, large ($ES = 0.12-0.25$). *Thorax*: Color yellow to light brown. Forewings (Fig. 94) without markings; veins not pigmented but crossveins brown and infuscated, numbering 21-27 between SC and R_1 and 12-18 between R_1 and R_2 ; radial region with 0-2 crossveins connecting IR_2 and R_3 basally; MAs 0.95-1.32x length of MA_1 ; cubital region with 3-4 intercalaries (2-3 forked). Hindwings (Fig. 112) without markings; veins not pigmented; crossveins not infuscated; Rs 0.74-1.38x length of R_2 ; MPs 0.23-0.36x length of MP_1 . Forelegs pale yellow, with reddish brown band at apex of foretibiae and each foretarsi suture; foretibiae 1.38-1.68x length of forefemora, 0.81-1.02x length of foretarsi; segment 2 of foretarsi 1.06-1.47x length of segment 3. Midlegs and hindlegs white. Claws light brown. *Abdomen*: Terga 1-10 each pale yellow, with light brown to dark brown, broad, midlongitudinal stripe containing pair of light, submedian, teardrop-shaped spots anteriorly and pair of round, tiny spots posteriorly, with pair of dark lateral spots; sterna white, without markings. Terminal segment of forceps (Fig. 125) rounded, sometimes slightly notched, not expanded laterally, 0.78-1.13x length of segment 2; segment 2 and 3 of forceps together 0.42-0.61x length of basal segment; penes as in Fig. 125. Caudal filaments pale yellow, with dark band at each suture; median terminal filament 0.93-0.97x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 10.5-15.4, antennae 0.6-0.7, forewings 10.7-15.2, hindwings 3.2-4.9, forelegs 5.4-7.5, cerci 11.6-18.8, median terminal filament 11.3-17.8; width of forewings 4.3-6.2, hindwings 2.0-2.9; dorsal diameter of compound eyes 0.55-0.70; distance between compound eyes 0.55-0.75. *Head*: Color pale yellow; compound eyes dark gray in alcohol, very small ($ES = 1.00-1.11$). *Thorax*: Color patterns of body, wings, and legs generally similar to male but less intense, and forewings with 24-32 crossveins between SC and R_1 , 14-21 crossveins between R_1 and R_2 . Foretibiae

1.05-1.17x length of forefemora, 1.32-1.38x length of foretarsi. *Abdomen*: Color pattern similar to male but lighter. Caudal filaments as per male.

DIAGNOSIS.— Larvae of *P. luteus* generally cannot be distinguished from *P. huoshanensis* morphologically. Distributional data may be of some aid in this respect (Fig. 4), although the two species may eventually be found to overlap. Adults of *P. luteus* can be easily distinguished from those of *P. huoshanensis* by the pigmented crossveins in their forewings (Fig. 94), less extensive crossvenation (ca. 21-28) between Sc and R₁ in their forewings, and the presence of 2 pairs of dark lateral spots on each abdominal tergum.

DISCUSSION.— We have designated, above, a neotype for *Ephemera lutea* Linnaeus, 1967, from McLachlan's collections at the BM that were determined and used by Eaton (1871, 1883-88) in his descriptions of *Potamanthus luteus*. Pictet's material of *P. ferreri* was missing in 1867 (Eaton 1883-88) and no material has been reported since. We synonymize Pictet's (1843) *P. ferreri*, from northwestern Italy, with *P. luteus* (subspecies *P. luteus luteus*) based on Pictet's drawing of the dorsal whole body of the male adult of *P. ferreri* (Fig. 1, Pl 25, in Pictet 1945), which agrees with *P. luteus* (Fig. 2, Pl. 25, in Pictet 1945) (particularly noteworthy are the eye size and abdominal markings). Its lighter coloration and slightly larger body size fall within the range of variation known for *P. luteus*. In addition, Gaino & Spanò (1979) reported *Potamanthus luteus* from Italy giving indirect support for this synonymy.

We recognize western and eastern populations of the species in Eurasia (Fig. 4) as distinct subspecies. Besides their geographic isolation, some minor morphological variation between the two is evident (see below).

Potamanthus luteus luteus (Linnaeus), NEW STATUS

Morphology Fig. 22, 36, 41, 46, 50, 59-60, 63, 69, 79, 94, 112

Distribution Fig. 4

DIAGNOSIS.— Larvae of *P. luteus luteus* can not be consistently told from those of *P. luteus oriens*, however, no larvae of the former have been found with rudimentary spine-like processes on the anterolateral corners of their pronota or a weak row of simple-stout setae dorsally on their forefemora, as some individuals of the latter have. In *P. luteus luteus* adults, MAs of the forewings of most individuals is much longer than MA₁. Also, some populations we have examined from northern Africa vary in having somewhat terminally notched forceps.

TYPE MATERIAL EXAMINED.— NEOTYPE: M (pinned, left forewing under cellophane, McLachlan Coll., B.M. 1938-674, determined by A. E. Eaton, BAE-36), ENGLAND, Surry, Weybridge, [date missing], deposited in BM.

OTHER MATERIAL EXAMINED.— ALGERIA: 2 L, SW Algeria, Oued Isser, 450 m, May 1981 (PERC); 4 L, SW Algeria, Oued Tafna, 830 m, May 1981 (PERC); 1 L S.W. Algeria, Oued Chouly, 535 m, V-30-1985 (PERC). CZECHOSLOVAKIA: 6 L, Bohemia, Pernstejn north-east, VI-20-1948 (PERC). ENGLAND: 1 M (pinned, McLachlan Coll., B.M. 1938-674, determined by A. E. Eaton, BAE-37), same data as Neotype (BM); 2 L, Herefordshire, R Wye, Whitney, Old Toll Br, VI-12-1986 (PERC). FRANCE: 1 M (pinned, McLachlan Coll., B.M. 1938-674, determined by A. E. Eaton, BAE-38), Brive, Haute Loire (BM); 1 M Quillan, 1879, A. E. Eaton (BM); 1 L, 2 M, 1 F, Brive, Loire, 1879, A. E. Eaton (MCZ); 1 F, B-Pyrenees, St-Jean-Piel-de-Port, VI-28-VII-3-1929 (BM); 1 Ms, B-Pyrenees, Itxassou, VI-19-27-1929 (BM). MOROCCO: 1 M, 1 F, 2 Fs, High Atlas, Souk Aghbar, Oued N'Fis, VII-14-1986 (PERC); 14 L, High Atlas, Aghbar, N'Pis, VII-12-1985 (PERC). POLAND: 18

L, 2 M, 2 F (reared), San R nr Priemusel [=Przemysl], VIII-6-1982, VIII-24-1985, VIII-14-1987 (PERC); 25 L, (V. R. Polen), Tucheler Heide, (BER). SPAIN: 1 M, Soria, Rio Duero, S Esteban de Gormaz, VIII-6-1982 (UGRA); 2 L, Granada, Rio Alhama, 720 m, Sta Cruz de Alhama, VI-9-1989 (UGRA). SWITZERLAND: 2 M, 2 F, Limmat R at Zurich, VII-5-1964 (PERC). SYRIA: 2 M (pinned, B.M. 1947-393, BAE-41, 42), NW Syria, Mt Cassius, V-12-1945 (BM). USSR: 2 M, 5 Ms, 3 Fs, Sudl Uralgebiet, Ungeb Kargalat (BER); 1 M, 1 F (reared), Lithuanian SSR, Vilnius, R Neris, VI-27-1988 (LENU); 3 M, 2 F, 2 Fs (reared), Georgian SSR, R Kura near Zages, VIII-28-1985 (LENU).

Potamanthus luteus oriens, NEW SUBSPECIES

Morphology Fig. 125

Distribution Fig. 4

Potamanthus luteus (Linnaeus): Uéno, 1928. Mem. Coll. Sci., Kyoto Imperial Univ., Ser. B, 4: 23 (L); Wu, 1987a. Acta Zootaxon. Sin. 12: 336 (F, L).

Potamanthus na: Imanishi, 1940. Rep. Limnobiol. Surv. Kwant. Manch. 1940: 180 (L), NEW SYNONYM.

Potamanthus naa: Imanishi, 1940. Rep. Limnobiol. Surv. Kwant. Manch. 1940: 181 (L), NEW SYNONYM.

DIAGNOSIS.— Some larvae of *P. luteus oriens* possess rudimentarily developed spine-like processes at the anterolateral corners of the pronotum, and some of them also possess a weakly developed row of small simple-stout setae dorsally on their forefemora. The larvae, however, can not be consistently told from *P. luteus luteus* or *P. huoshanensis*. The MAs of the forewings of adults is subequal to or slightly longer than MA₁ in most individuals.

ETYMOLOGY.— The subspecific name *oriens* is Latin, masculine, from oriens (east), thus alluding to the eastern Palearctic distribution of the subspecies.

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (alcohol, reared, larval and subimaginal exuviae, BAE-107, label written in Russian, translated by N. Ju. Kluge), USSR (Far East), Lower Amur, Slavyanka (lower than Troitskoe), NE from Khabarovsk, VIII-10-1984, deposited in LENU.

OTHER MATERIAL EXAMINED.— KOREA (NORTH): 3 Ms, 2 Fs, Pyongyang, Daedong R, 1988. KOREA (SOUTH): 1 Ms, Seoul, Yongsan, VI-7-1953 (UU); 1 Ms, 2 Fs, Seoul, Han R, Ttuksom, VI-29-1959, VIII-1959 (UU). USSR: 1 Ms (reared, larval exuviae, BAE-131), 2 F, same data and deposition as Holotype.

DISCUSSION.— This subspecies is restricted to Far East Asia and geographically isolated from *P. luteus luteus* by the Mongolian-Siberian dry lands.

Uéno (1928) described the larva of *Potamanthus luteus* from Japan (Seta River or outlet of Lake Biwa, Omi Province; Tenryu River, Shinano Province). Recently, N. Kobayashi collected adults of *Potamanthus* sp. on the shores of Lake Biwa, Omi Province, Japan, by light trap (Watanabe, personal communication). From the descriptive and collecting data it is clear that these are assignable to *P. luteus oriens*.

Imanishi (1940) reported larvae of *Potamanthus na* and *Potamanthus naa* from Tao'er River and Songhua River, respectively, in Jilin Province (Manchuria), China. Recently, Wu (1987a) reported female adults and larvae of *Potamanthus luteus* from Manchuria, China (Wuyian and Nancha, Yichun City, Heilongjiang Province; Songjiang River, Fusong County, Jilin Province). From the descriptive data associated with these reports, we conclude that these Manchurian potamanthids are *P. luteus oriens*. Landa & Soldán's (1983) report of *P. luteus* from Mongolia is probably also applicable to this subspecies.

Potamanthus (subgenus **Stygifloris**), NEW STATUS

Stygifloris Bae, McCafferty & Edmunds, 1990. Ann. Entomol. Soc. Am. 83: 887 [Type species: *Stygifloris sabahensis* Bae, McCafferty & Edmunds, 1990, by original designation].

MATURE LARVA.— *Head*: Compound eyes of male full-sized ($ES = 0.75$). Mandibles (Fig. 16, 23) 0.3x length of head. Paraglossae (Fig. 23) without ventral bipectinate-hairlike setae. Terminal segment of labial palpi (Fig. 23) falcate; medial margin of terminal segment with 2-3 rows each with 10-15 relatively large simple-stout setae. *Thorax*: Forefemora (Fig. 16, 72) with dorsal transverse row of 10-15 simple-stout setae. Foretibiae (Fig. 72) subequal to forefemora, 2.2x length of foretarsi, with ventral subapical tuft of 30-40 bipectinate-hairlike setae (setules rudimentary) (Fig. 73). *Abdomen*: Terga 1-10 (Fig. 16) with broad, longitudinal stripe, with each tergum containing 2 pairs of light spots. Gills 2-7 (Fig. 16) each with 20-30 marginal fibrillae arranged in single row on each lamellae.

ADULT. *Head*: Compound eyes of male large as in Fig. 146 (1.1 mm dorsal diameter) ($ES = 0.02$). *Thorax*: Prothorax and metathorax without longitudinal stripe on notum and pleura. Forewings (Fig. 96) without intermittent staining in costal region; MAs shorter than MA_1 ($MA_s/MA_1 = 0.85$); MP_2 originating from base of CuA; MP without basal crossveins between MP_1 and MP_2 ; A_1 fork nearly symmetrical. Hindwings (Fig. 114) with costal projections somewhat rounded and subacute ($93-108^\circ$); base of R_1 slightly arched toward Sc ($130-140^\circ$). Foretibiae of male 1.8x length of forefemora, subequal to foretarsi. Foretibiae of female subequal to forefemora, 2.0x length of foretarsi. *Abdomen*: Terga 1-10 each with U-shaped, dark marking extending across tergum. Male genitalia (Fig. 127, 140) with penes subbasally furcated, broadly convex laterally, somewhat flattened, with somewhat rounded apices. Median terminal filament of male 0.02x length of cerci. Median terminal filament of female 0.80-0.85x length of cerci.

DIAGNOSIS.— Larvae of *Stygifloris* (Fig. 16) are distinguished from those of the subgenera *Potamanthus* and *Potamanthodes* by the falcate apex of their labial palpi (Fig. 23) and the presence of a medial spot on each of the forewingpads (Fig. 16). Adults of *Stygifloris* are distinguished from other congeners by possessing a combination of large compound eyes as in Fig. 146, a MP_2 of the forewings that originates from CuA (Fig. 96), a slightly arched R_1 in the hindwings (Fig. 114), and peculiar male genitalia (Fig. 127, 140).

DISTRIBUTION.— Fig. 5: Oriental (Borneo).

DISCUSSION.— Bae et al. (1990) described *Stygifloris* as a new genus of Potamanthidae based on its unique combination of characteristics. However, our cladistic analysis had not been completed at that time. The phylogeny discussed by Bae et al. (1990) was therefore incomplete and somewhat premature. Our cladistic analysis, while indicating the taxon to be intermediate between *Potamanthus* s.s. and *Potamanthodes*, also indicates that a conservative phylogenetic classification would place it as a subgenus of *Potamanthus*, rather than giving it full generic status (see Phylogeny and Phylogenetic Classification section, below).

Potamanthus sabahensis (Bae, McCafferty & Edmunds), NEW COMB.

Morphology Fig. 16, 23, 57, 72-73, 78, 96, 114, 127, 140

Distribution Fig. 5

Stygifloris sabahensis Bae, McCafferty & Edmunds, 1990. Ann. Entomol. Soc. Am. 83: 889 [Holotype locality: East Malaysia, Sabah, Liwagu River; Holotype deposition: PERC].

MATURE LARVA.— *Dimensions* (mm): Length of body 11.0-13.0, antennae 4.35-4.40,

mandibles 0.35-0.40, caudal filaments 6.0-7.0; dorsal diameter of male compound eyes 0.7-0.8, female compound eyes 0.4-0.5. *Head*: Vertex (Fig. 16) without consistent or well-defined markings, sometimes central area lighter. Compound eyes of male full-sized ($ES = 0.75$). Antennae relatively long, 3.3x length of head. Mandibles (Fig. 16) 0.29x length of head; body of mandibles with 60-80 simple-stout setae mixed with 10-15 bipectinate-hairlike setae; tusks 0.89x length, and 0.06x width of body of mandibles. Terminal segment of maxillary palpi 1.34x length of segment 2. Terminal segment of labial palpi 1.20x length of segment 2. *Thorax*: Ground color generally pale brown; markings of nota (Fig. 16) not consistent or well defined, sometimes with light submedian C-shaped markings in medioposterior region of pronotum. Forewingpads (Fig. 16) with median spot. Legs without clearly defined stripes or markings. Forefemora (Fig. 72) with simple-stout setae along anterior and posterior margins; relatively short and sparse simple-hairlike setae distributed irregularly on dorsal surface. Foretibiae 1.0x length of forefemora, 2.19x length of foretarsi. *Abdomen*: Ground color generally brown to pale brown; markings of terga (Fig. 16) often not well defined; some individuals with terga 1-10 with slightly darker, broad, midlongitudinal stripe and each tergum with 2 pairs of small, light spots within stripe; some individuals with terga 2-9 each with dark, narrow, U-shaped marking extending throughout tergum. Gills (Fig. 16) 2-7 light brown, with lamellae somewhat irregularly twisted; fibrillae straight or curved, numbering 10-15 along lateral margins of dorsal lamellae, and 15-20 along lateral margins of ventral lamellae.

MALE ADULT.—*Dimensions* (mm): Length of body 12.0, forewing 10.8, hindwing 3.5, forelegs 9.8, forceps 0.90, cerci 21.5, median terminal filament 0.5; width of forewings 4.6, hindwings 2.0; dorsal diameter of compound eyes 1.08; distance between compound eyes 0.02. *Head*: Compound eyes large, nearly contiguous ($ES = 0.02$), gray in alcohol (ventrally darker gray). *Thorax*: Thorax pale yellow with pair of dark brown stripes extending from pronotum to mesopleura and with dark brown midlongitudinal stripe from pronotum to mesonotum. Forewings (as in Fig. 96) with 3 triangularly arranged, dark spots (near R_s fork, apex of wings, and at base of IMA); crossveins slightly infuscated, numbering 21 between SC and R_1 and 11 between R_1 and R_2 . Hindwings (as in Fig. 114) without maculations or infuscated crossvenation. Forelegs pale yellow, except claws, tarsal segment 5, and apex of tibiae dark brown. Midlegs and hindlegs white. *Abdomen*: Terga 1-10 pale yellow with dark, broad, midlongitudinal, stripe divided longitudinally by light pinstripe; each tergum with 2 pairs of small light spots arranged within broad median stripe and with narrow U-shaped dark marking encompassing most of tergum. Sterna of abdomen pale yellow, without markings. Terminal segment of forceps (Fig. 127) truncated terminally, slightly longer than segment 2 (1.11x segment 2) and 0.25x length of basal segment; penes (Fig. 127, 140) basally furcated for 1/4 of length visible beyond subgenital plate, subparallel beyond fusion but slightly divergent at tips, and apically somewhat rounded. Cerci white in basal half, darker in apical half, without bands.

FEMALE ADULT.—*Dimensions* (mm): Length of body 13.0, forewing 14.3, hindwing 4.5, forelegs 4.5, cerci 16.3, median terminal filament 13.3; width of forewings 5.7, hindwings 2.5; dorsal diameter of compound eyes 0.43; distance between compound eyes 0.85. *Head*: Compound eyes tiny, widely separated ($ES = 2.0$), black or gray in alcohol. *Thorax*: Body, wing, and leg color patterns generally similar to male. Forewings (Fig. 96) with 25-27 crossveins between SC and R_1 and 14-16 crossveins between R_1 and R_2 . Foretibiae 1.07x length of forefemora, 2.10x length of foretarsi. *Abdomen*: Color pattern similar to male. Caudal filaments white in basal half, darker in apical half, with dark band at every 2-4 sutures. Median terminal filament well developed, 0.80-0.85x length of cerci.

TYPE MATERIAL EXAMINED.— HOLOTYPE: L (mature male, alcohol, BAE-111),

MALAYSIA (East), Sabah, Liwagu R, Liwagu Cave, SE. of [Kinabalu National Park] Headquarters, 1525 m, (S7e), VIII-14-15-1972, G.F. & C.H. Edmunds (PERC). PARATYPES (alcohol): 27 L (11 mature male, 16 mature female), 4 F, same data as Holotype, 5 L, 2 F (UU), 5 L, 2 F (FAMU), 15 L, 2 F (PERC), 2 L, 1 F (USNM); 1 M, Liwagu River, N of Kundassan, 915 m, VIII-16-17-1972 (UU).

OTHER MATERIAL EXAMINED.— MALAYSIA (East): 150 L, 4 F, 4 Ms, same data as Holotype (UU, FAMU, PERC); 16 L, 1 Fs, Sabah, Liwagu R, N Kundassan, 915 m, VIII-16-17-1972 (UU); 1 F, Sabah, Liwagu R at Br, Ranau, 335 m, VIII-11-16-1972 (UU); 1 F, Sabah, Paring, Ranau, X-8-11-1958 (UU).

DISCUSSION.— This species and its known biology were discussed by Bae et al. (1990).

Potamanthus (subgenus Potamanthodes)

Potamanthodes Ulmer, 1920b. Arch. Nat. 85: 11 [Type species: *Potamanthus formosus* Eaton, 1892, by original designation].

Potamanthus (*Potamanthodes*): Imanishi, 1940. Rep. Limnobiol. Surv. Kwant. Manch. 1940: 178.

MATURE LARVA.— *Head*: Compound eyes of male full-sized (Fig. 142) to minute (Fig. 143) ($ES = 1.18-3.67$). Mandibles (Fig. 17, 24-25, 37, 42-43) 0.10-0.47x length of head. Paraglossae (Fig. 24-25) with ventral bipectinate-hairlike setae. Terminal segment of labial palpi (Fig. 24-25, 47) symmetrically pointed; medial margin of terminal segment with row of 15-30 relatively large simple-stout setae. *Thorax*: Forefemora (Fig. 17) with dorsal transverse row of 6-15 simple-stout setae. Foretibiae (Fig. 17) 0.75-0.99x length of forefemora, 1.26-1.82x length of foretarsi, with ventral subapical tuft of 5-20 bipectinate-hairlike setae (setules rudimentary) as in Fig. 73. *Abdomen*: Terga 1-10 each with midlongitudinal stripe and 2 pairs of submedian longitudinal stripes (but, markings sometimes unclear), or pair of somewhat round submedian markings on posterior margin as in Fig. 17. Gills 2-7 (Fig. 17) each with 20-40 marginal fibrillae arranged in single row.

ADULT.— *Head*: Compound eyes of male large to tiny (0.28-1.10 mm dorsal diameter) ($ES = 0.09-2.62$) (Fig. 146-147, 150). *Thorax*: Prothorax and mesothorax with longitudinal, mid-dorsal and lateral stripes. Forewings (Fig. 97-99) marked with intermittent dark staining in costal region; MAs shorter than MA_1 ($MA_s/MA_1 = 0.68-0.95$); MP_2 originating at base of CuA ; MP without basal crossveins between MP_1 and MP_2 ; A_1 fork nearly symmetrical. Hindwings (Fig. 115-117) with costal projections acute ($<90^\circ$); base of R_1 abruptly and strongly arched toward Sc ($90-100^\circ$). Foretibiae of male 1.25-2.71x length of forefemora, 0.65-1.71x length of foretarsi. Foretibiae of female 0.98-1.14x length of forefemora, 1.26-1.52x length of foretarsi. *Abdomen*: Terga 1-7 each sometimes with broad, sublateral, longitudinal stripes, but often not clearly defined. Male genitalia (Fig. 128-133, 141) with penes basally somewhat cylindrical, furcated at or beyond subgenital plate, and with each penis lobe either pointed, falcate, or notched, without pronounced lateral expansion. Median terminal filament of male fully developed, 0.62-0.88x length of cerci. Median terminal filament of female fully developed, 0.91-1.00x length of cerci.

DIAGNOSIS.— Larvae of the subgenus *Potamanthodes* (Fig. 17) can be distinguished from those of *Potamanthus* s.s. by the presence of a distinct dorsal transverse row of well-developed simple-stout setae on the forefemora (as in Fig. 72) and ventral, subapical tuft of hairlike setae on the foretibiae (as in Fig. 73). They are distinguished from *Stygifloris* by their more symmetrically pointed apex of labial palpi (Fig. 24-25). Adults of *Potamanthodes* are distinguished from those of *Potamanthus* s.s. and *Stygifloris* by their strongly arched R_1 in the hindwings (Fig. 115-117) and the conspicuous staining of the costal region of the

forewings (Fig. 97-99).

DISTRIBUTION.— Fig. 5: Eastern Palearctic (Korea, Japan, China); Oriental (southern China, Taiwan, Vietnam, Laos, Cambodia, Thailand, Burma, Malaysia).

DISCUSSION.— The subgenus *Potamantodes* represents a highly derived lineage of Potamantidae (see Phylogeny and Phylogenetic Classification section, below) that is best classified as a subgenus within *Potamantus*. It has been consistently recognized as a distinct taxon since Ulmer (1920b) noted the strongly arched R_1 of hindwings; however, its relationships have been unknown. Imanishi (1940) also recognized the group as a subgenus of *Potamantus* by noting a species he described as "*Potamantus (Potamantodes) kamonis*;" however, he provided no explanation for his interpretation. Although known larvae were instrumental in deciphering the group's relationships, the larvae of several species remain unknown.

***Potamantus macrophthalmus* (You), NEW COMB.**

Morphology Fig. 97, 115, 128, 146

Distribution Fig. 5

Potamantodes macrophthalmus You, 1984. Proc. 4th Intern. Conf. Ephem. 1984: 102 [Material: M (Holotype), F; Holotype locality: China (Shanxi Prov); Holotype deposition: NNU].

LARVA.— Unknown.

MALE ADULT.—*Dimensions* (mm): Length of body 10.0, antennae 1.0, forewings 9.6, hindwings (apices broken off), forelegs 8.6, forceps 0.60, cerci 20.5, median terminal filament 18.0; width of forewings 4.3; dorsal diameter of compound eyes 1.01; distance between compound eyes 0.09. *Head*: Color white. Compound eyes large, nearly contiguous ($ES = 0.09$) (Fig. 146), dorsally gray and ventrally dark gray in alcohol. *Thorax*: Color pale yellow. Forewings (Fig. 97) with longitudinal veins not pigmented; crossveins somewhat pigmented and infuscated in central region, numbering 25 between SC and R_1 and 12 between R_1 and R_2 ; radial region with 1 crossveins connecting IR_2 and R_3 basally; MAs 0.86x length of MA₁; cubital region with 3 forked intercalaries. Hindwings (Fig. 115) without markings; veins not pigmented; crossveins not infuscated; Rs 1.21x length of R_2 ; MP₁ 0.36x length of MP₁. Forelegs pale yellow with dark bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae 1.53x length of forefemora, 0.65x length of foretarsi; segment 2 of foretarsi 1.16x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga 1-7 each white, with slightly dark, broad, lateral stripes; sterna white, without markings. Terminal segment of forceps (Fig. 128) slightly notched apically, 1.09x length of segment 2; segments 2 and 3 together 0.31x length of basal segment; penes (Fig. 128) white, relatively long, ca. 0.8x length of forceps, furcated at midlength from subgenital plate and divergent laterally, pointed apically. Caudal filaments white, without markings; median terminal filament 0.88x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 11.1, antennae 1.0, forewings 11.2, hindwings (apices broken off), forelegs 5.3, cerci (broken), median terminal filament 13.0; width of forewings 4.8; dorsal diameter of compound eyes 0.53; distance between compound eyes 0.68. *Head*: Color pale yellow; compound eyes black, very small ($ES = 1.29$). *Thorax*: Color patterns of body, wings, and legs generally similar to those of male. Forewing venation similar to male except 26 crossveins between SC and R_1 , 15 crossveins between R_1 and R_2 . Hindwing venation similar to male. Foretibiae 1.03x length of forefemora, 1.26x length of foretarsi. *Abdomen*: Color pattern similar to male.

DIAGNOSIS.— Male adults of this species are distinguished from those of other

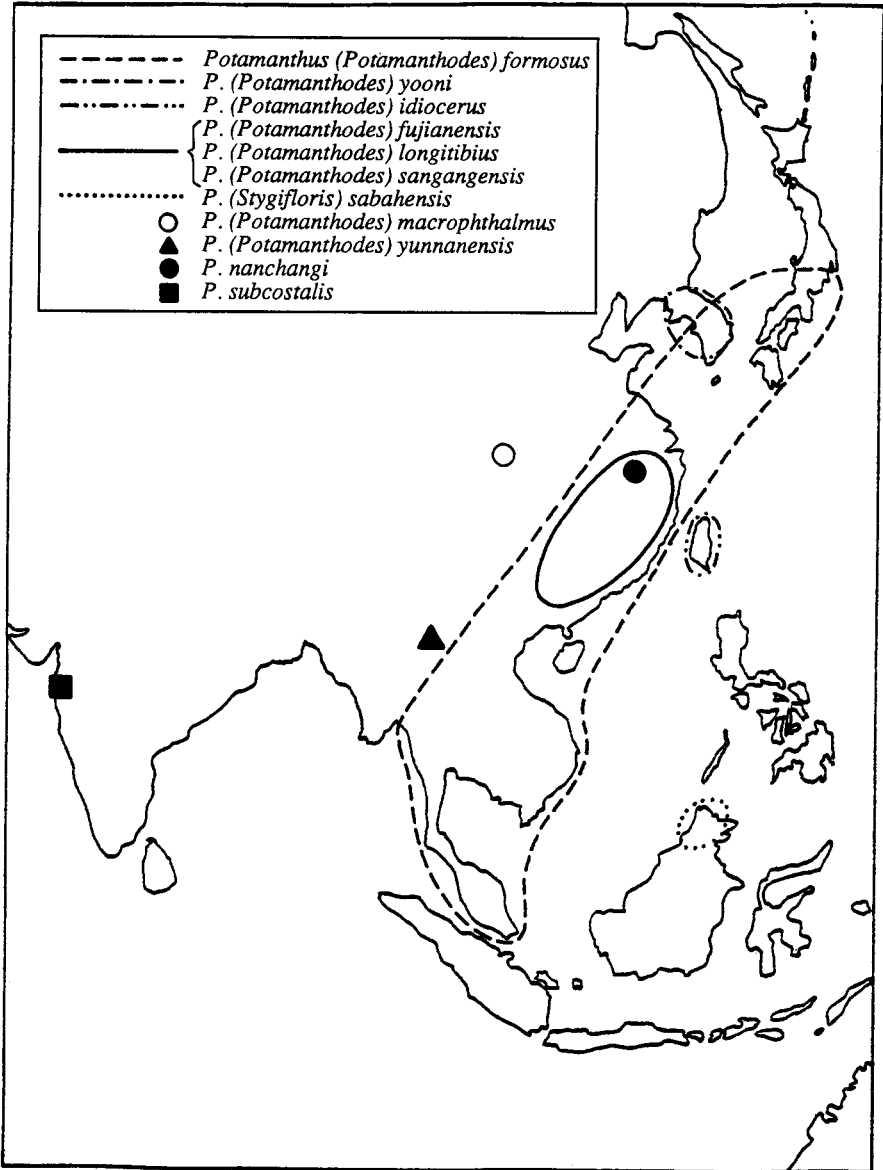


FIGURE 5. Distribution of *Potamanthus (Stygifloris)*, *Potamanthus (Potamanthodes)*, and *Potamanthus (incertae sedis)*.

Potamantodes by their large compound eyes ($ES = 0.09$) (Fig. 146) and relatively long (ca. 0.8x length of genital forceps) penes that are furcated at midlength (Fig. 128). Female adults of this species are distinguished from those of other *Potamantodes* by the combination of their very small compound eyes ($ES = 1.29$) and distribution in China (Fig. 5).

TYPE MATERIAL EXAMINED.— PARATYPES: 2 M, 2 F (alcohol, BAE-81), CHINA, Shanxi Prov, South of the Quiling Mountains, July 23-29, 1982, D. S. You (NNU).

Potamantus yooni, NEW SPECIES

Morphology Fig. 24, 42, 47, 51, 77, 98, 116, 129, 142, 147

Distribution Fig. 5

Potamantodes kamonis (Imanishi): Yoon & Bae, 1985. Entomol. Res. Bull., Korean Entomol. Inst., Seoul. 11: 94 (M, F, L), misidentification.

MATURE LARVA.— *Dimensions* (mm): Length of body 13.7-15.4, antennae 2.0-2.5; mandibles 0.20-0.25, caudal filaments 6.0-7.0; dorsal diameter of male compound eyes 0.75, female compound eyes 0.50-0.58. *Head*: Vertex brown to purplish brown with pair of irregular, light markings. Compound eyes of male full-sized ($ES = 1.18-1.33$) (Fig. 142); female compound eyes full-sized to minute ($ES = 1.79-2.30$). Antennae 1.3-1.6x length of head. Mandibles (Fig. 24, 42) short, 0.12-0.17x length of head; body of mandibles with ca. 50 simple-stout setae mixed with ca. 10 bipectinate-hairlike setae (setules weakly developed as in Fig. 51). Terminal segment of maxillary palpi (Fig. 24) 1.18-1.27x length of segment 2. Terminal segment of labial palpi (Fig. 24, 47) 0.83-1.36x length of segment 2. *Thorax*: Nota brown to purplish brown, with light markings; pronotum with 3-4 pairs of somewhat round markings, and with paired, C-shaped markings in medioposterior region (sometimes C-shaped markings narrower or not clearly visible); mesonotum and metanotum together with 6-10 pairs of somewhat round markings. Lateral expansions of pronotum white and moderately developed; anterolateral corners moderately developed. Legs pale yellow with brown to purplish brown markings; dorsal femora with elongated round marking in subbasal region; tibiae and tarsi with broad band at midlength. Foretibiae 0.82-0.84x length of forefemora, 1.36-1.38x length of foretarsi. *Abdomen*: Color light brown to brown; terga 1-10 each with light midlongitudinal stripe, and with pair of light submedian and sublateral longitudinal stripes (median and submedian stripes not clearly defined in some). Gills 3 with 28-40 marginal fibrillae along each lateral margin of dorsal lamellae, and 28-40 on ventral lamellae. Caudal filaments 0.39-0.49x length of body.

MALE ADULT.—*Dimensions* (mm): Length of body 13.5, antennae 0.9, forewings 11.9, hindwings 4.5, forelegs 11.7, genital forceps 1.15, cerci 25.8, median terminal filament 18.5; width of forewings 5.4, hindwings 2.7; dorsal diameter of compound eyes 1.10; distance between compound eyes 0.33. *Head*: Color pale yellow. Compound eyes black, medium-sized ($ES = 0.30$) (Fig. 147). *Thorax*: Color yellow. Forewings (Fig. 98) with longitudinal veins not pigmented; crossveins pigmented and infuscated throughout wing, numbering 28 between SC and R_1 , and 15 between R_1 and R_2 ; radial region with 1-2 crossveins connecting IR_2 and R_3 basally; MAs 0.78x length of MA_1 ; cubital region with 3-4 intercalaries (2-3 forked). Hindwings (Fig. 116) without markings; veins not pigmented; crossveins not infuscated; Rs 0.92x length of R_2 ; MPs 0.44x length of MP_1 . Forelegs pale yellow, with purplish brown bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae 1.60x length of forefemora, 0.77x length of foretarsi; segment 2 of foretarsi 1.17x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga 1-7 each white to pale yellow, with slightly dark, broad, lateral stripes; sterna white, without

markings. Terminal segment of forceps (Fig. 129) rounded apically, 1.07x length of segment 2; segments 2 and 3 together 0.37x length of basal segment; penes (Fig. 129) white, ca. 0.5x length of genital forceps, furcated at midlength from subgenital plate and divergent, pointed to slightly falcate apically. Caudal filaments pale yellow, with slightly dark band at each suture; median terminal filament 0.72x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 14.6-15.8, antennae 1.0, forewings 13.7-14.2, hindwings 4.8-5.0, forelegs 7.5-7.6, cerci 15.6-16.8, median terminal filament 15.8; width of forewings 6.3-6.5, hindwings 2.8-3.0; dorsal diameter of compound eyes 0.60-0.63; distance between compound eyes 0.80. *Head*: Color pale yellow; compound eyes apically gray, ventrally dark gray, very small (ES = 1.33). *Thorax*: Color yellow. Forewings with light yellowish tint, otherwise as in male; crossveins numbering 23 between SC and R₁, 14-17 between R₁ and R₂; MAs 0.68-0.78x length of MA₁. Hindwings as in male, except Rs 0.75-0.77x length of R₂ and MPs 0.36-0.43x length of MP₁. Legs similar to male, except foretibiae 1.04-1.12x length of forefemora, 1.31-1.45x length of foretarsi, and apex of foretarsi segment 3 and 4 dark purplish brown. *Abdomen*: Color pale yellow. Caudal filaments as in male; median terminal filament 0.94x length of cerci.

DIAGNOSIS.— Larvae of this species can be distinguished from those of other *Potamanthodes* by their full-sized compound eyes (ES = 1.18-1.33) in the males (Fig. 142), their larger body size (13.7-15.4 mm), and their distinct color pattern, which is similar to that of *P. luteus*. Male adults of this species can be distinguished from those of other *Potamanthodes* by the combination of medium-sized compound eyes (ES = 0.30) (Fig. 147) and medium-sized penes (ca. 0.5x length of genital forceps) that are furcated at midlength (Fig. 129). Female adults of this species can be distinguished from those of other *Potamanthodes* by the combination of very small compound eyes (ES = 1.33) and a distribution possibly limited to Korea (Fig. 5).

ETYMOLOGY.— This species is named in honor of Dr. I. B. Yoon, who has pioneered mayfly work in Korea.

TYPE MATERIAL EXAMINED.— HOLOTYPE: M (alcohol, BAE-161), KOREA (SOUTH), Kyonggi-do, Kapyong, Chojong R at Chongpyong, VI-11-1983, Y. J. Bae & T. H. Ro, deposited in KEI. PARATYPES: 1 M (alcohol, right wings on slide, BAE-162), 25 F (alcohol, BAE-50, 163, 164), same data as Holotype, deposited variously in KEI, PERC, USNM; 2 L (BAE-165, 166), same locale as Holotype, VI-12-1983, Y. J. Bae & T. H. Ro, deposited in PERC, USNM; 5 L, (BAE-19), Korea (South), Kyonggi-do, Kapyong, Mt Yumyong, V-14-1983, H. J. Park, deposited in PERC; 4 L, (BAE-167), Korea (South), Kangwon-do, Omi-ri at DMZ, VI-19-1983, I. B. Yoon, deposited in KEI.

OTHER MATERIAL EXAMINED.—KOREA (NORTH): 1 F, Heungson, Myohyang Mt, VII-7-1988 (S. Andrikovics). KOREA (SOUTH): 1 L (SEM stage), same data as paratype BAE-19; 3 L, Kapyong, Odae R nr Odae Mt Nat Pk, VIII-16-1978 (PERC).

DISCUSSION.— Yoon & Bae (1985) incorrectly treated this species under the name of *Potamanthodes kamonis* (Imanishi). *Potamanthodes kamonis* is a junior synonym of *P. formosus* (see discussion under *P. formosus*, below).

Potamanthus formosus Eaton

Morphology Fig. 17, 25, 37, 43, 61, 99, 117, 130, 141, 144, 150

Distribution Fig. 5

Potamanthus formosus Eaton, 1892. Trans. Entomol. Soc. London. 1892: 186 [Material: M, F (Syntypes); M Lectotype (designated by Kimmins, 1960) locality: Burma (Tenasserim Valley); Lectotype deposition: BM].

Potamanthodes formosus (Eaton): Ulmer, 1920b. Arch. Nat. 85: 11.

Potamanthus iyonis Matsumura, 1931. 6000 illustrated insects of the Japan Empire. Tokyo. 1931: 1469
[Material: F; Type information: unknown], NEW SYNONYM.

Potamanthus (Potamanthodes) kamonis Imanishi, 1940. Rep. Limnobiol. Surv. Kwant. Manch. 1940: 178 [Material: M (Holotype), F, L; Holotype locality: Japan (Kyoto); Holotype deposition: KYOU] (first L description), synonymized by Uéno (1969).

Potamanthodes kamonis (Imanishi): You, Wu, Gui & Hsu, 1982. Acta Zootaxon. Sin. 7: 410.

MATURE LARVA.— *Dimensions* (mm): Length of body 7.5-12.0, antennae 2.2-2.5, mandibles 0.13-0.30, caudal filaments 4.5-7.0; dorsal diameter of male compound eyes 0.28-0.30, female compound eyes, 0.28-0.33. *Head*: Vertex (Fig. 17) light brown to brown with pair of irregular, light markings. Compound eyes of male minute (ES = 2.80-3.67) (Fig. 17); female compound eyes minute (ES = 2.96-3.67). Antennae 1.8-2.2x length of head. Mandibles (Fig. 17, 25, 37, 43) short, 0.10-0.23x length of head; body of mandibles with 30-40 simple-stout setae mixed with 10-15 bipectinate-hairlike setae. Terminal segment of maxillary palpi (Fig. 25) 1.14-1.47x length of segment 2. Terminal segment of labial palpi (Fig. 25) slightly falcate in some, 0.83-1.36x length of segment 2. *Thorax*: Nota (Fig. 17) light brown to brown, with light markings often not clearly defined; pronotum with 3-4 pairs of irregular, somewhat round markings, and with paired, C-shaped markings in medioposterior region; mesonotum and metanotum with 5-10 pairs of irregular markings. Lateral expansions of pronotum white and moderately developed; anterolateral corners (Fig. 17) not developed into spine-like processes. Legs (Fig. 17) pale yellow with light brown to brown markings; dorsal femora with elongated round marking in subbasal region; tibiae and tarsi with broad band at midlength. Foretibiae 0.75-0.87x length of forefemora, 1.26-1.51x length of foretarsi. *Abdomen*: Color light brown to brown; terga 1-10 (Fig. 17) each either with light midlongitudinal stripe and pair of light submedian and sublateral longitudinal stripes, or with markings not clearly defined. Gills 3 with 20-30 marginal fibrillae along each lateral margin of dorsal lamellae, and 20-30 on ventral lamellae. Caudal filaments 0.50-0.71x length of body.

MALE ADULT.— *Dimensions* (mm): Length of body 8.0-9.4, antennae 0.6-0.7, forewings 7.7-8.9, hindwings 3.0-3.6, forelegs 6.2-7.4, forceps 0.68-0.75, cerci 19.6-22.2, median terminal filament 13.5-15.7; width of forewings 3.7-4.6, hindwings 1.8-2.3; dorsal diameter of compound eyes 0.28-0.33; distance between compound eyes 0.60-0.70. *Head*: Color pale yellow. Compound eyes black, tiny (ES = 2.15-2.55) (Fig. 150). *Thorax*: Color yellow. Forewings (Fig. 99) with slight yellowish tint in some (some individuals with at least 5 brown to purplish brown stained spots variously at bases of IR₂, IMA, IMP, MP₂, and cubital intercalaries); veins not pigmented; crossveins between C and Sc, Sc and R₁, R₁ and R₂, and in central region somewhat infuscated, numbering 18-22 between Sc and R₁, and 11-20 between R₁ and R₂; radial region with 0-1 crossveins connecting IR₂ and R₃ basally; MAs 0.83-0.94x length of MA₁; cubital region with 2-3 intercalaries (2 forked). Hindwings (Fig. 117) without markings; veins not pigmented; crossveins not infuscated; Rs 0.72-1.75x length of R₂; MPs 0.24-0.46x length of MP₁. Forelegs pale yellow, with purplish brown to dark brown bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae 1.43-1.66x length of forefemora, 0.82-0.89x length of foretarsi; segment 2 of foretarsi 1.17-1.60x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga 1-7 each white to pale yellow, with light brown, broad, lateral stripes (often not clearly visible); sterna white, without markings. Terminal segment of forceps (Fig. 130) rounded apically (slightly falcate in some), 1.25-1.67x length of segment 2; segments 2 and 3 together 0.36-0.45x length of basal segment; penes (Fig. 130, 141) white, ca. 0.5x length of genital forceps, furcated at

midlength from subgenital plate and divergent, and pointed to slightly falcate apically. Caudal filaments pale yellow, with slightly dark band at each suture; median terminal filament 0.69-0.72x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 8.4-10.6, antennae 0.7-0.8, forewings 8.1-10.5, hindwings 2.5-3.8, forelegs 3.9-5.3, cerci 10.0-11.5, median terminal filament 10.0-10.5; width of forewings 3.2-4.6, hindwings 1.3-1.9; dorsal diameter of compound eyes 0.23-0.33; distance between compound eyes 0.63-0.78. *Head*: Color pale yellow; compound eyes black, tiny (ES = 2.31-2.78). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male but lighter in intensity. Forewing venation similar to male except 21-24 crossveins between SC and R₁, 13-15 crossveins between R₁ and R₂. Hindwing venation similar to male. Foretibiae 0.98-1.09x length of forefemora, 1.42-1.51x length of foretarsi. *Abdomen*: Color pattern similar to male but lighter in intensity. Caudal filaments as in male; median terminal filament 0.91-1.00x length of cerci.

DIAGNOSIS.— Larvae of *P. formosus* (Fig. 17) can be distinguished from those of other *Potamanthodes* by the combination of minute compound eyes (ES = 2.80-3.67) in the male (Fig. 17), relatively short foretibiae (1.26-1.51x length of foretarsi), and relatively short mandibular tusks (0.10-0.23x length of head) (Fig. 144), and their relatively small body length (7.5-12.0 mm). Male adults of this species can be distinguished from those of other *Potamanthodes* by the combination of tiny compound eyes (ES = 2.15-2.55) (Fig. 150) and medium-sized penes (ca. 0.5x length of genital forceps) that are furcated at midlength (Fig. 130). Female adults of this species can be distinguished from those of *P. yooni* by their tiny compound eyes (ES = 2.31-2.78), but they cannot be distinguished from those of other *Potamanthodes* except by their distribution (consult adult key, below).

TYPE MATERIAL EXAMINED.— **LECTOTYPE** (*Potamanthus formosus* Eaton, 1892): M (pinned, McLachlan Col., determined by A. E. Eaton, B.M. 1938-674, BAE-35), BURMA, Tenasserim Valley [date & collector missing] (BM). **HOLOTYPE** (*Potamanthus (Potamanthodes) kamonis* Imanishi, 1940): M (alcohol, BAE-198), JAPAN, Kyoto, Kamogawa, 3 Sep. 1934, K. Imanishi (KYOU). **PARATYPES** (*Potamanthus (Potamanthodes) kamonis* Imanishi, 1940): 1 F, same data and deposition as Holotype; 6 L, 2 M, 1 F (BAE-199, 200), Japan, Kyoto, Kamigamo, IX-3-1934, K. Imanishi (KYOU).

OTHER MATERIAL EXAMINED.— **CHINA**: 1 Ms, Hubei Prov, Lui Shin Tze, VIII-1912 (BM); 1 M, Kouy-Tcheou, 1908 (HAM); 1 F (pinned, BAE-97), Kwangsi Prov, Kweiling, IV-1933 (MCZ). **JAPAN**: 1 L, Wakamatsu City, River Yu, VIII-10-1950 (UU); 1 L, Tsuruya, VIII-29-1917 (LENU); 5 L, 8 Ms, 8 Fs, Hatsukagawa, VII-30, VIII-30-1979, VII-22-1980 (KAGU); 3 M, 4 F, 4 Ms, 2 Fs, Koto R, Kagawa Pref, VII-23-1986 (KAGU). **MALAYSIA** (West): 1 M, 2 F, 1.6 mi NE K Lumpur, 1000', VI-8-1962 (PERC); 1 Fs, Gombok R & Univ Malaya Studies Center, 16.5 mi N Kuala Lumpur on Bentong Rd, VI-1-2-1968 (FAMU); 20 L, 1 F, Gombok R, 4.5 mi N Kuala Lumpur nr Bentong Road, XII-12-1968, II-6, III-8, IV-3, VIII-20-1969 (FAMU); 1 L, 1 M, Selangor, Large Trib, Sungai Selangor, 5 mi & 6 mi NE Kota Kuba Baharu (mi 43 & 44), 24.0-24.5°C, IX-1, 13-1978 (UU); 1 L, Selangor, Small Trib, Sungai Selangor (mi 42), 20°C, IX-13-1978 (UU); 24 L, Selangor, Sungai Tua, 6 mi & 2 mi N Batu Caves, IX-14, 15-1978 (UU); 6 L, Perak, Sungai Jor, Cameron Highlands Road, mi 19, IX-22-1978 (UU). **KOREA (SOUTH)**: 3 Ms, 1 Fs, Seoul, VII-17-1958 (UU); 5 Ms, 2 Fs, Seoul, Ttuksom, VI-28-29-1959 (PERC); 3 Ms, 5 Fs, Seoul, Mojin-dong, VIII-20, 27, 31-1959, IX-17-1959 (UU); 1 M, Kyonggi-do, Kapyong, Chojong R at Chongpyong, IX-5-1985 (KEI). **THAILAND**: 1 Ms, Nakhon, Nayok, VII-4-1929 (BM); 9 L, Chiangmai Prov, Mae Ping, 56 Km NE Chiangmai, XI-21-1964 (PERC); 3 L, 1 M, 1 F, 1 Ms, 1 Fs, Chiangmai Prov, Mae Ping, Chiangmai, 1000', X-5, XI-17, 20, 23, 27-1964 (PERC, UU); 1 L, Chiangmai Prov, Mae Mao R, SW Fang Horticultural, CL 2200, 500 m, XI-16-1985 (UU); 1 L, R Kwai Noi,

18 Km above Namtok, XI-30-1987 (PERC). VIETNAM: 2 Fs, 14 Km W Phan Rang, 60', VI-22-1960 (PERC); 1 M, Sonla Prov, Song Ma, V-1986 (LENU).

DISCUSSION.— Eaton (1892) did not specify or label a type series of specimens for this species. Kimmins (1960), however, designated a lectotype for it from among Eaton's (1892) original material (Syntypes). The drawing of male genitalia of the lectotype by Kimmins (1960) did not agree with Ulmer's (1925) drawing of male genitalia of *P. formosus* [Fig. 88 in Ulmer (1925)], and this created some misunderstanding (e.g., Imanishi 1940, Hsu 1937-38a, You et al. 1982, You 1984). The penes drawn by Ulmer are longer (0.67x length of genital forceps) than those drawn of the lectotype by Kimmins (0.5x length of genital forceps). We conclude that Ulmer's (1925) drawing is either inaccurate or actually a drawing of *P. macrophthalmus* genitalia (0.8x length of genital forceps, see Fig. 128).

Uéno (1931) mentioned similarities between Matsumura's (1931) description of *Potamanthus iyonis* from Japan and *P. formosus*. Although specimens of Matsumura's species in Hokkaido University could not be shipped for examination because of their fragile condition (S. Takagi, personal communication), markings of the wings and body size indicate that it is a junior synonym of *P. formosus*. Our examination of the adult holotype and larval paratypes of *Potamanthus kamonis* Imanishi (1940) from Japan confirmed its synonymy with *P. formosus* by Uéno (1969). The characters of male genitalia, wing venation, markings of wings, compound eye size, adult body size, and additional larval characters substantiate the synonymy.

We have in our possession an adult specimen of *P. formosus* that was taken at Hickam Air Force Base in Hawaii by E. H. Davidson in 1954. It quite probably was transported to Hawaii by a military plane from Korea or Japan at the time (the Korean War had just concluded), and there is no present indication that the species has colonized to the Hawaiian Islands.

Potamanthus idiocerus, NEW SPECIES

Morphology Fig. 145

Distribution Fig. 5

?*Potamanthus* sp.: Uéno, 1928. Mem. Coll. Sci. Kyoto Imperial Univ., Ser. B, 4: 25 (first L. description).
Potamanthodes formosus (Eaton): Uéno, 1969. Oriental Insects 3: 232 (M, F), misidentification.

MATURE LARVA.— *Dimensions* (mm): Length of body 11.0, antennae 2.5, mandibles 0.45, caudal filaments 6.0; dorsal diameter of female compound eyes 0.33. *Head*: Vertex light purplish brown with pair of irregular, light markings. Compound eyes of female minute (ES = 3.12). Antennae 2.0x length of head. Mandibles (Fig. 145) short, 0.34-0.36x length of head; body of mandibles with 40-50 simple-stout setae mixed with 10 bipectinate-hairlike setae. Terminal segment of maxillary palpi 1.33x length of segment 2. Terminal segment of labial palpi 1.05x length of segment 2. *Thorax*: Nota light purplish brown to brown, with distinct light markings; pronotum with 3 pairs of irregular, somewhat round markings, and with paired, C-shaped markings in medioposterior region; mesonotum and metanotum with 5-10 pairs of irregular markings. Lateral expansions of pronotum white and moderately developed; anterolateral corners not developed into spine-like processes. Legs pale yellow with light purplish brown markings; dorsal femora with elongated round marking in subbasal region; tibiae and tarsi each with broad band at midlength. Dorsal forefemora with 10-12 simple stout setae in transverse row at midlength, with scattered simple-stout setae and with few scattered simple-hairlike setae. Foretibiae 0.93x length of forefemora, 1.51x length of foretarsi, with 10-15 bipectinate-hairlike setae in tuft at ventral subapical position. *Abdomen*: Color light purplish brown, with distinct light markings; terga 1-10 each with midlongitudinal and pair

of submedian longitudinal stripes, and 2 pairs of round lateral markings. Gills 2-7 white, with slightly darker tracheae; gills 3 with 26 marginal fibrillae along each lateral margin of dorsal lamellae, and 26 on ventral lamellae. Caudal filaments 0.55x length of body.

MALE ADULT.—*Dimensions* (mm): Length of body 9.0, antennae 0.9, forewings 9.0, hindwings 3.4, forelegs 7.4, forceps 0.83, cerci 21.4, median terminal filament 13.2; width of forewings 4.4, hindwings 2.1; dorsal diameter of compound eyes 0.30; distance between compound eyes 0.70. *Head*: Color pale yellow. Compound eyes black, tiny (ES = 2.33). *Thorax*: Color yellow. Forewings (as in Fig. 99) with somewhat dark stains at bases of IR₂, IMA, IMP, MP₂, and cubital intercalaries; veins not pigmented; crossveins somewhat infuscated in central region, numbering 21 between SC and R₁ and 14 between R₁ and R₂; radial region with 1 crossvein connecting IR₂ and R₃ basally; MAs 0.89x length of MA₁; cubital region with 3 intercalaries (2 forked). Hindwings (as in Fig. 117) without markings; veins not pigmented; crossveins not infuscated; Rs 0.89x length of R₂; MPs 0.29x length of MP₁. Forelegs pale yellow, with purplish brown bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae 1.25x length of forefemora, 0.75x length of foretarsi; segment 2 of foretarsi 1.29x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga and sterna 1-10 each white, without markings. Terminal segment of forceps (as in Fig. 130) rounded or slightly falcate apically, 1.25x length of segments 2; segment 2 and 3 together 0.38x length of basal segment; penes (as in Fig. 130, 141) white, ca. 0.5x length of genital forceps, furcated at 1/3 length beyond subgenital plate, and pointed to slightly falcate apically. Cerci and median terminal filament white, with somewhat darkened band at each suture; median terminal filament 0.62x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 10.0, antennae 0.8, forewings 9.9, hindwings 3.3, forelegs (missing), cerci (missing), median terminal filament (missing); width of forewings 4.2, hindwings 1.7; dorsal diameter of compound eyes 0.31; distance between compound eyes 0.76. *Head*: Color pale yellow; compound eyes black, tiny (ES = 2.44). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male. Forewing venation similar to male, except 24 crossveins between SC and R₁, 16 crossveins between R₁ and R₂. Hindwing venation similar to male. *Abdomen*: Color pale yellow, without markings.

DIAGNOSIS.— Larvae of *P. idiocerus* are similar to those of *P. formosus* except their mandibular tusks (Fig. 145) are longer (0.34-0.36x length of head). Adults of this species are also similar to those of *P. formosus* (see diagnosis under *P. formosus*), however, they can be separated from adults of all other species of the subgenus *Potamanthodes* by their distribution in Taiwan (Fig. 5).

ETYMOLOGY.— The trivial name *idiocerus* is Greek, masculine, from *idios* (distinct, peculiar), and *keras* (horn), an allusion to the peculiar, somewhat longer mandibular tusks of the larvae.

TYPE MATERIAL EXAMINED.— HOLOTYPE: L (mature female, BAE-204), TAIWAN, Ta-tu River, 4 Km N of Tsaotun, X-11-1978, G. F. & C. H. Edmunds, deposited in PERC. PARATYPES: 2 L (mature female, BAE-217, 220), same data as Holotype, 1 L deposited in USNM, 1 L deposited in FAMU.

OTHER MATERIAL EXAMINED.—TAIWAN: 6 L, same data & deposition as Holotype; 1 L (exuviae), 1 Ms (reared), same data & deposition as Holotype; 1 F, 12 Ms, 12 Fs, Taipei, VIII-7-31, IX-1-10, IX-21-30-1964, VI-13-20, VII-13-20, XI-13-20-1965 (UU); 1 M (BAE-216), 290 Ms, 283 Fs, Taipei, IV-1-7, VI-11-17, VII-21-27, VIII-1-7, VIII-11-17, VIII-21-27, IX-1-7, X-1-7, XI-1-7-1966 (UU); 30 Ms, 30 Fs, Taichung, 1966 (UU); 4 F, Taihorin, V-1910, IX-1910, X-1910, XI-1910 (BER, HAM).

Potamanthus kwangsiensis (Hsu), NEW COMB.

Morphology Fig. 131

Distribution Fig. 5

Potamanthodes kwangsiensis Hsu, 1937-38a. Peking Nat. Hist. Bull. 12: 126 [Material: Ms (Holotype), Fs; Holotype locality: China (Jiangxi Prov); Holotype deposition: Y. C. Hsu's collection (destroyed); Neotype (designated herein) locality: China (Fujian Prov); Neotype deposition: NNU].

Potamanthodes fujianensis You, Wu, Gui & Hsu, 1980. J. Nanjing Normal Univ. 2: 1 [Material: Ms (Holotype), Fs; Holotype locality: China (Fujian Prov); Holotype deposition: NNU]; You, Wu, Gui & Hsu, 1982. Acta Zootaxon. Sin. 7: 410 (M, L), NEW SYNONYM.

LARVA.— Unknown.

MALE ADULT.—*Dimensions* (mm): Length of body 11.0, antennae 0.6, forewings 9.1, hindwings 3.6, forelegs 7.9, forceps 0.90, cerci 21.5, median terminal filament 17.3; width of forewings 4.5, hindwings 2.3; dorsal diameter of compound eyes 0.30; distance between compound eyes 0.65. *Head*: Color white. Compound eyes black, tiny (ES = 2.17). *Thorax*: Color pale yellow. Forewing veins not pigmented; crossveins somewhat infuscated in central region, numbering 20 between SC and R₁ and 13 between R₁ and R₂; radial region with 1 crossvein connecting IR₂ and R₃ basally; MAs 0.95x length of MA₁; cubital region with 3 forked intercalaries. Hindwings without markings; veins not pigmented; crossveins not infuscated; Rs 1.14x length of R₂; MPs 0.37x length of MP₁. Forelegs pale yellow, with purplish brown to dark brown bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae 1.26x length of forefemora, 0.88x length of foretarsi; segment 2 of foretarsi 1.35x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga 1-7 each white to pale yellow, with somewhat darkened, broad, lateral stripes; sterna white, without markings. Terminal segment of forceps (Fig. 131) notched apically and somewhat expanded medially, 1.50x length of segment 2; segments 2 and 3 together 0.41x length of basal segment; penes (Fig. 131) white, ca. 0.3x length of genital forceps, basally furcated at level of subgenital plate and divergent laterally, and pointed to slightly falcate apically. Caudal filaments white, without markings; median terminal filament 0.80x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 7.4, antennae (broken), forewings 7.1, hindwings 2.3, forelegs (missing), cerci 9.5, median terminal filament 9.5; width of forewings 3.0, hindwings 1.2; dorsal diameter of compound eyes 0.23; distance between compound eyes 0.53. *Head*: Color pale yellow; compound eyes black, tiny (ES = 2.33). *Thorax*: Color patterns of body, wings, and legs generally similar to male. Forewing venation similar to male, except 18 crossveins between SC and R₁, 9 crossveins between R₁ and R₂, and 2 forked cubital intercalaries. Hindwing venation similar to male. *Abdomen*: Similar to male, except median terminal filament 1.00x length of cerci.

DIAGNOSIS.— Male adults of this species are distinguished from those of other species of the subgenus *Potamanthodes* by their V-shaped (basally furcated) penes (Fig. 131) and their terminally notched genital forceps.

TYPE MATERIAL EXAMINED.— NEOTYPE: M (alcohol, BAE-232), CHINA, Fujian Province, Chongan, VII-22-1980, D. S. You, deposited in NNU.

OTHER MATERIAL EXAMINED.— 1 M, 2 F (alcohol, identified as *Potamanthodes fujianensis* by You, BAE-80), CHINA, Fujian Prov, Chongan, VII-22-1980, D. S. You (NNU).

DISCUSSION.— Hsu (1937-38a) described *Potamanthodes kwangsiensis* from Kiangsi (=Jiangxi) Province in China based on male and female subimagos. Even though his de-

scription and figure of male genitalia [Fig. 43 in Hsu (1937-38a)] were based on male subimagos, the basally furcated penes and terminally notched genital forceps, which are unique among the subgenus *Potamanthodes*, were clearly evident. Adult and subimaginal genitalia and other characteristics of *Potamanthodes fujianensis* You (1984), which was also collected from Jinggang Shan in Kiangsi Province near the type locality of *P. kwangsiensis*, agree with those of *P. kwangsiensis*. We therefore consider the two names to be synonymous. It should be noted that Hsu's figures of the wings of *P. kwangsiensis* [Fig. 40 in Hsu (1937-38a)] do not agree with his written description that MP_2 of the forewings originates from CuA, the costal projection is sharply pointed, and R_1 of hindwings is strongly arched toward Sc. The figures were evidently mislabeled and should not be associated with the species.

You et al. (1980) described *P. fujianensis* based on male and female subimagos and designated a male subimago as the holotype. You et al. (1982) subsequently described male and female adults of *P. fujianensis*. The subsequent designation of a new adult holotype and paratypes in that latter paper, however, is not valid and must be disallowed, since there is no provision for such in the ICZN. However, because those adult specimens are not types of *P. fujianensis*, we selected one of them as the neotype of *P. kwangsiensis* (see above).

You & Su's (1987) larval description of *P. fujianensis* was based on larvae collected near the type locality but not reared. We do not believe that those larvae are associated with adults described as *P. fujianensis* because the larval characteristics that are always closely associated with adult characteristics (i.e., compound eye size and relative length of foretibiae) are not consistent between those larvae and the adults. We furthermore recognize those larvae as a new species (see *P. longitibius*, below).

Potamanthus longitibius, NEW SPECIES

Morphology Fig. 143

Distribution Fig. 5

Potamanthodes fujianensis You et al.: You & Su, 1987. Acta Zootaxon. Sin. 12: 333 (L), misidentification.

MATURE LARVA.— *Dimensions* (mm): Length of body 12.2-14.6, antennae 3.0, mandibles 0.43-0.63. caudal filaments 7.0-7.3; dorsal diameter of male compound eyes 0.35, female compound eyes 0.35. *Head*: Vertex light brown to purplish brown with pair of irregular, light markings. Compound eyes of male minute (ES = 3.29) (Fig. 143); female compound eyes minute (ES = 3.57). Antennae 2.3x length of head. Mandibles (Fig. 143) 0.30-0.47x length of head; body of mandibles with 40-50 simple-stout setae mixed with 10-15 bipectinate-hairlike setae. Terminal segment of maxillary palpi 0.96-1.50x length of segment 2. Terminal segment of labial palpi 0.93-1.08x length of segment 2. *Thorax*: Not light brown to purplish brown, with distinct light markings; pronotum with 3 pairs of nearly round markings, and with paired, C-shaped markings in medioposterior region; mesonotum with 4-5 pairs of irregular markings and with transverse band of light markings through base of forewingpads. Pronotum moderately developed laterally; anterolateral corners only slightly developed. Legs pale yellow with light brown to purplish brown markings; dorsal femora with elongated round marking in subbasal region, with broad band at midlength; tibiae with broad band at midlength; foretarsi nearly dark brown. Dorsal forefemora with 10-12 simple-stout setae in transverse row at midlength, with scattered simple-stout setae, and with moderately developed hairlike setae. Foretibiae 0.97-0.99x length of forefemora, 1.57-1.82x length of foretarsi, with moderately developed bipectinate-hairlike setae dorsally and laterally, and with 10-20 bipectinate-hairlike setae in tuft at ventral subapical position.

Abdomen: Color light brown to purplish brown, with distinct light markings; terga 1-10 each with pair of teardrop-shaped spots and pair of tiny round spots, and pair of rounded markings on posterior margin. Gills 2-7 white, with slightly darker tracheae; gills 3 with 30-32 marginal fibrillae along each lateral margin of dorsal lamellae, and 28-30 on ventral lamellae. Caudal filaments 0.48-0.60x length of body.

MALE ADULT.—Unknown.

FEMALE ADULT.—Unknown.

DIAGNOSIS.— Larvae of *P. longitibius* can be easily distinguished from other larvae of the subgenus *Potamantodes* by their relatively long foretibiae (1.57-1.82x length of foretarsi). Their relatively long mandibular tusks (0.30-0.47x length of head) (Fig. 143) and the minute compound eyes of the male (ES = 3.29) (Fig. 143) are similar to those of *P. idiocerus*, but their long foretibiae, setation of forelegs, and distinct markings are different from *P. idiocerus* and other known larvae of the subgenus *Potamantodes*.

ETYMOLOGY.— The name *longitibius* is Latin, masculine, from longus (long), and tibia (tibia), an allusion of the relatively long foretibiae of the larvae.

TYPE MATERIAL EXAMINED.— HOLOTYPE: L (mature male, BAE-158, previously identified as *P. fujianensis* by You & Su 1987), CHINA (Fujian Prov), Shangang, V-8-1981, D.S. You, deposited in NNU. PARATYPES: 2 L (mature female, BAE-233, 234), same data as Holotype, 1 L deposited in PERC, 1 L deposited in USNM.

DISCUSSION.— Although the adults of *P. longitibius* are unknown, the unique characteristics of the larvae have prompted us to describe the species. Given the fact that a number of species of the subgenus *Potamantodes* remain unknown as larvae, future larval-adult associations could show that the larvae belong to another nominal species now unknown as larvae. For example, it is possible that the larvae we describe are the larvae of *P. sangangensis* (see below) because the adults of the latter species also possess unusually long foretibiae; also they are known from the same province of China. For the time being, however, it is important to give these larvae nominal recognition.

***Potamantus sangangensis* (You), NEW COMB.**

Morphology Fig. 133

Distribution Fig. 5

Potamantodes sangangensis You, 1984. Proc. 4th Intern. Conf. Ephem. p. 105 [Material: M (Holotype), F; Holotype locality: China (Fujian Prov); Holotype deposition: NNU].

LARVA.— Unknown.

MALE ADULT.—*Dimensions* (mm): Length of body 11.6, antennae 11.3, forewings (broken posteriorly) 10.2, hindwings (broken apically), forelegs 7.0, forceps 0.84, cerci > 25.0 (broken apically), median terminal filament 20.4; dorsal diameter of compound eyes 0.33; distance between compound eyes 0.85. *Head*: Color pale yellow. Compound eyes black, tiny (ES = 2.62). *Thorax*: Color yellow. Forewing veins not pigmented; crossveins somewhat infuscated in central region, numbering 25 between SC and R₁ and 17 between R₁ and R₂; radial region with 0-1 crossvein connecting IR₂ and R₃ basally; MAs 0.82x length of MA₁; cubital region with 3 forked intercalaries. Hindwings without markings; veins not pigmented or infuscated. Forelegs pale yellow, with purplish brown to dark brown bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae relatively long, 2.71x length of forefemora, 1.71x length of foretarsi; segment 2 of foretarsi 1.70x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga 1-7 each pale yellow, with

slightly dark, broad, lateral stripes; sterna white, without markings. Terminal segment of forceps (Fig. 133) rounded apically, 1.48x length of segment 2; segments 2 and 3 together 0.47x length of basal segment; penes (Fig. 133) white, 0.6x length of genital forceps, furcated at midlength from subgenital plate and divergent, and notched apically. Caudal filaments pale yellow, with somewhat darkened band at each suture; median terminal filament ca. 0.7x length of cerci.

FEMALE ADULT.—*Dimensions* (mm): Length of body 11.9, antennae 0.80, forewings (broken posteriorly) 12.0, hindwings 4.0, forelegs 5.3, cerci 15.5, median terminal filament 14.8; width of hindwings 1.9; dorsal diameter of compound eyes 0.33; distance between compound eyes 0.83. *Head*: Color pale yellow; compound eyes black, tiny (ES = 2.54). *Thorax*: Color patterns of body, wings, and legs generally similar to that of male. Forewing venation similar to male, except 24 crossveins between SC and R₁ and 14 crossveins between R₁ and R₂. Hindwings similar to male. Foretibiae 1.14x length of forefemora, 1.52x length of foretarsi. *Abdomen*: Caudal filaments white, without markings; median terminal filament 0.95x length of cerci.

DIAGNOSIS.— Male adults of this species are distinguished from those of other species of the subgenus *Potamanthodes* by their relatively long foretibiae (ca. 2.71x length of forefemora and 1.71x length of foretarsi) and their Y-shaped (furcated at midlength) and terminally notched penes (Fig. 133).

TYPE MATERIAL EXAMINED.— PARATYPES: 2 M, 2 F (alcohol, BAE-82), CHINA (Fujian Prov), Wuyi Shan, June 1981, D. S. You (NNU).

DISCUSSION.— It is highly probable that larvae we described as *P. longitibius* will eventually prove to be the larvae of *P. sangangensis*. They have unusually long foretibiae in common.

Potamanthus yunnanensis (You, Wu, Gui & Hsu), NEW COMB.

Morphology Fig. 132

Distribution Fig. 5

Potamanthodes yunnanensis You, Wu, Gui & Hsu, 1982. Acta Zootaxon. Sin. 7: 412 [Material: M (Holotype), F; Holotype locality: CHINA (Yunnan Prov); Holotype deposition: NNU].

LARVA.— Unknown.

MALE ADULT.—*Dimensions* (mm): Length of body 9.5, antennae (broken), forewings 8.6, hindwings 3.3, forelegs 6.9, forceps 0.76, cerci 21.0, median terminal filament (missing); width of forewings 4.3, hindwings 2.0; dorsal diameter of compound eyes 0.45; distance between compound eyes 0.63. *Head*: Color white. Compound eyes black, very small (ES = 1.40). *Thorax*: Color pale yellow. Forewing veins not pigmented; crossveins somewhat infuscated in central region, numbering 20 between SC and R₁ and 12 between R₁ and R₂; radial region with 1 crossvein connecting IR₂ and R₃ basally; MAs 0.92x length of MA₁; cubital region with 3 forked intercalaries. Hindwings without markings; veins not pigmented or infuscated; Rs 0.96x length of R₂; MPs 0.24x length of MP₁. Forelegs pale yellow, with dark brown bands in distal half of femora, at base and apex of tibiae, and at each tarsal suture; foretibiae 1.49x length of forefemora, 0.92x length of foretarsi; segment 2 of foretarsi 1.32x length of segment 3. Midlegs and hindlegs white. Claws white. *Abdomen*: Terga 1-7 each white, with slightly dark, broad, lateral stripes; sterna white, without markings. Terminal segment of forceps (Fig. 132) rounded apically, 1.30x length of segment 2; segments 2 and 3 together 0.32x length of basal segment; penes (Fig. 132) white, reduced, relatively short (ca.

0.2x length of genital forceps), basally furcated at level of subgenital plate, not divergent laterally, slightly notched apically. Caudal filaments white, slightly darker at each suture.

FEMALE ADULT.— (based on You et al. 1987). *Dimensions* (mm): Length of body 12.0, forewings 11.0, hindwings 3.5, forelegs ca. 5.5. Body: Generally similar to male. Compound eyes tiny (ES = 2.70).

DIAGNOSIS.— Male adults of this species are distinguished from those of other species of the subgenus *Potamanthodes* by their relatively short (ca. 0.2x length of genital forceps), basally furcated, and apically notched penes (Fig. 132).

TYPE MATERIAL EXAMINED.— PARATYPE: 1 M (alcohol, BAE-83), CHINA (Yunnan Prov), Xishuangbanna, Jinghong, May 1980, X. Wu (NNU).

POTAMANTHUS (subgenus *incertae sedis*)

Potamanthus nanchangi (Hsu), NEW COMB.

Potamanthodes nanchangi Hsu, 1935-1936. Peking Nat. Hist. Bull. 10: 322 [Material: M (Holotype);

Holotype locality: China (Jiangxi Prov); Holotype deposition: Y. C. Hsu's collection (destroyed)].

Neopotamanthodes nanchangi (Hsu): Hsu, 1937-38b. Peking Nat. Hist. Bull. 12: 223.

LARVA.— Unknown.

MALE ADULT.— [based on Hsu (1935-36, 1937-38b)]. *Length (mm) & Coloration*: Body 10.0, forewings 10.5, caudal filaments 19.0. General coloration yellowish brown. *Head*: Compound eyes large, round, grayish brown, and nearly contiguous. Ocelli prominent, pale, with black ring at base. Antennae pale; terminal filament short. *Thorax*: Pronotum yellowish; middle of posterior margin brownish and deeply notched. Mesonotum yellowish; lateral margin brownish. Metanotum brownish. Ventral surface of thorax yellowish. Legs light yellowish. Wings transparent white, with distal costal margin dull white. Forewings with MAs longer than MA₁ (MAs/MA₁ > 1.0); MP₂ connected to CuA basally; A₁ forked. Hindwings with R₁ not strongly arched toward Sc; costal projection rounded. *Abdomen*: Color dorsally brownish, ventrally light yellowish; posterior margin of each abdominal tergum dark brown. Posterior margin of tenth tergum with a quadrangular extension at the middle covering base of median filament; subgenital plate concave. Caudal filaments light brown, with dark brown ring on suture; median terminal filament subequal to cerci. Forceps with segments 2 and 3 together only half as long as segment 1. Penal lobes united, sharply pointed at apices, constricted at middle just beyond subgenital plate.

FEMALE ADULT.— Unknown.

DISCUSSION.— Hsu (1935-36) described this enigmatic species based on one male adult specimen collected by Dr. W. I. Yang from Nanchang, Jiangxi Province, China, on May 30, 1930. Hsu (1937-38b) redescribed and recombined the species with *Neopotamanthodes* Hsu. Unfortunately, the specimen was lost during the Sino-Japanese War (You, personal communication), and no additional material has been collected. The species is very likely valid because Hsu's original description (Hsu 1935-36), redescription (Hsu 1937-38b), and figure of male adult genitalia [Fig. 5 in Hsu (1935-36)] indicate a potamanthid with genitalia not matching any other species in the family. In our reformatting of Hsu's descriptions, above, we have updated morphological terminology, including wing venation.

This species could not belong to *Rhoenanthus* (*sensu novum*) because it lacks the convex subgenital plate and short terminal filament that typify *Rhoenanthus*. It is also not applicable to *Anthopotamus* because of its large male compound eyes as well as the fact that the base

of MP_2 of the forewings is attached to CuA and the costal projection of the hindwings is rounded. On the other hand, coloration, the large, nearly contiguous compound eyes, and the concave subgenital plate strongly suggest that it belongs to *Potamanthus*. We can not, however, place it to subgenus at this time on the basis of existing data.

It is possible that when fresh material and larvae are studied, *P. nanchangi* will be assignable to the subgenus *Stygifloris*. Like *Potamanthus (Stygifloris)*, it possesses such critical characters as large male compound eyes, forewings with MP_2 basally originating from CuA, hindwings with R_1 not strongly arched toward Sc, and rounded costal projections of the hindwings. Unlike *P. sabahensis*, however, it possesses a well-developed median terminal filament.

Potamanthus subcostalis Navás

Potamanthus subcostalis Navás, 1931. Rev. Acad. Cienc. Zaragoza 15: 17 [Material: F (Holotype); Holotype locality: India (Bombay); Holotype deposition: PM (lost)].

LARVA.— Unknown.

MALE ADULT.—Unknown.

FEMALE ADULT.— [transliterated from Navás' (1931) original Latin description and forewing figure] *Dimensions (mm) & Coloration*: Length of body 11, forewings 15.5, hindwings 5.3, caudal filaments 20.0. *Head*: Head brownish yellow with dark marking; pair of dark transverse stripes similarly placed on both sides toward occiput behind compound eyes; antennae white. *Thorax*: Thorax brownish yellow; pleura dark; pronotum broader than long, with pair of well-marked dark spots; mesonotum with pair of lateral, longitudinal lines in anterior region, and with 3 dark lines in posterior region. Wings clear and glossy. Forewings with some veins brownish yellow; subcostal area brownish yellow stained (basally more intense); crossveins in subcostal area dark; MAs slightly longer than MA_1 ; MP_2 basally originated from CuA; CuA basally arched, with 3 cubital intercalaries (2 forked); A_1 forked apically. Legs brownish yellow; claws dark. Hindwings pale; Rs forked slightly beyond midlength of hindwings. *Abdomen*: Abdomen brownish yellow, ventrally with pair of longitudinal stripes; terga 1-4 and posterior margin of other terga dark. Caudal filaments 3 in number, long (20 mm), subequal, brownish yellow, becoming more reddish brown in apical one third.

DISCUSSION.— This species is based on one female adult collected from Khandala (Bombay) in India on October 18, 1928. Unfortunately, the holotype, deposited in the Paris Museum and catalogued by Berthélémy (1965) is evidently missing (J. Legrand, personal communication). We were also unable to locate it in other collections where Navás material is deposited (i.e., BAR, BER, BM, HAM, UGRA, WIEN) (see Alba-Tercedor & Peters 1985).

Although Navás' (1931) original description and forewing drawing (his Fig. 25) are relatively incomplete, the species is clearly a potamanthid and most likely belongs to the genus *Potamanthus*. Although the description was based on a female adult, we have come to this conclusion because MP_2 of forewings originates from CuA and the median terminal filament is well developed. Color pattern of the subcostal region of the forewings may be unique and has prompted our continued recognition of the species; it could, however, be associated with the irregular markings in the costal area of the forewings of the subgenus *Potamanthodes*. There is not sufficient evidence to place the species to subgenus at this time.

KEY TO GENERA, SUBGENERA, SPECIES, AND SUBSPECIES
KNOWN LARVAE

- 1a. Mandibular tusks subequal to, or longer than, head length (Fig. 11-14); Holarctic & Oriental (Fig. 1) **2**
- 1b. Mandibular tusks shorter than 1/2 length of head (Fig. 15-17); Palearctic & Oriental (Fig. 1) **Genus *Potamanthus*, 9**
- 2a. Foretibiae relatively long (2.3-2.8x length of foretarsi), with dense hairlike setae on dorsal and lateral surface (Fig. 11-13); East Asia, Southeast Asia & India (Fig. 1) **Genus *Rhoenanthus*, 3**
- 2b. Foretibiae relatively short (1.2-1.9x length of foretarsi), with dense hairlike setae along anterior margin (Fig. 14); eastern half of North America (Fig. 1) **Genus *Anthopotamus*, 6**
- 3a. Mandibular tusks with large lateral subapical spine, appearing apically forked (Fig. 11, 26); maxillary palpi slender, with weakly developed hairlike setae on terminal segment (Fig. 18); Southeast Asia & India (Fig. 2) **Subgenus *Rhoenanthus* (only *Rhoenanthus speciosus* known as larvae)**
- 3b. Mandibular tusks without large lateral subapical spine, not appearing apically forked (Fig. 12-13), but sometimes with small lateral subapical spine (Fig. 13, 28); maxillary palpi thick, with strongly developed hairlike setae on terminal segment (Fig. 19-20); Far east Asia, China & Indochina (Fig. 2) **Subgenus *Potamanthindus*, 4**
- 4a. Mandibular tusks strongly convergent and abruptly curved inward (Fig. 12, 27); crown and lateral margin of galealaciniae forming right angle, with rows of long hairlike setae covering entire crown; Indochina (Fig. 2) ***Rhoenanthus obscurus***
- 4b. Mandibular tusks only gradually curved inward (Fig. 13, 28); crown and lateral margin of galealaciniae forming gradual angle conspicuously greater than 90°, with hairlike setae covering only 3/4 of crown surface; Far E Asia & China (Fig. 2) **5**
- 5a. Abdominal terga each with pair of light markings at posterior margin extending anteriorly into paired submedian stripes; caudal filament segments with whorls of simple-stout setae; mandibular tusks without subapical spine or pronounced seta; China (Fig. 2) ***Rhoenanthus youi***
- 5b. Abdominal terga each with pair of light markings at posterior margin but lacking light, submedian stripes; caudal filament segments without whorls of simple-stout setae; mandibular tusks often with small subapical spine (Fig. 13, 28) or pronounced seta; Far East Asia (Fig. 2) ***Rhoenanthus coreanus***
- 6a. Mandibular tusks attenuated but also with abrupt constriction at base (Fig. 33-34); foretibiae with long setae relatively well developed in three rows along anterior margin (Fig. 71), and with prominent apical spine (Fig. 34); mature larvae relatively short (9-11 mm) **7**

- 6b. Mandibular tusks gradually attenuated throughout, not abruptly constricted at base (Fig. 14, 30-31); foretibiae with long setae distributed irregularly (not in defined rows) along anterior margin (Fig. 30-31, 70), without prominent apical spine (Fig. 30-31); mature larvae relatively long (13-18 mm) **8**
- 7a. Color brown or dark brown with less distinct light markings (last instar larvae solid dark brown) (Fig. 39 in Needham 1920); compound eyes of male relatively large (ES = 2.00-2.15); mandibular tusks relatively long (0.9-1.3x length of head)
Anthopotamus verticis
- 7b. Color brown, purplish brown, or dark brown with distinct light markings in early to late instars (as in Fig. 14); compound eyes of male relatively small (ES = 2.58); mandibular tusks relatively short (0.7-0.8x length of head)
Anthopotamus neglectus
- 8a. Lateral margins of pronotum distinctly expanded laterally, with anterolateral corners produced into spinelike processes (Fig. 31); forefemora without hairlike setae on dorsal surface (Fig. 3 in McCafferty 1975a); foretibiae relatively long (1.5-1.9x length of foretarsi), and hairlike setae along anterior margin relatively long (Fig. 31); Northeast & Southeast North America (Fig. 3) *Anthopotamus myops*
- 8b. Lateral margins of pronotum moderately expanded laterally, with anterolateral corners not produced into spinelike processes (Fig. 14, 30); forefemora with hairlike setae on dorsal surface (Fig. 14, 30, 70); foretibiae relatively short (1.2-1.5x length of foretarsi) (Fig. 14), and hairlike setae along anterior margin relatively short (Fig. 30); Appalachian range (Fig. 3) *Anthopotamus distinctus*
- 9a. Forefemora with distinct dorsal transverse row of well-developed simple-stout setae at midlength (Fig. 16-17, 72); foretibiae with ventral, subapical tuft of hairlike setae (Fig. 73); pronotum not patterned as in Fig. 15, and body markings often not clearly defined; mature male larvae with full-sized to minute compound eyes (ES = 0.73-3.60); Far East Asia, China & Southeast Asia (Fig. 5) **11**
- 9b. Forefemora without dorsal transverse row of simple-stout setae at midlength, or only cluster of small simple-stout setae in that area (Fig. 15); foretibiae without ventral, subapical tuft of hairlike setae; color brown to dark brown with various markings on body, including submedian pair of C-shaped markings on pronotum as in Fig. 15 (also see Fig. 124 in Schoenemund 1930); mature male larvae with full-sized compound eyes (ES = 0.75-1.00) (Fig. 15); Europe, Central Asia & East Asia (Fig. 4)
Subgenus *Potamanthus*, **10**
- 10a. Found in Europe, Central Asia & North Africa (Fig. 4)
Potamanthus luteus luteus
- 10b. Found in China & Far East Asia (Fig. 4)
Potamanthus luteus oriens
Potamanthus huoshanensis

- 11a. Terminal segment of labial palpi falcate (with distinct apicomedial margin) (Fig. 23); forewingpads of older (not including last instar) larvae each with distinct spot medially (Fig. 16); Borneo (Fig. 5)
 Subgenus *Stygifloris*, *Potamanthus sabahensis*
- 11b. Terminal segment of labial palpi symmetrically pointed (Fig. 24-25); forewingpads of older larvae without medial spot (Fig. 17); Far East Asia, China, Taiwan & Indochina (Fig. 5)
 Subgenus *Potamanthodes*, **12**
- 12a. Mature male larvae with full-sized compound eyes (ES = 1.18-1.33) (Fig. 142); Korea (Fig. 5)
Potamanthus yooni
- 12b. Mature male larvae with minute compound eyes (ES = 3.12-3.60) (Fig. 143); Far East Asia, China, Taiwan & Indochina (Fig. 5) **13**
- 13a. Foretibiae relatively long (1.57-1.82x length of foretarsi); China (Fig. 5)
Potamanthus longitibius
- 13b. Foretibiae relatively short (1.26-1.51x length of foretarsi); Far East Asia, China & Indochina (Fig. 5) **14**
- 14a. Mandibular tusks 0.34-0.36x length of head (Fig. 145); Taiwan (Fig. 5)
Potamanthus idiocerus
- 14b. Mandibular tusks 0.10-0.23x length of head (Fig. 144); Far East Asia, China & Indochina (Fig. 5)
Potamanthus formosus

KNOWN ADULTS

- 1a. MP_2 of hindwings originating from MP_1 , forming symmetrical fork with MP_1 (Fig. 107-117), sometimes coalescing with CuA for short distance near base (Fig. 109); subgenital plate of male concave (Fig. 124-133); Palearctic, Oriental & Nearctic (Fig. 1)
11
- 1b. MP_2 of hindwings originating from CuA (MP_1 and MP_2 never forming symmetrical fork) (Fig. 100-106); subgenital plate of male convex (Fig. 118-123); East Asia, Southeast Asia & India (Fig. 1)
 Genus *Rhoenanthus*, **2**
- 2a. MP_2 of forewings basally connected to MP_1 (Fig. 84-88); 3-5 costal crossveins of forewings concentrated near bullae (Fig. 84-88); Far East Asia, China & Indochina (Fig. 2)
 Subgenus *Potamanthindus*, **4**
- 2b. MP_2 of forewings basally connected to CuA (Fig. 82-83); costal crossveins of forewings not concentrated near bullae (Fig. 83); Southeast Asia & India (Fig. 2)
 Subgenus *Rhoenanthus*, **3**
- 3a. A_1 of forewings forked only once (Fig. 83); penial lobes of male distinctly narrowed apically (Fig. 119); Malay Peninsula, Sumatra, Java & Borneo (Fig. 2)
Rhoenanthus speciosus

- 3b. A_1 of forewings forked twice (with distal and subdistal fork) (Fig. 82); penal lobes of male not distinctly narrowed apically (Fig. 118); Indochina & India (Fig. 2)
Rhoenanthus distafurcus
- 4a. Male 5
- 4b. Female 8
- 5a. Forewings with purplish brown stained markings scattered throughout wing (Fig. 84); Indochina (Fig. 2)
Rhoenanthus magnificus
- 5b. Forewings with purplish brown stained marking concentrated transversely in midregion (Fig. 85, 87); Far East Asia, China & Indochina (Fig. 2) 6
- 6a. Costal projection of hindwings rounded (Fig. 104); R_1 of hindwings moderately arched at base (Fig. 104); Indochina (Fig. 2)
Rhoenanthus obscurus
- 6b. Costal projection of hindwings acute (Fig. 103, 106); R_1 of hindwings straight to slightly arched at base (Fig. 103, 106); Far East Asia & China (Fig. 2) 7
- 7a. Penal lobes relatively narrow-elongated, with notched asymmetrical apices (Fig. 123); China (Fig. 2)
Rhoenanthus youi
- 7b. Penal lobes short and broad, without notched asymmetrical apices (Fig. 122); Far East Asia (Fig. 2)
Rhoenanthus coreanus
- 8a. Forewings purplish brown over most of membrane (Fig. 86); hindwings purplish brown throughout (Fig. 105); southern China & Indochina (Fig. 2) 9
- 8b. Forewings with purplish brown stained marking concentrated transversely in midregion as in Fig. 87; hindwings purplish brown in apical half as in Fig. 106; Far East Asia & China (Fig. 2) 10
- 9a. R_1 of hindwings slightly arched at base as in Fig. 102; southern China & Indochina (Fig. 2)
Rhoenanthus magnificus
- 9b. R_1 of hindwings moderately arched at base (Fig. 105); Indochina (Fig. 2)
Rhoenanthus obscurus
- 10a. Found in Far East Asia (Fig. 2)
Rhoenanthus coreanus
- 10b. Found in southern China (Fig. 2)
Rhoenanthus youi
- 11a. MP_2 of forewings basally connected to MP_1 (Fig. 89-93) and compound eyes of male small to tiny ($ES = 0.68-2.89$) as in Fig. 148-150; Nearctic (Fig. 1)
Genus *Anthopotamus*, 12

- 11b. Either MP_2 of forewings basally connected to MP_1 (Fig. 94-95) and compound eyes of male large (ES = 0.08-0.25) as in Fig. 146, or MP_2 of forewings basally connected to CuA (Fig. 96-99) and compound of eyes of male variable in size (ES = 0.08-2.62); Palearctic & Oriental (Fig. 1) Genus *Potamanthus*, 21
- 12a. Male 13
- 12b. Female 17
- 13a. Compound eyes small (ES = 0.68-0.94) (Fig. 148); crossveins of forewings not infuscated (Fig. 92) *Anthopotamus verticis*
- 13b. Compound eyes very small (ES = 0.92-1.25) (Fig. 149) or tiny (ES = 1.91-2.89) as in Fig. 150; crossveins of forewings infuscated (Fig. 89-90) or not infuscated (Fig. 91) 14
- 14a. Compound eyes very small (ES = 0.92-1.25) (Fig. 149); crossveins of forewings strongly infuscated (Fig. 89); Appalachian range (Fig. 3) *Anthopotamus distinctus*
- 14b. Compound eyes tiny (ES = 1.91-2.89) as in Fig. 150; crossveins of forewings infuscated (Fig. 90) or not infuscated (Fig. 91); northeast & nouttheast North America (Fig. 3) 15
- 15a. Crossveins of forewings not infuscated (Fig. 91); body 11.3-13.0 mm long *Anthopotamus myops*
- 15b. Crossveins of forewings infuscated in midregion (Fig. 90); body 7.2-9.2 mm long *Anthopotamus neglectus*, 16
- 16a. Northeast North America (Fig. 3) *Anthopotamus neglectus neglectus*
- 16b. Southeast North America (Fig. 3) *Anthopotamus neglectus disjunctus*
- 17a. Crossveins of forewings not infuscated (as in Fig. 91) *Anthopotamus myops*
- 17b. Crossveins of forewings slightly to strongly infuscated (Fig. 93, as in Fig. 89-90) 18
- 18a. Body 8.5-9.2 mm long; compound eyes tiny (ES = 2.27-2.61) as in Fig. 150 *Anthopotamus neglectus*, 19
- 18b. Body 9.5-14.0 mm long; compound eyes very small (ES = 1.42-1.66) as in Fig. 149 20
- 19a. Found in Northeast North America (Fig. 3) *Anthopotamus neglectus neglectus*
- 19b. Found in Southeast North America (Fig. 3) *Anthopotamus neglectus disjunctus*

- 20a. Crossveins of forewings strongly infuscated (as in Fig. 89); crossveins of hindwings strongly infuscated (as in Fig. 107); Appalachian range (Fig. 3)
Anthopotamus distinctus
- 20b. Crossveins of forewings slightly infuscated (Fig. 93); crossveins of hindwings not infuscated (Fig. 111); northeast & southeast North America (Fig. 3)
Anthopotamus verticis
- 21a. MP_2 of forewings basally connected to MP_1 (Fig. 94-95); compound eyes of male large (ES = 0.08-0.25) as in Fig. 146; Europe, Central Asia & East Asia (Fig. 4)
Subgenus *Potamanthus*, 22
- 21b. MP_2 of forewings basally connected to CuA (Fig. 96-99); compound eyes of male large to tiny (ES = 0.09-2.62) as in Fig. 146-150; Far East Asia, China & Southeast Asia (Fig. 5) 24
- 22a. Wing veins dark (Fig. 94, 112); forewings (Fig. 94) with 21-27 crossveins between Sc and R_1 , and 12-18 crossveins between R_1 and R_2 ; abdominal terga 1-10 each with 2 pairs of dark lateral spots; Europe, Central Asia & Far East Asia (Fig. 4)
Potamanthus luteus, 23
- 22b. Wing veins clear (Fig. 95, 113); forewings (Fig. 95) with 35-38 crossveins between Sc and R_1 , and 23-25 crossveins between R_1 and R_2 ; abdominal terga 1-10 without pairs of dark lateral spots; China (Fig. 4) *Potamanthus huoshanensis*
- 23a. Found in Europe & Central Asia (Fig. 4) *Potamanthus luteus luteus*
- 23b. Found in Far East Asia (Fig. 4) *Potamanthus luteus oriens*
- 24a. R1 of hindwings straight, not strongly arched toward Sc at base (Fig. 114); forewings without blotches in costal region (Fig. 96); Borneo (Fig. 5)
Subgenus *Stygifloris*, *Potamanthus sabahensis*
- 24b. R1 of hindwings strongly arched toward Sc at base (Fig. 115-117); forewings with distinctive blotches in costal region (Fig. 97-99); Far East Asia, China, Taiwan & Indochina (Fig. 5)
Subgenus *Potamanthodes*, 25
- 25a. Male 26
- 25b. Female 32
- 26a. Compound eyes large (ES = 0.09) (Fig. 146); penes greatly elongated (0.8x length of genital forceps) (Fig. 128); China (Fig. 5) *Potamanthus macrophthalmus*
- 26b. Compound eyes medium-sized (ES = 0.30) (Fig. 147) or very small to tiny (ES = 1.40-2.62) (Fig. 149-150); penes not greatly elongated (shorter than 0.6x length of genital forceps); Far East Asia, China, Taiwan & Indochina (Fig. 5) 27
- 27a. Compound eyes medium-sized (ES = 0.30) (Fig. 147); body 13.0-14.0 mm long; Korea (Fig. 5) *Potamanthus yooni*

- 27b. Compound eyes very small to tiny (ES = 1.40-2.62) (Fig. 149-150); body 8.0-11.6 mm long; Far East Asia, China, Taiwan & Indochina (Fig. 5) **28**
- 28a. Penes apically pointed (Fig. 130-131); Far East Asia, China, Taiwan & Indochina (Fig. 5) **29**
- 28b. Penes apically notched (Fig. 132-133); China (Fig. 5) **31**
- 29a. Penal lobes separated to base (Fig. 131); terminal segment of genital forceps notched apically (Fig. 131); China (Fig. 5) *Potamanthus kwangsiensis*
- 29b. Penal lobes separated at about midlength (Fig. 130); terminal segment of genital forceps rounded to slightly falcate apically (Fig. 130); Far East Asia, China, Taiwan & Indochina (Fig. 5) **30**
- 30a. Found in Taiwan (Fig. 5) *Potamanthus idiocerus*
- 30b. Found in Far East Asia (Korea & Japan), China & Indochina (Fig. 5) *Potamanthus formosus*
- 31a. Penes 0.6x length of genital forceps (Fig. 133) *Potamanthus sangangensis*
- 31b. Penes 0.2x length of genital forceps (Fig. 132) *Potamanthus yunnanensis*
- 32a. Compound eyes very small (ES = 1.29-1.33) as in Fig. 149 **33**
- 32b. Compound eyes tiny (ES = 2.31-2.78) as in Fig. 150 **34**
- 33a. Found in Korea (Fig. 5) *Potamanthus yooni*
- 33b. Found in China (Fig. 5) *Potamanthus macrophthalmus*
- 34a. Found in Taiwan (Fig. 5) *Potamanthus idiocerus*
- 34b. Found in Far East Asia (Korea & Japan), China & Indochina (Fig. 5)
Potamanthus formosus
Potamanthus kwangsiensis
Potamanthus sangangensis
Potamanthus yunnanensis

PHYLOGENY AND PHYLOGENETIC CLASSIFICATION

Cladistic methods for hypothesizing phylogeny (sensu Ross 1937, 1974; Hennig 1950, 1966) have been employed rigorously in the analysis of the evolutionary relationships of the Ephemeroptera in the recent past (e.g., McCafferty 1979, McCafferty & Edmunds 1979, Peters 1980, Savage & Peters 1983). Only more recently, however, have cladistic analyses resulted in strict phylogenetic classifications for Ephemeroptera (McCafferty 1991a, 1991b). We have used such cladistic methodology to hypothesize the phylogenetic relationships within the Potamanthidae. Furthermore, we have revised the supraspecific taxa and se-

quenced the species within those taxa to conform to a strict phylogenetic classification expressive of that phylogeny. The reasons for using a phylogenetic classification rather than an evolutionary classification or some other system for Ephemeroptera were presented in detail by McCafferty (1991b). We have selected outgroups for the purpose of determining character state polarity based on the phylogeny of the Ephemeroptera and Ephemeroidea presented by McCafferty (1991b). In the present study, the familial relationships were not researched beyond that of McCafferty (1979, 1991b); however, it is germane to consider that subject as well as the uniqueness of Potamanthidae since they are important to our study of relationships within the family.

INTEGRITY OF THE FAMILY POTAMANTHIDAE

As pointed out in the Introduction, a distinct potamanthid taxon has been recognized beginning with Eaton (1883-88). Ever since the Edmunds & Traver (1954) reclassification of the Ephemeroptera, with the exception of Riek's (1973) classification, the taxon has been universally recognized at the family level. This general acceptance had undoubtedly been on phenetic grounds prior to demonstrating a sequential phylogenetic position of the lineage that supported its recognition as a separate family (McCafferty 1991b). We have been able to identify several synapomorphies that support this classification and therefore essentially define the family in a phylogenetic sense. These include the nine numbered synapomorphies indicated at the stem of the family clade (Fig. 6). These numbers correspond to the numbered character and character state descriptions appearing in Table 1.

The presence of bipectinate-hairlike setae on the mandibular tusks of the larvae (synapomorphy 3₁) is considered an apomorphy unique to the potamanthids because all other ephemerooids, including the earlier derived Polymitarcyidae, possess only simple-hairlike setae.

The structure of gill 1 of Potamanthidae larvae (synapomorphies 22₁-24₁) is unique among the infraorder Lanceolata (Leptophlebioidea, Behningioidea, and Ephemeroidea). Considering larvae of the Leptophlebiidae, particularly the ancestral genera *Paraleptophlebia* and *Leptophlebia* (Peters & Edmunds 1970, Peters 1980), as well as the other ephemerooids (but excluding the Behningioidea because their gills 1 are so specialized), it becomes apparent that the ventrolateral orientation, segmentation, and apical setation are synapomorphies common only to the potamanthid lineage. Whereas all ephemerooids have reduced gills 1, all but potamanthids have retained the plesiomorphic posterolateral position and unsegmented condition. It is curious that the Ephemerellidae and Caenidae of the Caenoidea (same suborder Rectracheata, but infraorder Pannota rather than Lanceolata) also have gills 1 similar to the Potamanthidae. At this time we can explain this only as a convergence for an as yet unknown adaptation. To consider these states commonly derived is untenable because it would require the acceptance of a inordinate number of character convergences involving a large number of family lineages.

Wing venation in Potamanthidae is essentially similar to that of other ephemerooids, especially Ephemeridae, except for three nearly consistent differences (synapomorphies 30₁, 33₁, 36₁). In the forewing, A₁ has become conspicuously forked and the angle between R₁ and A₁ (as measured between straight lines drawn from the base to the tip of the basal fork of A₁ and from the base to the tip of R₁) has increased. These wing characteristics are unique among the Lanceolata. The forewings of Neophemeridae (Pannota) also have a similarly forked A1 that must be explained as a convergence. In the hindwing, the costal projection in the potamanthid lineage has shifted to an extreme basal position and become acute apically. This characteristic is difficult to quantify precisely and the hindwings of some nonpotamanthid

genera, e.g., *Ephoron* (Polymitarcyidae) may have a similar appearance that presumably evolved independently. In addition, *R. obscurus*, *P. sabahensis*, and *P. nanchangi* are potamanthid species that have subsequently lost the typical strongly produced point of the projection, and thus the costal projection appears more rounded. Although these exceptional potamanthid costal projections are reminiscent of the obtuse plesiomorphic state, they are still basally oriented and most probably represent apotypic reversals (see the relatively apotypic phylogenetic positions of these species below).

Egg morphology in Ephemeroptera appears to be highly subject to convergent evolution, and thus, is of limited use in phylogeny reconstruction (see discussion below); however, two characteristics of the Potamantidae appear to represent synapomorphies (44₁ and 45₁). Instances of egg structure convergences are scattered through the Lanceolata as well as other distantly related groups of mayflies. The potamanthid lineage appears to have independently evolved two large type II polar caps and a tagenofrom micropyle (see Koss & Edmunds 1974) that are evidently maintained throughout the family (we were unable to examine eggs of some species).

INTERFAMILIAL RELATIONSHIPS

The phylogenetic position of the Potamantidae within the Ephemeroptera, and superfamily Ephemeroidea in particular, has been hypothesized and depicted either in phylograms or cladograms by Edmunds (1962, 1972, 1973), Landa (1973), Koss (1973), Koss & Edmunds (1974), McCafferty (1979), Landa & Soldán (1985), and McCafferty (1991b). Prior to these more modern treatments, several mayfly taxonomists suggested interrelationships of the potamantids either explicitly, or implicitly via their proposed higher classifications. For the most part, these would have to be regarded as phenetic interpretations; and relationships may not always have been thought to be genealogical by all of these workers since several did not have a known position on evolution.

Although Eaton (1883-88) had placed potamantids closer to leptophlebiids than to other ephemeroids, other early workers, beginning with Lestage (1917) and Lameere (1917), generally recognized what are now considered ephemerids and polymitarcyids, along with potamantids, in the same family or superfamily (Ephemeridae or Ephemeroidea). They were thus conceptually in agreement with the phylogenetic classification of McCafferty (1991b), which we follow here. In that classification, Polymitarcyidae, Potamantidae, and Ephemeridae, which together include all extant tusked burrowing mayflies with fibrillate gills, are placed in the superfamily Ephemeroidea. Traver (1935) and Demoulin (1958) included neophemerids in the taxon, but Burks (1953) legitimately removed them. Edmunds and Traver (1954) added the behningiids to the ephemeroids, but they have been excluded by McCafferty (1991b).

Spith (1933), being a student of one of the pioneers of phylogenetic research, A. C. Kinsey, attempted the first study of mayfly phylogeny per se, but his analysis was restricted to the North American fauna and was phenetically based. He included potamantids within the Ephemeridae, but concluded that they were intermediate between Leptophlebiidae and Ephemeridae because he reasoned that *Anthopotamus* wing venation, mandibles, and gill fibrillae were related to those of other ephemerids, but that their genitalia, mouthparts, and gill lamellae were related to those of leptophlebiids, especially *Leptophlebia*. He also regarded potamantids as "semi-burrowers," representing an intermediate grade between sprawling leptophlebiids and burrowing ephemerids. His ideas may have been influenced by Eaton (1883-88) and in general can be taken to reflect the close phylogenetic relationship of the Leptophlebiidae and Ephemeroidea, which was later found by Landa (1969) to be

TABLE 1. Cladistic characters and character state polarities.

Character	Character State
1. Body size (mature larvae or adult)	0. 10-15 mm
	-1. < 10 mm
	+1. > 20 mm
2. Clypeus setation	0. Hairlike & simple-stout setae profuse (Fig. 27-29) 1. Setae sparse to absent (Fig. 30-31, 36-37)
3. Mandible setation	0. With simple-hairlike setae (Pl. 28: Fig. 8-9; Pl. 30: Fig. 7-8, Eaton 1883-88) 1. With weak bipectinate-hairlike setae (Fig. 38-43, 48-51)
4. Basal tusk setae	0. On dorsal & lateral surface (Fig. 30-31, 41-43) 1. On medial & lateral surface (Fig. 26-29, 38)
5. Tusk length	0. 0.9-2.3x head length (Fig. 11-14) 1. 0.1-0.5x head length (Fig. 15-17)
6. Tusk curvature	0. < 20° (Fig. 11) 1. > 20° (Fig. 12-13)
7. Tusk attenuation	0. Evenly attenuated (Fig. 30-31) 1. With abrupt attenuation at base (Fig. 27, 34)
8. Maxillary palp setation	0. Long & dense on segment 3 (Fig. 18-21) 1. Short & sparse on segment 3 (Fig. 22-25)
9. Apex, labial palp	0. Falcate (Fig. 18, 23, 44) 1. Symmetrical (Fig. 24, 46-47)
10. Paraglossa shape	0. Broad (Fig. 18-21) 1. Narrowly reduced (Fig. 22-25)
11. Bipectinate-hairlike setae, dorsal forefemora	0. Long & dense (Fig. 11-13, 26) 1. Shorter & sparse to absent (Fig. 14-17, 70, 72)
12. Simple-stout setae row, dorsal forefemora	0. Absent (Fig. 11-15) 1. Present (Fig. 16-17, 72)
13. Length, hairlike setae of foretibia anterior margin	0. Medium length (Fig. 26) -1. Short (Fig. 72) +1. Long (Fig. 30) +2. Very long (Fig. 71)
14. Arrangement, hairlike setae of anterior foretibia	0. Irregular (Fig. 70) 1. In 3 rows (Fig. 71)
15. Length, setules of setae of foretibia anterior margin	0. Short (Fig. 66, 69) 1. Long (Fig. 67-68)
16. Arrangement, setules of setae of anterior foretibia	0. All setules even in length (Fig. 67) 1. 1 long setule alternating with 3 short setules (Fig. 68)
17. Distribution, foretibia bipectinate-hairlike setae	0. On dorsal & anterior margin (Fig. 11-13) 1. On anterior margin (Fig. 14-17)
18. Foretibial apical spine	0. Absent (Fig. 30) 1. Present (Fig. 34)
19. Ventral apex, foretibia	0. Without tuft of bipectinate-hairlike setae (Fig. 71) 1. With tuft of bipectinate-hairlike setae (Fig. 73)

Table 1 continued

Character	Character State
20. Ratio, foretibia to forefemur length	0. > 1.2 (Fig. 11-13)
	1. 0.8-1.2 (Fig. 14-17)
21. Ratio, foretibia foretarsus length	0. > 2.2 (Fig. 11-13)
	1. 1.5-2.2 (Fig. 14-17)
22. Origin, gill 1	0. Posterolateral (Fig. 12, McCafferty 1975a)
	1. Anterolateral (Fig. 11-17)
23. Segmentation, gill 1	0. 1-segmented (Fig. 191 & 193, Edmunds et al. 1976)
	1. 2-segmented (Fig. 11-17)
24. Apical setation, gill 1	0. Without setae (Fig. 191 & 193 in Edmunds et al. 1976)
	1. With hairlike setae (Fig. 11-17)
25. Gill fibrillae	0. Multiple-rowed basally (Fig. 11-13)
	1. Single-rowed basally (Fig. 14-17)
26. Eye size, male adult (inter-eye distance/dorsal diameter)	0. Large (0.0-0.2) (Fig. 146)
	1. Medium sized (0.3-0.5) (Fig. 147)
	2. Small to very small (0.6-1.6) (Fig. 148-149)
	3. Tiny (1.7-3.0) (Fig. 150)
27. Markings between C & Sc, forewing	0. Absent (Fig. 94-96)
	1. Distinctive blotches present (Fig. 97-99)
28. Costal crossveins arrangement, forewing	0. Not concentrated near bulla (Fig. 82-83)
	1. Concentrated near bulla (Fig. 84-88)
29. Crossveins between Sc & R ₁ , forewing	0. < 38
	1. > 38
30. Angle between R ₁ & A ₁ , forewing	0. < 80° (Fig. 339-341 in Edmunds et al. 1976)
	1. > 80° (Fig. 82-99)
31. Basal connection of MP ₂ , forewing	0. Originating from MP ₁ & not closely connected to of CuA by crossveins at arch (Fig. 89-95)
	1. Originating from MP ₁ but closely connected to CuA by crossveins at arch (Fig. 84-88)
	2. Originating from CuA at usual point at arch (Fig. 82-83, 96-99)
32. Number of basal MP ₁ -MP ₂ crossveins, forewing	0. 0 (Fig. 89-93)
	1. 1-2 (Fig. 94-95)
33. Termination of A ₁ , forewing	0. Not forked (Fig. 339-341, Edmunds et al. 1976)
	1. Forked (Fig. 82-99)
34. Crossvein infuscation, forewing	0. Present in at least one sex (Fig. 89-90, 92-93)
	1. Absent in both sexes (Fig. 91, 95)
35. Pigmentation pattern, forewing	0. Without large areas of pigment (Fig. 83)
	1. With basal pigmentation & broad medial stain somewhat developed in both sexes (Fig. 87-88)
	2. Male as per apomorphy 1, female wing almost completely pigmented (Fig. 85-86)
36. Costal projection	0. Subbasal-obtuse (Fig. 339-341 in Edmunds et al. 1976)
	1. Basal-Acute (Fig. 100-103, 106-113, 115-117)

Table 1 continued

Character	Character State
37. Basal arch of R ₁ , hindwing	0. Slightly to moderately arched toward Sc (103-158o) (Fig. 100-114) 1. Strongly arched toward Sc (90-100°) (Fig. 115-117)
38. MP-cell, hindwing	0. Absent (Fig. 107-117) 1. Present (Fig. 100-106)
39. Subgenital plate	0. Concave (Fig. 124-133) 1. Convex (Fig. 118-123)
40. Penes	0. Fused for nearly entire length (Fig. 124-126) 1. Furcated for at least ca. 1/2 exposed length (Fig. 123, 130) 2. Furcated for entire exposed length (Fig. 118-119, 131)
41. Apex of penis	0. Falcate to pointed (Fig. 124-126, 128-131) -1. Notched (Fig. 120-123, 132-133) +1. Rounded (Fig. 118-119, 127)
42. Penis cross section	0. Not flattened dorsoventrally (Fig. 136-141) 1. Flattened dorsoventrally (Fig. 134-135)
43. Median terminal filament/ cerci ratio (male adult)	0. Developed (> 0.5) 1. Rudimentary (< 0.2)
44. Egg polar caps	0. Absent (Fig. 185, Koss & Edmunds 1974) 1. With 2 bipolar caps (Fig. 76-78)
45. Micropyle shape	0. Funnelform (Fig. 227-228, Koss & Edmunds 1974) 1. Tageniform (Fig. 80-81)

profoundly expressed by internal anatomical characters.

Edmunds (1962) depicted Potamanthidae and Euthyplociidae [=Polymitarciidae in part] as sister groups within the Ephemeroidea in his phylogram but presented no supporting data. Edmunds (1972, 1973), Landa (1973), and Landa & Soldán (1985) depicted Potamanthidae and Ephemeridae (sensu lato) as sister groups within the Ephemeroidea, but, as McCafferty (1991b) pointed out, this was evidently based on symplesiomorphy, particularly regarding internal anatomical characters. Koss (1973) and Koss & Edmunds (1974) presented a phylogram showing Potamanthidae to be a sister group to the Ephemerellidae/Tricorythidae lineage. Although such a conclusion might possibly be supported by the condition of gill 1, as discussed above, the preponderance of cladistic data and adherence to the principle of parsimony require that this situation be regarded as convergence. We do not know if the egg similarities between Potamanthidae and Ephemerellidae are fundamental, but further research into egg behavior, as was conducted for the Caenidae by Provonsha (1990), may shed light on this problem.

The entire phylogeny of Koss (1973) and Koss & Edmunds (1974) must be considered tenuous because it was based only on egg morphology, which is highly subject to parallelism, and it did not incorporate strict cladistic methodology. Besides the convergences between

TABLE 2. Matrix of character state distributions among species.

SPECIES	CHARACTER																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
coreanus	+1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
distafurcus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
distinctus	0	1	1	0	0	0	0	0	0	0	1	0	+1	0	1	0	1	0	0	1	1	1	1
formosus	-1	1	1	0	1	0	0	1	1	1	1	1	-1	0	0	0	1	0	1	1	1	1	1
huoshanensis	0	1	1	0	1	0	0	1	1	1	1	0	-1	0	0	0	1	0	0	1	1	1	1
idiocerus	-1	1	1	0	1	0	0	1	1	1	1	1	-1	0	0	1	0	1	1	1	1	1	1
kwangsiensis	-1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
longitibius	-1	1	1	0	1	0	0	1	1	1	1	1	-1	0	0	0	1	0	1	1	1	1	1
luteus	0	1	1	0	1	0	0	1	1	1	1	0	-1	0	0	0	1	0	0	1	1	1	1
macrophthalmus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
magnificus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
myops	0	1	1	0	0	0	0	0	0	0	1	0	+1	0	1	1	1	0	0	1	1	1	1
nanchangi	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
neglectus	-1	1	1	0	0	0	0	0	0	0	1	0	+1	1	1	1	1	1	0	1	1	1	1
obscurus	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
sabahensis	0	1	1	0	1	0	0	1	0	1	1	1	-1	0	0	0	1	0	1	1	1	1	1
sangangensis	-1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
speciosus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
subcostalis	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
verticis	0	1	1	0	0	0	1	0	0	0	1	0	+1	1	1	1	1	1	0	1	1	1	1
yooni	0	1	1	0	1	0	0	1	1	1	1	1	-1	0	0	0	1	0	1	1	1	1	1
youi	+1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
yunnanensis	-1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Ephemerellidae and Potamanthidae eggs, as discussed above, additional examples of similar convergences just within Polymitarciidae include two small polar caps in *Euthyplocia*, two type III polar caps in *Campylocia*, a single type II polar cap in *Ephoron*, and two type III polar caps in *Asthenopus* (Koss & Edmunds 1974). Also, according to those authors, the tageniform micropyle of Potamanthidae and Ephemerellidae is additionally found in *Pentagenia* (Ephemeridae) and *Povilla adusta* (Polymitarciidae).

McCafferty (1979) placed Potamanthidae as a sister group to a lineage that eventually split into the Ephemeridae-Palingeniidae [=Ephemeridae] lineage and the Euthyplociidae-Polymitarciidae [=Polymitarciidae] lineage. This was based on internal anatomical data given by Landa (1969); i.e., that these latter groups shared an additional ventral tracheal anastomosis in abdominal segment 2 (a highly probable apomorphy). Subsequent data from Landa & Soldán (1985), however, indicated that the apomorphy was not consistently found in those groups; and McCafferty (1991b) found forewing venational synapomorphies in Potamanthidae and Ephemeridae that did support their relationship as sister groups. These synapomorphies included an extreme basal arch of MP₂ and the absence of true cubital intercalary veins. McCafferty (1991b) also showed that the hypothetical common ancestor of Potamanthidae and Ephemeridae was derived in common with the extinct family Australphemeridae, recently discovered from the Lower Cretaceous of Brazil by McCafferty (1990).

The nearest outgroup for use in the cladistic analysis of lineages within the Potamanthidae

(Table 2: continued)

SPECIES	CHARACTER																					
	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
coreanus	1	0	0	0	1	0	1	1	0	1	0	1	1	0	1	1	1	-1	0	1	1	1
distafurcus	?	?	0	0	0	1	1	2	0	1	0	0	1	0	1	1	2	+1	1	1	1	1
distinctus	1	1	2	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1
formosus	1	1	3	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0	0	0	1	1
huoshanensis	1	1	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1
idiocerus	1	1	3	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0	0	1	0	1
kwangsiensis	?	?	3	1	0	0	1	2	0	1	0	0	1	1	0	0	2	0	0	0	1	1
longitibius	1	1	3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
luteus	1	1	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1
macrophthalmus	?	?	0	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0	0	0	1	1
magnificus	?	?	0	0	1	0	1	1	0	1	0	2	1	0	1	1	1	-1	0	1	1	1
myops	1	1	3	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	1
nanchangi	?	?	0	0	?	1	2	?	1	?	0	1	0	?	0	1	0	0	?	?	?	?
neglectus	1	1	3	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1
obscurus	1	0	0	0	1	0	1	1	0	1	0	2	1	0	1	1	1	-1	0	1	1	1
sabahensis	1	1	0	0	0	0	1	2	0	1	0	0	1	0	0	0	1	+1	0	1	1	1
sangangensis	?	?	3	1	0	0	1	2	0	1	0	0	1	1	0	0	1	-1	0	0	1	1
speciosus	1	0	0	0	0	1	1	2	0	1	0	0	1	0	1	1	2	+1	1	1	1	1
subcostalis	?	?	?	?	?	?	1	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?
verticis	1	1	2	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1
yooni	1	1	1	1	0	0	1	2	0	1	0	0	1	1	0	0	1	0	0	0	1	1
youi	1	0	0	0	1	0	1	1	0	1	0	1	1	0	1	1	1	-1	0	1	1	1
yunnanensis	?	?	3	1	0	0	1	2	0	1	0	0	1	1	0	0	2	-1	0	0	1	1

is therefore the Ephemeroidea. By employing the basic tenets of "levels of universality" and "outgroup rule" (Wiley 1975, 1981) along with McCafferty's (1991b) phylogeny, other usable outgroups in order of decreasing availability are Polymitarcyidae, Behningiidae (Behningioidea), Leptophlebiidae (Leptophlebioidea), infraorder Pannota, and Oniscigastridae (infraorder Vetulata).

INTRAFAMILIAL RELATIONSHIPS

Forty-five characters and their homologous plesiomorphic and apomorphic character states used in our cladistic analysis of Potamanthidae are itemized in abbreviated form and sequentially numbered in Table 1. Citations of morphological figures used herein or elsewhere augment the abbreviated descriptions of plesiomorphies and apomorphies and are not repeated in the discussion unless of special note. The plesiomorphic character states are listed as character state 0; a single apomorphic state for a character is listed as character state 1; when two or more character states for a character represent unrelated dipolar (independent) transitions, they are considered bidirectional and are listed as -1 and +1 to make this distinction; and when two or more apomorphies for a character represent a stepwise unidirectional transition they are listed as character states 1, 2, etc. With respect to transitional sequences of character states, the further character modifications, which we hypothesize to have occurred after the origin of the first descendants of each lineage, are treated as

phenoclines (Ross 1974) and thus incorporate concepts of levels of universality (Wiley 1975, 1981) and generality (Nelson 1978).

Table 2 is a data matrix indicating the distribution of the character states described in Table 1 among all species of Potamantidae that we recognize as valid. Species constituted our operational taxonomic units (OTU's). They are listed alphabetically only by their trivial names because no generic boundaries were assumed at the initiation of the cladistic analysis and no specific epithets were homonymic. Outgroup distribution may be taken to be 0 (the plesiomorphic state) for all characters unless there is some variability in the outgroup, in which case at least the plesiotypic lineages of the outgroup (e.g., within Ephemeridae) as well as other more remote outgroups are indicative of the plesiomorphic character state. Apomorphic character states are plotted with numbers as outlined for Table 1. A "?" appears in the matrix for characters of life stages that remain unknown for certain species (e.g., the larva is unknown for *R. magnificus* and the adult is unknown for *P. longitibius*) or for characters that could not be studied adequately because of the preserved state or availability of material at this time (e.g., *P. nanchangi* and *P. subcostalis* are known only from the written descriptions of adult specimens, all of which are now lost). A total of 36 characters were of use in intrafamilial comparisons.

The most parsimonious cladogram generated from our data matrix (Table 2) is presented in Fig. 6. Again, the OTU's are indicated only by trivial names; those with an asterisk are unknown as larvae, and a double asterisk indicates that the adult stage is unknown. Synapomorphies are listed to the right of the stem of the lineage to which they apply. The main numbers represent the characters (Tables 1 and 2), and subscript numbers appearing with these represent the apomorphic state (Tables 1 and 2) of the characters that are shared by all members of the lineage. This type of notation has been used, for example, by Alexander (1991). For any apomorphies that appear independently in different lineages included in Fig. 6, a dagger is placed next to them and indicates that they are probable convergences. If the convergence occurs in a terminal (species) lineage, it is not considered an autapomorphy. Characters involving autapomorphies, although autapomorphies are extensive in many individual species of Potamantidae (e.g., *R. obscurus*), are not included in Tables 1 and 2 and Fig. 6.

In order to incorporate as many species as possible into the cladogram, certain probable assumptions had to be made regarding the unknown stages of the few species that remain unknown in one stage. For example, of the nine synapomorphies discussed above that define the family, four of them involve larval characters. We assumed that the six species that remain unknown as larvae share these apomorphies because the adults of these species were typical potamantids, and there are no data to suggest otherwise. Parentheses surround the character apomorphies indicated in Fig. 6 in those instances where they cannot presently be confirmed as synapomorphies by all species in the lineage but can be assumed based on all species known from the pertinent life stages. New data from newly discovered material, especially metamorphic stages, can be used in the future to attempt to falsify our phylogenetic hypotheses.

Within the family, the probability of assumption varies somewhat depending on the species. Two species unknown as larvae and belonging to what we call the *Rhoenanthus* lineage could be cladistically placed in that lineage and analyzed within it entirely on the basis of adults. That was not possible for the other four species with unknown larvae that did not belong to the *Rhoenanthus* lineage (the opposite lineage is defined by larval synapomorphies). However, once an assumption was made based on phenetics as well as their lack of adult synapomorphies that would have placed them elsewhere, they could be variously analyzed. For example, *P. macrophthalmus* could be analyzed adequately on the basis of adults only,

but other species lacked sufficient data to completely analyze them. We are not confident that *P. nanchangi* or *P. subcostalis*, although obviously belonging to the relatively large *Potamanthus* lineage (see discussions below and Fig. 10), can be placed precisely within a lineage at this time. The general cladistic position could be deduced for the remainder, placing them in an apotypic lineage consisting of *P. formosus*, *P. idiocerus*, *P. kwangsiensis*, *P. sangangensis*, and *P. yunnanensis* (Fig. 6). However, the interrelationships of these species remain unresolved as a result of incomplete larval data (see further discussion, below).

We refer to the various lineages resulting from dichotomous branching, or cladogenesis, (Fig. 6, 10) by corresponding taxonomic group names when possible. For example, the lineages resulting from the first (earliest) bifurcation of our hypothesized potamanthid ancestor are referred to as the *Rhoenanthus* lineage and the *Anthopotamus-Potamanthus* lineage. Naming the lineages in this fashion keeps with our revised classificatory concepts used in the Taxonomy section and derived from the phylogeny (discussed below) and thus simplifies discussion.

As for almost all phylogenies generated by using numbers of OTU's and numbers of characters at least as great as ours, a percentage of character state distributions must be explained as convergences (discussed in detail below) after employing the principle of parsimony to choose the most probable cladogram. Once our most parsimonious cladogram was produced (Fig. 6), it indicated those characters in Potamanthidae that are subject to parallelism (e.g., those associated with certain penes structure and eye size reduction). Gosliner (1985) made a strong argument for excluding any characters highly subject to parallelism from cladistic analysis (and therefore de-emphasizing parsimony) because the nature of the universe is not always parsimonious. Parallelisms we discovered were minimal, but if overly common it would be counterproductive to rely on unqualified parsimony.

The *Rhoenanthus* and *Anthopotamus-Potamanthus* Dichotomy

Synapomorphies defining the *Rhoenanthus* lineage (Fig. 6) involve adult characters of fore- and hindwings, male genitalia and terminalia, and the larval tusks. At least half of the synapomorphies (4₁, 38₁, 39₁) are highly reliable in that they are not subject to convergence and their polarity is unquestioned. The penal lobe character (40) is perhaps the least reliable because the penal lobes have also become bifurcated in a number of the species of the *Anthopotamus-Potamanthus* lineage. In fact, various tendencies for the penes to become separated or fused occurs commonly in many Ephemeroptera families and therefore the character is difficult to use in cladistic analysis because the study of outgroup morphology is often inconclusive for establishing polarities. The development of the median terminal filament (character 43) in adult mayflies (i.e., two-tailed or three-tailed) is consistent in some families and in others is quite variable. The plesiomorphic condition in this regard is ultimately three-tailed, but ancestrally in some families it may be two-tailed, and reversals are common. In the *Rhoenanthus* lineage, the median terminal filament of male adults became rudimentary, if our hypothesis of polarity is correct. Convergence in this respect is not common within Potamanthidae, occurring only in one relatively specialized species in the *Anthopotamus-Potamanthus* lineage, *P. sabahensis*. The MP cell of the hindwing (apomorphy 38₁) is found in a very few species of Ephemeridae and Polymitarciidae, where it evidently independently evolved.

Character 31 requires some explanation because we maintain that it involves a phenocline in the *Rhoenanthus* lineage. McCafferty (1991b) indicated that the very strongly arched MP₂ of the forewings was a characteristic synapomorphy of the Potamanthidae-Ephemeridae lineage. Within this group this arch has become so strong sometimes that it has coalesced with

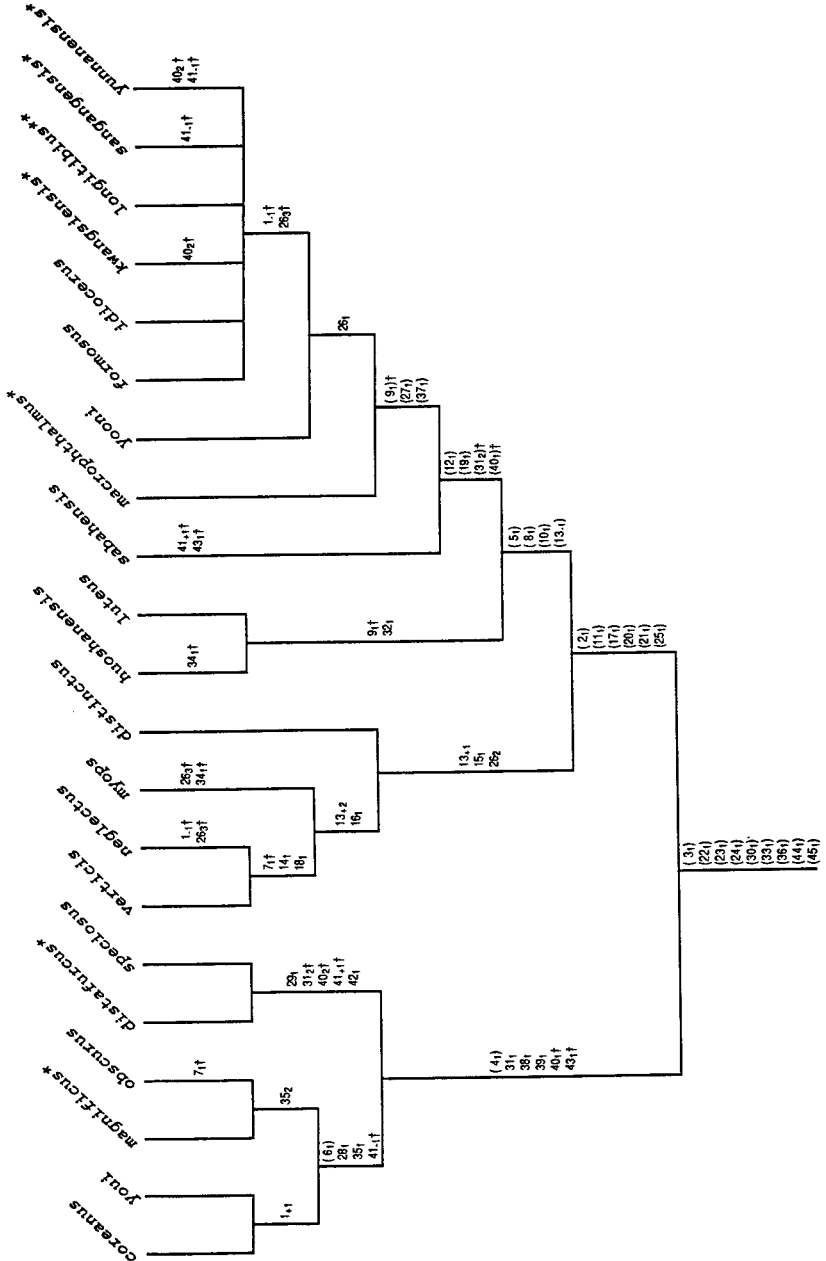


FIGURE 6. Potamantidae species cladogram (* = larva unknown; ** = adult unknown; (N) = N characteristic cannot presently be confirmed by all spp. of the lineage, but may be assumed based on all spp. known from the pertinent life stages; N_{+1} and N_{-1} = bidirectional apomorphies of character N; N_2 or N_3 = apomorphies in a phenoclinical progression for character N; $N\ddagger$ = N apomorphy possibly convergent in another lineage).

CuA and thus lost its original base. In Potamanthidae, we have designated this further modification as apomorphy 31₂. In the *Anthopotamus-Potamanthus* lineage, this apomorphy has evidently occurred independently and directly; however, in the *Rhoenanthus* lineage it may very likely have been attained in one sublineage via an intermediate character state (31₁). In this intermediate phenocline step, MP₂ arch became connected to CuA by minute crossveins, but it still maintained its base (compare, e.g., Fig. 89, 88, and 83 to visualize this hypothesized transition). Of note, the plesiomorphic state and the phenocline apomorphies also occur in the genus *Ephemer* in the family Ephemeridae.

As for the *Anthopotamus-Potamanthus* lineage, the six synapomorphies defining it (Fig. 6) involve a significant degree of larval evolution, none of which are convergent in the cladogram. Not only does this evidence offer compelling support for the major branches expressed by the cladogram, but it also tends to indicate the importance of the larval stage in deducing the relationships within the family (the larval stage of potamanthids has been virtually ignored in the taxonomy of the group prior to this study). Of particular note is the reduction of basal marginal fibrillae of gill 2-7 to a single row (synapomorphy 25₁). Of the Lanceolata with elongate fibrillate gills, the outgroups Behningiidae, Ephemeridae, and all Polymitarciidae with the exception of *Ephoron*, which is a relatively derived group (McCafferty 1991b), have two or more rows of fibrillae basally. Other synapomorphies (2₁, 11₁, 17₁) involve the reduction of certain setal fields in size, numbers, and complexity. The probable evolutionary significance of setal modification will be discussed below. Synapomorphies 20₁ and 21₁ involve the reduction in size of the foretibia relative to the tarsus and femur. The latter apomorphies were deduced by comparing character states in Potamanthidae with the more ancestral subfamilies of Polymitarciidae, in particular, because legs of other ephemeroids are structurally modified for digging.

The *Rhoenanthus* (*Rhoenanthus*) and *Rhoenanthus* (*Potamanthindus*) Dichotomy

All synapomorphies that define the *Rhoenanthus* (*Rhoenanthus*) lineage (Fig. 6) are referable to the adult stage (*R. distafurcus* remains unknown as larvae). Two of these evidently represent end points of phenoclines: MP₂ of the forewings has become directly attached to CuA and lost its base (apomorphy 31₂) and the penal lobes have become completely bifurcated beyond the subgenital plate (apomorphy 40₂). Both of these apomorphies occur as convergences within the *Anthopotamus-Potamanthus* lineage. Although the former is found extensively in the *Potamanthus* sublineage, the latter is convergent only in *P. kwangsiensis* and *P. yunnanensis*, which may or may not represent sister species. In addition, the rounded apices of the penes (synapomorphy 41₁), which partly define this lineage, are also found in *P. sabahensis* of the *Potamanthus* lineage; however, in addition to being an obvious convergence, it is quite possible that they are fundamentally different in the two groups because those of the *Rhoenanthus* (*Rhoenanthus*) lineage are broadly rounded (Fig. 118) and those of *P. sabahensis* are narrowly rounded (Fig. 127). Independent evolution is further inferred by the uniquely flattened nature of the penes of the former lineage (synapomorphy 42₁). Synapomorphy 29₁ is an expression of increased crossvenation. This does not occur in other Potamanthidae, but in Ephemeridae crossvenation has become well developed in the apotypic genus *Eatonigenia* (McCafferty 1973).

Of the species in the *Rhoenanthus* (*Rhoenanthus*) lineage, *R. distafurcus* possesses a noteworthy autapomorphy involving a doubly forked A₁ (Fig. 82). It is possible that the basal fork represents a fusion of the original A₂ with A₁. The fact that the base of A₂ is nearly connected to A₁ in other species of the *Rhoenanthus* lineage (e.g., Fig. 86), and in potamanthids in general, would seemingly support such a conclusion.

The *Rhoenanthus* (*Potamanthindus*) lineage is typified by striking modifications of the

forewings, particularly the development of patterning (synapomorphy 35₁) and crowding of crossveins near the bulla (synapomorphy 28₁). Extensive pigmentation of the forewings is not commonly found among Ephemeroptera, with some exceptions, such as among certain species of *Callibaetis* (Baetidae) and *Baetisca* (Baetiscidae). These latter taxa are only very distantly related to the Ephemeroidea. Crossveins near the bulla show some similar tendencies of modification in certain Heptageniidae, but again this group is only very distantly related. The other adult synapomorphy (41₁) involves notched apices of the penes. A notched condition evidently also arose in two specialized species of the *Potamanthus* lineage, *P. sangangensis* and *P. yunnanensis*; however, the notch is somewhat different in the two lineages (compare Fig. 120-123 with 132-133), further supporting the hypothesis of convergence regarding this character. The larval tusks also are much more curved (synapomorphy 6₁) in the *Rhoenanthus* (*Potamanthindus*) lineage than in any other potamanthids. We have made the assumption that this character state would apply to *R. magnificus* because its adults so typically fit this lineage.

Within the *Rhoenanthus* (*Potamanthindus*) lineage, two species pairs were indicated by the cladistic analysis (Fig. 6). Individuals of *R. coreanus* and *R. youi* are distinctly larger than any other potamanthids (synapomorphy 1₁). In *R. magnificus* and *R. obscurus*, the female adults have nearly completely pigmented forewings (synapomorphy 35₂), representing a further development of the wing pigmentation tendencies (apomorphy 35₁) first expressed early in the *Rhoenanthus* (*Potamanthindus*) lineage.

In terms of numbers of autapomorphies, *R. obscurus* is one of the most specialized species of Potamanthidae and certainly the most specialized in the *Rhoenanthus* lineage. Several autapomorphies occur in the larvae (Fig. 13, 19, 27), including enlarged simple-stout setae on the tusks, a laterally expanded hypopharynx, a truncated galealacinia, elongated bipectinate-hairlike setae on the galealacinia, and the profusion of bipectinate-hairlike setae over the entire terminal segment of the maxillary palp. In addition, *R. obscurus* larvae (Fig. 27) have a distinct and abrupt narrowing at the base of the otherwise gradually attenuated tusks (apomorphy 7₁). This also occurs in *A. verticis* of the *Anthopotamus*-*Potamanthus* lineage, but the tusks of the latter species, although fully developed, are not similarly shaped (Fig. 34). The hindwings of *R. obscurus* (Fig. 104) show a reduction of the well-developed point of the costal projection typical of Potamanthidae (synapomorphy 36₁), and R₁ has become conspicuously arched toward Sc. The former characteristic is also found in *P. sabahensis* and *P. nanchangi* of the *Potamanthus* lineage. A more developed variation of this latter characteristic (synapomorphy 37₁) defines the *Potamanthus* (*Potamanthodes*) lineage. We do not consider it a convergence in the strict sense because of the degree of difference involved.

The *Anthopotamus* and *Potamanthus* Dichotomy

The first (earliest) bifurcation of the *Anthopotamus*-*Potamanthus* lineage gave rise to the *Anthopotamus* lineage (defined by three synapomorphies) and the more diverse *Potamanthus* lineage (defined by four synapomorphies). In the *Anthopotamus* lineage, the bipectinate-hairlike setae along the anterior margin of the foretibia are very long and their setules are long and dense (synapomorphies 13₁ and 15₁). In addition, the eyes of the males in this lineage are relatively small (apomorphy 26₂). This tendency is also found in the *Potamanthus* (*Potamanthodes*) lineage (see below); there could be phenoclines involved when viewed as progressively decreasing size ranges (Table 1, Fig. 6, 146-150). Although polarity of eye size can be well documented, it is evidently subject to a degree of parallelism. Within the *Anthopotamus* lineage, *A. myops*, *A. verticis*, and *A. neglectus* share a immediate common ancestor, evidenced by further lengthening of hairlike setae along the anterior margin of the larval foretibiae (synapomorphy 13₂), a peculiar alternating arrangement of setules on those

foretibial setae (synapomorphy 16₁, Fig. 68), and a various weakening of crossvenation infuscation of the forewings. The interrelationships of these species are more difficult to deduce. Males of *A. myops* and *A. neglectus* have tiny compound eyes (apomorphy 26₃), falling into the smallest size range found in Potamanthidae. On the other hand, males of *A. myops* and *A. verticis* share the complete loss of crossvein infuscation in the forewings (apomorphy 34₁). The sister species relationship among the three species is ambivalent based on adults; and parallelism of both of these apomorphies can be found in certain species of *Potamanthodes*, weakening their credibility. Fortunately, the larvae do exhibit apomorphies (7₁, 14₁, 18₁) that strongly suggest a sister relationship. The tusks of *A. verticis* and *A. neglectus* both demonstrate an abrupt constriction at their base, and their foretibiae show special modifications in that the anterior setae are arranged in three distinct rows and an apical spine is developed. Moreover, *A. myops* shares no apparent larval apomorphies with one or the other of the latter species.

Synapomorphies (5₁, 8₁, 10₁, 13₁) defining the *Potamanthus* lineage are considered very strong evidence for the integrity of this grouping, with no instances of convergence elsewhere in the Potamanthidae. Some setation in both mouthparts and legs is reduced in the larvae (opposite of the tendency expressed in *Anthopotamus*), but the most conspicuous characteristic of the lineage is the reduction in size of the mandibular tusks so that only a short length of tusk is visible beyond the anterior margin of the head (Fig. 15-17). Among Ephemeroidea, distinct reduction in tusk size is found elsewhere only in the Ephemeridae and only in the few species of the genus *Afromera* and the apotypic subgenus *Aethephemera* of *Ephemer*a (McCafferty & Edmunds 1973, McCafferty & Gillies 1979).

The *Potamanthus* (*Potamanthus*) and *Potamanthus* (*Stygifloris*-*Potamanthodes*) Dichotomy

In this dichotomy (Fig 6), the *Potamanthus* (*Potamanthus*) lineage could be considered the most plesiotypic in that it demonstrates little change from the common ancestor. The apex of the labial palp is narrow and more-or-less symmetrically pointed (apomorphy 9₁), but this characteristic is subject to considerable convergence both outside and within the Potamanthidae (see the *Potamanthus* (*Potamanthodes*) lineage. The lineage does, however, have at least one unique synapomorphy (32₁) involving presence of one or two crossveins connecting the bases of MP₁ and MP₂ of the forewings. Within the *Potamanthus* (*Potamanthus*) lineage, the crossvein infuscation in the forewings is absent in both sexes of *P. huoshanensis*. This apparently represents a convergence with the similar condition of *A. myops* in the *Anthopotamus* lineage.

The *Potamanthus* (*Stygifloris*-*Potamanthodes*) lineage is defined by both larval (12₁ and 19₁) and adult synapomorphies (31₂ and 40₁). Apomorphy 31₂ involves the convergent loss of the arched base of CuA in the forewings as discussed above, under the *Rhoenanthus* and *Rhoenanthus* (*Potamanthindus*) lineages, and apomorphy 40₁ involves the furcation of the penial lobes, also discussed above. Thus, the most convincing evidence for the clade involves the appearance of a distinct row of simple-stout setae on the dorsum of the forefemora (synapomorphy 12₁) as well as a tuft of bipectinate-hairlike setae ventrally and subapically on the foretibiae (synapomorphy 19₁).

Based on available written descriptions of *P. nanchangi* (Hsu 1937-38b) and *P. subcostalis* (Navás 1931), both of these species are most likely members of the *Potamanthus* (*Stygifloris*-*Potamanthodes*) lineage. Unfortunately, they cannot be placed beyond this at this time because no material now exists for further study.

The *Potamanthus* (*Stygifloris*) and *Potamanthus* (*Potamanthodes*) Dichotomy

The single species *P. (Stygifloris) sabahensis* represents a phylogenetic lineage clearly

TABLE 3. Phylogenetic classificatory arrangement of Potamantidae species.

Genus *Rhoenanthus* EatonSubgenus *Rhoenanthus* Eaton*Rhoenanthus distafurcus* Bae & McCafferty*Rhoenanthus speciosus* EatonSubgenus *Potamanthindus* Lestage*Rhoenanthus magnificus* Ulmer*Rhoenanthus obscurus* Navás*Rhoenanthus coreanus* (Yoon & Bae)*Rhoenanthus youi* (Wu & You)Genus *Anthopotamus* McCafferty & Bae*Anthopotamus distinctus* (Traver)*Anthopotamus myops* (Walsh)*Anthopotamus verticis* (Say)*Anthopotamus neglectus* (Traver)Genus *Potamanthus* PictetSubgenus *Potamanthus* Pictet*Potamanthus huoshanensis* Wu*Potamanthus luteus* (Linnaeus)*Potamanthus, incertae sedis: Potamanthus nanchangi* (Hsu)*Potamanthus, incertae sedis: Potamanthus subcostalis* NavásSubgenus *Stygifloris* Bae, McCafferty & Edmunds*Potamanthus sabahensis* (Bae, McCafferty & Edmunds)Subgenus *Potamanthodes* Ulmer*Potamanthus macrophthalmus* You*Potamanthus yooni* Bae & McCafferty*Potamanthus formosus* Eaton, *sedis mutabilis**Potamanthus idiocerus* Bae & McCafferty, *sedis mutabilis**Potamanthus kwangsiensis* (Hsu), *sedis mutabilis**Potamanthus longitibius* Bae & McCafferty, *sedis mutabilis**Potamanthus sangangensis* (You), *sedis mutabilis**Potamanthus yunnanensis* (You, Wu, Gui & Hsu), *sedis mutabilis*

intermediate between the more ancestral *Potamanthus* (*Potamanthus*) lineage and the *Potamanthus* (*Potamanthodes*) lineage (Fig. 6). Although it does not possess any autapomorphies, its sister lineage *Potamanthus* (*Potamanthodes*), containing a number of species, is clearly set off by three synapomorphies (9₁, 27₁, 37₁). Irregular markings in the costal interspace of the forewings (27₁) and the very strongly arched R₁ of the hindwings (37₁) are not subject to convergence, with the possible exception of the somewhat less arched R₁ of the highly specialized *R. obscurus*, as discussed above, under the *Rhoenanthus* (*Potamanthindus*) lineage.

The only species with large-eyed males in the *Potamanthus* (*Potamanthodes*) lineage is *P. macrophthalmus*. Others have males with medium-sized eyes (synapomorphy 26₁), and all but *P. yooni* have males with tiny eyes (synapomorphy 26₃). This character, its character states, and convergence were discussed above, under the *Anthopotamus* and *Potamanthus* dichotomy.

The six remaining species apparently share a more recent common ancestor, all having a distinctly small body size (synapomorphy 9₁) and the tiny male eyes mentioned previously.

The adult stage of *P. longitibius* is unknown, however, adult male eye size can easily be extrapolated from the mature male larvae in Potamanthidae. Larval characters could not be reliably used to deduce interrelationships within this sublineage because three of the six species are unknown as larvae. Left with adult characters only, the distribution of character states is inconclusive; i.e., although various pairs of the species share adult apomorphies, we could not find three or more of the species sharing any one adult apomorphy (e.g., see distributions of apomorphies 40₂ and 41₁, Fig. 6).

PHYLOGENETIC CLASSIFICATION

The linear phylogenetic classification of the species of Potamanthidae is presented in Table 3. We have incorporated a sequencing convention (Nelson 1972, 1974) to recognize three genera as well as three subgenera within the genus *Potamanthus*. We have also used conventions of Wiley (1979, 1981) for applying the designations of "*incertae sedis*" ("of uncertain taxonomic position") and "*incertae mutabilis*" ("of interchangeable taxonomic sequence"). Thus, *P. nanchangi* and *P. subcostalis* are designated *incertae sedis* and listed at the first place where their relationships are understood; and *P. formosus*, *P. idiocerus*, *P. kwangsiensis*, *P. longitibius*, *P. sangangensis*, and *P. yunnanensis* are listed to reflect their phylogenetic position as a group, but are each designated as *sedis mutabilis* to indicate that their phylogenetic relationships with each other remain unknown.

By recognizing only three genera we have been conservative in our classification and at the same time primarily emphasized the major branches in the phylogeny of the Potamanthidae and the importance of the larval stage in delineating these branches. It is significant that all species of Potamanthidae can be determined to genus even though their full characterization may remain unknown. This would not have been possible if additional genera were alternatively recognized (see, e.g., our treatment of *P. nanchangi* and *P. subcostalis*). Our conservative classification is further supported by the major biogeographic and evolutionary patterns in Potamanthidae, discussed below.

The use of subgenera has been variously employed in the taxonomy of the mayflies, but appears appropriate here for two reasons. First, major sublineages within *Rhoenanthus* and *Potamanthus* can be expressed, and second, some of the historical genus-group names can be retained, albeit at a more subordinate rank (see generic and subgeneric synonymies in the Taxonomy section, above). Incidentally, all subgenera can be satisfactorily keyed in both the larval and adult stages. This is not always the case, even at the generic level in some Ephemeroptera taxa, e.g., some Ephemerellidae and some Baetidae.

When phylogenetic relationships have been hypothesized by cladistic techniques, resulting classifications should be phylogenetic (e.g., Cracraft 1974a, Farris 1979, 1980, McCafferty 1991b). Previous schemes, that included our *Anthopotamus* and *Potamanthus* (*Potamanthus*) in the same genus and at the same time recognized *Potamanthodes* as a separate genus, would, however, not only certainly be paraphyletic and ill-advised in light of the phylogenetic relationships, but also would not be defensible in terms of overall differentiation in light of the increased descriptive data we have amassed.

HISTORICAL BIOGEOGRAPHY

We agree with Edmunds (1972, 1981, 1982) that mayflies are classic candidates for studying historical biogeography because of their short and fragile alate stages and apparent conservative vagility. To perform such analyses effectively, however, both detailed distributional data and comprehensively researched phylogenetic data must be available on the

taxa to be studied because only these data allow biogeographic history to be inferred with the least amount of assumption and speculation. Myers & Giller (1988) argued that current biogeographic hypotheses are based on too incomplete distributional data, and that it is the further documentation of distribution patterns that will determine the future advancement in analytical biogeography. At the same time, Brundin (1988) concluded that, on the basis of the present status of historical biogeography, what is needed most for improving our ability to investigate the subject is cladistic based phylogenetic data on a far larger scale than has generally been available. These two data sets are critical whether vicariance (e.g., Croizat et al. 1974) or dispersal (e.g., Ross 1974) are viewed as the primary mechanisms for explaining observed patterns, although the analogy between vicariant events and allopatric speciation, or cladogenesis, would appear to emphasize the former (Nelson 1981, Nelson & Platnick 1981). Our extensive distributional and phylogenetic data have thus allowed us to develop certain hypotheses regarding the historical biogeography of the Potamantidae, which we present below.

DISTRIBUTION PATTERNS

As a group, the Potamantidae has a typical Laurasian distributional pattern (Fig. 1), involving the Palearctic (throughout, including northern Africa), Nearctic (only eastern), and Oriental Regions. Within the Orient, Potamantidae occurs in Southeast Asia up to Wallace's Line, but no species are known from the Philippines. In addition, two species occur in India, which is generally considered to have originated in Gondwana, but has been adjacent to the Laurasian land mass since the Tertiary. Although there have been reports of Potamantidae from Ceylon, Hubbard (1983) showed these reports to be erroneous since they were actually based on ephemerids.

Species ranges (Fig. 2-5) are based primarily on materials examined for this study; however, additional distributional data from the literature were incorporated when deemed valid. Ranges are well known for North America and western Eurasia, but should still be considered somewhat preliminary for the eastern Palearctic and the Orient because extensive field work has yet to be carried out in much of these areas. No species are Holarctic, but *P. luteus*, the most widespread species, occurs across Eurasia.

Genera (Fig. 1) and subgenera of Potamantidae demonstrate relatively consistent and well-demarcated distribution patterns. *Rhoenanthus* occurs in both the eastern Palearctic and Oriental Regions, however, the subgenus *Potamanthindus* is restricted to temperate East Asia and Indochina, and the subgenus *Rhoenanthus* is limited to tropical Oriental areas, where it is relatively widespread. *Anthopotamus* is restricted to the humid, eastern area of North America, where all four species occur in both the Northeast and Southeast (excluding Florida) Subregions of McCafferty & Waltz (1990). *Potamanthus* occurs throughout Eurasia, with the subgenus *Potamanthus* distributed in the temperate Palearctic and northern Africa, the subgenus *Stygifloris* confirmed only from north Borneo, and the subgenus *Potamanthodes* widely distributed in the eastern Palearctic and the Orient, excluding the Sunda Islands. The species *P. subcostalis*, which may belong to either *Stygifloris* or *Potamanthodes*, is known from northern India.

AREA AFFINITIES

An area cladogram is given in Fig. 7 and was derived directly from our species distributional data (Fig. 2-5) and cladogram of the Potamantidae (Fig. 6), both of which have been presented previously. Distributional areas in area cladograms are noted by abbrevia-

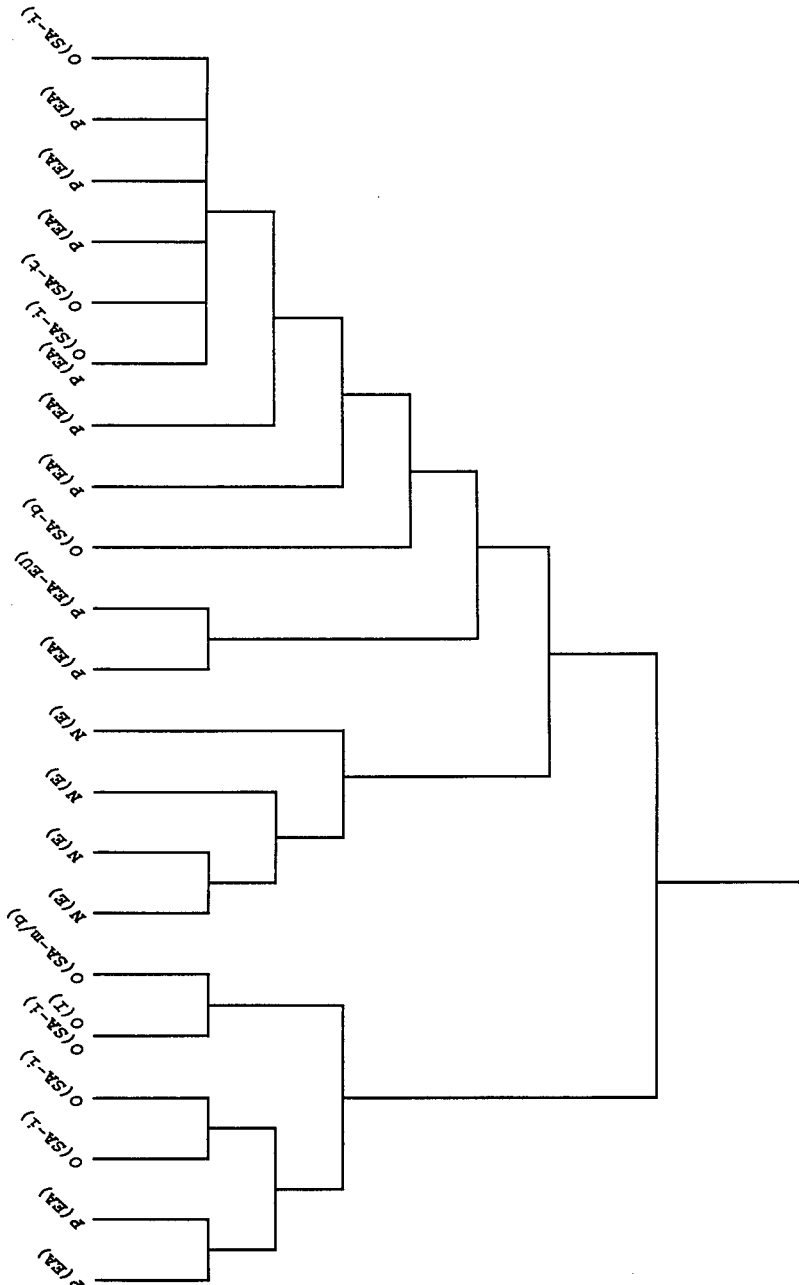


FIGURE 7. Area cladogram of Potamanthidae [P(EA) = Palearctic East Asia, P(EU) = Europe, O(SA) = Southeast Asia, N(E) = Eastern North America, b = Borneo, i = Indochina, m = Malay Archipelago, t = Taiwan].

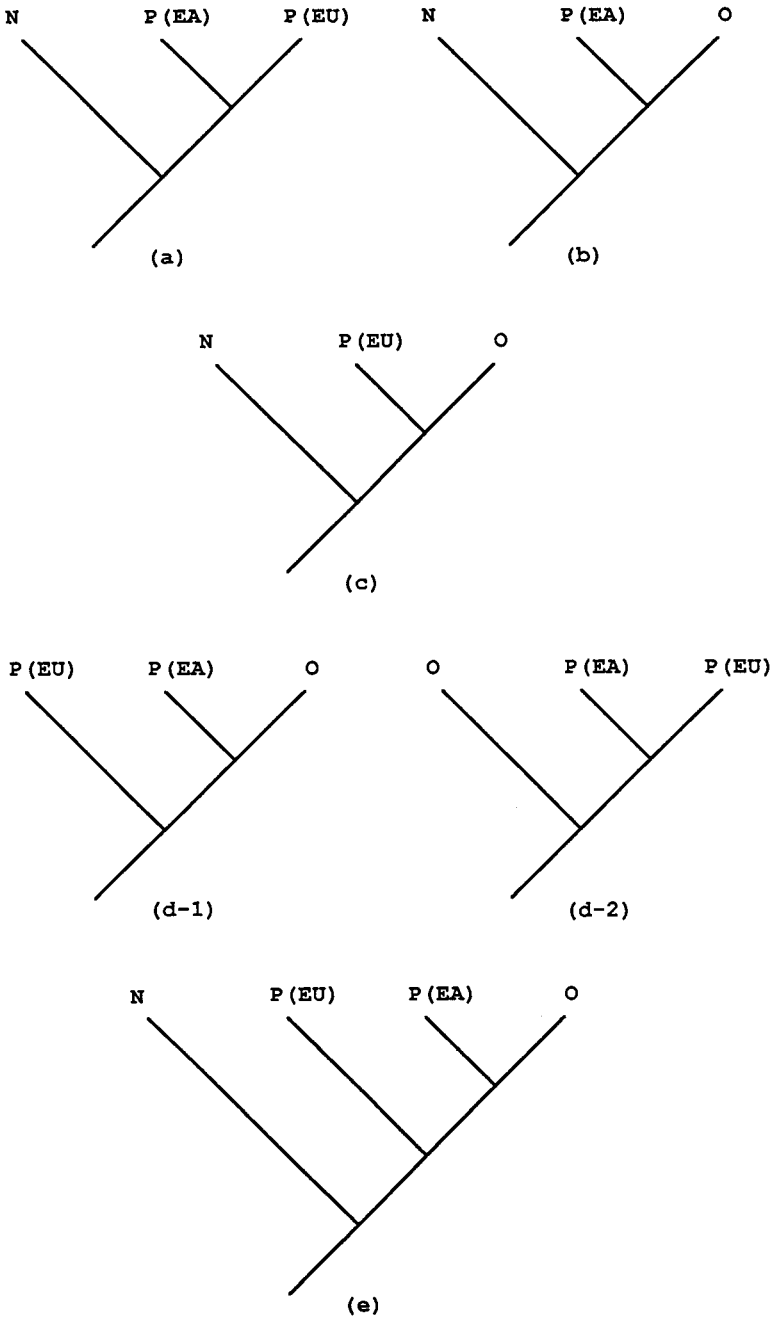


FIGURE 8. Reduced area cladograms of Potamantidae representing three- or four-area relationships among five major geographic subregions: see text for discussion [N = Eastern Nearctic, O = Southeast Asia, P(EA) = Palearctic East Asia, P(EU) = Europe].

tions for the biogeographical regions as follows: P = Palearctic, N = Nearctic, and O = Oriental.

When appropriate, the major biogeographic regions are further subdivided into subregions and provinces as suggested by Nelson & Platnick (1981). Thus, the Palearctic Region contains three subregions: East Asia, Central Asia, and Europe, delineated respectively by the Mongolian-Siberian Highlands and the Ural Mountains. East Asia is cited as (EA), Europe is cited as (EU), and a distribution that includes all three Palearctic subregions it is cited as (EA-EU); there are no exclusively Central Asia distributions among the Potamanthidae. Northern Africa is generally not considered part of the Afrotropical Region; we therefore consider northern African distributions (Morocco, Algeria) of the otherwise European *P. luteus luteus* as being in the Palearctic Europe Subregion.

We demarcate the Oriental Region from the Palearctic as being south of the Himalayan Mountains and the Hongshui River in China, where atmospheric winter temperatures remain above 10°C and precipitation is over 1,000 mm from May to October. We subdivide the Oriental Region into two subregions: Southeast Asia (SA) and India (I). Southeast Asia contains four provinces parenthetically abbreviated as follows: Indochina (SA-i), the Malay Archipelago, including the Malay Peninsula, Sumatra, and Java, (SA-m), Taiwan (SA-t), and Borneo (SA-b).

For analyzing area affinities, we employed Rosen's (1975) method of constructing reduced area cladograms based on our species and area cladograms. Congruence was then used to infer area affinities from the reduced area cladograms. Four major potamanthid geographic areas [Nearctic, Palearctic (Europe), Palearctic (East Asia), and Oriental] were compared. All four possible three-way comparisons involving these areas were derived from Fig. 7 and are presented in Fig. 8a-d. The four-area cladogram resulting from such an analysis is given in Fig. 8e.

In comparing the three Holarctic areas, it can be seen from Fig. 8a that, according to relationships among Potamanthidae, the two Palearctic areas are closer related to each other than either is to eastern North America. Our data therefore do not appear to lend support to the Asiamerica-Euramerica hypothesis of Cox (1974). That hypothesis suggests that East Asia and Europe are closer related to eastern North America than they are to each other, having historically (until the Oligocene) been separated by the Turgai Strait east of the Ural Mountains. Studies of various other organisms (e.g., Cracraft 1974b, Platnick 1976, Allen 1983, McKenna 1983) support the Asiamerica-Euramerica hypothesis. Our data appear contradictory because the Palearctic (Europe) area is occupied by one widespread species, *P. luteus*. Otherwise, the cladogram (Fig. 6) shows quite clearly that eastern Asia and eastern North America are very closely related, vis-à-vis the common ancestry of *Anthopotamus* and *Potamanthus*.

As seen in Fig. 8b and 8c, the Oriental Region and the Palearctic Region are more closely related to each other than either is to the Nearctic. These relationships would perhaps be expected; however, no prediction about the area cladogram is obvious when making the three-way comparison between the Palearctic (Europe), Palearctic (East Asia), and Oriental. In fact, from the data in Fig. 7, two alternative arrangements can be derived (Fig. 8d-1 and 8d-2). When parsimony is used to choose the most likely alternative, the first alternative (Fig. 8d-1), which shows East Asia and the Orient to have closer affinity than either does with the Europe Subregion, is favored. Evidence for this is found in the genus *Rhoenanthus*, and the subgenera *Stygifloris* and *Potamanthodes* of the genus *Potamanthus*, whereas only the subgenus *Potamanthus* provides support for a stronger relationship between Europe and East Asia.

BIOGEOGRAPHIC HYPOTHESES

Of the families of Ephemeroidea, Potamanthidae is the only one that can be considered to have a strictly Laurasian distribution. The other extant families, Ephemeridae and Polymitarciidae, are more cosmopolitan, and the extinct family Australiphemeridae is known only from Brazil (West Gondwana of the Lower Cretaceous). When the phylogenetic relationships of these four families are considered in light of their primary geographic affinities, some idea of the biogeographic origin of the Potamanthidae may be visualized. McCafferty (1991b) showed the first major branching of the Ephemeroidea to result in the Polymitarciidae lineage and a lineage leading to the other three families (the A-E branch). The Polymitarciidae is primarily a Gondwanian group with numerous Pantropical lineages. Of the A-E branch, the Australiphemeridae (at least Gondwanian but possibly more widespread) was derived earliest, leaving the Ephemeridae and Potamanthidae as sister lineages.

We consider Ephemeridae to be primarily a Laurasian group. Even though Ephemeridae are found in the Neotropics and Afrotropics, these areas involve only relatively few apotypic species, with those of the Neotropics evidently having Nearctic ancestry (McCafferty 1987) and those of the Afrotropics evidently having Oriental ancestry (Edmunds 1979, McCafferty & Gillies 1979) and possibly European ancestry (McCafferty unpublished). Therefore, if the common ancestor of the A-E branch was widespread-Pangaeian, the evolution of the Ephemeridae-Potamanthidae lineage could have corresponded to a Gondwana-Laurasia vicariance via the breakup of Pangaea in the Upper Triassic. The presence of the genus *Ichthybotus* (presently classified as an early derived subfamily Ichthybotinae of the Ephemeridae) in New Zealand is an anomaly because it is the only ephemerid known from any Amphinotic area. Also, New Zealand is a Gondwanian element that has been historically distant from Laurasia, and even recently would have been difficult to reach via overseas dispersal from Asia. However, *Ichthybotus* may be truly Gondwanian if it was derived prior to the origins of Ephemeridae and Potamanthidae. If this is so, it would require separate familial status for *Ichthybotus*, and such a possibility is being researched by the second author.

The scarce paleobiogeographic data available for the Ephemeroidea (see McCafferty 1990), while not conflicting with a hypothesis that the Ephemeridae-Potamanthidae lineage arose in the mid-Mesozoic, can confirm only that Polymitarciidae and Australiphemeridae occurred in West Gondwana as early as Lower Cretaceous and that recent genera of Ephemeridae occurred in both eastern and western areas of Laurasia during the Tertiary [a report of an ephemerid (Palingeniinae) from the Jurassic in Siberia (Tshernova 1977) cannot be confirmed]. Potamanthidae are not known from the fossil record.

Thus, little can be deduced regarding a precise place and time of origin of the Potamanthidae. Nonetheless, from the above, it appears that the Potamanthidae-Ephemeridae bifurcation most likely occurred within Laurasia sometime between the end of the Triassic and the beginning of the Cenozoic. There is no evidence of any large-scale vicariant event corresponding with that bifurcation. Both families are currently best represented in East Asia and the Orient. The origin of the families could have been in this general vicinity, or conversely, the common ancestor of the two lineages could have been widespread in Laurasia, although this appears less likely.

Either a vicariant model (e.g., Croizat et al. 1974) or a dispersal model (e.g., Ross 1974) may be used as a basis for explaining historical biogeography within the Potamanthidae. Actually, both of these models incorporate aspects of dispersal and vicariance to various degrees (e.g., species range expansions via dispersal alternate with range splitting and

allopatric speciation via vicariance). Both models require different assumptions that are arguably valid, depending on the organisms, geography, and time scale involved (see e.g. Pielou 1979). The vicariant model appears to be an incontrovertible explanatory tool when dealing with clearly fractionated and isolated geographic distributions such as among continental land masses in the Southern Hemisphere or island archipelagos. Thus, Edmunds (1981) was able to use a strict vicariant model in explaining the historical biogeography of Southern Hemisphere (in particular Amphitotic) mayflies by directly correlating phylogenetic branching with Transantarctic continental drift patterns.

Below, we present an analysis of the historical biogeography of Potamanthidae based on a vicariant model. However, where obvious, (i.e., when a distributional pattern demonstrated by an area cladogram is not congruent with a well-known past geological event), dispersal is accepted as a rational alternative explanation, as suggested by Rosen (1978). In particular, distributions in India and northern Africa may best be explained as resulting from dispersal because vicariance with respect to the area cladogram does not properly explain the Gondwanian origins of these areas. Unfortunately, the lack of fossil data precludes dating many of the biogeographic events very precisely by limiting hypothetico-deduction in this respect. Our main hypotheses concerning the historical biogeography of the Potamanthidae are summarized graphically in Fig. 9.

Based on our interpretations thus far, the common ancestor of the Potamanthidae was possibly widespread in Laurasia. Our analysis of the Holarctic area affinities (Fig. 7, 8a-c) suggests that this Holarctic biota was subjected to a major vicariant event involving the isolation of the Eastern and Western Hemispheres and oceanic disjunction. From Fig. 6 and 7, that would obviously have involved the bifurcation and geographic isolation of the Western Hemisphere *Anthopotamus* lineage and the Eastern Hemisphere *Potamanthus* lineage. The distributions of *Rhoenanthus* spp. were not applicable to the analysis of North American affinities (Fig. 8a-c) and the *Rhoenanthus* lineage (Fig. 6 and 7) was evidently restricted to Asia at the time of the *Anthopotamus-Potamanthus* bifurcation, as it is today.

Within the *Rhoenanthus* lineage, species are found in temperate East Asia and in the tropical Orient, including both Southeast Asia and India. It is quite possible that the common ancestor of *Rhoenanthus* was widespread in eastern Asia (East Asia and Southeast Asia), however, it is quite improbable that this ancestral range included India. India is generally regarded to have a Gondwanian origin and to have not become connected with Laurasia until the Eocene. Therefore, the area cladogram (Fig. 7) does not properly explain the history of the Indian subcontinent, and the presence of *R. distafurcus* in India is explicable only in terms of dispersal (range expansion from Indochina since the Eocene). In Ephemeridae, there is apparently a strong affinity between Thailand and India expressed by the distribution of a number of species (McCafferty unpublished).

No direct evidence of a major vicariant event associated with the bifurcation of the *Potamanthindus* and *Rhoenanthus* s.s. lineages exists. However, within *Potamanthindus*, the bifurcation leading to the *coreanus-youi* and *magnificus-obscurus* species pairs apparently corresponded with a vicariant event involving isolation of the common ancestor of the former species pair in temperate East Asia and that of the latter pair in tropical Indochina. Such a vicariance was most likely mitigated by adaptations to factors related to the differences in climate in the two areas, perhaps at a time when the climate was becoming less uniform in eastern Asia, such as one of the three late Eocene cooling pulses. Within *Rhoenanthus* s.s., speciation of *R. distafurcus* and *R. speciosus* evidently involved isolating the former in Indochina (later expanding into India, see above) and the latter in the Sunda Islands. These areas are separated by the South China Sea, and vicariance probably occurred at a time when the sea level in the Gulf of Thailand rose to a relatively high level, perhaps corresponding to

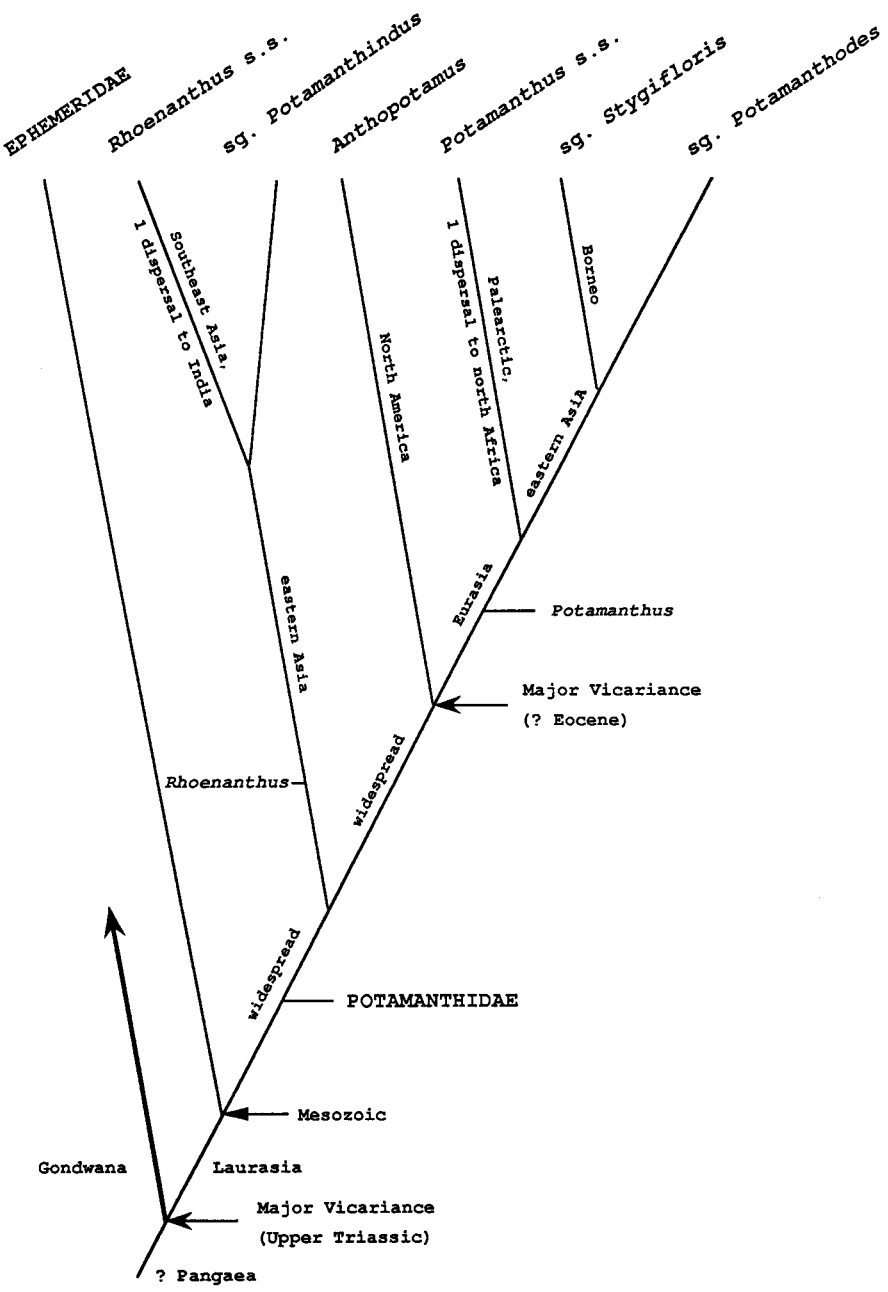


FIGURE 9. Phylogram summarizing biogeographic hypotheses.

one of the many warm pulses during the Cenozoic.

As suggested above, in the *Anthopotamus-Potamanthus* lineage, bifurcation into the *Anthopotamus* lineage and the *Potamanthus* lineage most likely was the result of vicariance of a widespread Laurasian biota into a Western Hemisphere and Eastern Hemisphere lineage, respectively. The Eocene, at a time about 49 million years before present, is often suggested as the time when such a vicariance took place because it is when the North Atlantic became considerably wider. An actual physiographic split and oceanic barrier however, need not have been necessary to have caused vicariance in this respect. Historical connections between the North America and Eurasia are far northern, and therefore, any severe cooling pulse such as would be associated with an ice age would provide an extensive isolating effect in both the Beringia area and the Greenland area (the *Potamanthidae* are not known to be northern boreal but primarily mid-boreal to tropical).

Within *Anthopotamus*, the relatively broad species ranges of each of the extant species may suggest that the associated speciation events were correlated with well-documented Northern Hemisphere glaciation pulses in the last 10 million years. The cycle of vicariance, range reduction, and range extension could lead to the basically sympatric species ranges now evident (Fig. 3), much as is apparently exemplified by many of the species of the eastern North American heptageniid genus *Stenonema* (see Bednarik & McCafferty 1979). The subspecies of *A. neglectus* (Fig. 3) are presently clearly disjunct, and if given sufficient time, could potentially result in speciation. We cannot postulate the basis of this particular disjunction.

Within the *Potamanthus* lineage, the initial bifurcation into a *Potamanthus* s.s. lineage and a *Stygifloris-Potamanthodes* lineage does not appear to have involved a major vicariant event. Although *Potamanthus* s.s. is exclusively a Palearctic group, species of the opposite lineage are about equally divided between tropical Southeast Asia and temperate East Asia. In *Potamanthus*, *P. huoshanensis* is exclusively found in East Asia, and *P. luteus* occurs across Eurasia (Fig. 4), with *P. luteus luteus* found mainly in the Europe Subregion and *P. luteus oriens* found in East Asia. The degree of disjunction between these two subspecies is not clear at this time. Tshernova (1958) reported *P. luteus* from Central Asia, but gave no details and we have not been able to confirm these records or determine which subspecies might be involved, although we suspect that *P. luteus luteus* will extend into Central Asia (Fig. 4) because we have seen that subspecies from Syria as well as the Republic of Georgia. The presence of *P. luteus luteus* in northern Africa is explicable as dispersal because the geological history of the African continent is not congruent with our cladogram; that is, Africa is Gondwanian and *Potamanthidae* is Laurasian. This dispersal may have coincided with the rejoining of Africa and Europe some 17 million years ago.

The bifurcation into the *Stygifloris* lineage and the *Potamanthodes* lineage apparently involved a vicariant event in which *Stygifloris* became isolated in north Borneo and *Potamanthodes* was isolated in East Asia and Southeast Asia. As for one of the vicariant events deduced for within *Rhoenanthus*, this most likely corresponded with a rise in water level in the South China Sea. Because of the *incertae mutabilis* status of most of the species of *Potamanthodes* due to the lack of known larval stages that prevent complete cladistic analysis, little can be said about their biogeography. The completed phylogeny will undoubtedly indicate that at least one, but perhaps more, vicariant events were associated with climatological differences between the two areas represented. This is so because, of the eight species involved, five are known exclusively from East Asia and two are known exclusively from Southeast Asia. One species, *P. idiocerus*, is known from Taiwan and may very well be the sister species of the Asian mainland species *P. formosus*, suggesting another vicariant event isolating an island population.

Potamanthus subcostalis cannot definitively be placed to either *Stygifloris* or *Potamanthodes* at this time. Nevertheless, the distribution of this exclusively Indian species is most likely a result of a dispersal to India since the Eocene, for the reasons explained above in the discussion of *R. distafurcus*. It is, of course, unclear as to whether speciation took place in Southeast Asia prior to dispersal or took place as a result of a subsequent isolation following dispersal.

EVOLUTION

A Wagner groundplan-divergence phylogram (Wagner 1961, 1980) of the genera and subgenera of Potamanthidae was generated from our cladistic data (i.e., relative numbers of apomorphies) and is presented in Fig. 10. It provides a visualization of the relative degree of overall evolutionary change in each of the major lineages. It shows, for example, that as a group Potamanthidae is evolutionarily distinct, *Anthopotamus* is least changed overall from the hypothetical ancestor, and the greatest degree of divergence is found within *Potamanthus*.

In addition to simply showing relative specialization, a limited amount of data regarding behavior and ecology associated with the habitat and feeding of larvae allows some descriptive assessment of evolutionary specialization. Our technique has been to examine such data with respect to the phylogeny of the Ephemeroidea (McCafferty 1991b) and the species cladogram (Fig. 6), and then present a hypothetical narrative based on the apparent patterns expressed, e.g., as per Ross (1974). Most nonstructural data regarding potamanthid larvae are based on a few species from the USA, Europe, and Japan. However, in certain instances we have taken the liberty of extrapolating function for all species based on similarities and differences in morphology with those species for which function is known (e.g., with regard to feeding and mouthpart ultrastructure).

SUBSTRATE RELATIONS

The known habitats of potamanthid larvae (*R. speciosus*, *R. obscurus*, *R. coreanus*, *A. distinctus*, *A. myops*, *A. verticis*, *P. sabahensis*, *P. luteus*, *P. yooni*, *P. formosus*) are erosional areas where substrate consists of various mixtures of sand, gravel, and rocks (Argo 1927, McCafferty 1975, Bartholomae & Meier 1977, Munn & King 1987b, Watanabe 1988, Bae & McCafferty unpublished, Bae unpublished, G. F. Edmunds personal communication, A. G. B. Thomas personal communication). We have recently found in both field and laboratory settings that *A. verticis*, and presumably other potamanthids, are crude burrowers that live in crevices in such habitats (Bae & McCafferty unpublished). Larvae of *R. coreanus* and *P. formosus* (Bae unpublished) and *P. idiocerus* (G. F. Edmunds personal communication) have also been observed to live interstitially, and thus representatives of all three genera have been confirmed to burrow.

We conclude from this that the ancestor of Potamanthidae was such a burrower and crevice dweller. We also hypothesize that the common ancestor of the Ephemeridae and Potamanthidae and earlier ephemeroid ancestors were also similar burrowers (see McCafferty 1991b). Cylindrical bodies and burrow-tube formation evolved in the Ephemeridae, but the more ancestral dorsoventrally flattened body and crevice dwelling habit was retained in Potamanthidae. A somewhat parallel evolution occurred in the Polymitarcyidae, where cylindrical bodies and tube dwelling is present in the apotypic subfamilies (McCafferty 1979, 1991b).

The prolongation of mandibles into tusks in Ephemeroptera is apparently related at least in part to the larva's ability to excavate or burrow, whether a crevice dweller or tube dweller. All Ephemeroidea (*sensu novum*) are tusked, and leptophlebiids that burrow and are crevice

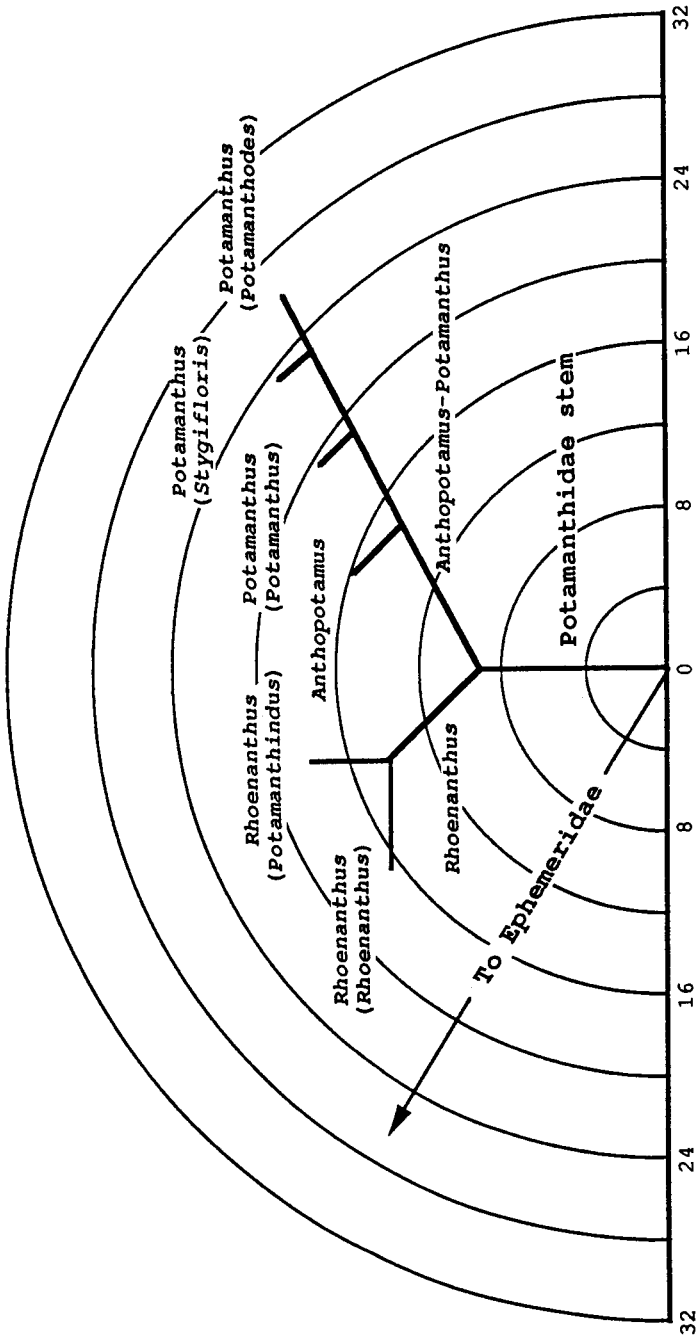


FIGURE 10. Wagner groundplan-divergence phylogram for genera and subgenera.

dwellers (e.g., some *Paraleptophlebia* in North America and *Jappa* in Australia) are also tusked, although the tusks in the two groups are not homologous. Keltner & McCafferty (1986) showed the functional relationships of tusks to excavating fine and compacted substrates in tube-dwelling Ephemeridae. We observed that *A. verticis* used tusks to help remove sand and gravel from in front of the head while burrowing and maintaining themselves interstitially (Bae & McCafferty unpublished). We infer from this that the original ephemeroid was a flattened and fully tusked burrowing crevice dweller such as *Rhoenanthus* or *Anthopotamus* in Potamanthidae or genera of the plesiotypic subfamily Euthyplociinae in Polymitarcyidae. Although the Euthyplociinae larvae have not been observed to live interstitially, their general facies are very similar to plesiotypic potamanthid larvae, and we predict similar substrate relations.

Watanabe (personal communication) and Bae (unpublished) have found fully mature larvae of *P. formosus* and *P. yooni* to sprawl on the substrate surface. This could be explained as pre-emergence behavior of otherwise primarily interstitial larvae. On the other hand, it could indicate that species of the apotypic genus *Potamanthus* are less prone to burrow or only facultative burrowers. If the latter is the case, the greatly reduced tusks in this particular genus could be related to disuse in burrowing. This is highly speculative at this time, and additional observations on substrate relations in *Potamanthus* are critically needed. An alternative or additional explanation is associated with feeding and is discussed below.

FEEDING

Casual observations of the gut contents of preserved larvae of *R. speciosus*, *R. obscurus*, *A. distinctus*, *A. myops*, *A. verticis*, *P. sabahensis*, *P. luteus*, *P. yooni*, and *P. formosus* suggest that they are all detritivores since approximately 95% of the contents involved fine detritus. This approach is less desirable than studying fresh larvae for gut content, however, the few existing studies of fresh individuals of *A. myops* by Munn & King (1987b) and Meier & Bartholomae (1980) and of *A. verticis* by Bae & McCafferty (unpublished) are consistent with our data from preserved specimens.

We have recently observed the feeding behavior of *A. verticis* larvae using the videomacroscopy techniques developed by Keltner & McCafferty (1986) and McShaffrey & McCafferty (1986, 1988, 1990, 1991). They were found to be primarily active filter feeders [deposit feeders sensu McShaffrey & McCafferty (1988)]. Larvae loosened and filtered fine detritus from interstitial areas in front of, and below, the head with a sweeping motion of the setaceous forelegs and palps. They were also able to passively filter fine detritus already suspended in the current. More feeding behavior details will be presented by Bae & McCafferty (unpublished).

Detailed feeding observations for other potamanthids are not currently available. Fortunately, however, relatively strong correlations between ultrastructure and functional morphology related to feeding in aquatic arthropods (e.g., Froelich 1964, Strenger 1973 1979, Farmer 1974, McShaffrey & McCafferty 1988, Soldán 1979, Wallace & O'Hop 1979, Wallace & Merritt 1980, Zimmerman & Wissing 1980) has allowed us to draw inferences about the evolution of feeding specialization in potamanthids with some confidence. The well-developed setaceous maxillary and labial palps (Fig. 18-25) as well as the setaceous forelegs (Fig. 11-17, 70-71) found in all potamanthid larvae have led us to hypothesize that potamanthid larvae in general are filter feeders. The gut content data reported above support the hypothesis. Furthermore, the commonness of filtering apparatus throughout the Ephemeroidea suggest that the common ancestor of the group was capable of filter feeding.

Within the Potamanthidae, there are differences in the degree and position of setation

among the three genera, and we infer from this that there are corresponding differences in the feeding behavior among the three genera. In *Rhoenanthus*, an ability to be a collector/gatherer as well as a filter feeder is suggested by the presence of falcate apices of the labial palps and relatively long forelegs, all of which may allow some manipulation of food not possible in the other genera. The position of *Rhoenanthus* in the cladogram (Fig. 6) along with its more generalized behavior further suggest that its behavior may be the most primitive in the family.

The setae of the forelegs of *Rhoenanthus* are generally distributed, but in *Anthopotamus* and *Potamanthus*, the forelegs are shorter and apparently more specialized for filtering, with well-developed bipectinate-hairlike setae located along the anterior margin of the foretibiae. This must have been the condition of the common ancestor of the two genera (Fig. 6). *Anthopotamus* and *Potamanthus* have the most highly developed filtering apparatus that we have found among the Ephemeroidea.

Anthopotamus is evidently the most specialized filterer among the genera. Suggestive of this is their foretibial filtering setae, which are very long and regularly spaced (Fig. 71) and have long and complex setules (Fig. 67-68). In addition, bipectinate-hairlike setae are well developed laterally on the labial palps.

In *Potamanthus*, some reduction in the mouthpart appendages, including tusks and maxillary and labial palps (Fig. 22-25) occurred, and the bipectinate-hairlike setae of the mouthparts and forelegs (Fig. 69) are not as highly developed as in *Anthopotamus*. This may indicate differences in resources or efficiency in filtering in the two genera.

Above, we postulated that the reduction of tusks in *Potamanthus* could be related to the possibility that they do not burrow as much and therefore do not profit from having tusks that aid in excavation as in other potamanthids. However, videomicroscopy revealed that larvae of *A. verticis* regularly clean the setae of their forelegs by raking the tibiae across the tops of the tusks, and thus the tusks may have an indirect feeding function as well as direct excavating function. This may also indicate an alternative explanation for the reduction of the tusks in *Potamanthus* if the forelegs are not used extensively in filter feeding. Then again, perhaps *Potamanthus* does not burrow as much, and its forelegs are therefore not subjected to becoming clogged with fine substrate and requiring cleaning to the same extent as other potamanthids.

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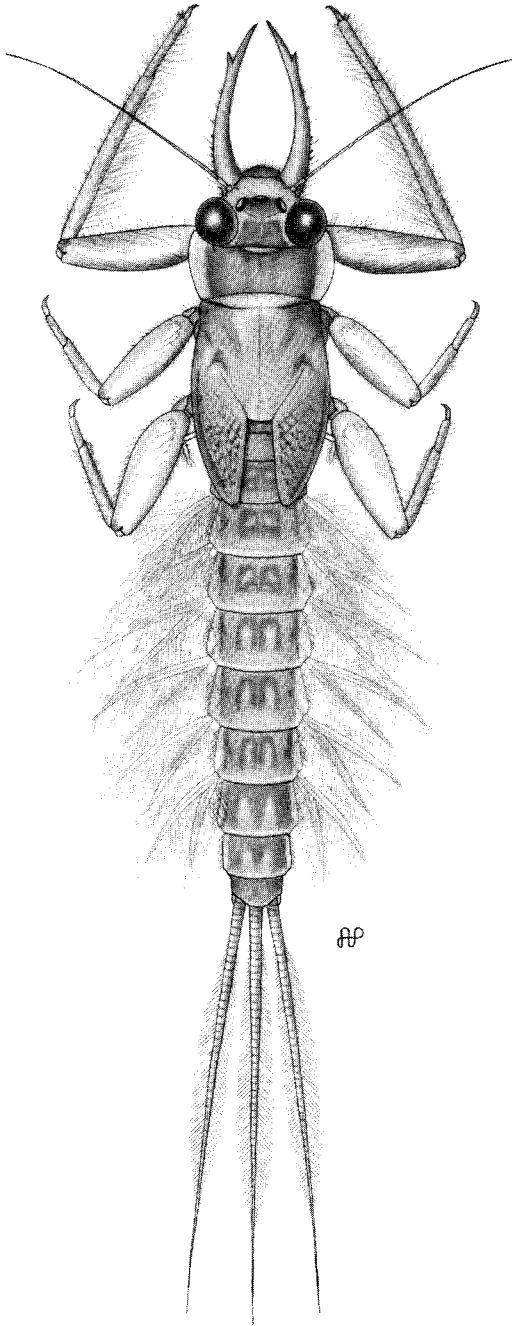


FIGURE 11. *Rhoenanthus (Rhoenanthus) speciosus*, larval habitus.

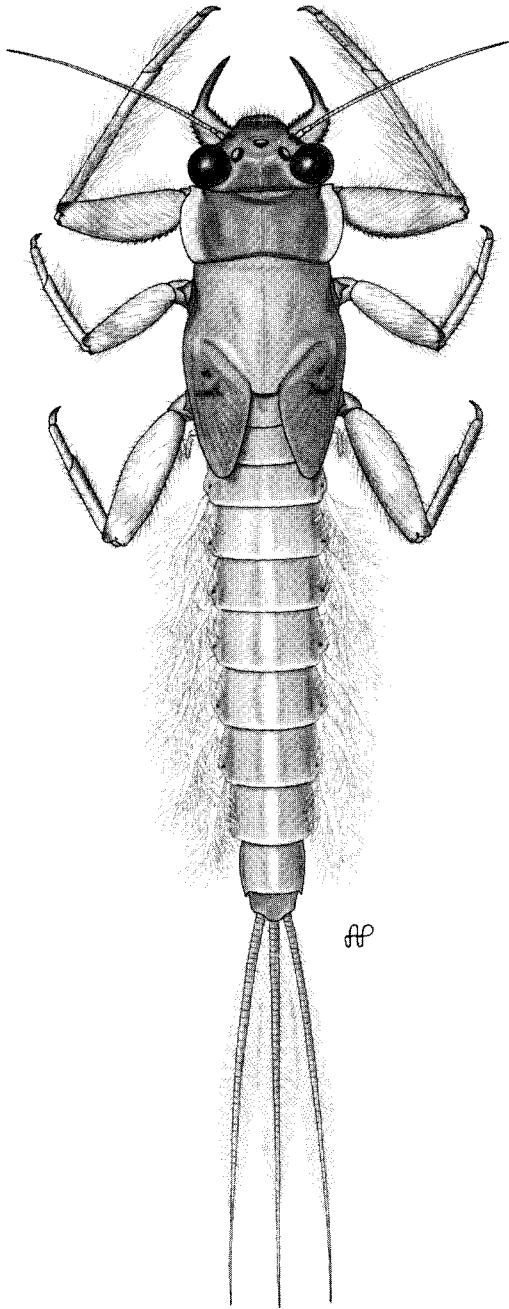


FIGURE 12. *Rhoenanthus (Potamanthindus) obscurus*, larval habitus.

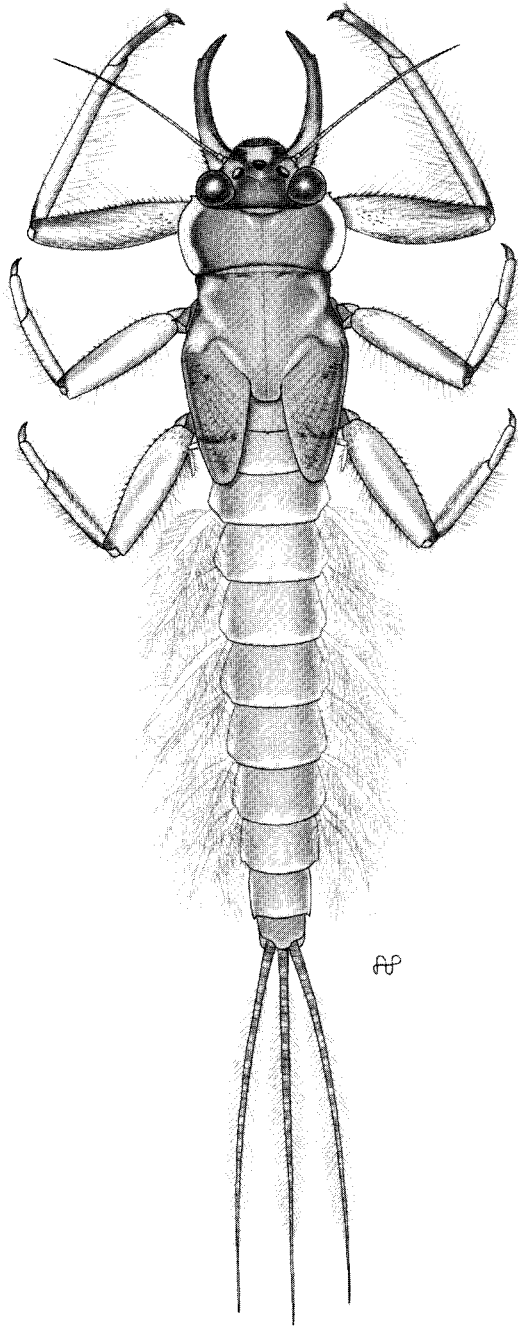


FIGURE 13. *Rhoenanthus (Potamanthindus) coreanus*, larval habitus.

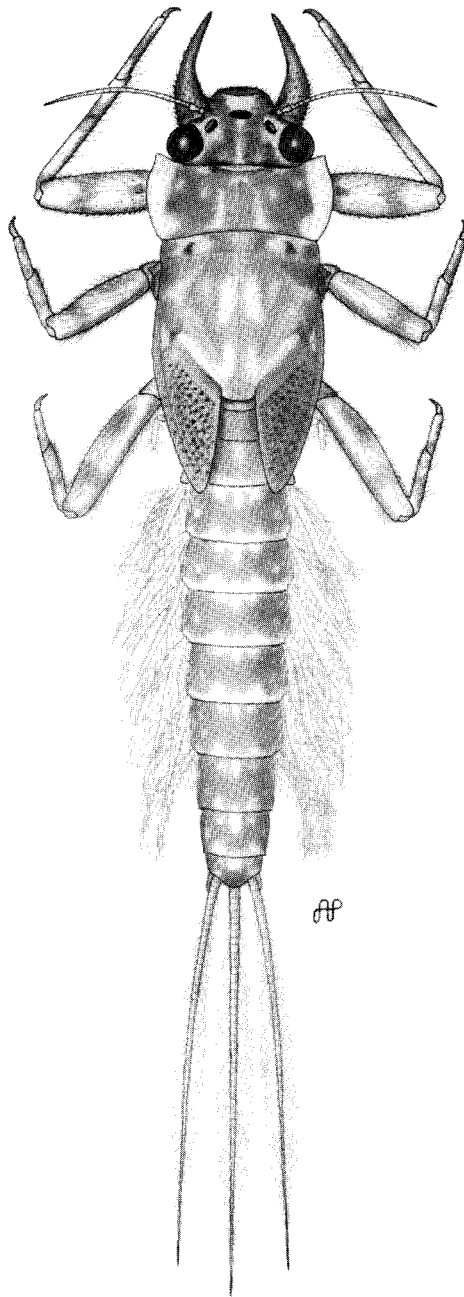


FIGURE 14. *Anthopotamus distinctus*, larval habitus.

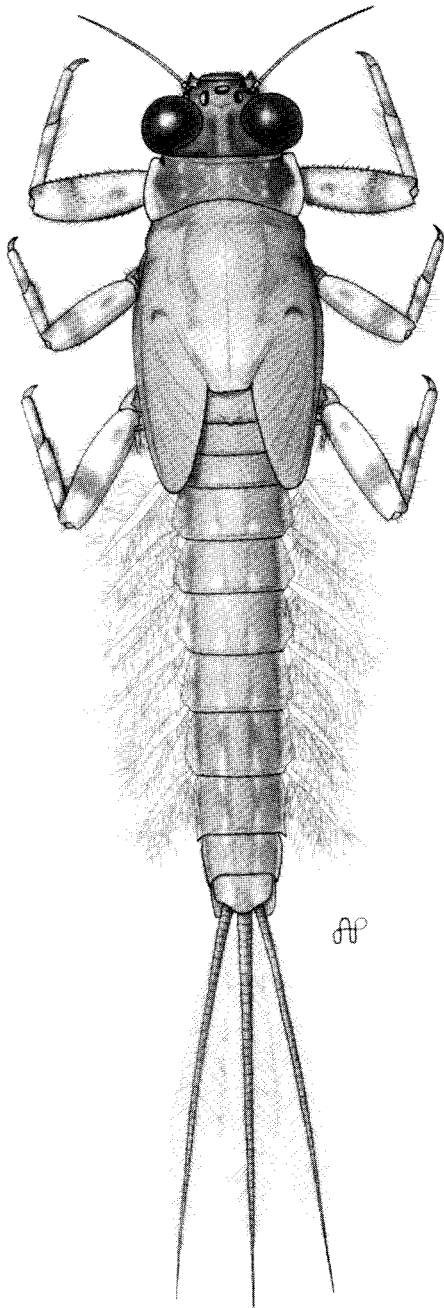


FIGURE 15. *Potamanthus (Potamanthus) huoshanensis*, larval habitus.

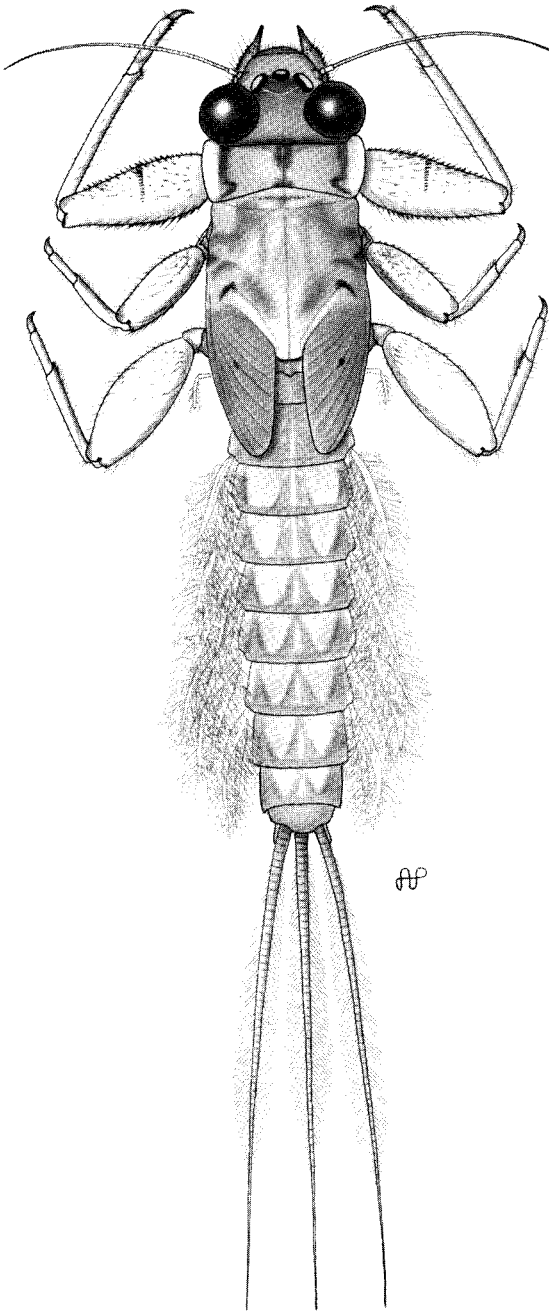


FIGURE 16. *Potamanthus (Stygifloris) sabahensis*, larval habitus.

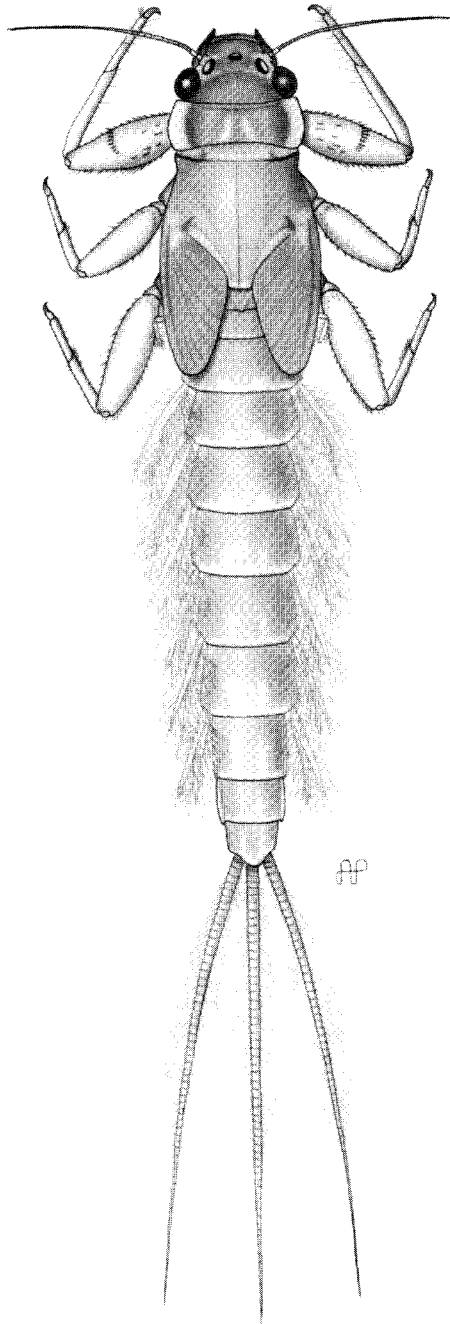
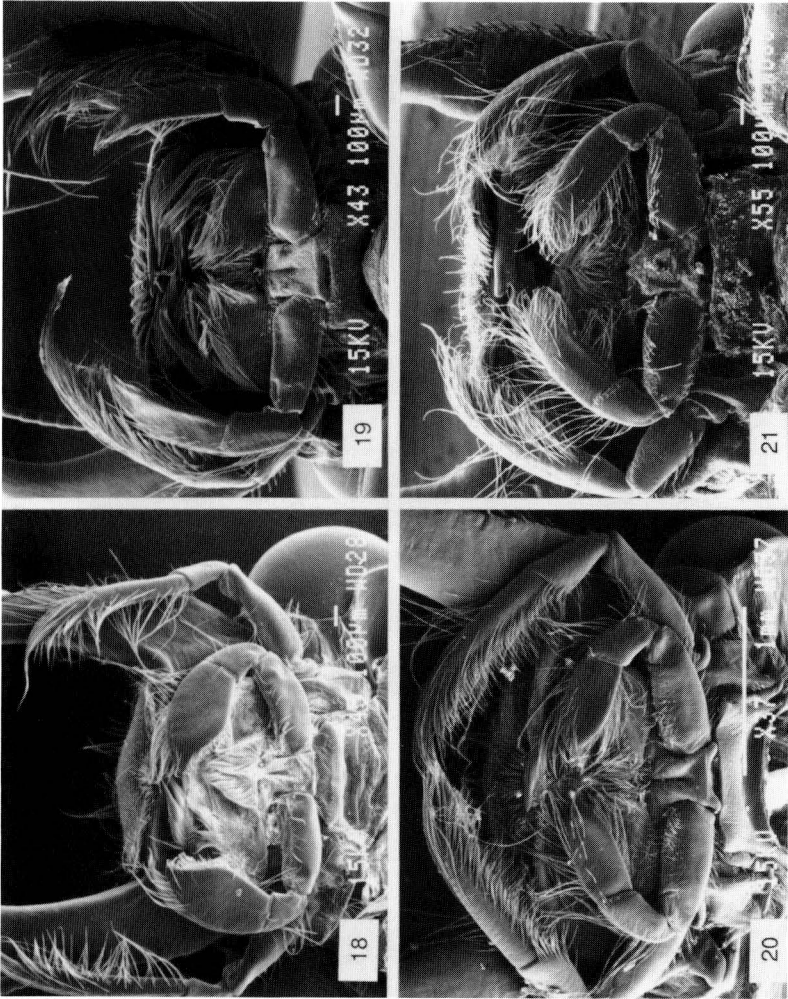
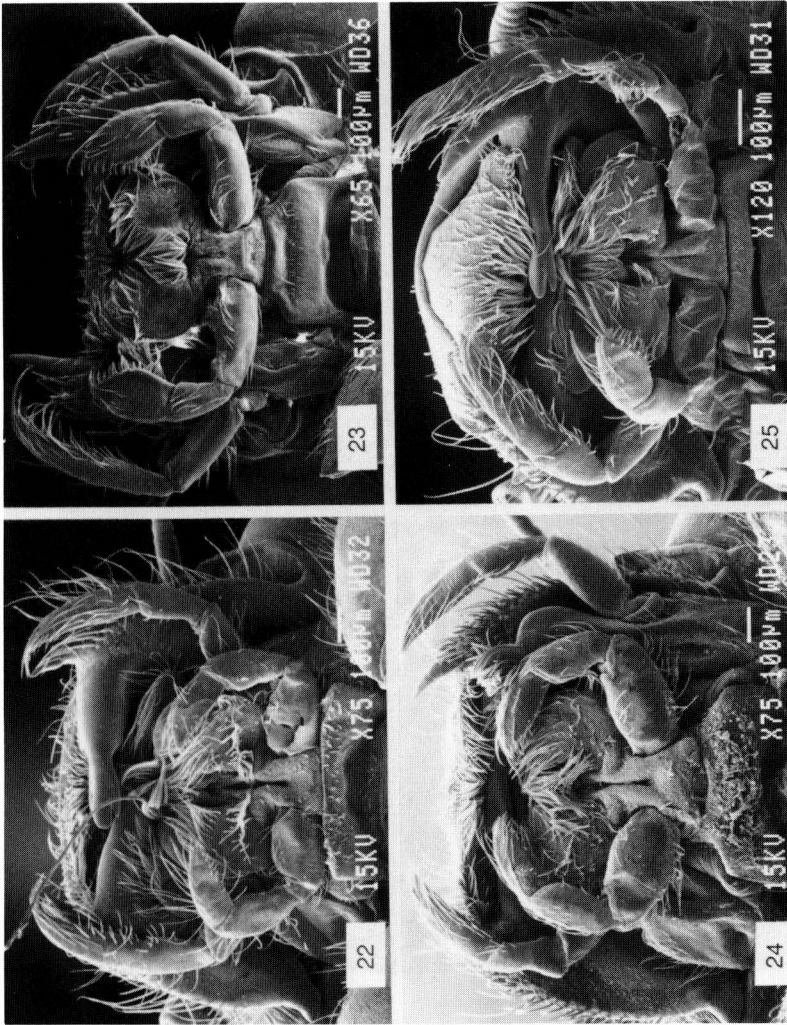


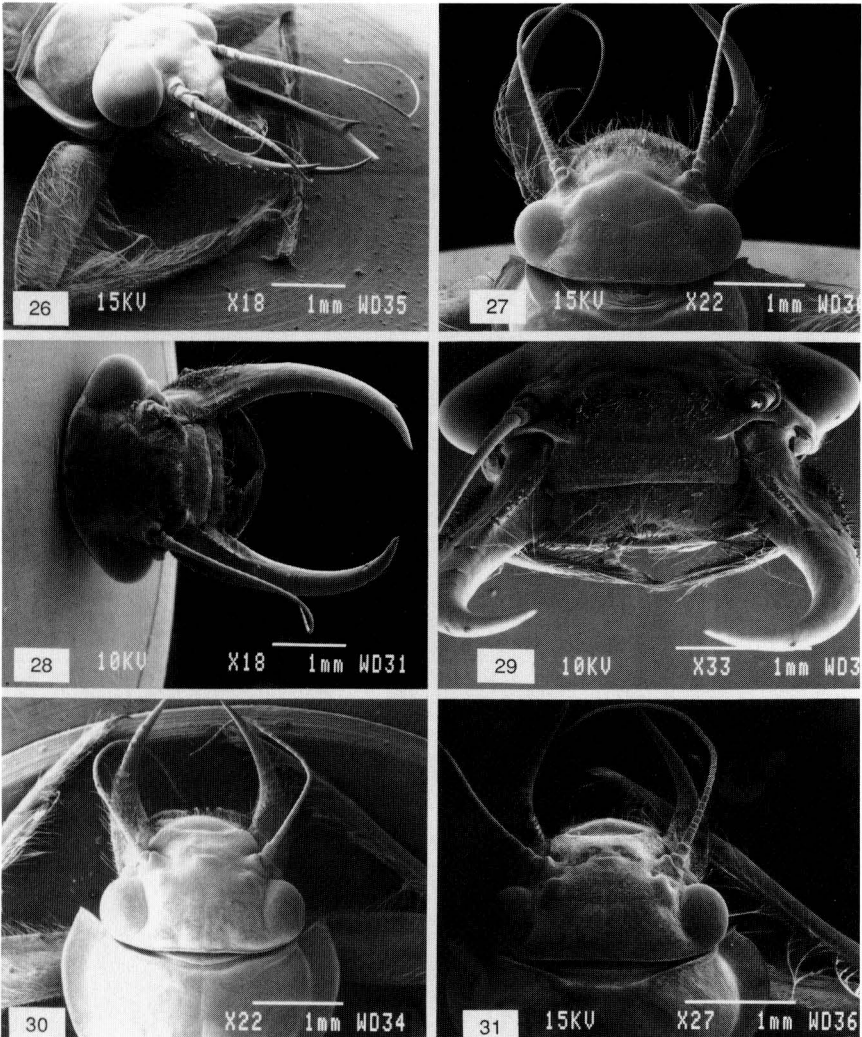
FIGURE 17. *Potamanthus (Potamanthodes) formosus*, larval habitus.



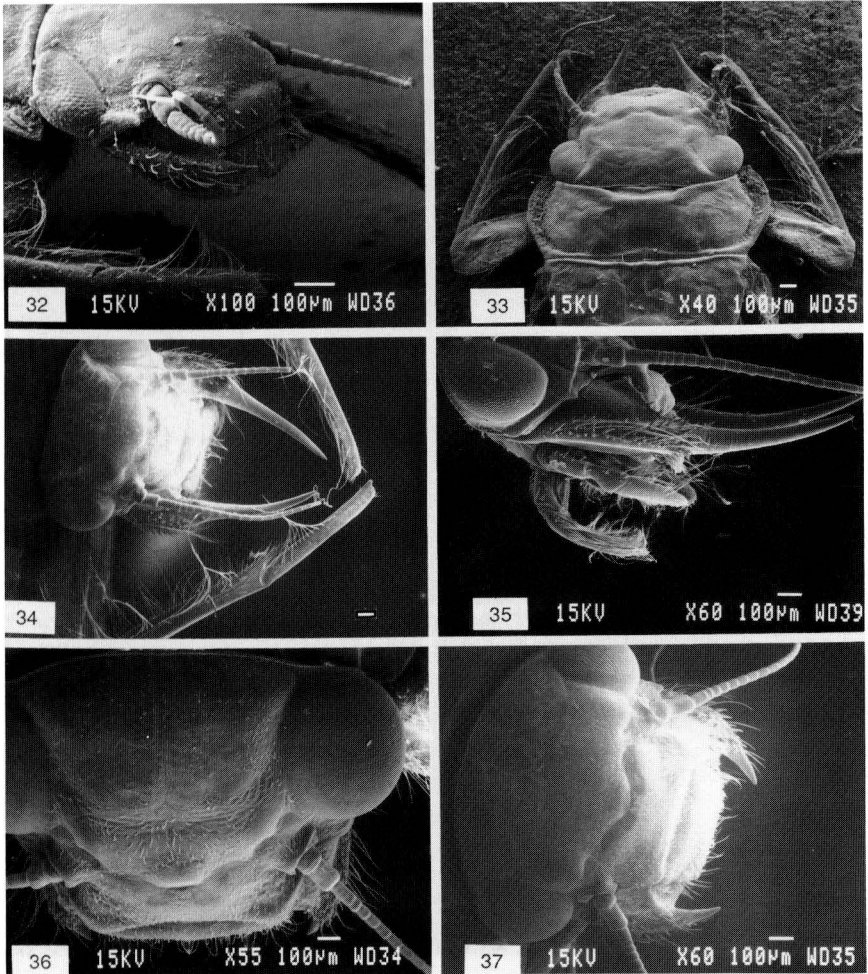
FIGURES 18-21. Larval mouthparts. 18, *R. (Rhoenanthus) speciosus*. 19, *R. (Potamanthindus) obscurus*. 20, *R. (Potamanthindus) coreanus*. 21, *A. myops*.



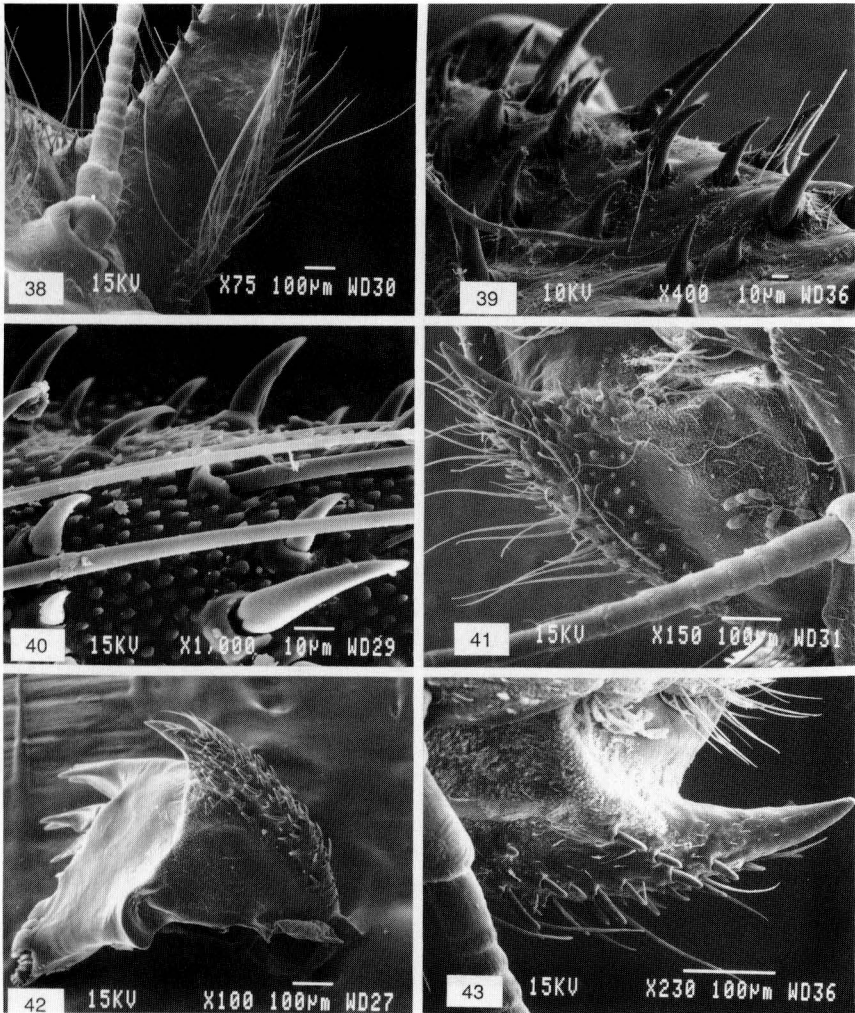
FIGURES 22-25. Larval mouthparts. 22, *P. (Potamantus) luteus*. 23, *P. (Stygifloris) sabdshensis*. 24, *P. (Potamantodes) yooni*. 25, *P. (Potamantodes) formosus*.



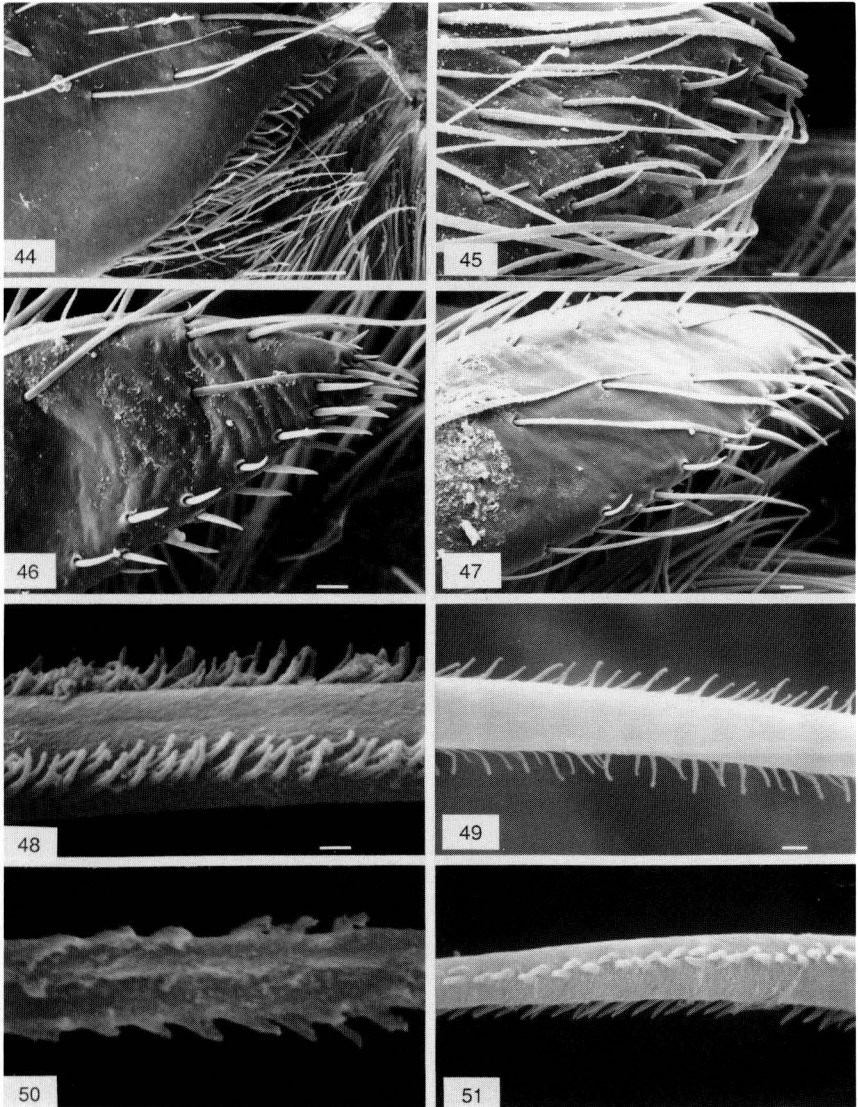
FIGURES 26-31. Larval head and thorax. **26**, *R. (Rhoenanthus) speciosus*, anterolateral. **27**, *R. (Potamanthindus) obscurus*, dorsal. **28**, *R. (Potamanthindus) coreanus*, dorsal. **29**, *R. (Potamanthindus) coreanus*, frontal. **30**, *A. distinctus*, dorsal. **31**, *A. myops*, dorsal.



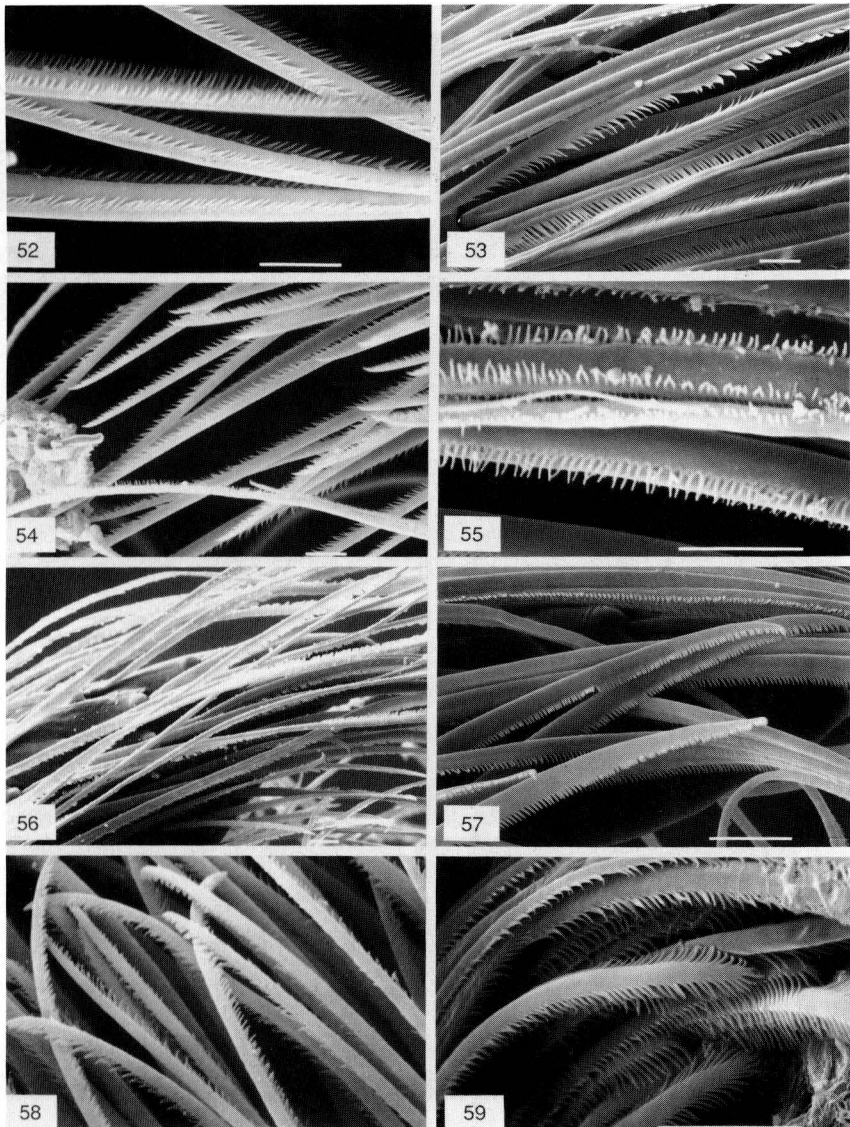
FIGURES 32-37. Larval head and thorax. 32-35. *A. verticis*. 34, Early instar, anterolateral. 33, Middle instar, dorsal. 34, Late instar, dorsal (bar = 100 µm). 35, Late instar, lateral. 36, *P. (Potamanthus) luteus*, dorsal. 37, *P. (Potamanthodes) formosus*, dorsal.



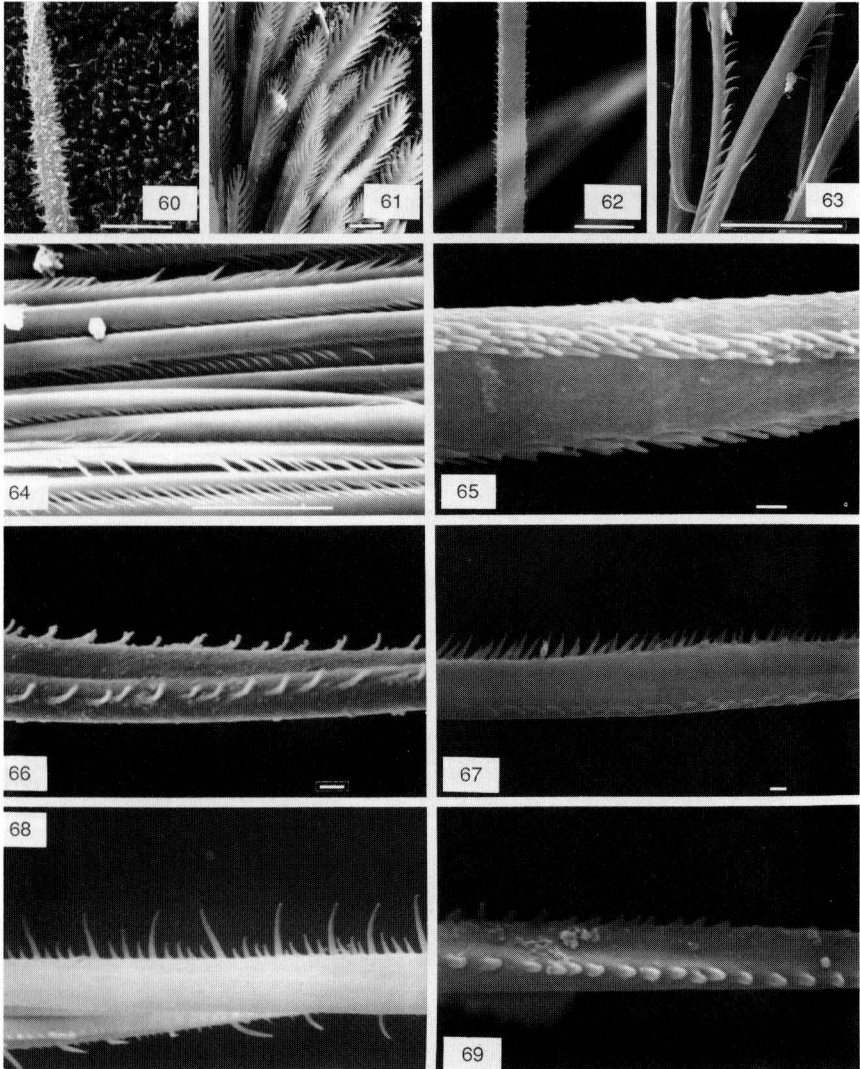
FIGURES 38-43. Mandibular tusk. 38, *R. (Potamanthodes) obscurus*, basal, in part. 39, *R. (P.) coreanus*, basal, in part. 40, *A. myops*, basal, in part. 41, *P. (Potamanthodes) luteus*, dorsal. 42, *P. (Potamanthodes) yooni*, dorsal. 43, *P. (Potamanthodes) formosus*, dorsal.



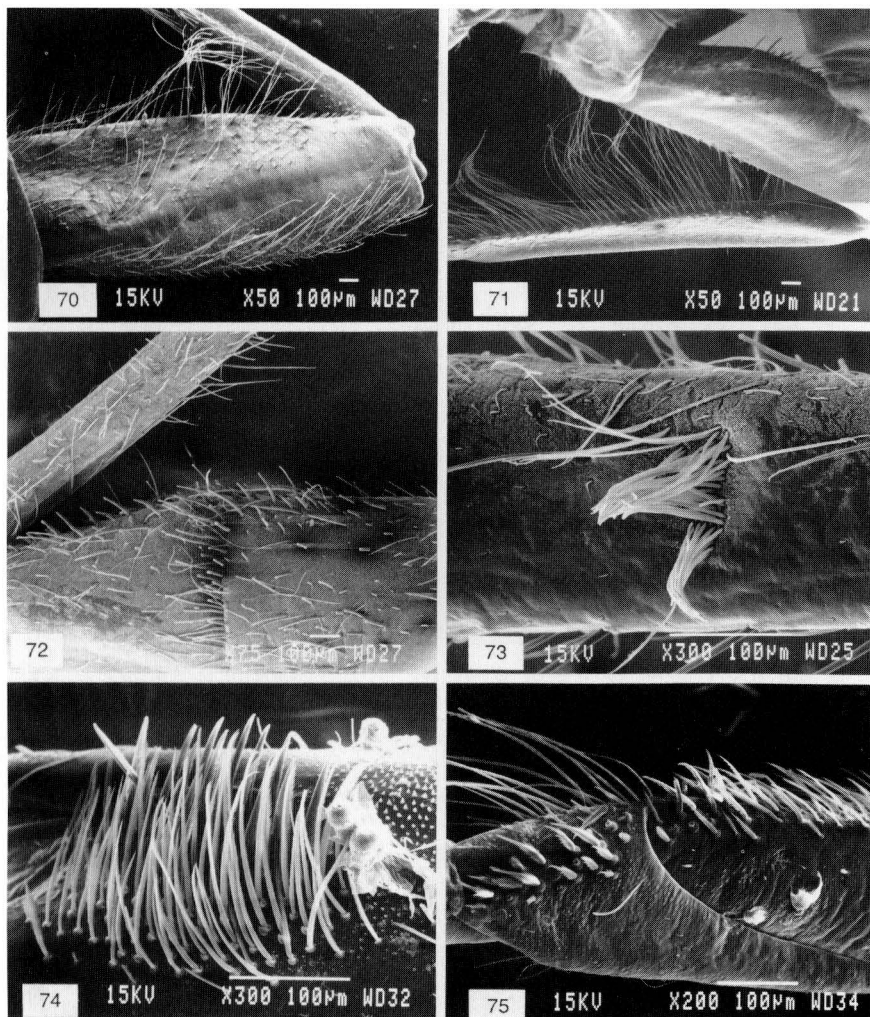
FIGURES 44-51. Larval mouthparts. 44-47. Labial palp 44: bar = 100 μm ; 45-47: bar = 10 μm). 44, *R. (Potamanthindus) coreanus*. 45, *A. myops*. 46, *P. (Potamanthus) luteus*. 47, *P. (Potamanthodes) yooni*. 48-51. Mandibular tusk setae (bar = 1 μm). 48, *R. (Potamanthindus) obscurus*. 49, *A. myops*. 50, *P. (Potamanthus) luteus*. 51, *P. (Potamanthodes) yooni*.



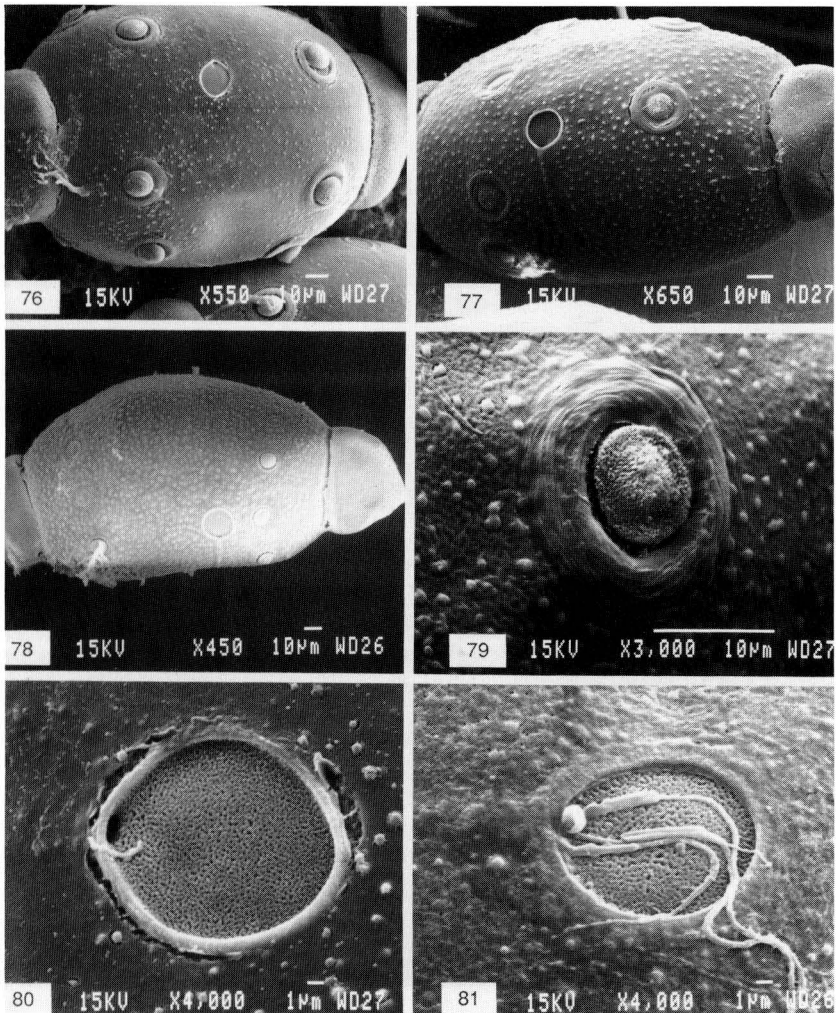
FIGURES 52-59. Mouthpart setae. 52-57. Setae, maxillary palp (bar = 10 μ m). 52, *R. (Rhoenanthus) speciosus*. 53, *R. (Potamanthindus) obscurus*. 54, *R. (Potamanthindus) coreanus*. 55, *R. (Potamanthindus) coreanus*. 56, *A. myops*. 57, *P. (Stygifloris) sabahensis*. 58-59. Setae, galealacinia crown (bar = 10 μ m). 58, *A. myops*. 59, *P. (Potamanthus) luteus*.



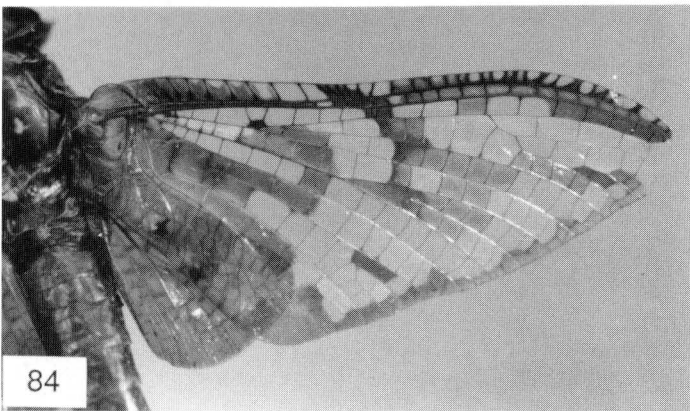
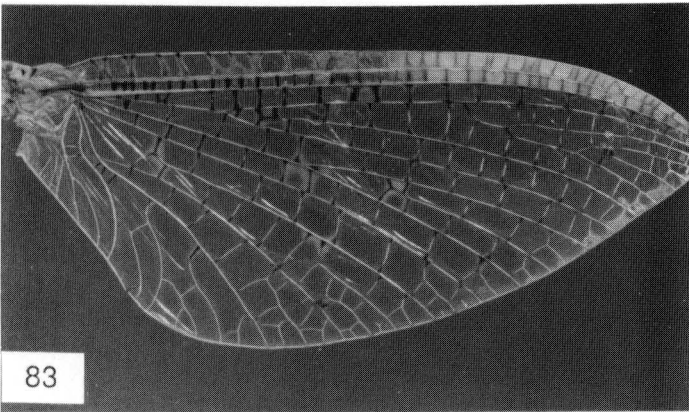
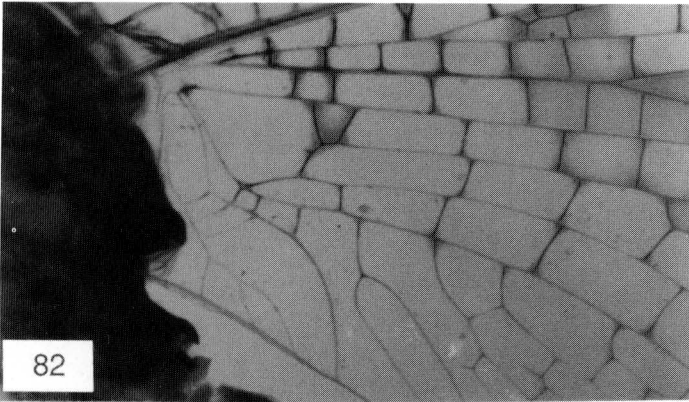
FIGURES 60-69. Larval setation 60-64, bar = 10 μm ; 65-69, bar = 1 μm). **60**, Dorsal head, *P. (Potamanthus) luteus*. **61**, Anterior surface of hindtibia, *P. (Potamanthodes) formosus*. **62**, Dorsal forefemur, *R. (Potamanthindus) obscurus*. **63-64**, Hypopharynx. **63**, *P. (Potamanthus) luteus*. **64**, *R. (Potamanthindus) obscurus*. **65**, Clypeus, *R. (Potamanthindus) obscurus*. **66-69** Foretibia. **66**, *R. (Potamanthindus) coreanus*. **67**, *A. distinctus*. **68**, *A. myops*. **69**, *P. (Potamanthus) luteus*.



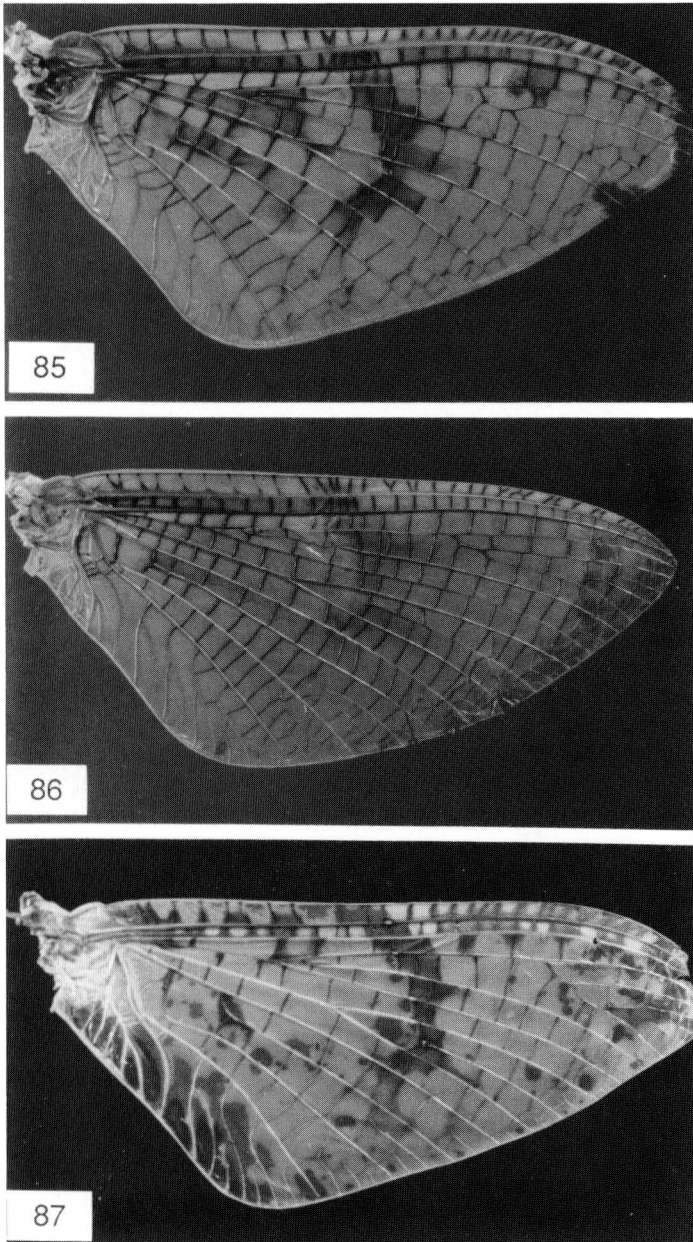
FIGURES 70-75. Larval leg setation. 70-72. Forefemur and foretibia. **70**, *A. distinctus*, dorsal. **71**, *A. verticis*, ventral. **72**, *P. (Stygifloris) sabahensis*, dorsal. **73**, Ventral, subapical foretibia, *P. (Stygifloris) sabahensis*. **74-75**. Hindfemur and hindtibia, *A. verticis*. **74**, Distal anterior margin of femur. **75**, Anterior margin of tibia.



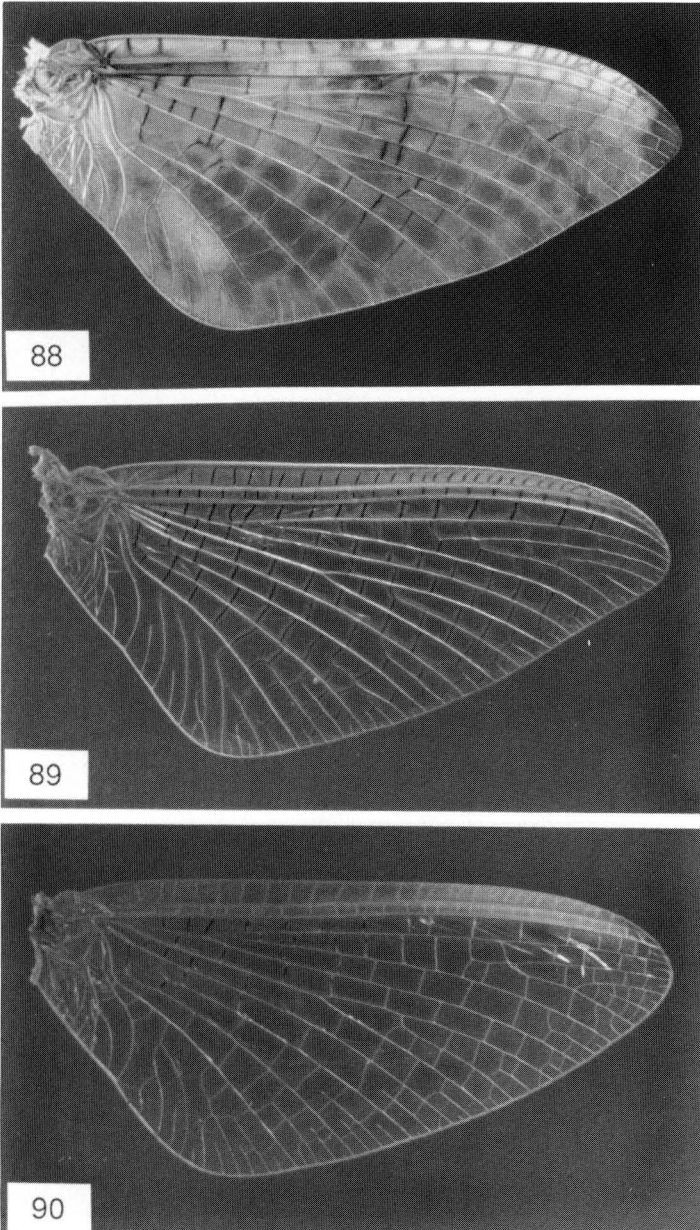
FIGURES 76-81. Egg. **76**, *R. (Potamanthindus) coreanus*. **77**, *P. (Potamanthodes) yooni*. **78**, *P. (Stygifloris) sabahensis*. **79**, Knob-terminated coiled thread, *P. (Potamanthus) luteus*. **80**, Micropyle, *R. (Potamanthindus) coreanus*. **81**, Sperm guide (with sperm), *A. verticis*.



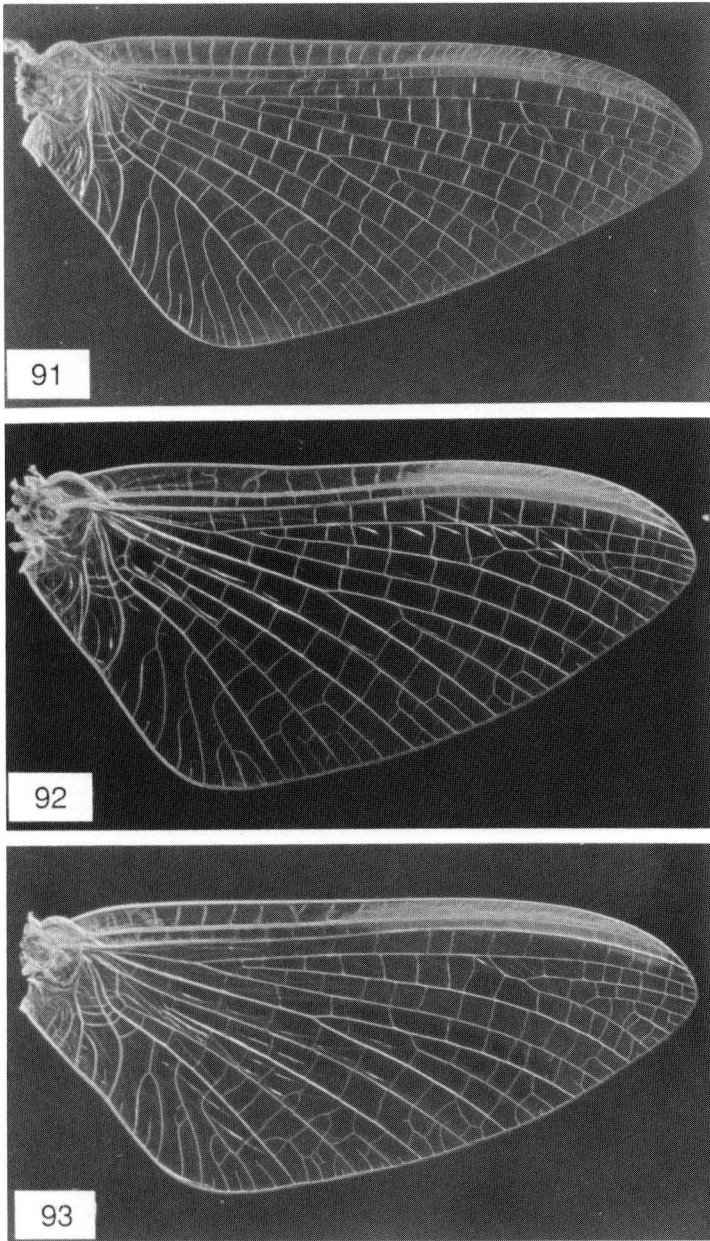
FIGURES 82-84. Adult forewing, male. **82**, *R. (Rhoenanthus) distafurcus*. **83**, *R. (Rhoenanthus) speciosus*. **84**, *R. (Potamanthindus) magnificus*.



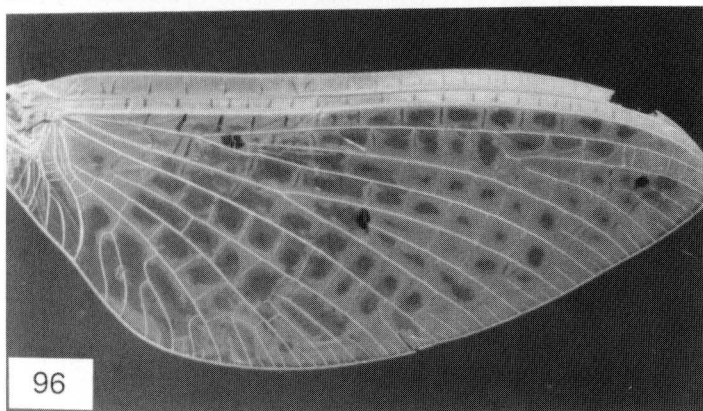
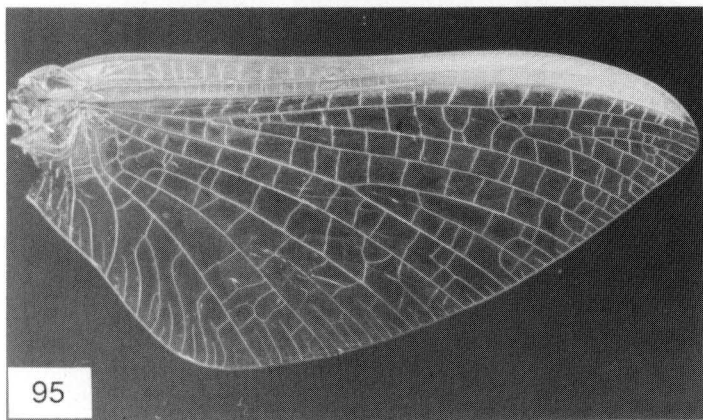
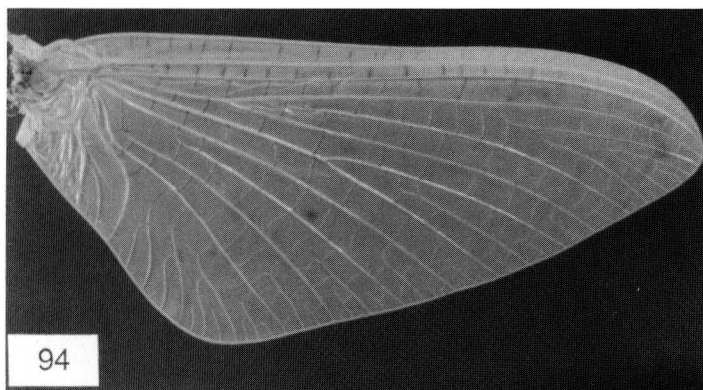
FIGURES 85-87. Adult forewing. **85**, *Rhoenanthus (Potamanthindus) obscurus*, male. **86**, *R. (Potamanthindus) obscurus*, female. **87**, *R. (Potamanthindus) youi*, male.



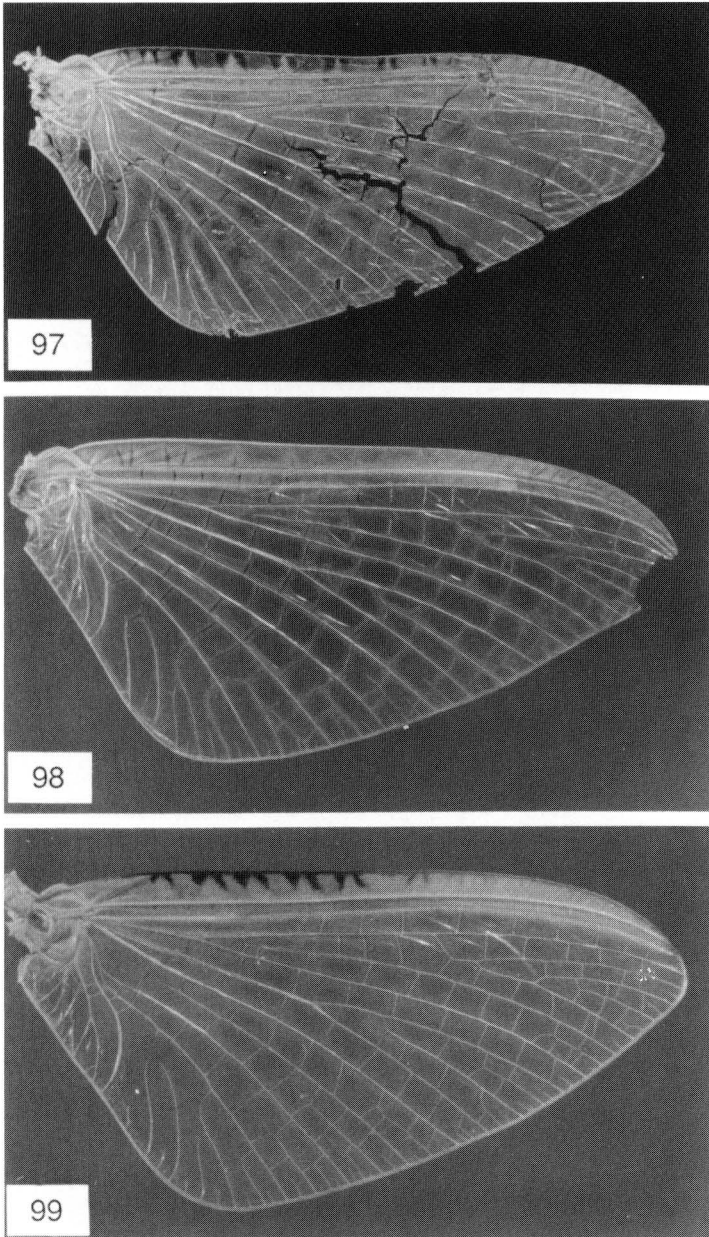
FIGURES 88-90. Adult forewing, male. **88**, *R. (Potamanthindus) coreanus*. **89**, *A. distinctus*. **90**, *A. neglectus*.



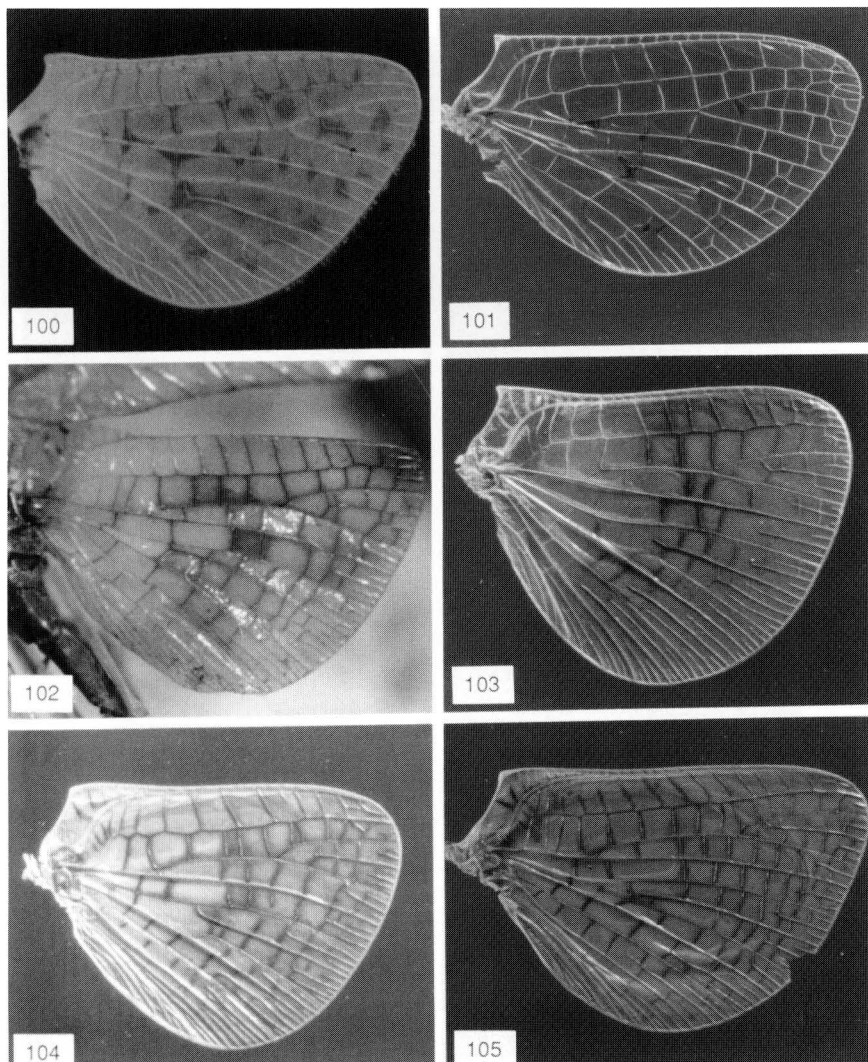
FIGURES 91-93. Adult forewing. **91**, *A. myops*, male. **92**, *A. verticis*, male. **93**, *A. verticis*, female.



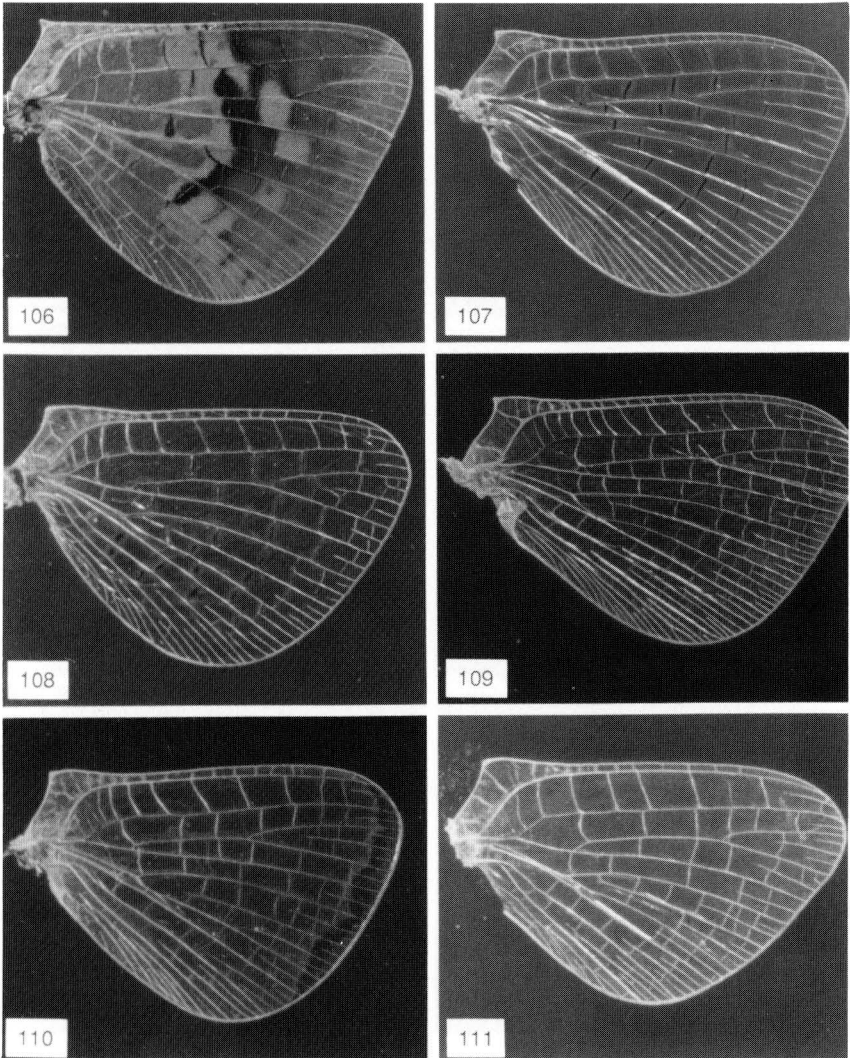
FIGURES 94-96. Adult forewing. **94**, *P. (Potamanthus) luteus*, male. **95**, *P. (Potamanthus) huoshanensis*, male. **96**, *P. (Stygifloris) sabahensis*, female.



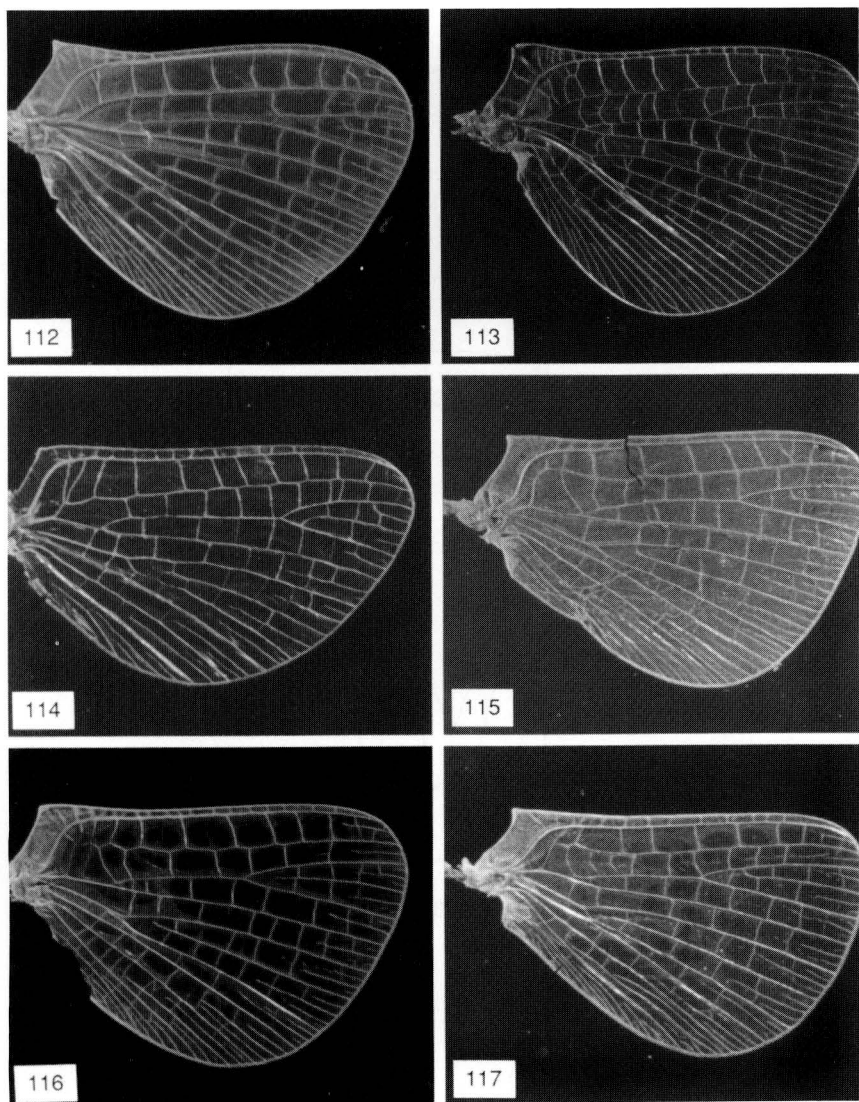
FIGURES 97-99. Adult forewing, male. 97, *P. (Potamantodes) macrophthalmus*. 98, *P. (Potamantodes) yooni*. 99, *P. (Potamantodes) formosus*.



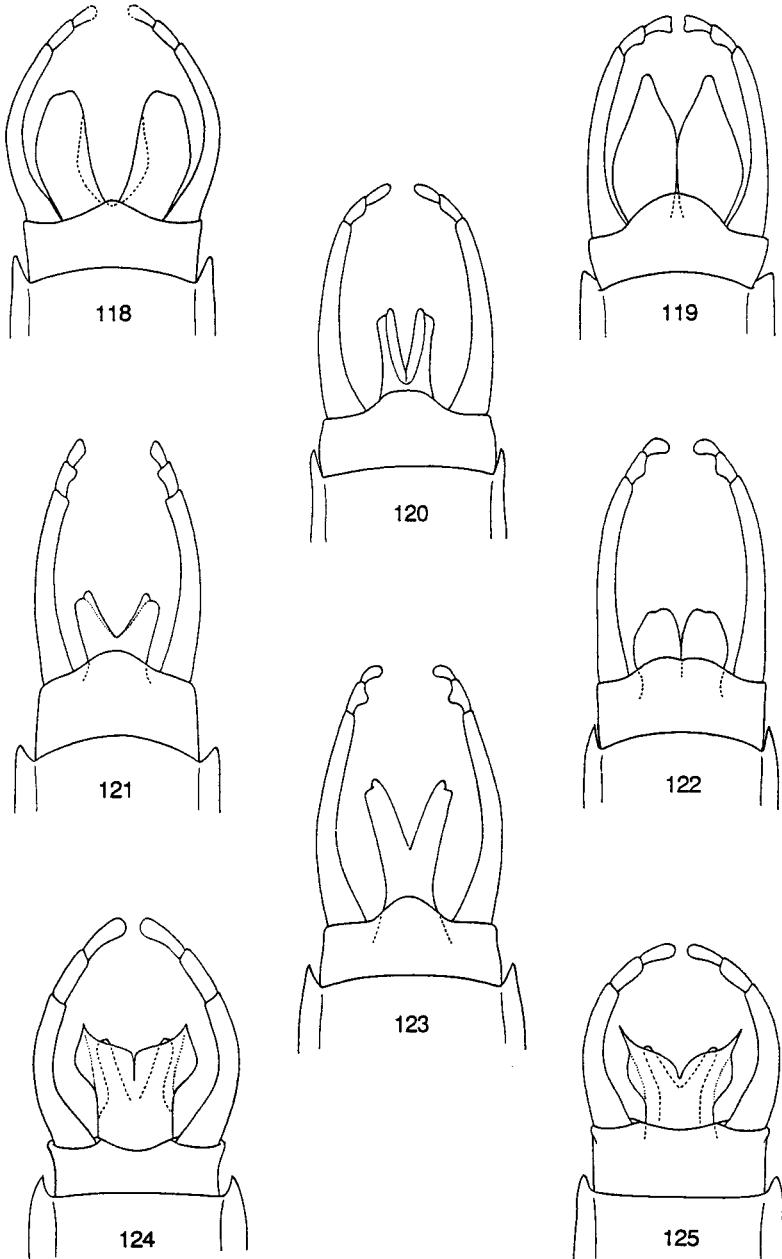
FIGURES 100-105. Hindwing. **100**, *R. (Rhoenanthus) distafurcus*, male subimago. **101**, *R. (Rhoenanthus) speciosus*, male adult. **102**, *R. (Potamanthindus) magnificus*, male adult. **103**, *R. (Potamanthindus) coreanus*, male adult. 104-105, *R. (Potamanthindus) obscurus*. **104**, Male adult. **105**, Female adult.



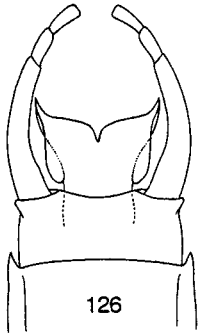
FIGURES 106-111. Adult hindwing. **106**, *R. (Potamanthindus) youi*, male. **107**, *A. distinctus*, male. **108**, *A. neglectus*, male. **109**, *A. myops*, male. **110**, *A. verticis*, male. **111**, *A. verticis*, female.



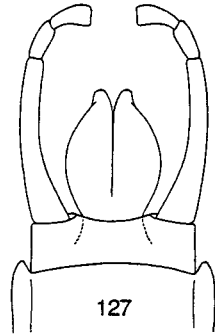
FIGURES 112-117. Adult hindwing. 112, *P. (Potamanthus) luteus*, male. 113, *P. (Potamanthus) huoshanensis*, male. 114, *P. (Stygifloris) sabahensis*, female. 115, *P. (Potamanthodes) macrophthalmus*, male. 116, *P. (Potamanthodes) yooni*, male. 117, *P. (Potamanthodes) formosus*, male.



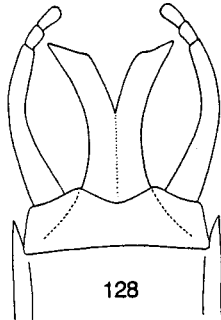
FIGURES 118-125. Male adult genitalia, ventral. **118**, *R. (Rhoenanthus) distafurcus*. **119**, *R. (Rhoenanthus) speciosus*. **120**, *R. (Potamanthindus) magnificus*. **121**, *R. (Potamanthindus) obscurus*. **122**, *R. (Potamanthindus) coreanus*. **123**, *R. (Potamanthindus) youi*. **124**, *A. distinctus*. **125**, *P. (Potamanthus) luteus*.



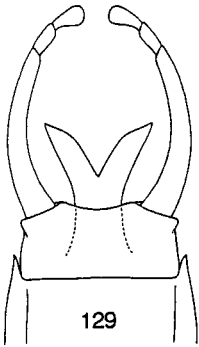
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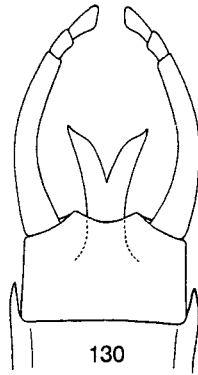
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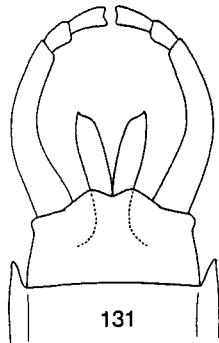
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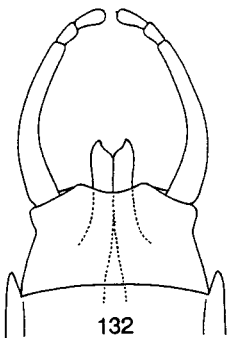
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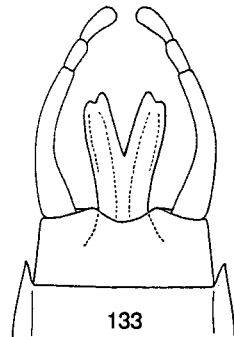
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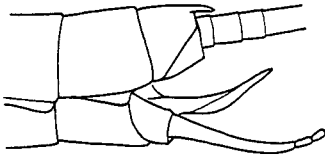


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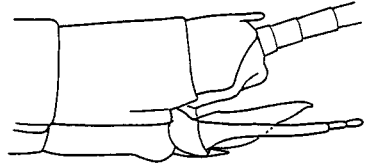


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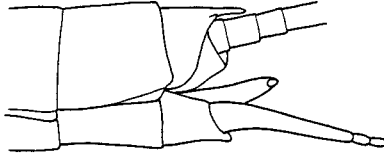
FIGURES 126-133. Male adult genitalia, ventral. **126**, *P. (Potamanthus) huoshanensis*. **127**, *P. (Stygifloris) sabahensis*. **128**, *P. (Potamanthodes) macrophthalmus*. **129**, *P. (Potamanthodes) yooni*. **130**, *P. (Potamanthodes) formosus*. **131**, *P. (Potamanthodes) kwangsiensis*. **132**, *P. (Potamanthodes) yunnanensis*. **133**, *P. (Potamanthodes) sangangensis*.



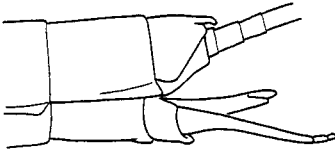
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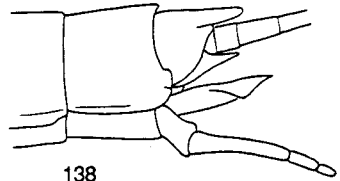
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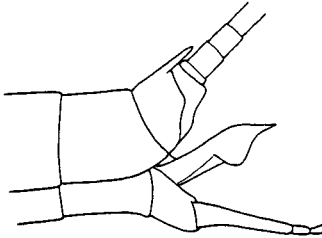
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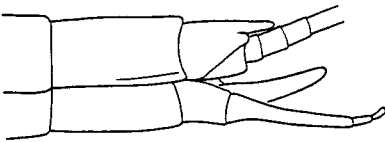
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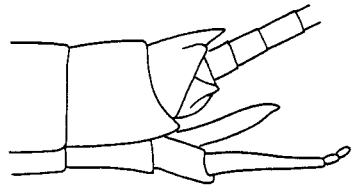
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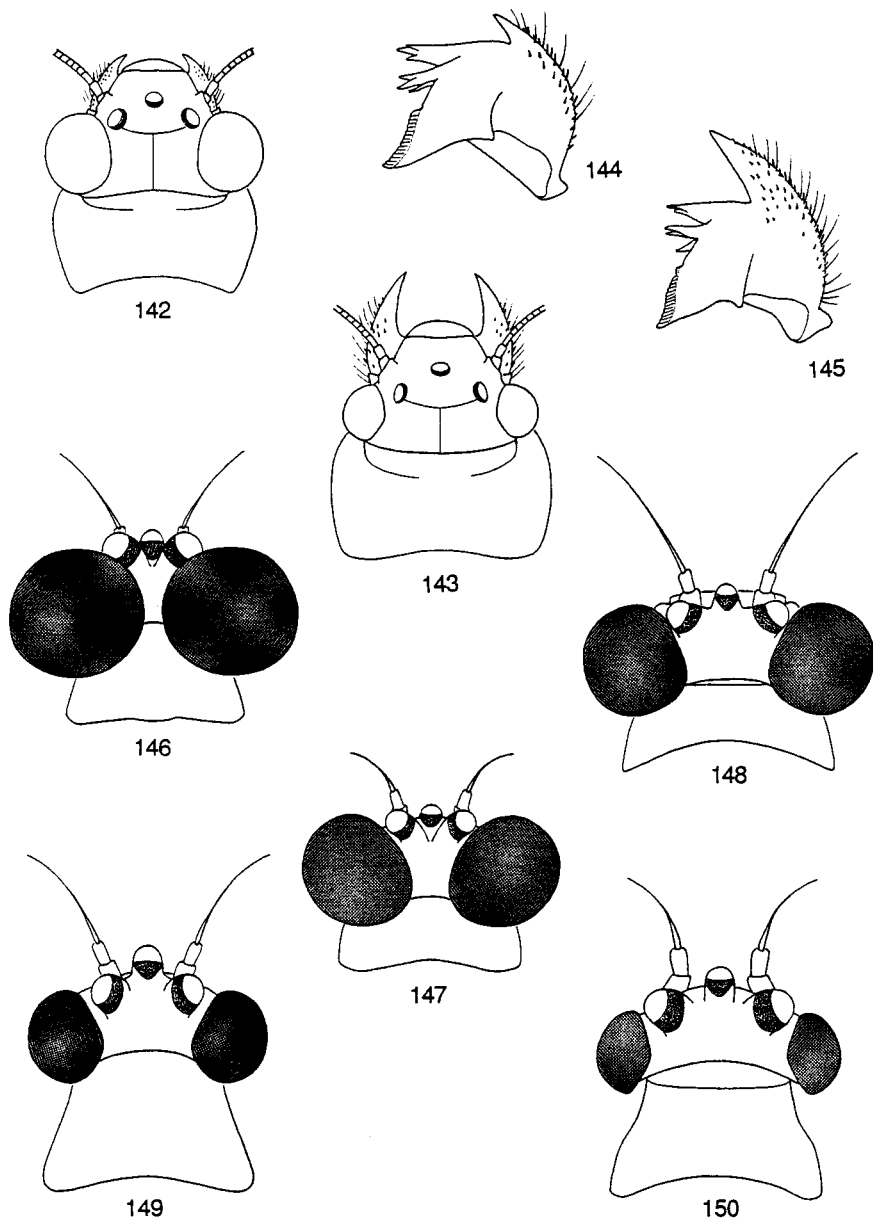


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FIGURES 134-141. Male adult genitalia, lateral. 134, *R. (Rhoenanthus) distafurcus*. 135, *R. (Rhoenanthus) speciosus*. 136, *R. (Potamanthindus) obscurus*. 137, *R. (Potamanthindus) youi*. 138, *A. distinctus*. 139, *P. (Potamanthus) huoshanensis*. 140, *P. (Stygifloris) sabahensis*. 141, *P. (Potamanthodes) formosus*.



FIGURES 142-150. Compound eyes and mandible. 142-143. Larva dorsal head. **142**, *P. (Potamanthodes) yooni*. **143**, *P. (Potamanthodes) longitibius*. 144-145. Larva dorsal mandible **144**, *P. (Potamanthodes) formosus*. **145**, *P. (Potamanthodes) idiocerus*. 146-150. Head, male adult. **146**, *P. (Potamanthodes) macrophthalmus*. **147**, *P. yooni*. **148**, *A. verticis*. **149**, *A. distinctus*. **150**, *P. formosus*.