THE MALE IMAGO OF PROTOBEHNINGIA TSHERNOVA FROM THAILAND (EPHEMEROPTERA: BEHNINGIIDAE)

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ABSTRACT

A new species, *Protobehningia merga*, is described from male imagos and nymphal exuviae collected in Mai Nam Khwae Noi (River Kwai), Thailand. The adult of Protobehningia was formerly unknown. Notes on the biology of the new species are included. Phylogenetic and zoogeographic relationships of the genera of Behningiidae are discussed.

INTRODUCTION

The three extant genera of the family Behningiidae are among the rarest Ephemeroptera in the world and the nymphs live in clean shifting sand rivers. Only isolated populations of behningiid species have been found and all occur only in the Northern Hemisphere.

The genus *Protobehningia* was originally established for the species *P. asiatica* Tshernova from the lower reaches of the Ussuri River, U.S.S.R. The type series of the species contained only three nymphal specimens.

One of us (MTG) recently collected male imagos and nymphal exuviae of Protobehningia in the Mai Nam Khwae Noi (River Kwai), Thailand. Based on a comparison of the nymphal exuviae from Thailand and recently collected nymphs of *P. asiatica* from the Ussuri River, the Thai specimens represent a new species of *Protobehningia*.

In this paper we describe the male imago of *Protobehningia* at the generic and specific level. As the male imagos and nymphs are now known for all three extant genera of the Behningiidae, the phylogenetic relationships and zoogeography of the family are discussed.

Overview and Strategies of Ephemeroptera and Plecoptera. J. Alba-Tercedor & A. Sanchez-Ortega (eds.), Sandhill Crane Press, Gainesville, Florida, 1991. [Proceedings of: VIth International Ephemeroptera Conference (24-28 July 1989) and Xth International Symposium on Plecoptera (27-30 July 1989), Granada, Spain].

Protobehningia Tshernova
(Figs. 1-7)

Protobehningia Tshernova, 1960, in Tshernova and Bajkova, Entomol. Obozr. 39:411.

Male imago. Antennae inserted on prominent anterolateral projections on head; scape 4 X length of pedicel, flagellum 1-1/2 X length of scape. Eyes well developed, large, bulbous, not divided into upper and lower portions. Lateral ocelli large, a little less than 1/2 width of an eye; median ocellus smaller, 1/2 width of a lateral ocellus. Wings (Fig. 4-5): maximum width of fore wings a little more than 1/2 maximum length of fore wings; vein Rs of fore wings forked 1/7 of distance from base to margin, vein R^3 unforked, veins in radial field evenly spaced; vein MA forked 1/6 of distance from base to margin, fork symmetrical, veins in MA field evenly spaced; veins IMP and MP_2 attached to vein CuA near base; long, unforked, evenly spaced intercalaries between veins in CuA field (Fig. 4). Hind wings with a small costal projection near base of wings (Fig. 5); veins evenly spaced throughout wings. Prothoracic legs (Fig. 1-2): tibiae a little less than 2 X length of femora; tarsi 1-segmented, weakly annulated, a little less than 1/2 X length of tibiae; fore claws very small, pad-like (Fig. 2). Mesothoracic legs: tibiae 1-1/2 X length of femora; legs abscised near base of tarsi. Metathoracic legs: coxae well developed, elongated; tibiae small, less than 1/4 length of femora; legs abscised near apex of tibiae. Abdomen long, slender; posterolateral corners of terga 2-7 flared with single slender paranotal remnants; well developed posterolateral spines on tergum 9; segments 9 and 10 well developed, segment 9 equal to length of segment 8. Male genitalia (Fig. 3): median area of styliger plate deeply incised, a broad based projection on median line; forceps 2-segmented, segmentation indistinct, segment 1 short (Fig. 3), with a well developed knob on inner margin, segment 2 long, smoothly tapered toward apex, apex sometimes coiled; penes divided except at base, each penis lobe tubular and slender, penes 3 X length of forceps and 3/5 to 4/5 length of abdomen. Cerci well developed, 1-1/3 X length of body, each segment with scattered long setae; terminal filament well developed, base a little narrower than bases of cerci, 1/2 X length of cerci, each segment with scattered long setae.

Female. Unknown. Females of *Dolania* and *Behningia* never undergo an imaginal molt. This may also be true for *Protobehningia.*

Mature nymph. See Tshernova and Bajkova (1960) for description.

Protobehningia merga new species
(Figs. 1-6 and Fig. A)

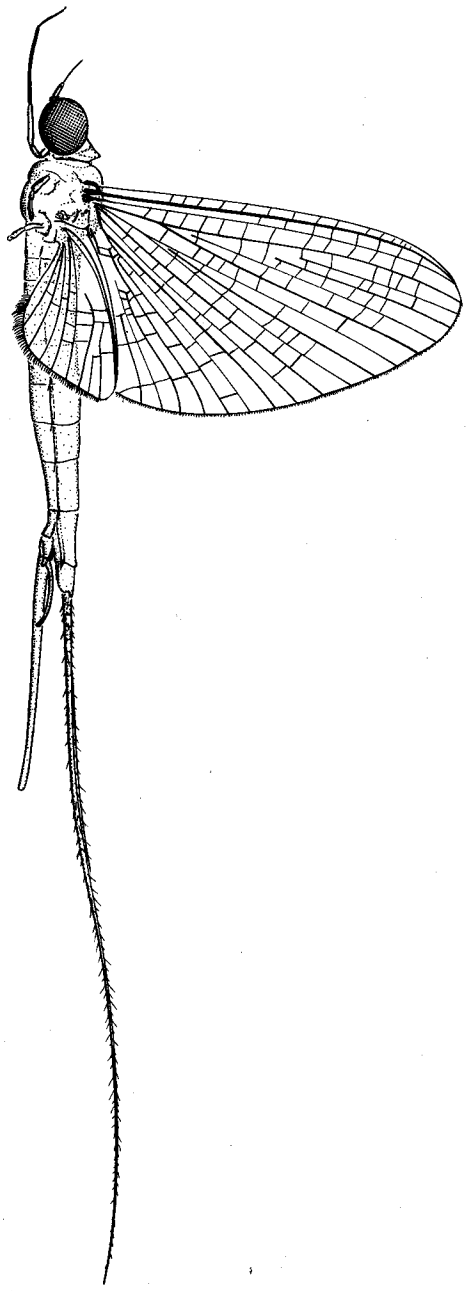
Male imago (in alcohol). Length of body (anterior margin of pronotum to apex of abdomen): 8.2-9.0 mm; length of fore wings: 6.7-7.5 mm. Eyes black. Antennae white, except flagellum brown, scape and pedicel washed with blackish-brown especially along lateral margins. Head white, carinae

washed with blackish-brown. Thorax cream, carinae darker. Legs white, femora of prothoracic legs 0.75-0.85 mm in length, washed with blackish-brown on dorsal surface (Fig. 1). Wings (Fig. 4-5): membrane of fore and hind wings colorless, transparent, except cells C and Sc of fore wings brownish; veins of fore and hind wings hyaline, except C, Sc and R of fore wings blackish-brown, fading towards apex. Abdomen white, hyaline between muscles; apex of tergum 10 outlined with blackish-brown. Genitalia (Fig. 3): white. Caudal filaments whitish, hyaline.

Female. Unknown.

Mature nymph. Unknown, but female and male nymphal exuviae are included in type series. These exuviae appear similar to the nymphs of *P. asiatica* as described by Tshernova and Bajkova (1960). Diagnostic characters for the nymphal exuviae of P. merga include the following: Body length (thorax and abdomen), ca. 10 mm. Maxillary palpi 3-segmented; segment 2 of palpi 2/3 length of segment 1, segmentation between segments 1 and 2 complete; segment 3 of palpi a little longer than length of segment 2, segmentation between segments 2 and 3 complete but indistinct. Ventral surface of glossae of labium with >20 long, stout setae (Fig. 6).

Specimens. Holotype male imago, THAILAND, Kanchanaburi Prov., Mai Nam Khwae Noi, 18 km N of Nam Tok, 1-XII-87, M. T. Gillies. Paratypes, 11 male imagos, M. T. Gillies, 3 male nymphal exuviae and 7 female nymphal exuviae, E. H. F. Gillies, remaining data as for holotype. All types are in alcohol. All specimens are deposited in the following collections: holotype, 5 male imaginal paratypes, 2 male and 2 female nymphal exuviae paratypes at Florida A&M University; 3 male imaginal paratypes, 2 male and 3 female nymphal exuviae paratypes at British Museum (Natural History); and 3 male imaginal paratypes and 2 female nymphal exuviae paratypes at



(Fig. A)

Leningrad State Museum.

Etymology. merga, L. meaning two-pronged pitchfork.

Discussion. The nymphal exuviae of *P. merga* were compared with two nymphs of *P. asiatica* collected from the Ussuri River in 1984 by Dr. N. Kluge. Both nymphs of P. asiatica were immature (body length 7.0-8.2 mm). Nymphs of *P. asiatica* appear larger than those of *P. merga*. The body length (thorax and abdomen) of the extended nymphal exuviae of *P. merga* are all about 10 mm, while Tshernova and Bajkova (1960) reported "the not fully grown larvae are 12.5 and 14.0 mm." We are not sure if these measurements include head length.

Illustrations of the glossae and paraglossae of *P. asiatica* by Tshernova and Bajkova (1960) and comparative material (Fig. 7) show few (<5) long, stout setae on the ventral surface. The glossae and paraglossae of *P. merga* have more than 20 long, stout setae on the ventral surface (Fig. 6).

Biology. We have only the most fragmentary information about the biology of this rarely seen mayfly. The collecting site was on the River Mae Nam Khwae Noi at a point where it is 50-100 m wide and flows between steeply wooded hills. The river bed was of sand or sand with stones, interspersed with rocky outcrops and occasional series of rapids. At that time there were no exposed sandbanks and it was not possible to wade in further than a few meters from the bank. Because of the depth of the water we were unable to sample established sandbanks, and no nymphs of *Protobehningia* were found. From the stony areas small numbers of Baetidae, Heptageniidae and Potamanthidae were collected.

A watch was kept on the river on two mornings in December from soon after first light at 0600 h local time until something like 20 minutes after sunrise which, though obscured by the hills, would have been at 0633. On both mornings small numbers of males were on the wing from 0615 for about half an hour. They were patrolling rapidly up and down the river, from a half to two meters above the water, with frequent changes in direction. They kept away from the banks of the river and it was only possible to net them by operating from a dugout canoe paddled by two local boatmen. We saw no female Protobehningia, either spent or on the wing. A drift-net held over the side of the canoe yielded small numbers of nymphal exuviae of both sexes.

DISCUSSION

The male imago of Protobehningia can be distinguished from that of *Behningia* and *Dolania* by the following combination of characters: (1) vein CuA of the fore wings is not forked (Fig. 4); (2) tibiae of prothoracic legs are a little shorter than 2 X length of femora (Fig. 1); (3) forceps of male genitalia are 2-segmented, and segment 1 is short with a well developed knob on the inner margin (Fig. 3); (4) length of penes is 3/5 to 4/5 length of abdomen; and (5) terminal filament is well developed and is 1/2 length of cerci. Tshernova and Bajkova (1960) give an excellent key to the nymphs of the three

genera of Behningiidae. Included herein is a key and comparative illustrations of the male imagos of the three genera.

Key to the Male Imagos of Behningiidae

1. Vein CuA of fore wings not forked (Fig. 4); length of penes 3/5 to 4/5 length of abdomen. ..... *Protobehningia*
-- Vein CuA of fore wings forked (Fig. 10, 12); length of penes 1/4 to less than 1/4 length of abdomen. **2**

2. Longitudinal veins form geminate pairs in fore wings (Fig. 12); length of forceps nearly as long as length of penes (Fig. 9). ..... *Behningia*
-- Longitudinal veins evenly spaced in fore wings (Fig. 10); length of forceps 1/2 length of penes (Fig. 8). ..... *Dolania*

McCafferty (1979) concluded that the most ancient furcation within the evolution of the Ephemeroidea gave rise to the Behningiidae and to the remainder of the Ephemeroidea. Further, he discussed the monophyletic nature of the Behningiidae based on a relatively large number of apomorphic character states which he considered to have been present early in the evolution of the lineage. With the discovery of the male imago of *Protobehningia*, it appears that the morphological and behavioral/ecological adaptations common to the nymphs and adults of all three genera arose in the ancestral lineage and probably at an early time. In the nymphs these adaptations include many modifications of the legs, head and body to burrow into shifting sand, and the modifications of the mouthparts for predaceous feeding. In the adults these adaptations include the elongated penes and male leg abscision. Tshernova (1979) established *Archaeobehningia* for the fossil species *A. edmundsi* collected in Buryat A.S.S.R. from Mid or Upper Jurassic strata. She noted the head and legs of the fossil nymph resembled those of extant Behningiidae; however, the placement of *A. edmundsi* into the Behningiidae is debatable.

Fig. 14 represents the phylogeny of the three extant genera of the Behningiidae. The phylogeny is based on an analysis of both nymphal and adult character states using methods of phylogenetic systematics. Out group comparisons included various genera of the Leptophlebiidae, especially the Leptophlebiinae, and the Ephemeroidea, especially the Polymitarcyidae. Table 1 lists character states used to prove monophyletic relationships.

Based on the known distribution of Protobehningia, the genus appears to be Oriental in origin. Tshernova (1958) concluded that the mayfly fauna of the Amur Intermediary Subregion contained elements of the Oriental Region. Bajkova (1979) and Levanidova (1982) have continued to study the mayfly fauna of the Far Eastern U.S.S.R., and Bajkova (1979) stated that Oriental species of Ephemeroptera extend north to the eastern parts of the Sajan mountains. A review of the keys to Ephemeroptera of the Far East U.S.S.R.

by Tshernova *et al.* (1986) indicated a number of tropical genera distributed from the Oriental Region to the Amur Intermediary Subregion [such as *Rhoenanthus, Choroterpes* (*Euthraulus*), and *Cincticostella*].

The evolution of the sister group (ancestor of *Dolania* and *Behningia*) to *Protobehningia* appears to have arisen in the Oriental Region or Amur Intermediary Subregion. *Behningia* is known from the Far East U.S.S.R. to Eastern Europe; Tshernova (1958), Levanidova (1982), and Tshernova *et al.* (1986) have listed many genera with similar distributions.

Dolania is known from the coastal rivers in the Southeastern United States. Peters (1988) discussed the vicariant distribution of some Leptophlebiidae between the Oriental Region and Eastern United States, and stated that such distributions correlate with the Arcto-Tertiary forest that covered most of the Northern Hemisphere, including *Beringia*, from the Early Tertiary into the Pleistocene.

ACKNOWLEDGMENTS

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Table 1. Explanation of character states of Behningiidae used in Fig. 14. Apomorphic condition indicated by dark oval.

No.	Character state	*Proto-behningia*	*Dolania*	*Behningia*
9.	Imago ♂. Length ratio penes:forceps.	● >2	● >2	O < 1.5
8.	Imago wing. Geminate vein pairs present.	O No	O No	● Yes
7.	Nymph. Galea-lacinia of maxilla ovoid.	O No	O No	● Yes
6.	Nymph. Length ratio labial palp 3:2.	O <1-1	O <1-1	● 1.5-2
5.	Imago wing. Fork of vein CuA lost.	● Yes	O No	O No
4.	Imago ♂. Basal forceps segment fused.	O No	● Yes	● Yes
3.	Nymph. Tibiae of hind legs reduced.	O No	● Yes	● Yes
2.	Nymph. Tarsi of fore legs fused to tibiae.	● Yes	O No	O No
1.	Nymph. Claws absent.	O No	● Yes	● Yes

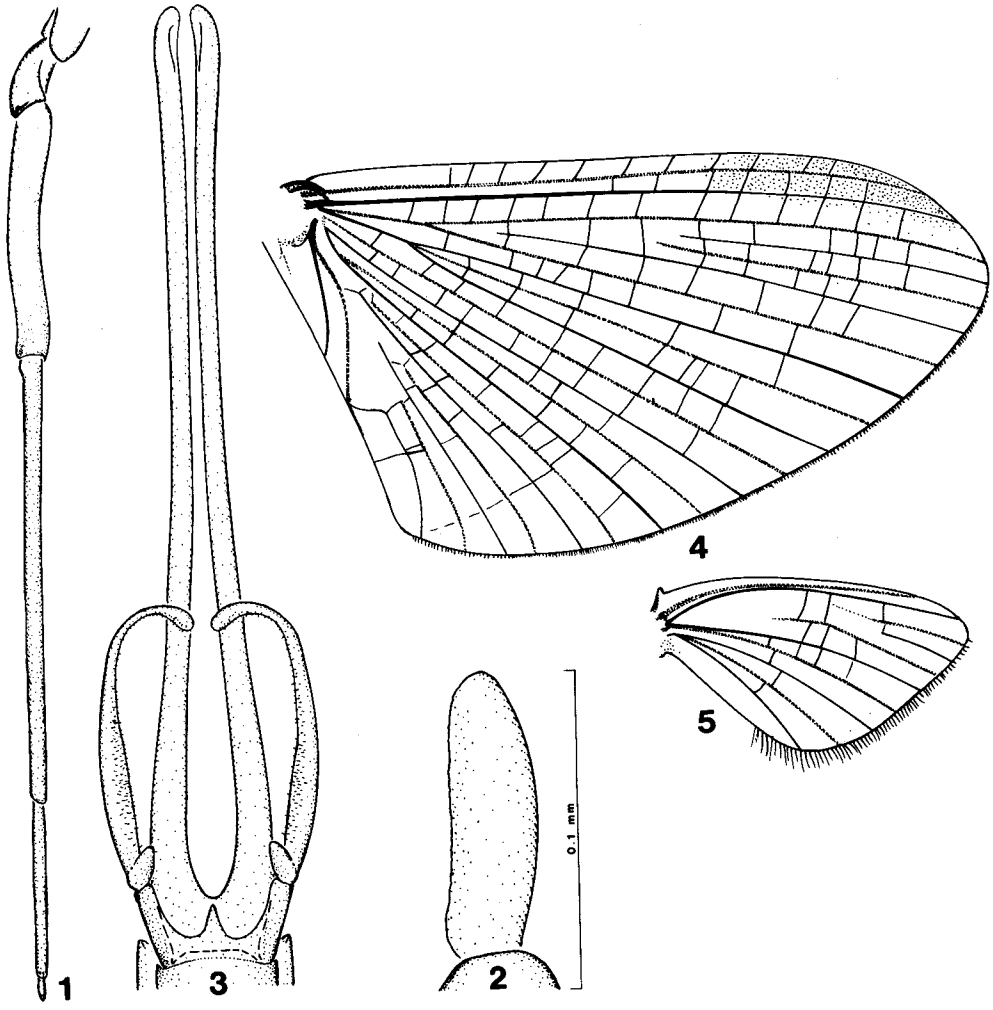

Fig. 1-5. Male imago of *Protobehningia merga* sp. n.: 1, fore leg; 2, fore claw; 3, male genitalia, ventral; 4, fore wing; 5, hind wing. Note: convex longitudinal wing veins are drawn with solid lines and concave veins with broken lines.

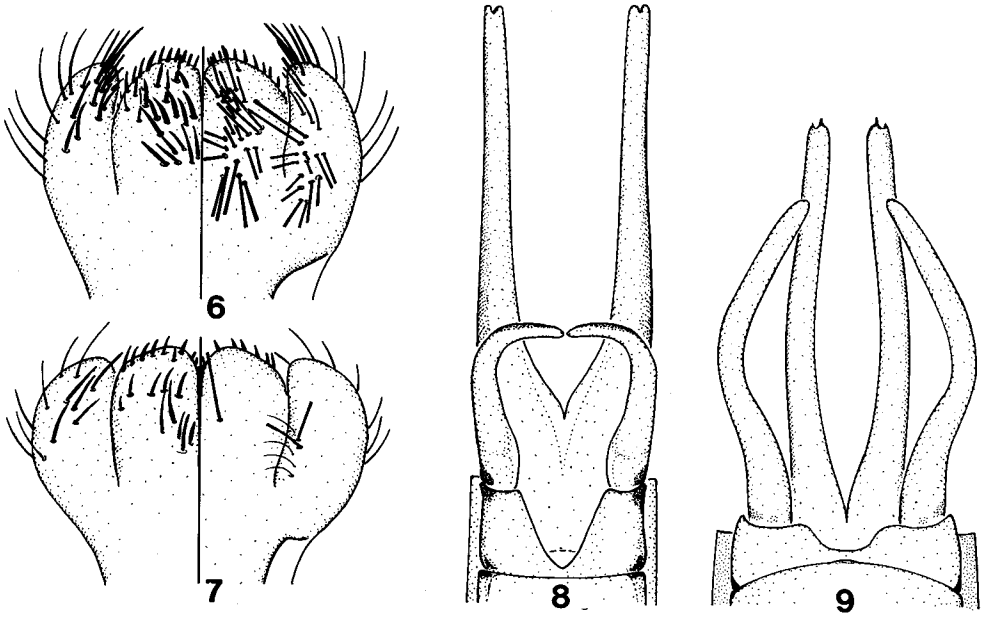

Fig. 6-7. Paraglossae and glossae of nymphs of Protobehningia (venter on right, dorsum on left): 6, P. merga; 7, P. asiatica. Fig. 8-9. - Ventral view of genitalia: 8, *Dolania americana* Edmunds and Traver; 9, *Behningia ulmeri* Lestage.

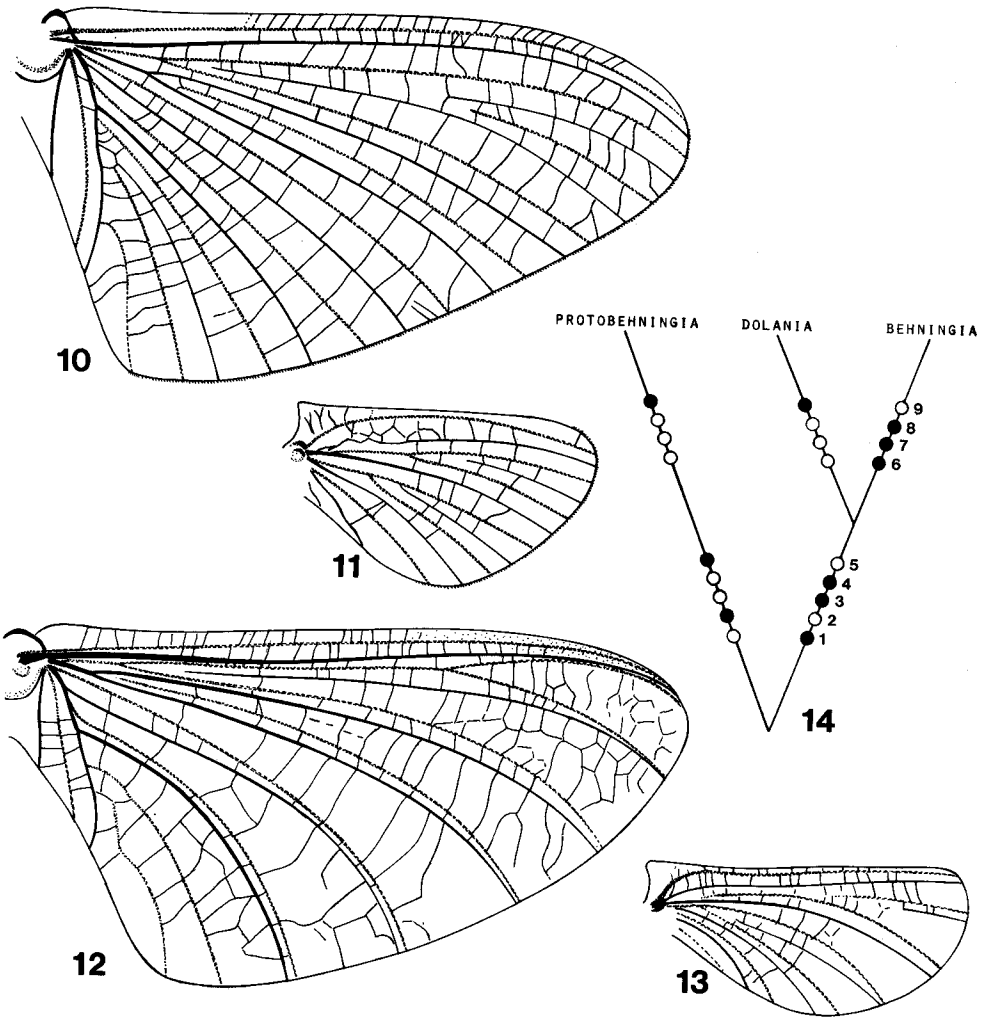

Fig. 10-13. - Fore and hind wings of adults of Behningiidae veins position as in Fig. 4-5): 10-11, *Dolania americana*; 12-13, *Behningia ulmeri*. Fig. 14. Cladogram of extant genera of Behningiidae.