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# THE CLASSIFICATION OF THE EPHEMEROPTERA
## I. EPHEMEROIDEA: BEHNINGIIDAE[1]

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ABSTRACT

The two previously known Old-World species of *Behningia* are reviewed. *B. ulmeri* Lestage is known from 2 nymphs from the Volga River of Russia, *B. lestagei* Motas and Becesco from 1 nymph from the Dniester River in Moldavian S.S.R. and 3 from the Warta River in Poland. The 2 adult males, 1 nymph, and 4 nymphal exuviae from the lower Amur River of Eastern Siberia, which Tshernova earlier referred doubtfully to *B. ulmeri*, are placed in *B.* **tshernovae**, n. sp. The first American representative of the family, **Dolania americana**, is described from four nymphs from the Savannah River and its tributaries in South Carolina. All these nymphs have remarkable adaptive features for burrowing in sand. The Behningiidae seem derived from potamanthid-like ancestors, and pertain to the superfamily Ephemeroidea. A new subfamily, Anepeorinae, is erected for the heptageniid genus *Anepeorus* whose nymphs, like those of Behningiidae, have truly ventral gills.

The mayfly family Behningiidae is one of the rarest and least known families of mayflies. The first known representative of the group was described by Georg Ulmer (1924) from two mature nymphs (one male, one female) collected June, 1922, in the Volga River by A. Behning. The mayfly was not named. Figures were given of the dorsal view of the whole nymph, antenna, developing genitalia of the male nymph, mouthparts, gills one and two, legs, and venation of the nymphal wing pad. Principally because of the incipient wing venation, Ulmer thought the nymph might be allied to the Oligoneuriidae, although he noted that the developing male

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genitalia resembled those of *Ephoron* (=*Polymitarcys*). Lestage (1929) named the nymph *Behningia ulmeri*, thus honoring both the discoverer and the describer. Little was added except to note the similarity of the gills to the Ephemeroidea, particularly Potamanthidae, to remark upon the unique combination of characters, and to suggest inclusion of the form in the Ephemeroidea.

In 1938, two papers of importance added to the knowledge of the genus. Motas and Bacesco described a female nymph of the genus from the Dniester River of Roumania (now Moldavian

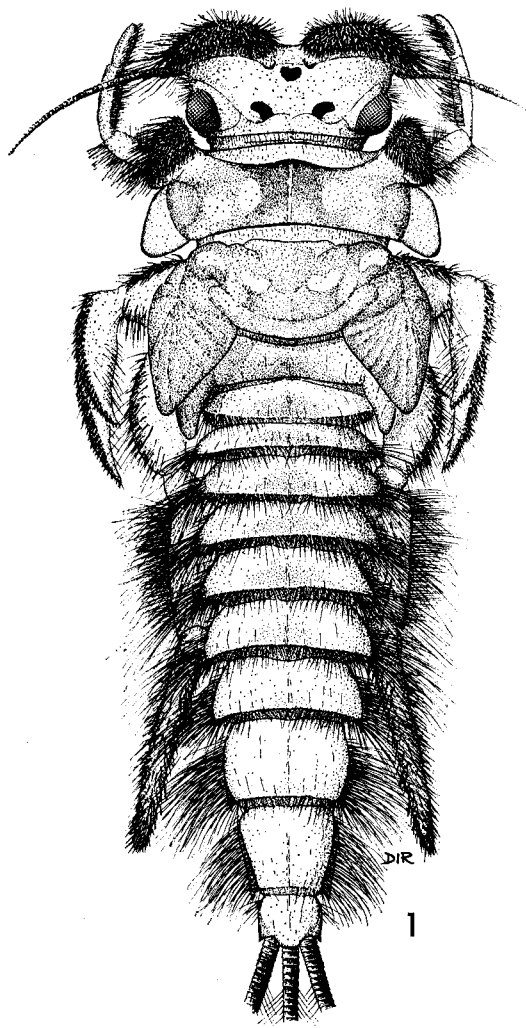



FIG. 1.—*Dolania americana*, dorsal view of female nymph, holotype. Gills not figured.

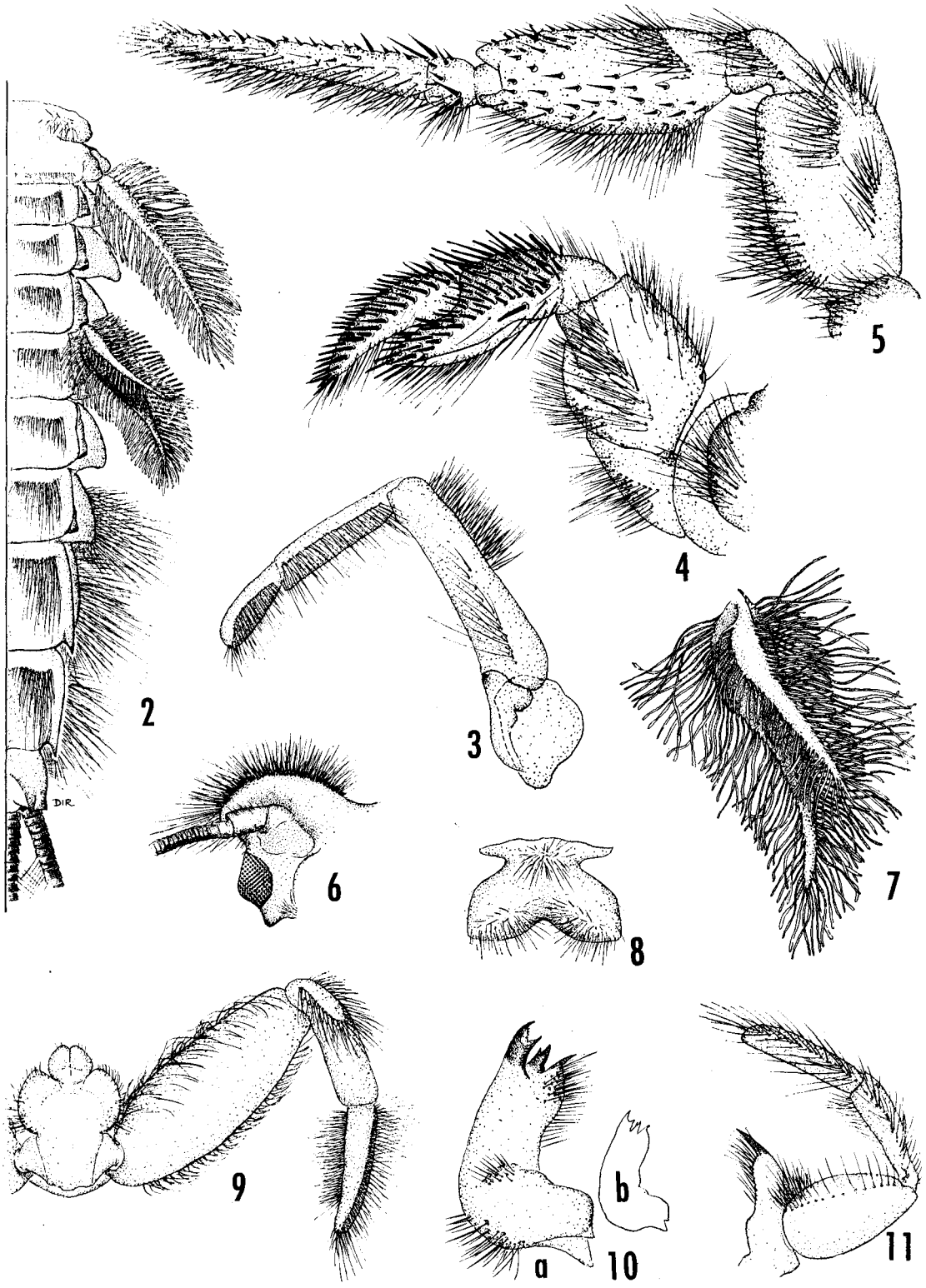
S.S.R.). They gave dorsal and ventral views of the nymph, and named it *Behningia lestagei*. Noting the unique combination of characters, they erected for the genus *Behningia* a separate family Behningiidae.

Tshernova (1938) reported a female nymph from the lower Amur River which she attributed with question to *Behningia ulmeri*, and also described two adult males which she thought were the same species as the Amur nymph. She noted a large number of characters common to the adult and nymph, of which the primary ones were the same postion of the ocelli on the posterior border of the head, the feeble legs of like structure, and the similarity between the genitalia of her male specimens and those figured for the developing nymph by Ulmer (op. cit.). She gave the figures of the adult which we have reproduced in this paper, and independently concluded from her material that the genus should be placed in a separate family, Behningiidae. We had been uncertain as to which of the two proposals of the family name had priority, but Dr. Tshernova (in letter) has informed us that the paper by Motas and Bacesco was published in January, 1938, and her own paper in April, 1938.

Later in this same year Lestage (1938) reviewed the genus and placed *Behningia* as a highly specialized nymph of the Oligoneuriidae, thus reducing the name Behningiidae to synonymy. Motas and Bacesco (1940) again reviewed the affinities of the genus and decided that *Behningia* deserved at least its own subfamily, Behningiinae, within the Oligoneuriidae. They repeated the earlier figures of *B. lestagei* and added the figures which we have reproduced here (figs. 13–21), as well as figures of gills one and two. Wesenberg-Lund (1943) has reproduced the dorsal and lateral views of the nymph of *B. lestagei* provided by Motas and Bacesco.

Tshernova (1952) gave notes and figures of the Amur nymph which she had previously referred with doubt to *B. ulmeri*, and recorded the collection of four cast nymphal exuvia from the Amur River. She also gave a table of comparison between the true *B. ulmeri* (of the Volga) and the Amur specimens doubtfully referred to that species.

*Demoulin* (1952) again reviewed the systematic position of *Behningia* and decided that it merits a separate family, Behningiidae, having common origin with the families Oligoneuriidae and Palingeniidae but greater affinities with the latter. Edmunds and Traver (1954) recognized family rank for the Behningiidae and included it within the Ephemeroidea, the same superfamily which contains the Palingeniidae, but placed it nearest the Potamanthidae; the Oligoneuriidae were placed in the superfamily Heptagenioidea. Demoulin (1955a) reaffirmed his views of the relationship of the Behningiidae and Palingeniidae, regarding the two families as having stemmed from the fossil family Mesephemeridae and considering the Oligoneuriidae as more remotely related. He has also published (1955c) a note in which he considers the possibility that the ventral gill position of *Behningia* is primitive rather than specialized. Keffermüller (1957) reported the collection of three young nymphs of *B. lestagei* from the Warta River of Poland.




FIGS. 2–11.—*Dolania americana*, paratype nymph. FIG. 2. Abdomen, ventral, showing gills one and four. FIG. 3. Prothoracic leg. FIG. 4. Mesothoracic leg. FIG. 5. Metathoracic leg. FIG. 6. Right side of head, ventral, showing insertion of antenna. FIG. 7. Gill two. FIG. 8. Labrum. FIG. 9. Labium, with left palpus, ventral. FIG. 10a. Mandible; b. outline to same scale as other mouthparts. FIG. 11. Maxilla.

In 1951 and 1952 Mr. Thomas Dolan, IV, collected five nymphs of Behningiidae from the Savannah River and its tributaries in South Carolina. (One of the nymphs could not be located for the present study.) These were forwarded to us for study. We advised Mr. Dolan to publish his find, but the press of his other duties prevented this and he later turned the material back to us with permission to publish the data. Demoulin (1955b) has indicated the presence of the family Behningiidae in North America from information contained in letters to him from Dolan and Edmunds. We feel certain that this North American form deserved generic rank, distinct from the Eurasian genus.

### Genus **Dolania,** new genus

*Adult.*—Unknown, except for the wing venation as determined from the nymph (figs. 31, 32).

*Nymph* (figs. 1–11).—Outer edge of mandibles sharply curved inward apically, a distinct spine present below the inner canine (fig. 10); maxillary galea-lacinia about one-third as wide as long (fig. 11); glossae of labium not fused; paraglossae wide, short and broadly attached to mentum (fig. 9). The short tibia of the metathoracic leg cylindrical and tarsus-like, as long as broad, coxa at least ⅕ as long as femur; tarsus only slightly longer than femur (fig. 5).

The genotype is the following species.

#### **Dolania americana,** new species

*Nymph* (fig. 1).—Length: body, 13; tails 7. General color light yellowish brown dorsally, yellowish white ventrally, with numerous dark goldenbrown hairs and spines (figs. 1, 2). Dorsum of head light yellowish brown, yellowish white ventrally, crown of spines dark-golden-brown; eyes and ocelli gray. Thoracic notum light yellowish brown, with paler pattern as indicated in figure 1, posterolateral flanges of pronotum paler. Prothoracic legs white with light yellowish brown setae (fig. 3). Mesothoracic and metathoracic legs yellowish white with brown articulation points and dark golden-brown setae and spines; some of spine-like setae on the legs vary according to the age of the nymph, being more tuberculate in older specimens (figs. 4, 5). Dorsum of abdomen yellowish brown; the lateral setae dark golden-brown (fig. 1). The sternites (fig. 2) pale with dark golden-brown setae; the point of insertion of each gill marked with a black tranverse streak. Gills pale, trachea unpigmented (figs. 2, 7). Cerci and terminal filament pale; pale setae occur on the medial edges of the cerci and both sides of the terminal filament except at the base, and on the outer edges of cerci in the apical half.

*Holotype.*—Female nymph, South Carolina, Upper Three Runs, 25 miles S. Aiken (near 1952 location of Highway S. C. 28), 1951, Thomas Dolan, IV, and S. S. Roback, deposited in Academy of Natural Sciences of Philadelphia. Paratypes, female nymph, South Carolina, Savannah River, 8 miles above Allendale Bridge, 1952, Dolan and Roback, in University of Utah; young (male?) nymph, South Carolina, Savannah River, groins above former site of Ellenton on the Aiken-Barnwell county border,9-VII-1951, Dolan, in Academy of Natural Sciences of Philadelphia; young (female?) nymph, South Carolina, Upper Three Runs near former site of Ellenton, 9-VII-1951, Dolan, in collection of Jay R. Traver (on slides).

### Genus **Behningia** Lestage

*Imago.*—Eyes simple, ocelli behind the eyes on the posterior edge of the head (fig. 29). The concave and convex veins of the disc of the fore-wing form geminate pairs (see fig. 24). Legs obsolescent (figs. 26–28), tarsal segments of prothoracic legs fused; the meso- and metathoracic legs reduced in size; tibiae and tarsi of mesothoracic legs fused. Forceps of male one-segmented; penes extend well beyond the forceps (fig. 30). Cerci long; median filament short.

*Nymph.*—Outer edge of mandible (fig. 18) sinuate, gently curved inward apically, no spine present below canines; maxillary galea-lacinia ovoid (fig. 17); glossae of labium (figs. 22, 23) fused to form an hexagonal plate, the paraglossae long and narrow. The tibia of the metathoracic leg (fig. 13) much shorter than broad; the coxae about half as long as femur; the tarsus more than twice as long as femur.

#### **Behningia ulmeri** Lestage

(Without name) Ulmer, 1924: 3–7, 6 figs.
*Behningia ulmeri* Lestage, 1929: 436.

This species was described and figured by Ulmer, and named by Lestage. We have redrawn Ulmer's figure of the labium (fig. 22).

*Distribution and Material.*—Volga River, by Myschkin (70 km. above Rybinsk), Russia, 23-VI-1922, A. Behning; two mature nymphs, one male, one female.

#### **Behningia lestagei** Motas and Bacesco

*Behningia lestagei* Motas and Bacesco, 1938: 25–29, 2 figs.; Motas and Bacesco, 1940: 78–90, 4 figs., 1 pl.; Wesenberg-Lund, 1943: 37, figs. 21–22; Keffermüller, 1957: 255.

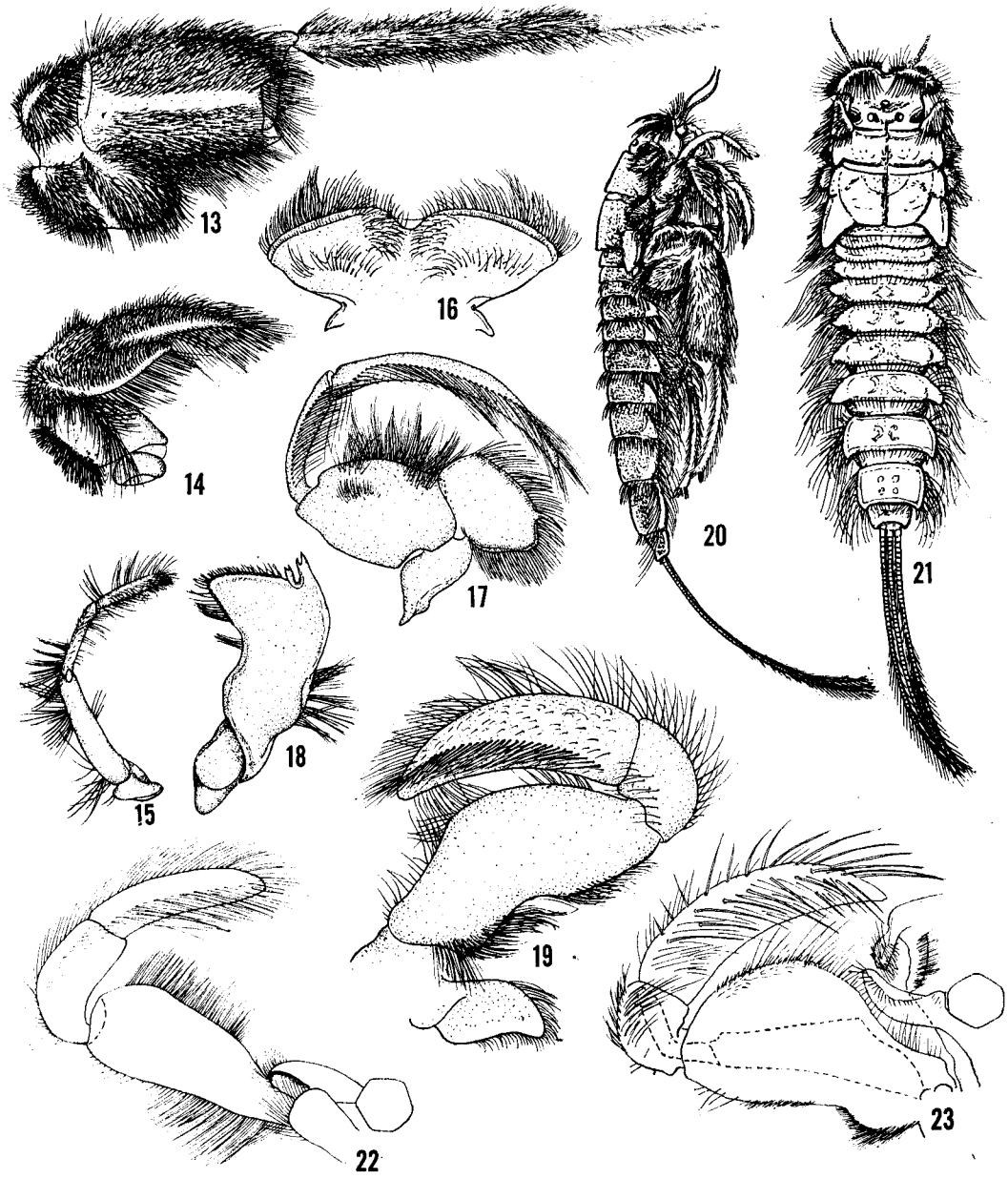
This species has been adequately described and discussed by Motas and Bacesco (1938, 1940). We have copied the drawings of the dorsal and lateral views (figs. 20, 21), the mouthparts (figs. 16–19), and the legs (figs. 13–15) of this species from their 1940 paper.

*Distribution and Material.*—Moldavian S. S. R. (formerly Roumania), Dniester River, Vadul lui Voda, 18 km. E. Kishinev (Dep. de Lapusna), 9-VI-1936, M. Bacesco; one female nymph. Poland, River Warta, Prov. Poznam, distr. Konin, 4-VIII-1955, M. Keffermüller; three young nymphs.

**Behningia tshernovae,** new species

*Behningia ulmeri* Lestage (?), Tshernova, 1938: 129–37, 4 figs.; Tshernova, 1952: 248–50, figs. 20–24.

This species is the only member of the family known in the imago stage (Tshernova, 1938). The nymphal stage is partially described by Tshernova (1952) and is compared in a table with *B. ulmeri* Lestage of the Volga. Both adult and nymph are questionably referred to *B. ulmeri*. The nymph of *Behningia tshernovae* from the Amur bears more similarity to *B. lestagei* than to *B. ulmeri*, but also seems to be distinct from the latter species. We have redrawn the labium of this species (fig. 23). Even though our knowledge of *Behningia* is still fragmentary, continued reference of the Amur form to *B. ulmeri* (which obviously it is not) or reference of the specimens to *B. lestagei* (which it also does not seem to be) can only lead to confusion. For this reason we take pleasure in naming the Amur form for




FIGS. 13–23.—*Behningia lestagei*, female nymph (after Motas and Bacesco, 1940, all except 20–21 redrawn). FIG. 13. Metathoracic leg. FIG. 14. Mesothoracic leg. FIG. 15. Prothoracic leg. FIG. 16. Labrum. FIG. 17. Maxilla. FIG. 18. Mandible. FIG. 19. Labial palpus. FIG. 20. Lateral view of whole nymph. FIG 21. Dorsal view of same. FIG. 22. *Behningia ulmeri*, nymph, labium with one palpus (redrawn from Ulmer, 1923). FIG. 23. *Behningia tshernovae*, nymph, labium with one palpus (redrawn from Tshernova, 1950).

Olga Tshernova. We are designating the male (one of two) figured by Tshernova (1938) as the type.

*Distribution and Material.*—U. S. S. R., Siberia, all from the lower Amur. Two male imagoes, mouth of Amur, Litvinzevo, B. K. Soldatov, 21-VII-1910; Amur River near Sophijsk, 10-VIII-1911, B. K. Soldatov, one nymph; Lower Amur, Nameless lake (Besimjamoye Ozero) (probably not standing, but flowing water), 28-VII-1946, one nymphal skin; at Malmizh, 1-VIII-1947, one nymphal skin; 1 km. above upper Tomborsk, 1-VIII-1946, one nymphal skin; 2 km. above village of M. Gorky, 28-VII-1946, one nymphal skin. The four nymphal skins are all from material collected by the Amur Ichthyological Expedition.

Family BEHNINGIIDAE Motas and Bacesco

*Imago.*—It is difficult to characterize the imago stage of the Behningiidae because *Dolania* is unknown in this stage. We have briefly characterized the known adult of *Behningia* under that genus. The only known feature of the adult of *Dolania* is the wing venation (figs. 24, 25), and this is strikingly different from that of *Behningia*. One unique feature in the wings of both genera is the strong divergence of $CuA_2$ from $CuA_1$ with the intercalary or intercalaries paralleling $CuA_1$. The forks of Rs and MA are very deep with MA being forked slightly more basally than Rs. (The venation of *Dolania* was reconstructed from the nymphal wing pad by examining the wing pad under a phase contrast microscope. One error inherent in this technique results from the fact that the tracheae and developing veins are often inseparable, and in several instances, particularly at the basal connections, the tracheae depart from the paths of developing veins. Therefore, the wings of *Dolania* may prove to be a little different than interpreted in figures 24 and 25.) The divergence of $MP_2$ and CuA from $MP_1$, which is a characteristic of the Ephemeroidea, is seen in wings of both genera but more clearly in *Dolania*. The great difference in venation of wings between *Behningia* and *Dolania* might be regarded as evidence that the similarities of the nymphs of the two genera are a result of convergence, or that the adult referred to *Behningia* is in reality a species of another genus. We feel that the similarities of the nymphs are a result of common ancestry, and that Tshernova (1938) was correct in referring the adult to *Behningia*. Indeed, the wing venation of *Behningia* is probably derived through specialization for speed flight from a wing much like that of *Dolania*. If there were several genera with venation intermediate between *Dolania* and *Behningia*, there would be no problem of classification of these two genera. For those who regard venation as some magic key to mayfly classification, the venation of the two genera may seem incongruous, and might even suggest to some that a new sub-family is necessary for *Dolania*.

*Nymph* (figs. 1–23).—Head flattened, the antennae inserted ventrally (fig. 6); the anterior margin with a pair of patches of spines and setae; three ocelli present; labrum emarginate medially; mandibles small, without a mandibular tusk; galea-lacinia of maxilla terminating in a spine, palpi three-segmented; labium with large three-segmented palpi. Anterolateral corners of pronotum produced and crowned with spines, the posterolateral corners produced; prothoracic legs palp-like; mesothoraic legs highly modified, the tibia and tarsus forming a spinous pad; metathoracic legs highly modified; all legs without claws. Abdominal tergites with dense, laterally extended setae and a row of setae on the posterior margin of each segment; sternites with setae; gills on segments one to seven, carried in a ventral position; all gills with fringed margins, the first gill single, the others with two branches. (In *Dolania*, young nymphs have gill one *shorter* than the gills of the middle segments, but in mature nymphs gills one is *longer* than the middle gills.) Cerci variable in length, the median filament as long as or nearly as long as the cerci.

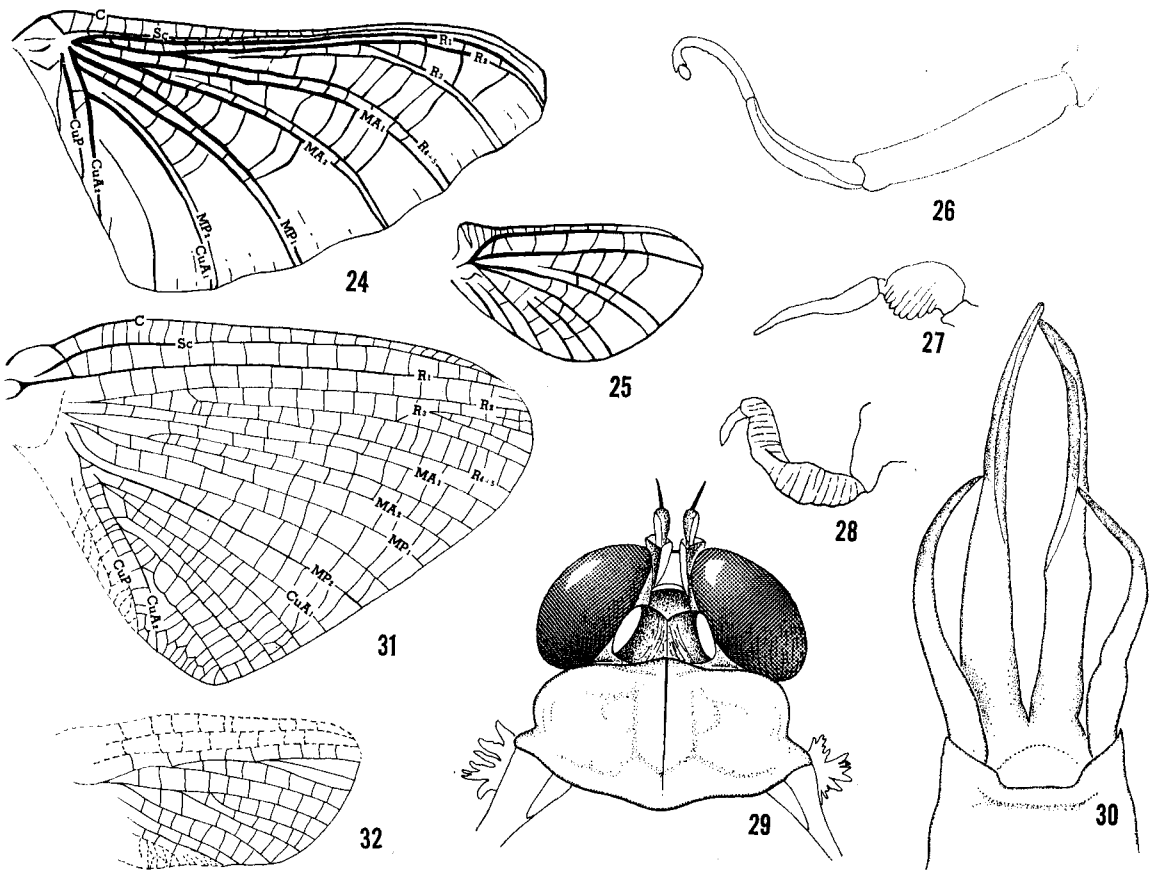
*Systematic Position.*—The systematic position of the family Behningiidae within the Ephemeroptera continues to remain uncertain, but the discovery of *Dolania* has clarified it somewhat, and the discovery of the adult of this genus will undoubtedly be of further aid.

The adult of *Behningia* and the incipient wing venation of the *Dolania* adult as seen in the nymph give some clues as to the relationship. The rearward sag of $MP_2$ and CuA, which is the classic trait of the Ephemeroidea (but also found in the Neophemeridae, superfamily Caenoidea as delimited by Edmunds and Traver, 1954), is present in the wings of both genera, indicating the affinity to other Ephemeroidea. We do not agree with Demoulin (1952, etc.) that the wing venation is evidence of a close relationship of Behningiidae to the Palingeniidae and to the Oligoneuriidae. Edmunds and Traver (1954b) have maintained that the reduction in venation and the gemination of veins is an adaptation for speed flight, and we have been, and remain, of the opinion that the reduction and gemination of veins in Oligoneuriidae, Palingeniidae, and Behningiidae represents three distinct phyletic lines. *Our reasons for this opinion are based on two impressive facts.* First, the occurrence of wings with very little or no gemination of veins in all three families (*i.e.*, *Palingenia longicauda* Olivier in the Palingeniidae, *Pseudoligoneuria feuerborni* Ulmer and/or *Chromarcys magnifica* Navas in the Oligoneuriidae, and *Dolania americana* in the Behningiidae) indicates that the gemination of veins has originated *after* the separation of the three families rather than in a common ancestor, unless one is to assume separate

evolutions to the non-geminate form in each family. Secondly, the diverse nymphal forms in each of these three families give no hint of close affinity; the differences are seen not only in adaptive structures but in basic conservative features.

Despite the adaptive features illustrated among the Oligoneuriidae, several features remain strikingly constant, e.g., the consistent shape of the mouthparts, with two-segmented palpi on maxillae and labium, the presence of maxillary gills, and the presence of long hairs on the forelegs. The evidence seems to be reasonably good that the Oligoneuriidae arose from the Isonychiinae of the family Siphlonuridae. The nymphs of the two groups share such common features as the long hairs on the forelegs, the presence of maxillary gills, and similar abdominal gills in some members of both groups (i.e. *Isonychia* and all Oligoneuriidae except *Homoeoneuria*). The mouthparts of the Oligoneuriidae are not strikingly different from *Isonychia*; the maxillae are more specialized, and the palpi are more flattened, the labium and its palpi are more flattened, and the mandibles are quite different. The genus *Pseudoligoneuria* is clearly an oligoneurid, but it has so many isonychiine features that Ulmer (1939) placed it in the family Siphlonuridae. *Pseudoligoneuria* shares the dorsal position of the gill on the first segment with *Isonychia* rather than a ventral position as in the other Oligoneuriidae. The wing venation appears intermediate between the isonychiine and oligoneuriid types, although known only from the nymphal wing pad. Perhaps *Chromarcys* is the adult of the nymphal *Pseudoligoneuria*, but even if this is so the figures of wing venation of *Chromarcys* by Navas (1932) seem to be of little value.

The nymphs of Palingeniidae are specialized burrowers with no similarity to any oligoneurid, but instead share many common features with the Polymitarcidae. The nymphs of both Palingeniidae and Polymitarcidae are specialized silt burrowers with very similar mouthparts in which the labial and maxillary palpi are two-




FIGS. 24–32.—Adult male of *Behningia tshernovae* (redrawn from Tshernova, 1938). FIG. 24. Forewing, with labels on veins added. FIG. 25. Hindwing. FIG. 26. Prothoracic leg. FIG. 27. Mesothoracic leg. FIG. 28. Metathoracic leg. FIG. 29. Head and prothorax. FIG. 30. Male genitalia. FIGS. 31–32. *Dolania americana*, venation of wings as determined from study of nymphal wingpads, dotted portions of veins highly questionable. FIG. 31. Forewing. FIG. 32. Hindwing.

segmented. The distinction between the nymphal stages of Palingeniidae and Asthenopodinae of the Polymitarcidae is hardly greater than that separating Asthenopodinae from Polymitarcinae [Eaton's (1883–88) figures of the nymphs of "*Palingenia*" are actually the genera *Asthenopus* or *Asthenopodes* from Brazil (pl. 25, figs. 20–24) and *Povilla* from Ceylon (pl. 25, figs. 1–19); true nymphs of Palingeniidae have been described by Schoenemund (1929), Gravely (1920), and Tshernova (1952).]

The nymphs of Behningiidae are so strikingly unusual that it is difficult to evaluate their relationship. The gills are, except for their ventral position, typical of the Ephemeroidea. In fact, such gills are remarkably constant in, and exclusive to, the Ephemeroidea. We do not attach great significance to ventral gill position because it appears that abdominal gills of all mayflies arise from the pleurae. The difference between the lateral gill positions of *Potamanthus* and the ventral position of the gills in *Behningia* is no more significant than the difference between the lateral gill positions of *Potamanthus* and the dorsal gill position of Ephemeridae, Polymitarcidae or Palingeniidae. All degrees of gill positions can be found among the various mayfly genera. In regard to Demoulin's (1955b) supposition that the ventral gill position of the family Behningiidae is primitive, it is interesting to note that the only mayflies with truly ventral abdominal gills (*Behningia*, *Dolania*, the supposed nymph of *Anepeorus*[4]) are specialized sand-dwellers, in which the ventral gill position gives protection from the molar action of sand and silt.

The mouthparts of the Behningiidae are reminiscent of some Ephemeroidea, although they are extremely specialized, especially in the enlarged palpi which are used in burrowing in the sand.

If as we believe, the Behningiidae are authentic members of the superfamily Ephemeroidea, one might expect that a hypothetical ancestral nymph of this family would have approximately the following features. It would probably have been an unspecialized dweller on the surface of a sandy bottom, with unmodified legs, mandibles with a moderately developed tusk or none at all, maxillary and labial palpi three-segmented, and with lateral gills of the Ephemeroidea type. Such a mayfly nymph would not be expected among living forms, but such a form as *Potamanthus luteus* Linn. is probably not too unlike the possible ancestor of the Behningiidae. Certainly the burrowing Palingeniidae and Polymitarcidae with specialized fossorial legs, large mandibular tusks, two-segmented maxillary and labial palpi, and dorsal gills give little suggestion of either ancestry or close relationship to Behningiidae. The Ephemeridae are also specialized silt burrowers which equally show little suggestion of ancestry or relationship to the sand-burrowing Behningiidae; however, some members do have three-segmented maxillary and labial palpi. The more primitive Euthyplociidae are not too unlike the probable ancestor of Behningiidae, but they have very well developed mandibular tusks. We conclude that, among living forms, the primitive Potamanthidae with very small mandibular tusks are most likely to be the closest living relatives of the Behningiidae.

The following key will serve to distinguish the nymphs of the species of Behningiidae. The adult stage is described only for *Behningia tshernovae*, new species.

KEY TO THE SPECIES OF NYMPHS OF THE BEHNINGIIDAE

1. Coxae of metathoracic legs about four-fifths as long as femora (fig. 5); paraglossae broader than long (fig. 9) (*Dolania*, new genus) ..... **Dolania americana,** n. sp.
   Coxae of metathoracic legs about one-half as long as femora (fig. 13); paraglossae much longer than broad (figs. 22, 23) (*Behningia* Lestage) ..... 2
2. Second segment of labial palpi at least two-thirds as long as third (fig. 22); Volga River ..... **Behningia ulmeri** Lestage
   Second segment of labial palpi less than one-half as long as third (figs. 19, 23) ..... 3
3. First segment of labial palpi shaped as in figure 23; Amur River ..... **Behningia tshernovae,** n. sp.
   First segment of labial palpi shaped as in figure 19; Dniester and Warta rivers ..... **Behningia lestagei** Motas and Bacesco

## Biology of the Behningiidae

The nymphs of Behningiidae are apparently adapted for burrowing in sand. In all accounts of the family, it appears that the collections were made from large rivers or tributaries with sandy bottoms. According to Mr. Dolan, one of the nymphs of *Dolania* was collected in silt near the stream margin, but the regular habitat for both *Dolania* and *Behningia* is probably in moderately clean sand in fairly swift current. Keffermüller (*op. cit.*) remarks that the nymphs of *Behningia lestagei* were collected "in a place with strong current, from sandy bottom at a depth of 1–2 m."

Mr. Dolan has kindly supplied us with some notes on the behavior of *Dolania* which were given by him at the 15th annual meeting of the American Society of Limnology and Oceanography at Ithaca, New York, September 9, 1952. We are taking the liberty of publishing some of these notes as follows:

"In transporting the specimen from the field to the laboratory, I was able to observe how well its external structure fitted it to its environment.

"Placed in a gallon bottle of water, the nymph immediately swam for the glass bottom and remained there head-down on a 60° to 70° angle, attempting to burrow in.

[4]We believe that Burks (1953) correctly assigned this unusual nymph to the genus *Aneperous*. This genus is an authentic heptageniid, but certainly it should be in a separate subfamily. Therefore, we propose for it the new subfamily *Anepeorinae*.

"Placed in a jar half full of sand, it immediately disappeared beneath the sand, not to appear again until it reached a wall of the bottle. Here it traveled along, burrowing in full sight.

"The forward motion was effected by the burrowing action of fore legs, and elongated labial and maxillary palpi. These extended forward through the notch between the head prolongations. With head tucked under slightly these prolongations acted partly as bulldozer blade, and in part to protect the mouthparts and the eyes which were further shielded by the lateral prolongations of the prothorax.

"The thoracic prolongations and drawn-up chelipod-like middle legs completely boxed in the ventral anterior bulky half of the animal, thus increasing its efficiency as a burrower. Trailing hind tibia and tarsi lie just below ventral rows of gills, maintaining a space free of sand at all times in which the gills could move.

"The long red-brown hair may well act as a cushioning effect from the pressure of the sand, as well as an anti-abrasive to the wearing action of the sand grains."

We believe that probably another important function of the hair on the nymph is to exclude sand but to let water enter to the ventral gill area.

The biology of adult stages of the Behningiidae is unknown. The wing and leg structure of the adult of *Behningia* suggests that it is a rapid-flying, short-lived form. We can only speculate as to the nature and biology of the adult of *Dolania*.

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REFERENCES CITED

**Demoulin, G.** 1952. Les *Behningia* Lestage 1929, et leur position dans la classification des Éphémères. Inst. Roy. Sci. Nat. Belgique. Bull. 28(21): 1–15, 5 figs.

1955a. Contribution à l'étude morphologique, systématique et phylogénique des Éphéméroptères Jurassiques d'Europe Centrale. I. Mesephemeridae. Inst. Roy. Sci. Nat. Belgique. Bull. 31(39): 1–13, 1 pl.

1955b. Contribution à l'étude des Éphéméroptères Jurassiques d'Europe Centrale. III. Phylogénie et zoogéographie. Mém. Soc. Ent. Belgique 27: 176–86, 6 maps.

1955c. À propos de la position ventrale des trachéobranchies chez la larva des Behningiidae (Ephemeroptera). Bull. Ann. Soc. Roy. Ent. Belgique 91: 207–208.

**Edmunds, G. F., Jr.,** and **J. R. Traver.** 1954. An outline of a reclassification of the Ephemeroptera. Proc. Ent. Soc. Washington 56: 236–40.

1954b. The flight mechanics and evolution of the wings of Ephemeroptera, with notes on the archetype insect wing. Jour. Wash. Acad. Sci., 44: 390–400, 14 figs.

**Gravely, F. H.** 1920. Notes on some Asiatic species of *Palingenia*. Rec. Indian Mus. 18: 137–43, pls. 18–20.

**Keffermüller, M.** 1957. Some rare species of may-flies (Ephemeroptera) in Poland. Fragmenta Faunist. Polska Akad. Nauk, Inst. Zool., 7: 254–62. [In Polish; English summary.]

**Lestage, J. A.** 1929. Contribution à l'étude des larves des Éphéméroptères V. Les larves à trachéobranchies ventrales. Bull. Ann. Soc. Ent. Belgique 69: 433–40.

1938. Contribution à l'étude des Éphéméoptères XIX. L'inclusion des Behningiidae parmi les Oligoneuriidae. Bull. Ann. Soc. Ent. Belgique 78: 315–19.

**Motas, C.,** and **M. Bacesco.** 1938. La découverte en Roumanie d'une nymphe d'Éphémère appartenant au genre *Behningia* J. A. Lestage 1929. Ann. Scient. Univ. Jassy 24: 25–29, 2 figs.

1940. Notes complémentaries sur la nymphe de *Behningia lestagei* Motas 1937, trouvée en Roumanie. Ann. Scient. Univ. Jassy 26: 78–90, 4 figs., 1 pl.

**Schoenemund, R.** 1929. Beitrag zur Kenntnis der Nymphe von *Palingenia longicauda* Oliv. Zool. Anz. 80: 106–20, 6 figs.

**Tshernova, O. A.** 1938. Sur une nouvelle famille d'Ephemeroptera. Bull. Acad. Sci. U. R. S. S., Sér. Biol., 1938: 129–37, 4 figs.

1952. Podenki (Ephemeroptera) basseina reki Amura i prilejashtchich vod i ich rol v pitanii amurskich rib. Trudi Amurskoi ichtiolog. ekspeditskii 1945–1949 gg., 3: 229–360, 21 pls. (141 figs.).

**Ulmer, G.** 1924. Eine merkwürdige Ephemeriden-Nymphe aus der Wolga. Arb. Biol. Wolga-Station 7: 3–7, 6 figs.

**Wesenberg-Lund, C.** 1943. Biologie der Süsswasserinsekten. Copenhagen: Gyldenalske Bogenhandel, and Berlin: J. Springer. (11)+682 pp., 13 pls., 501 figs.