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NORTH AMERICAN MAYFLIES OF THE FAMILY OLIGONEURIIDAE[1]

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ABSTRACT

Present knowledge of the family in this continent is reviewed, and a key is given to its two North American genera, both as nymphs and as adults. Males from Kansas are described as probable adults of *Homoeoneuria ammophila* (Spieth), originally described in *Oligoneuria* from nymphs taken in Indiana and later found also in Illinois. Adults and nymphs of *H. dolani*, n. sp., are described from Georgia and South Carolina, chiefly from the Savannah River. *Homoeoneuria* nymphs, unassociated with adults and not identifiable to species, have been collected in Florida, Mississippi, Texas, and Nebraska. The genus was first known from Guatemala. In its body form and legs the nymph strongly resembles the Russian genus *Oligoneurisca*, but its distinct nature and the unique absence of forceps indicate that *Homoeoneuria* occupies an isolated position within the family. The nymphs are inhabitants of larger streams, where they live buried in the shifting sand bottom; some observations on their activities are included. Adults emerge from early June through late October. *Lachlania saskatchewanensis* Ide and *L. powelli* Edmunds, the other North American representatives of the Oligoneuriidae, are briefly discussed.

At the time of Traver's (1935) revision of the North American mayfly fauna, the family Oligoneuriidae was not known from North America north of Mexico. In the present paper we record two genera and several species from ten states and one Canadian province. The members of this family are easily identified in both nymphal and adult stages. The adults are readily recognizable by the unique wings in which cross venation is greatly reduced or absent, intercalary veins are reduced or absent, and the concave veins are hidden beneath the convex veins to give the appearance of a greatly simplified wing (figs. 10 and 30). The males are unusual in that the fore legs (fig. 7) are *shorter* than the middle or hind legs (figs. 5 and 6). The nymphs (figs. 15 and 31) resemble *Isonychia* (Siphlonuridae: Isonychiinae) in having long setae on the femur and tibia of each fore leg, but may be immediately distinguished by the much smaller gills on segments two to seven, and by the ventral position of the gills on segment one. The North American genera of Oligoneuriidae may be distinguished by the following key.

1. Adult 2
   Nymph 3
2. Terminal filament present and as well developed as the cerci; veins R_3+IR_3 not present in forewing, thus the wing has only three apparent longitudinal veins in the disc (fig. 10); male lacking genital forceps (fig. 4) . . . . . **Homoeoneuria** Eaton
   Terminal filament lacking, only the two cerci present; veins R_3+IR_3 present in forewing, thus the wing has four apparent veins in the disc (fig. 30); males with genital forceps . . . . . **Lachlania** Hagen
3. Lamellate portion of gills on segments two to seven oval, fibrilliform portion well developed; ventral first gill similar to others; coxae of metathoracic legs much smaller than femora (fig. 31) . . **Lachlania**
   Lamellate portion of gill on segments two to seven lanceolate, fibrilliform portion wanting (figs. 24 and 25); ventral fibrilliform portion of first gill greatly enlarged (fig. 23); coxae of metathoracic legs larger than femora (fig. 29) . . . . . **Homoeoneuria**

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Genus **Homoeoneuria** Eaton

The genus *Homoeoneuria* was described by Eaton (1881) from females of *H. salviniae* collected at Dueñas (4950 feet elevation), and at Aceytuno (5100 feet elevation), Guatemala. Subsequently Eaton (1892) added some notes, but the genus remained unmentioned for many years.

Spieth (1937) reported an unusual oligoneurid nymph from the White River at Decker, Indiana, the first record of the family in North America. After he collected additional specimens he named this form *Oligoneuria ammophila* (1938). Burks (1953) reported the same species in Illinois.

In the summer of 1951, Edmunds secured two cast skins of nymphs at Kearney, Nebraska, that were very similar to *Oligoneuria ammophila*. From raised ridges on the wing pads of these nymphal exuviae it was possible to reconstruct the very characteristic wing venation of the genus and the unique absence of forceps, it would appear that *Homoeoneuria* occupies an isolated position within the Oligoneuriidae. The absence of the forceps is not due to their loss in preserved material, for they are missing from all our specimens and the developing genitalia of the nymph also confirm their complete absence.

The absence of genital forceps (fig. 4) and the shape of the hind legs, with their strongly bowed coxae and femora (fig. 5), indicate that the female must be held by these legs during mating. Further, the presence of short, coarse, curved spines on the inner surfaces of the femur and tibia provide additional support for this conclusion. It is likely that the legs are swung dorsally so that the femora can embrace the female abdomen, and at the same time the spines of the femora and tibiae prevent slipping. The large, bulb-like claws (fig. 8) with their pubescent surface also may assist in holding the mating insects together as they do in *Lachlania*.

FIG. 1. The Homochitto River, Mississippi, at June, 1956, level showing exposed sand bed. That part of the bed covered with water was similar to the exposed portion.

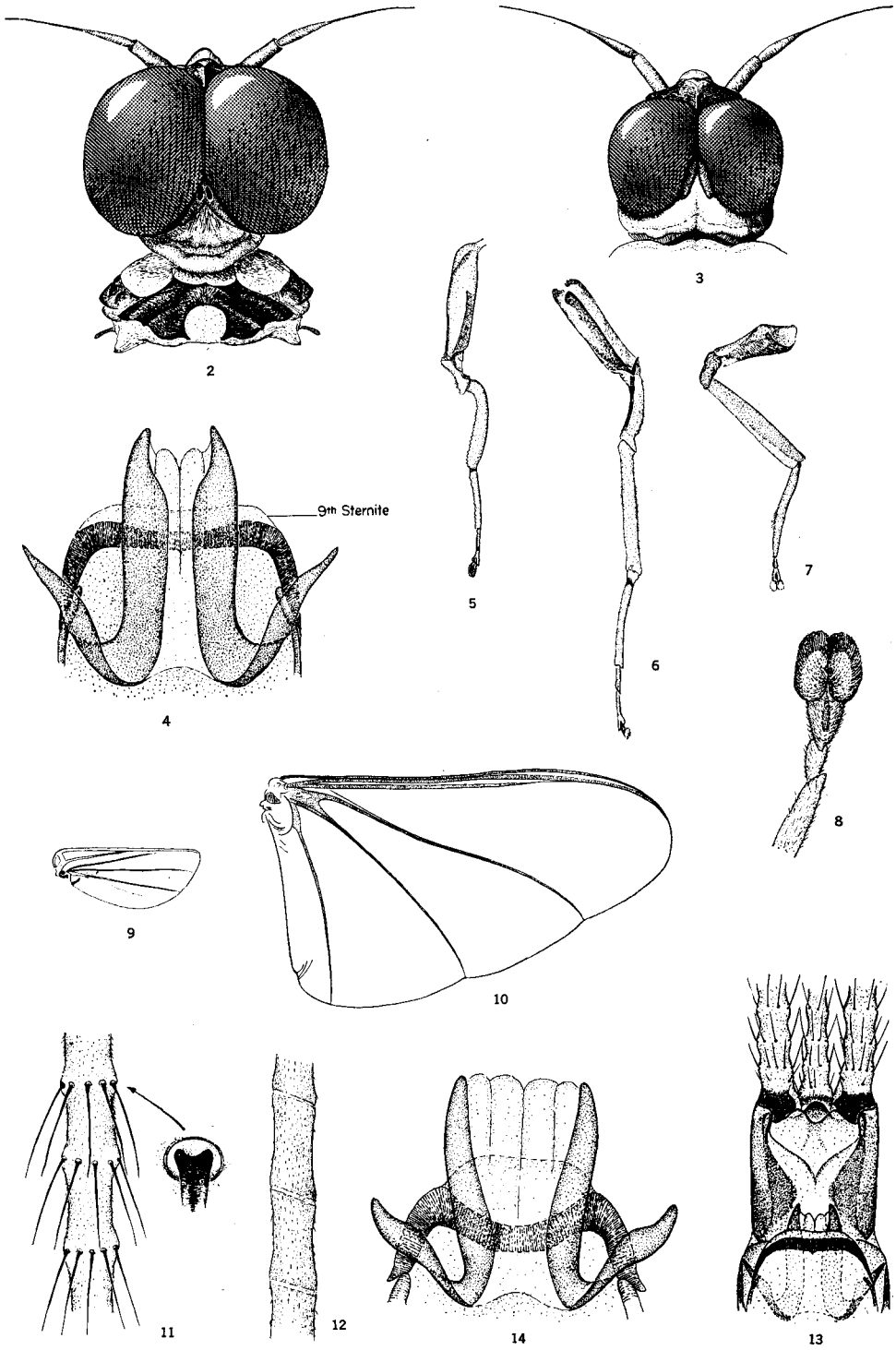
Homoeoneuria, and *ammophila* was subsequently transferred to that genus by Edmunds and Allen (1957: 318).

In the summer and fall of 1951, while surveying the Savannah River in Georgia and South Carolina, Thomas Dolan IV and Selwyn S. Roback collected a number of adults of this genus from the surface of the river's waters and also collected nymphs from the river. Since 1951, nymphs or adults of *Homoeoneuria* have been collected also from various localities in Georgia, South Carolina, Florida, Mississippi, Texas, and Kansas.

Because of the distinct nature of the nymph

The wing venation of *Homoeoneuria* (fig. 10) is the most reduced of any in the order but is most similar to that of *Elassoneuria*, the two sharing the feature of the absence of R_3 and IR_3. The nymph of *Elassoneuria* (Lestage 1916, and Ulmer 1920) is quite unlike that of *Homoeoneuria*, with little suggestion that *Homoeoneuria* and *Elassoneuria* are closely related.

The nymph of the Russian genus *Oligoneurisca* bears a great resemblance in body form and legs to that of *Homoeoneuria*, and may be closely related, although the similarity might be a result of convergent evolution. The incipient wing



FIGS. 2 to 13.—*Homoeneuria dolani*, imago paratypes.

FIG. 2.—Head and prothorax of male, dorsal view.
FIG. 3.—Head of female, dorsal view.
FIG. 4.—Male genitalia, dorsal view.
FIG. 5.—Male metathoracic leg.
FIG. 6.—Male mesothoracic leg.
FIG. 7.—Male prothoracic leg.
FIG. 8.—Detail of prothoracic claw of male.
FIG. 9.—Male metathoracic wing.
FIG. 10.—Male mesothoracic wing.
FIG. 11.—Detail of male cercus.
FIG. 12.—Detail of female cercus.
FIG. 13.—Male terminalia, ventral view.

FIG. 14.—*Homoeoneuria ammophila* (Spieth)?, male genitalia, dorsal view.

venation is reminiscent of *Oligoneuriella*, but if the first two apparent veins in Tshernova's (1937) drawing are actually C and R_1, then the wing venation would be very similar to that of *Homoeoneuria*. Although this is possible, it does not appear likely; an adequate knowledge of the venation will have to await adults of *Oligoneurisca* and a more thorough study of all the genera in the family.

The taxonomic relations within this genus are difficult because of the fragmentary nature of most collections. We are able to distinguish two species of adults which are recognizable only on the basis of minor differences in color and the male genitalia. After careful examination of nymphs from all localities, we have been unable to find any characteristics for separating them.

Even though we are unable to distinguish the nymphal forms, we feel that it is best to consider the Savannah River forms as being a separate species. It is probable that the males which we have from Kansas represent the adults of *H. ammophila* Spieth, and these are certainly not conspecific with the Savannah River specimens.

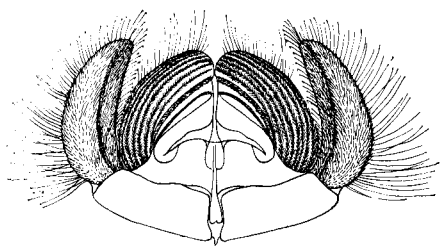
Homoeoneuria dolani, new species

Male imago.—Length: body 8–9; wing 6–7; terminal filament and cerci 7–8 mm. *Head:* Dark brown; eyes dark brown, contiguous dorsally (fig. 2); antennae placed very near the nasal carina. *Thorax:* Prothorax very short, dark brown; the postero-lateral areas membranous; a finger-like projection extends from near the lateral margin; a large circular pale spot on the mid-line based on the posterior margin but not attaining the anterior margin; postero-lateral corners pale; these three pale areas connected by a narrow pale posterior edge (fig. 2). Meso- and meta-thorax fuscous with extensive pale membranous areas at the leg bases and at the wing bases. Inner parapsidal furrows of mesonotum pale, narrowed anteriorly and mostly closed, a pale transverse stripe connects the two furrows, thus forming a pale, roughly H-shaped mark, a small tapering median stripe extends caudad a short distance from the transverse stripe; the outer parapsidal furrows pale, but somewhat obsolescent at and anterior to the wing base. *Legs:* Fore legs (fig. 7) shorter than middle or hind legs; tarsi two segmented; femora dark brown, ventral (posterior) edge pale; tibia and tarsus pale brown, darkest dorsally; claws (fig. 8) large and bulb-like, similar, pale brown. Middle and hind legs (figs. 5 and 6) light brown, darkest dorsally; femora darkest, with pale ventral and dorsal edges; tarsi three-segmented. *Wings:* Bright reflection of blue or purple may show in alcoholic specimens; reflections probably evident in living specimens. Venation as in figures 9 and 10; medium brown. Microchaetae cover the base of the fore wing, the costal border, all veins, and the posterior edge, while the membrane between the veins is covered with microtubercules. The entire surface of the hind wing is covered with microchaetae. *Abdomen:* Abdominal tergites uniformly dark brown; a dark narrow stripe near the pleural and posterior margins and on the anterior margin, a pair of submedian dark streaks or spots near the middle of each tergite; these better developed on the anterior tergites. Abdominal sternites one to eight considerably paler than tergites, the edges slightly darker; paired submedian markings consist of pale streaks or spots outlined in dark brown, on the anterior sternites these are largely streaks with one or two detached spots, on subsequent sternites the streak breaks up into spots; tergites slightly paler between these markings; sternite nine with the anterior part dark brown, the posterior part pale, margins dark, sternite ten dark with pale central area; penes as in figures 4 and 13; no genital forceps present. Cerci and terminal filament light brown with conspicuous setae at each joining (fig. 11).

Female imago.—Length: body 9–10; wing 7–8; tails 2–3 mm. *Head:* Similar to that of male; eyes considerably smaller, contiguous dorsally (fig. 3). Thorax similar to that of male. Legs twisted and obsolescent.

Abdominal tergites similar to those of one to eight of male, but paler. Sternites similar to those of one to eight of male, but with median line paler and limited by poorly defined spots and streaks. Tails brown, darker than those of male, without setae (fig. 12).

Nymph.—Spieth's (1937) description of *H. ammophila* adequately covers the characteristics of *H. dolani* except in a few details, which are as follows: *Length:* Mature female nymph—body 11.5 mm., caudal filaments 3.2 mm.; mature male nymph—body 9.5 mm., caudal filaments 2.2 mm. *Head:* Median carina present between the antennal bases. In ventral view, when the forelegs are pulled forward, the multibranched gills of the maxillae can be seen projecting posteriorly between the bases of the legs to form a dense clump of white, thread-like structures protected by the very thick, overlaying labium. Mouthparts (figs. 16–22) are so large that they project posteriorly to the bases of the mesothoracic legs, forming a large and conspicuous clump under the head. *Legs* (figs. 27–29): Tibia of prothoracic leg strongly bowed with the proximal portion curved so that it fits into a groove in the femur. The groove of the fore femur extends almost the entire length of the ventral surface, but is deepest in the distal half, just before the origin of the long fringing hairs on the proximal half of this leg segment. At the angle of the curve of the tibia, it arches down in such a way that the long hairs bordering its inner surface are brought directly below the mouthparts so that when the tibia is folded into the femoral groove, the hairs of the tibia and of the femur form a continuous band. Thus a mass of hairs is brought directly under the mouth. *Abdomen:* Coloration of abdominal segments rather variable,



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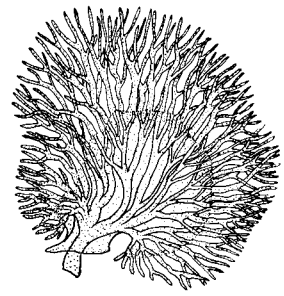

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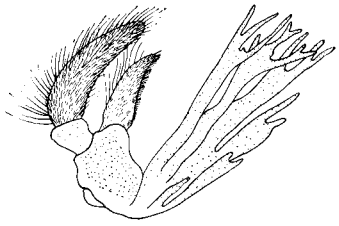

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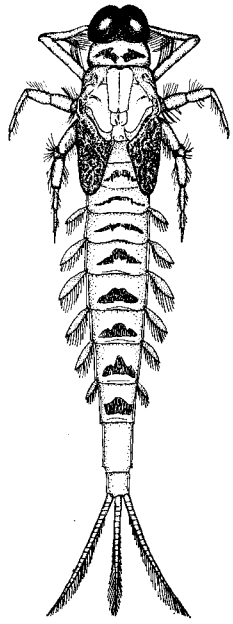

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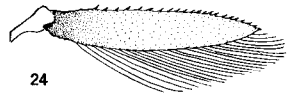

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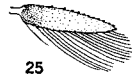

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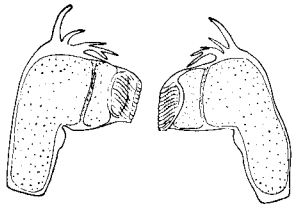

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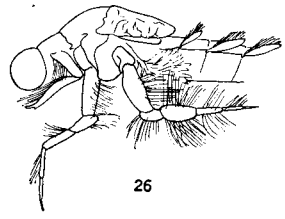

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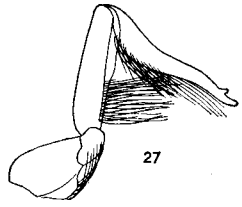

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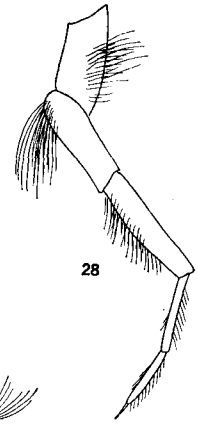

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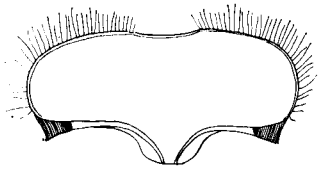

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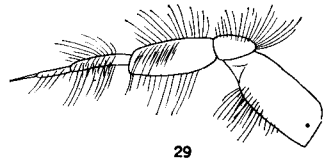

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FIG. 15 to 29.—*Homoeoneuria* sp., nymph, from Homochitto River, Mississippi.

FIG. 15.—Male nymph, dorsal view.
FIG. 16.—Labium, ventral view.
FIG. 17.—Left maxilla with attached gill.
FIG. 18.—Left mandible.
FIG. 19.—Right mandible.
FIG. 20.—Lacinia mobilis and canines, left mandible.
FIG. 21.—Lacinia mobilis and canines, right mandible.
FIG. 22.—Labrum.
FIG. 23.—First gill.
FIG. 24.—Fourth gill.
FIG. 25.—Seventh gill.
FIG. 26.—Anterior portion of nymph, lateral view.
FIG. 27.—Prothoracic leg.
FIG. 28.—Mesothoracic leg.
FIG. 29.—Metathoracic leg.

some nymphs virtually lacking the brown bands on the tergites, while they are broken in others. Dorsally, there is a covering of short spines rather heavily distributed over the entire surface, exclusive of the portion of the tergites overlaid by the gills. The sternites, except for that of segment one, are covered by long hairs, sharp spines, or both. On sternites two, three, and four there are long, posteriorly-directed hairs; those on two and three so arranged that they form a U-shaped pattern with the opening of the U directed anteriorly. The hairs on sternite two are concentrated at the postero-lateral angles, while on sternite three they are present along the lateral and posterior margins. There are also a few small spines present on sternite three. Sternite four has hair-like spines on the posterior margin and the postero-lateral angles of the segment. (This pattern of hairs and hairlike spines concentrated near the first pair of gills may form a protective covering to keep silt and trash away from them.) Other sternites covered with short, coarse spines, and sublateral rows of long hairs. The rows of hairs become sparser posteriorly and are absent from segments nine and ten. Median portion of posterior border of sternite nine prolonged posteriorly; the prolongation excavated with the lateral corners of the excavation terminating in spines. Between the spines there is a row of short spinules. Gills two to seven margined (figs. 24 and 25) on outer edge with short spines; inner edge bordered with long hairs.

Holotype. GEORGIA: Savannah River, October 20, 1951, T. Dolan IV and S. S. Roback (UU).[5] *Allotype.* Same data. *Paratypes.* GEORGIA: Savannah River, July 9 (UF) and 22 (UF, UU) 1952, adults, collected by D. C. Scott; August 27, 1955, nymph (ANSP), September 2 (UF), June 28, 1951 (JRT, UU), October 20, 1951 (UU, ANSP), adults, collected by T. Dolan and S. S. Roback; November 2, 1951, nymphal exuviae, collected by T. Dolan IV and S. S. Roback (ANSP); Savannah River, Brigham's Landing, August 27, 1955, nymph, collected by S. S. Roback (ANSP). SOUTH CAROLINA: Greenville County, South Saluda River, July 28, 1953, nymph, collected by M. J. Westfall (UF); Savannah River, 8 miles above Allendale Bridge, August 21, 1955, nymph, collected by S. S. Roback (ANSP).

Homoeoneuria ammophila (Spieth)

The description and figures of the nymph of this species are given by Spieth (1938: 1). We have found no way to distinguish the nymphs of the two (or more) species that we have studied. Further study of reared or associated material will probably result in the discovery of distinguishing characteristics.

Records.—INDIANA: White River, Hazelton, June 16, 1936, nymphs, collected by H. T. Spieth (AMNH); White River, Decker, July 27, 1932, nymph, collected by S. Denham. ILLINOIS: Hillsdale, Rock River at mouth of Canoe Creek, July 30, 1925, nymph, collected by R. E. Richardson (INHS); Rock River at foot of Lephardt's Island, July 30, 1925, nymph, collected by R. E. Richardson (INHS).

We are tentatively considering the males described below as representing the adult of *H. ammophila.*

Male imago.—The description of *H. dolani* will apply equally to the males which we tentatively assign to this species, except as follows. *Length:* body 10; wing 9–10 mm.; terminal filament and cerci, 10 mm. Spot on mid-line of prothorax quadrate (rather than circular). Abdominal tergites dark brown, a dark thin stripe near the pleural margin; posterior margin marked with a narrow fuscous stripe on tergites one and two, this stripe becoming progressively better developed in the middle area of segment to tergite seven, tergites eight and nine wholly fuscous. Penes as in figure 14. Cerci and terminal filament white with conspicuous setae at each joining.

If adults of *Homoeoneuria ammophila* can be reared or collected from the White River at Hazelton, Indiana, or the nymphs secured of the Kansas males, the latter might prove to be a separate species, although it is more likely that these males are *Homoeoneuria ammophila* (Spieth).

Records.—KANSAS: Wyandotte Co., Kansas River, ¼ m. SE Bonner Springs, two males, W. L. Peters (in Peters' personal collection).

Homoeoneuria sp.

These nymphs, which are unassociated with adults, we are unable to assign to any particular species, but include the records here.

Records.—FLORIDA: Escambia County, Escambia River at Florida Highway 4, August 12, October 23, 1954, nymphs, collected by C. D. Hynes and Lewis Berner (UF). MISSISSIPPI: Franklin County, Homochitto River at U. S. Highway 98, June 5, 1956, nymphs, collected by C. D. Hynes and Lewis Berner (UF, UU). NEBRASKA: Kearney, September 5, 1951, nymphal exuviae, collected by G. F. Edmunds (UU). TEXAS: Guadalupe River, S. of Victoria, September 4, 1950, nymphal exuvia, collected by T. Dolan IV (ANSP).

BIOLOGY OF *Homoenoeuria*

A series of nymphs of *Homoeoneuria* sp. collected at the Homochitto River (fig. 1) in Mississippi on June 5, permitted limited observations of the habitat and habits of the insects. At the time collections were made, the river

[5] The collections where specimens are located are indicated by abbreviations as follows: AMNH, American Museum of Natural History: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; CNC, Canadian National Collections; INHS, Illinois State Natural History Survey; JRT, collection of Jay R. Traver; ROM, Royal Ontario Museum, Toronto; UF, University of Florida; UM, University of Massachusetts; UU, University of Utah.

level was low, so low in fact that the water occupied only half the River basin. At few places was the depth of the stream more than 3 feet, a reflection of the semi-drought conditions which were prevalent in the southeast during 1956. Nevertheless, the water flowed rapidly so that considerable effort was needed to wade upstream. The stream bottom was clean-swept, composed mostly of loose, shifting sand with pebbly stretches, and there was no attached vegetation.

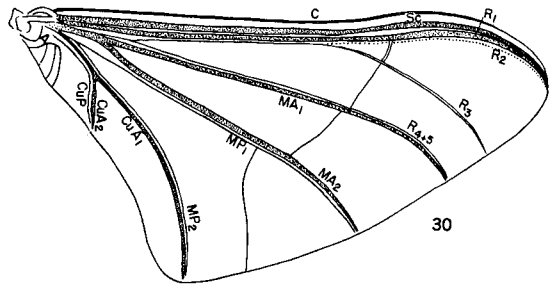
By stirring the sand by foot and holding a screen downstream as many as six to eight nymphs could be collected at each attempt. The living nymphs are very transparent so that they were at first difficult to see against the collecting screen; however, with a little practice, the insects could be picked up with ease. Against a white background, the bodies of some of the nymphs had a distinct greenish tinge and many showed brownish annulations on the abdomen. A few of the nymphs had blackened wing pads indicating that they were virtually ready to emerge.

To determine exactly where the nymphs were living, one person stirred the very top level of the sand bottom, perhaps the upper inch, and a second held a screen downstream. Only a single nymph was taken. By stirring somewhat deeper in the same area many additional specimens were taken. Further observations indicated that the nymphs live one to two inches below the surface of the sand.

Nymphs placed in a pan of water with no sand proved to be extremely awkward swimmers. In the water, the body was vibrated vigorously dorso-ventrally, but the insect scarcely moved. After a few seconds in this attempt to swim, the nymph turned over onto its dorsal surface, sank to the bottom of the pan and rested. When sand from the stream bottom was placed in the pan and the insects came in contact with it there was an immediate reaction. The body vibrated rapidly in the same pattern demonstrated in the weak swimming attempt, and this resulted in the very rapid disappearance of the nymphs into the sand. Apparently, this vibrating not only stirs up the sand so that it is pushed away from the nymph, but also permits rapid covering of the body. Orientation of the nymphs in the sand is probably upstream as evidenced by the apparent feeding mechanism. The forelegs, with their long hairs, are held directly below the mouthparts which are also covered with long hairs. Food is filtered from the loose sand, and the animal grazes on the material caught on the hairs. An examination of contents of the digestive tract showed only that the food was so thoroughly macerated that it could not be identified. The green color of some of the living nymphs may indicate that algae make up some of the food of this species.

Specimens collected from the Escambia River, Florida, were taken under similar circumstances to those taken from the Homochitto. The Escambia was at the lowest level observed in years and it was, therefore, possible to work in the stream bed with a screen. A few nymphs were taken by stirring the shifting sand bottom and collecting them downstream on the screen.

The period of emergence extends from at least early June through late October. Adults have been taken as late as October 20 from the Savannah River. On the basis of collections made thus far, the nymphs of *Homoeoneuria* appear to be inhabitants of larger streams.



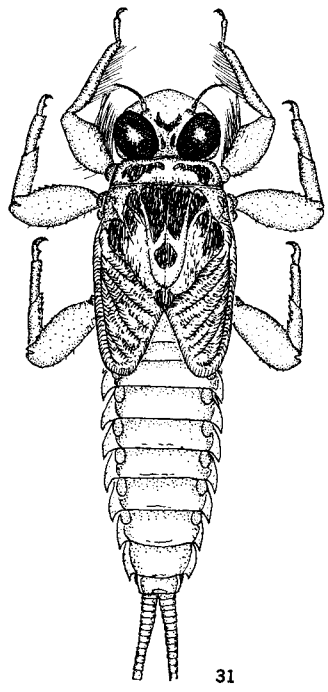


FIG. 30.—*Lachlania powelli*, wing of male imago.
FIG. 31.—*Lachlania powelli*, dorsal view of male nymph.

Genus **Lachlania** Hagen

The genus *Lachlania* was erected by Hagen (1868) for the species *Lachlania abnormis* Hagen from Cuba. Needham and Murphy (1924) referred a nymph from Guatemala to the genus. The first record of the genus north of Mexico was established by Ide (1941: 154) who described *Lachlania saskatchewanensis* from Saskatchewan.

The genus was next discovered in Utah by Edmunds (1948, 1951), who obtained a species which was named *Lachlania powelli*. The species was reared, thus positively associating the nymphs and adults, confirming the association previously established by Needham and Murphy. A few specimens of *L. powelli* have subsequently been collected from the type locality, but the known range of neither species of *Lachlania* has been extended.

The genus *Lachlania* (s.l.) is a very distinct one of widespread occurrence in the Americas. It is probably most closely related to the genus *Spaniophlebia* which it resembles in both the adult and nymphal stages, but any statement concerning the relationship of the New World Oligoneuriidae seems premature until we have a better knowledge of the genera *Oligoneuria* and *Oligoneuriodes*. There seems to be little reason for retaining subgeneric groupings in *Lachlania* in the present state of our knowledge.

Lachlania saskatchewanensis Ide

This species was described from a single female; the species differs from the only other known from North America north of Mexico, *L. powelli* Edmunds, as cited under that species. It is probable that the discovery of this specimen on the surface of a salt lake was accidental.

Records.—SASKATCHEWAN: Stoney Lake, near Humboldt, September 5, 1940, collected by J. E. Moore and J. S. Thompson (ROM).

Lachlania powelli Edmunds

This species appears to be very similar to *L. saskatchewanensis* and may eventually prove to be synonymous, although the series of approximately fifty females of *L. powelli* from Utah differ consistently from the drawings and description of the single female of *L. saskatchewanensis* Ide. The former has a pair of large paramedian pale spots on the anterior margin, while the latter has a continuous pale band; *Lachlania powelli* has less curvature in the veins of the forewing and a relatively broader hind wing. Several other species of mayflies occupying similar habitats are common to the Green River of Utah and the Saskatchewan River area. *L. powelli* will rest as an established species only after a series of females, males, and nymphs of *L. saskatchewanensis* becomes available.

The nymphs of *Lachlania powelli* were found chiefly attached to sticks, other trash, and on the surface of rocks in rapids. The river in this area is essentially a "warm water" river, being occupied by such widespread introduced fish species as carp and channel catfish, and also by such native forms as the Colorado River squawfish, some forms of Gila, and by flannelmouth and humpbacked suckers. From the distributional data, it seems that other species of the genus occupy similar habitats.

The nuptial flight of *L. powelli* takes place in midmorning, and is characterized by very rapid flight which is probably similar to that of all the Oligoneuriinae. The subimaginal skin is shed while the insects are in flight, but the pellicle is not shed from the wings. This habit is probably found in all Oligoneuriinae. Additional observations on the biology of *L. powelli* have been published by Edmunds (1951).

Records.—UTAH: Green River at Hideout Canyon, 5800 feet elevation, Daggett County, nymphs and adults, August 9, 1947, September 3–4, 1947, September 5, 1948, September 11, 1950, September 9, 1952, September 18, 1954 (UU, UF, AMNH, JRT, UM, CNC, CAS), all collected by G. F. Edmunds.

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