A REVISION OF THE GENUS *HOMOEONEURIA* (EPHEMEROPTERA: OLIGONEURIIDAE)

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INTRODUCTION

Eaton (1881) established the genus *Homoeoneuria* for the female of *H. salviniae* from Dueñas and Aceytano, Guatemala at an altitude of 4950 ft. (1510 m) and 5100 ft. (1550 m) respectively. Recently two other species, *H. ammophila* (Spieth) and *H. dolani* Edmunds, Berner and Traver, have been described from North America. In addition, another species has also been reported as *Homoeoneuria* sp. by Edmunds, Berner and Traver (1958). Herein we redescribe *H. ammophila, H. dolani, H. salviniae* and describe three new species: *H. alleni, H. cahabensis,* and *H. fittkaui.*

At the present time, little is known about the relationships of *Homoeoneuria* to the other genera in the family Oligoneuriidae. Edmunds, Berner and Traver (1958) indicated that *Homoeoneuria* seems to be related to *Elassoneuria* based on the absence of R_3 and IR_3 in the fore wings of both genera. However, the nymphs do not show close resemblance, suggesting that the relationship of the two genera is remote. Interestingly the body form and legs of *Oligoneurisca* nymphs are similar to those of *Homoeoneuria*, although Edmunds, Berner and Traver (1958) cautioned that the similarity might be a result of convergent evolution. The imagos of both genera have similar wing venation although *Homoeoneuria* lacks vein R_3 and cross veins (Fig. 1). Edmunds (1979) stated that *Oligoneurisca* and *Homoeoneuria* are sister groups. *Oligoneuriella* and *Homoeoneuria* have similar wing venation although the former has vein R_3 and IR_3. The nymphs of the two genera, however, are morphologically very different.

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Except for Eaton's description of *Homoeoneuria* which was based on female imagos, no attempt has been made to redescribe the genus. Since specimens of all known oligoneuriid genera are available to us with both nymphs and imagos represented, a more definitive description of the genus is herein presented.

Materials, Methods and Deposition

In addidion to the *Homoeoneuria* specimens collected and reared in the field and laboratory, several other collections were also made available for study. For SEM study, the technique by Towns and Peters (1978) was followed to prepare the specimens. Egg counts were made on nymphs with black wing pads. *Homoeoneuria cahabensis* n. sp. and *H. dolani* were the only species with sufficient numbers of black wing pad nymphs and 5 nymphs of each were dissected for egg counts. Female gonads dissected, and placed in small plastic petri dishes and eggs were counted under a dissecting microscope.

Type deposition has been listed to facilitate access to specimens for future reference. Localities and deposition of recently collected specimens of previously described species and new species are listed under geographical distribution. Abbreviations for collections in which specimens are deposited are as follows: American Museum of Natural History (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); Brigham Young University (BYU); British Museum of Natural History (BMNH); California Academy of Sciences (CAS); Canadian National Collections (CNC); Clemson University (CLU); Cornell University (CU); Florida A&M University (FAMU); Illinois Natural History Survey (INHS); Institute National de Pesquisas da Amazonia (INPA); P.H. Carlson personal collection (PHC); University of Florida (UF); and University of Utah (UU).

The following terms and procedures used in the description of the imagos and nymphs require further explanation. Each segment of the prothoracic legs of male imago is compared to the length of prothoracic tibiae which is given in parentheses. Male genital terminology proposed by Brinck (1957) and Grandi (1960) is used as indicated in Fig. 9-10.

Genus HOMOEONEURIA Eaton

Homoeoneuria Eaton, 1881:197; Edmunds, Berner and Traver, 1958:376; Edmunds, Berner and Jensen, 1976:182. Type species: *Homoeoneuria salviniae* Eaton, by original designation.

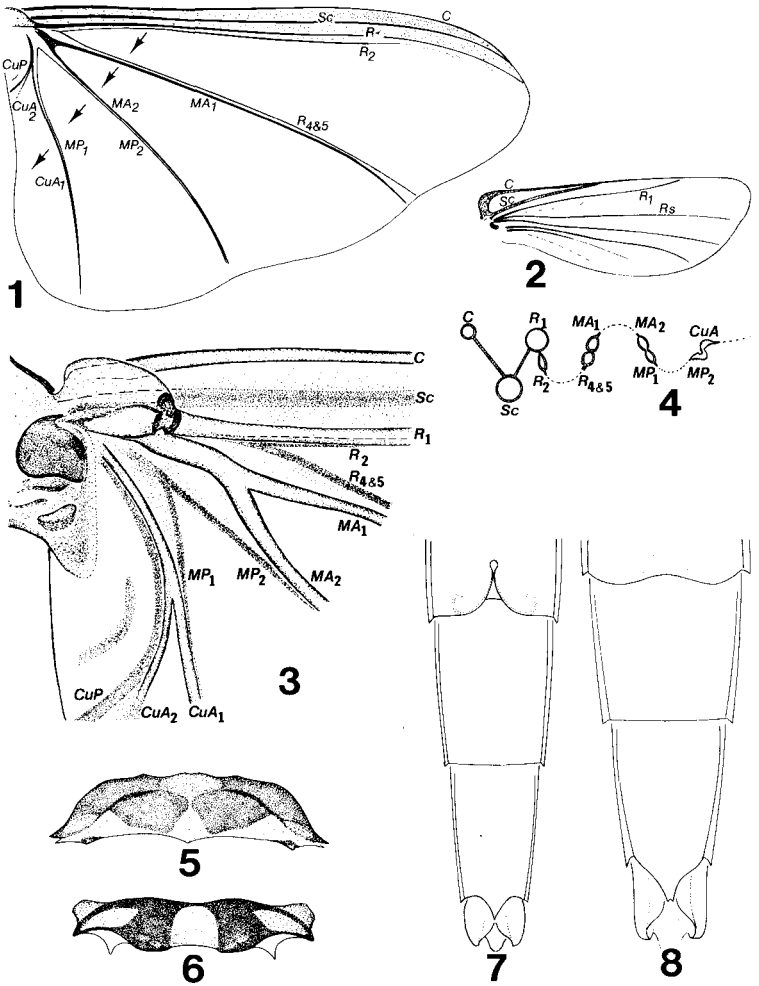
Species included: *H. alleni* new species; *H. ammophila* (Spieth) 1937:1 *(Oligoneuria); H. cahabensis* new species; *H. dolani* Edmunds, Berner and Traver, 1958:375; *H. salviniae* Eaton, 1881:197; *H. fittkaui* new species.

Imago. — Length: ♂ body 6.0-10.0 mm, fore wing 6.8-11.0 mm; ♀ body 7.0-11.0 mm; fore wings 6.8-11.0 mm. Eyes of male and female meet on meson of head. Wings (Figs. 1-4): membranes and longitudinal veins of fore and hind wings

thickly covered with granulate setae and evenly spaced papilla-like setae (Fig. 71-72): maximum width of fore wings slightly more than 1/2 maximum length; maximum width of hind wings 1/3 to 1/2 maximum length; vein R_3 of fore wings absent, cross veins of fore and hind wings absent (Fig. 1-2). Legs. Male: ratio of segments in prothoracic legs, 1.3:1.00 (0.71 mm):0.18:0.18; prothoracic legs approximately 3/4 length of mesothoracic legs, 1¼ length of metathoracic legs; tarsal segment 2 of prothoracic legs enlarged; femora of metathoracic legs bowed forming an intersegmental keel with the trochanters; inner margins of trochanters, femora and tibiae of metathoracic legs with blunt spicules; coxae of metathoracic legs longer than either femora or tibiae; claws of a pair bulb-like, surface pubescent, fore claws much larger. Female: coxae developed, remaining segments of legs membranous, twisted and vestigial. Male genitalia (Fig. 9-14): styliger bar present; genital forceps absent; penes with developed arms (Fig. 9-12); ejaculatory ducts greatly eversible (Fig. 16-22). Sternum 7 of female with broad, shallow emargination (Fig. 8) to deep, narrow constriction (Fig. 7); sternum 9 posteromedially extended, minutely cleft apically (Fig. 7) to pointed (Fig. 8). Caudal filaments. Male: terminal filament slightly longer than cerci; whorls of setae on articulations. Female: terminal filament 3/5 to 5/6 length of cerci; basal 3/5 of inner lateral margins of cerci, inner and outer margins of terminal filaments with a narrow longitudinal groove.

Egg. — Ovoid, polar caps absent; chorion covered with reticulated fiber coils (Fig. 69) or minute granules (Fig. 68); 1 to 2 oval sperm guides with micropyle and micropylar canal on tapered end (Fig. 69); attachment structures on chorionic depressions, cauliflower- (Fig. 68) to lettuce-shaped (Fig. 70) with single broad stalk (Fig. 68) to 2-3 slender stalks (Fig. 70).

Mature Nymph. — Head hypognathous; frontoclypeal region not expanded, thick anteromarginal hairs present. Antennae inserted below eyes, length approximately 4/5 length of head with 11-13 segments; pedicel approximately twice length of scape, extends beyond anterior margin of head. Mouthparts (Fig. 41-48): maximum width of mandibles approximately 3/4 maximum length excluding incisors, outer incisors broader than inner incisors, inner lateral margin of incisors weakly serrated; prostheca with 3-4 major branches (Fig. 46-48). Maxillary gills multibranched; segment 2 of maxillary palpi approximately 4 times length of segment 1. Linguae of hypopharynx broad, dome-shaped apically entire (Fig. 42, 45), submarginal setae short, anteromedian margin bare. Segment 2 of labial palpi 1-1/2 length of segment 1; setae of ventral surface of paraglossae as in Fig. 74. Thorax: Pronotum with prominent posterolateral extension overlapping base of prothoracic coxae (Fig. 56). Legs (Fig. 56, 58-66). Prothoracic legs: trochanters approximately 1/3 length of coxae; tibiae approximately 1-1/6 length of femora; coxae medially enlarged with prominent apical keel; coxae and trochanters with long thick hairs; outer lateral margin of femora with slender spinous setae (Fig. 56); tarsi reduced, papilla-like (Fig. 58-62). Mesothoracic legs (Fig. 56): mesothoracic legs 1-1/3 length of prothoracic legs and metathoracic legs; coxae cylindrical (Fig. 56); coxae and trochanters equal in length; tarsi slightly shorter than tibiae, dorsal surface of trochanters with long thick hairs, remainder of segments with long spinous setae, shorter on tibiae and tarsi; tarsal claws slender without denticles. Metathoracic legs

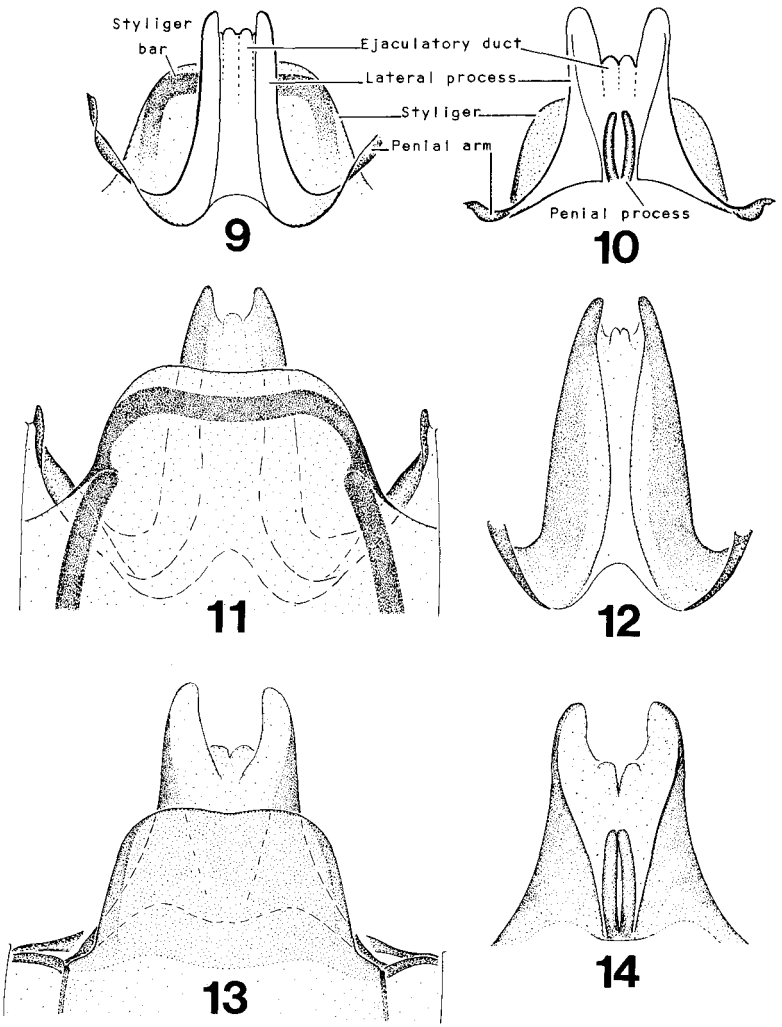


FIGURES 1-8. Imago of *Homoeoneuria*. 1-4, *H.* (s.s.) *cahabensis:* 1, fore wing, 2, hind wing; 3, basal area of fore wing enlarged; 4, cross section of fore wing (section marked by arrows in Fig. 1; membrane shortened between medial and cubital veins). 5-6, pronotal color pattern of male: 5, *H. (Notochora) fittkaui;* 6, *H.* (s.s.) *cahabensis.* Fig. 7-8, outline of abdominal sterna 7-9 of female: 7, *H. (Notochora) fittkaui;* 8, *H.* (s.s.) *dolani.*

(Fig. 56): coxae cylindrical with prominent apical keel (Fig. 56); trochanters 1/2 length of coxae; tibiae approximately 2/3 length of femora; tarsi approximately 2/3 length of tibiae; trochanters with apical spur (Fig. 56); tarsal claws straight, long and slender without denticles (Fig. 63-66); setae as on mesothoracic legs. Abdomen: Posterolateral spines on segments 8-9; sternum 1 with a short finger-like posteromedian process (Fig. 57); tergum 10 approximately 1/2 length of tergum 9; sternum 9 with a pair of weakly sclerotized posteromedian spines (Fig. 38-40); terga and sterna covered with clubbed setae (Fig. 73); surface of sterna 2-4 and sterna 1-8 with long, thick posterior hairs. Gills: gill 1 ventral, large multibranched without plate-like lamellae; gills 2-7 slender, without fibrilliform portion, maximum width approximately 1/6 maximum length, flat, anteriorly bordered with moderately long hairs, dorsal and ventral surface glabrous. Caudal filaments: Cerci slightly longer than terminal filament, with long inner marginal setae; terminal filament with long inner and outer marginal setae.

Discussion. — *Homoeoneuria* can be distinguished from all other genera of Oligoneuriidae by the following combination of characters. In the imagos: (1) veins R_3 and IR_3 of fore wings and cross veins of fore and hind wings are absent (Fig. 1); (2) prothoracic legs are approximately 3/4 length of metathoracic legs; (3) male metathoracic trochanters are flat and attached almost at right angles to the coxae forming an intersegmental keel with the prominently bowed femora; (4) metathoracic coxae are longer than either femora or tibiae; (5) genital forceps are absent; and (6) sternum 9 of female is posteromedially extended and apically pointed (Fig. 7) to minutely cleft (Fig. 8). In the egg: (1) polar caps are absent (Fig. 67, 69); and (2) cauliflower- (Fig. 68) to lettuce-shaped attachment structures (Fig. 70) are nestled on chorionic depressions. In the nymph: (1) pronotum has a prominent posterolateral extension that overlaps the base of prothoracic coxae (Fig. 57); (2) metathoracic coxae are cylindrical, and have a prominent apical keel (Fig. 56); (3) tarsi of prothoracic legs are reduced and papilla-like (Fig. 58-62); (4) mesothoracic and metathoracic claws are slender, unhooked and lack denticles (Fig. 63-66); (5) abdominal sternum 1 has a short finger-like posteromedian process (Fig. 57); and (6) lamella of abdominal gills 2-7 are slender, anteriorly and posteriorly bordered with short spinous setae and long hairs respectively, and fibrilliform portions are absent.

Homoeoneuria shares several common morphological characters with *Oligoneurisca* but can be distinguished from it by any of the



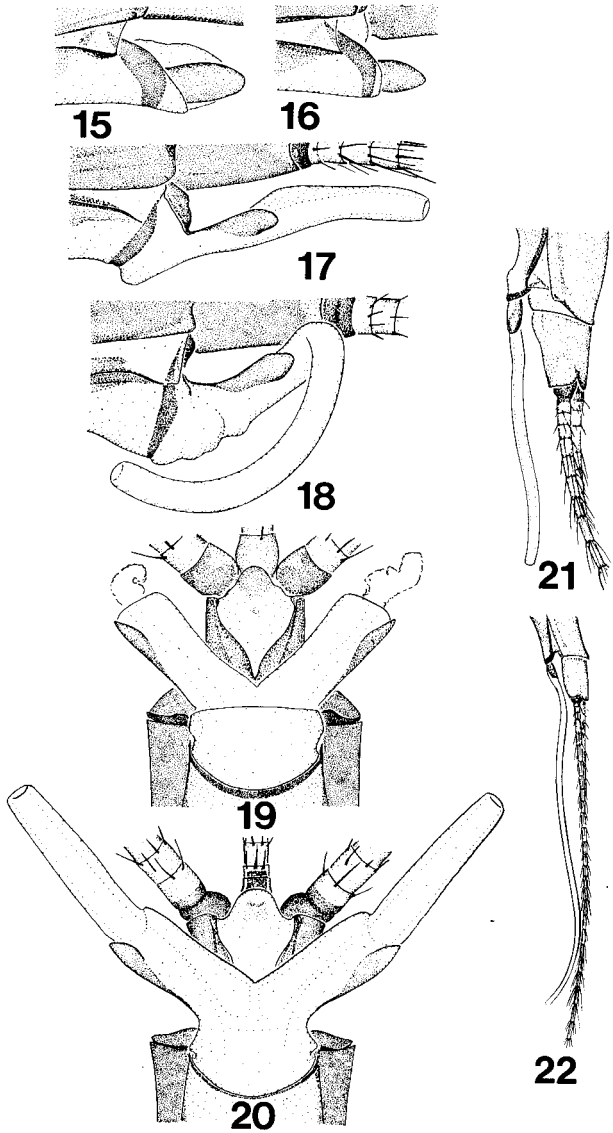
FIGURES 9-14. Genitalia of male imago of *Homoeoneuria* (9-11, 13, ventral; 12, 14, dorsal); 9-10, terminology; 11-12, *H.* (s.s.) *cahabensis;* 13-14, *H. (Notochora) fittkaui.*

following characters. In the imagos: (1) veins R_3 and IR_3 of the fore wings and cross veins of fore and hind wings are absent (Fig. 1-2); (2) males have flat metathoracic trochanters which are attached almost at right angles with the coxae and form an intersegmental keel with the prominently bowed and flat femora; and (3) male genital forceps are absent. In the nymph: (1) unexpanded frontoclypeal area has thick anteromarginal hairs; (2) prothoracic tarsi are greatly reduced to papilla-like structures (Fig. 58-62); (3) mesothoracic and metathoracic tarsi are distinctly shorter than tibiae; (4) mesothoracic and metathoracic claws are unhooked and lack denticles (Fig. 63-66); (5) abdominal sternum 1 has a finger-like posteromedian process (Fig. 57); and (6) fibrilliform portions of gills are absent, and lamellae are slender.

From the published figures of *Homoeoneuria* (and other genera of Oligoneuriidae), the shape of the penes seems to differ in each species. We decided against the use of this character for reasons that will become evident. In the family Oligoneuriidae the ejaculatory ducts are capable of extrusion, at least in some genera (Eaton 1883, under "Subsection B of *Palingenia*"). This may be true for all genera, but there has been little study or discussion of the possibility, probably because a series of male imagos with penes in various stages of extrusion is necessary for comparative study, and most collections are relatively small. We have such a series for representatives of three genera *(Oligoneuriella, Lachlania, Homoeoneuria)* and it seems valuable at this time to document what is known.

Eaton (1883, Plate III, Fig. 2a) figured the ventral aspect of the genitalia of *Oligoneuriella rhenana* (Imhoff) (as *Oligoneuria*); a lateral view of the same species is given in Fig. 23-25. It is possible to understand somewhat how extrusion occurs in *Oligoneuriella* by referring to Grandi's (1947, Fig. XXIII) work on the anatomy and morphology of *O. rhenana*.

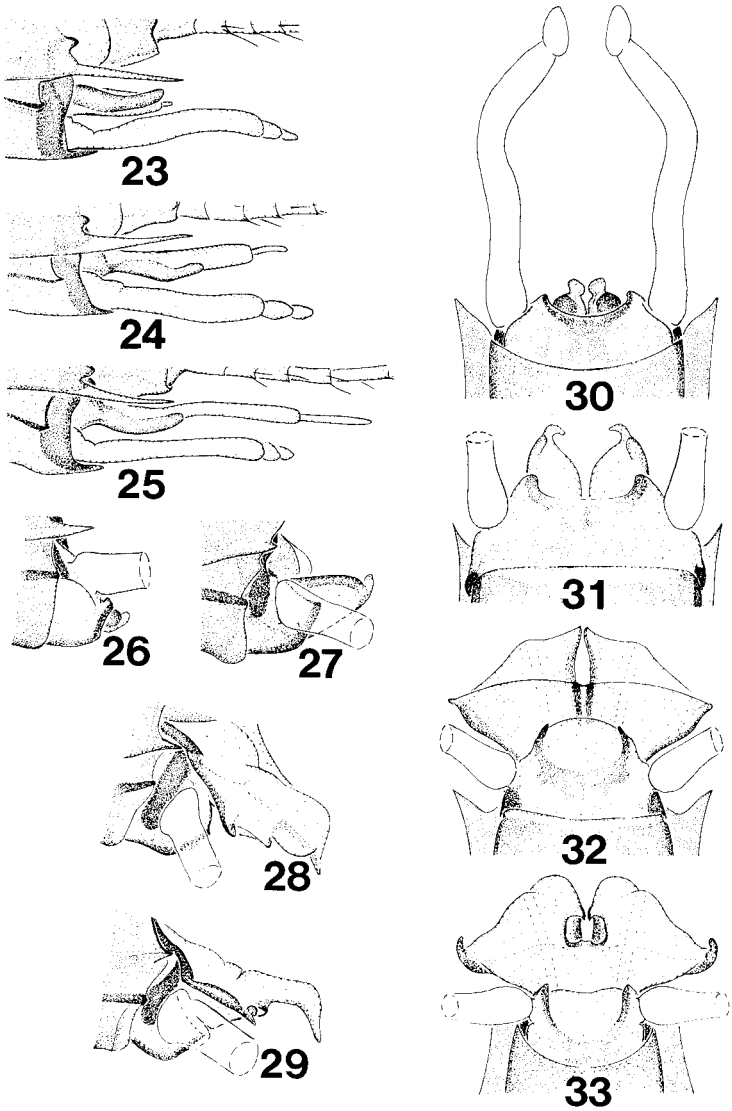
Penes of *Lachlania* (unidentified species from Peru) in different stages of ejaculatory extrusion are given in Fig. 26-33. Dorsal and ventral figures of *Lachlania dencyanna* Koss appear in Koss and Edmunds (1970). Koss and Edmunds (1970) refer to the finger-like projections on the dorsal surface of the penes as titillators, but from the extended penes of the Peruvian species (Fig. 27-29, 31-33)



FIGURES 15-22. Extrusion of ejaculatory ducts of male imago of *Homoeoneuria* (s.s.) (15-18, 21-22, lateral; 19-20, ventral): 15, *H. ammophila;* 16-20, *H. cahabensis;* 21-22, *H. dolani.*

it appears that these are sclerotized areas used to pull or hold the membranous penes erect something like the spokes of an umbrella. These sclerotized processes are separate from the gonoducts (gonoducts visible in membranous portion of penes in Fig. 31). *Homoeoneuria (Notochora) fittkaui* n. sp. has similar finger-like projections on the dorsal surface of the penes which might serve the same purpose, but it is difficult to speculate based on the limited series of material available. For *Homoeoneuria cahabensis,* the normal (or closed) position is shown in Fig. 11-12, 16 (dorsal, ventral, lateral); the most extruded portion of the ejaculatory ducts is shown in Fig. 17-20 (dorsal, lateral). In Fig. 18, the ejaculatory ducts have stretched and flopped laterally and anteriorly after extrusion; either the ejaculatory ducts are not retracted in this species or the specimens figured were captured with penes extruded. In two specimens of *H. dolani* from the original paratype series, the lateral sclerotized processes and penial arms of the penes and the sclerotized area of the styliger are in the normal position, but the ejaculatory ducts are highly elastic and stretched out as in Fig. 21-22, again suggesting that *Homoeoneuria* may not retract the ducts. Edmunds, Traver and Berner (1958) show the normal position for *H. dolani* but the figure of the penes of *H. ammophila* shows beginnings of extrusion. In the other available specimen of a male imago of *H. ammophila,* the penes are similar to *H. dolani* and *H. cahabensis* when ejaculatory ducts are not extruded (lateral view, Fig. 15). The penes of all known species of *Homoeoneuria* (s.s) lack the dorsal, median, sclerotized finger-like process and are highly membranous and apparently elastic. If a method could be developed so that the penes are extruded in a consistent manner, characters to separate the species based on the male genitalia might be developed. The same is probably true for other oligoneuriid genera.

The nymphs of the different species of *Homoeoneuria* are distinguishable. Characters such as the shape of mandibular prosthecae and hypopharyngeal superlinguae, setation of antennal pedicel, and relation of the tarsi to the tibiae and width of tibiae and femora of prothoracic legs (Table 1) are good species group characters. Abdominal color patterns, although somewhat variable within species, are consistent between species, and between nymphs



FIGURES 23-33. Extrusion of ejaculatory ducts of male imago of other genera of Oligoneuriidae (23-29, lateral; 30-33, ventral): 23-25, *Oligoneuriella rhenana;* 26-33, *Lachlania* sp. (from Peru).

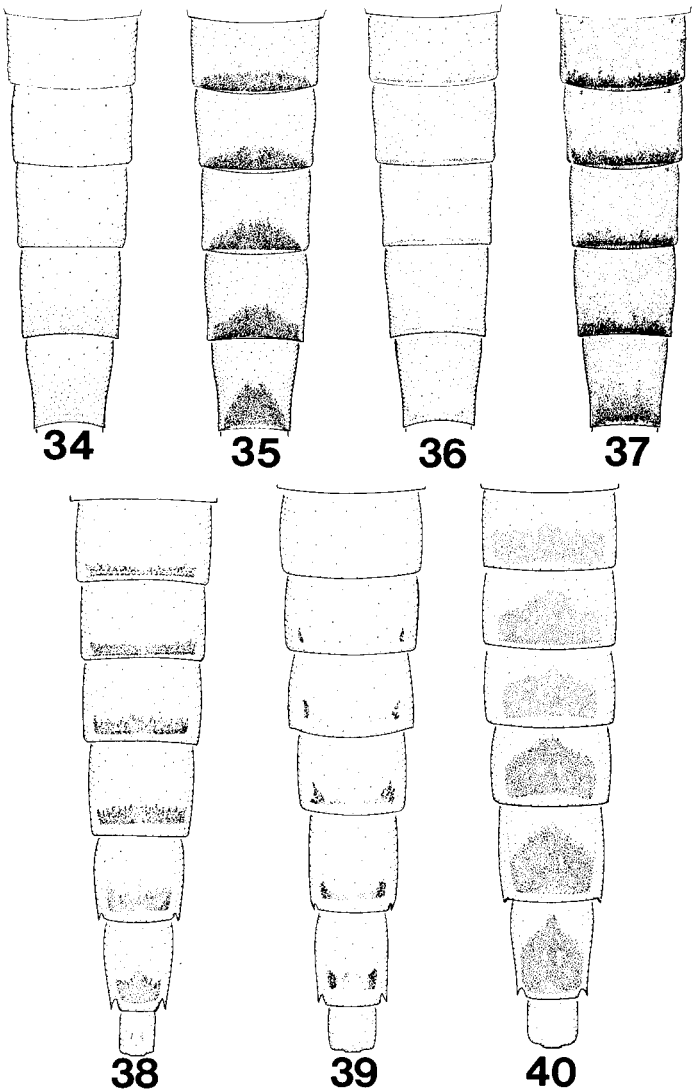
and adults of species- at least for those species where material is reared (*H. dolani* and *H. cahabensis*). Figures are given of the abdominal terga of a nymph and imago of *H. cahabensis*. Although the base color of the body is much darker in imagos, the pattern of an irregular band of even width across the posterior margin of terga 4-7 is repeated in nymphs and imagos (Fig. 37-38). Association of nymphs and imagos of *H. ammophila* from midwestern localities is also based on the similar color patterns on abdominal terga. Only in the last few days prior to emergence is the color pattern obscured by the developing imaginal color pattern under the nymphal cuticle, as in Fig. 15 in Edmunds, Berner, and Traver (1958) of *H. cahabensis (Homoeoneuria* sp.).

Key to Imagos

1. Penes with paired finger-like processes (Fig. 10, 14); female sternum 7 with deep, narrow posteromedian constriction (Fig. 7) ..... subgenus *Notochora, H. fittkaui* new species
   Penes without finger-like processes (Fig. 9, 11-12); female sternum 7 with shallow, broad posteromedian emargination (Fig. 8) ..... subgenus *Homoeoneuria* s.s. 2
2. Head, thorax and abdomen dark smoky brown; pattern of reddish-brown markings on abdominal terga as in Fig. 37 ..... *H. cahabensis* new species
   Head, thorax andd abdomen brown; pattern of brown markings on abdominal terga not as above (Fig. 35-36) 3
3. Abdominal terga with narrow brown markings (Fig. 36) or without markings ..... *H. dolani* Edmunds, Berner and Traver
   Abdominal terga with broad brown markings (Fig. 35) ..... *H. ammophila* (Spieth)

Key to Nymphs

1. Antennal pedicel with short, thick setae (Fig. 53-54); maximum width of tibiae of prothoracic legs 9/10 to equal width of femora; posterior margin of superlingua strongly curved (Fig. 41-42) 2
   Antennal pedicel glabrous (Fig. 55); maximum width of tibiae of prothoracic legs 2/3 to 5/6 width of femora; posterior margin of superlingua slightly curved (Fig. 43-45) 3
2. Vertex and thoracic nota with purplish-brown markings; distance of tarsi of prothoracic legs from apex of tibiae approximately 1/5 maximum width of tibiae; purplish-brown markings on abdominal terga as in Fig. 40 ..... *H. alleni* new species



FIGURES 34-40. Markings on abdomen of *Homoeoneuria* (34-37, terga 4-8 of male imago; 38-40, terga 4-10 of mature nymph): 34, *H. (Notochora) fittkaui;* 35, *H.* (s.s.) *ammophila;* 36, *H.* (s.s.) *dolani;* 37-38, *H.* (s.s.) *cahabensis;* 39, *H.* (s.s.) *salviniae;* 40, *H.* (s.s) *alleni.*

Vertex and thoracic nota without markings; distance of tarsi of prothoracic legs from apex of tibiae approximately 2/3 maximum width of tibiae; dark brown markings on abdominal terga as in Fig. 39 ..... *H. salviniae* Eaton

3. Pattern of dark brown markings on abdominal terga as in Fig. 35; tibiae of prothoracic legs slightly bowed (Fig. 60); galea-lacinia of maxillae with submarginal row of 13-15 long, spinous setae ..... *H. ammophila* (Spieth)

Pattern of markings on abdominal terga not as above; tibiae of prothoracic legs strongly bowed (Fig. 61-62); galea-laciniae of maxillae with submarginal row of 18-25 long, spinous setae 4

4. Coxae of prothoracic legs with reddish-brown basal spot (Fig. 56); vertex and thoracic nota with reddish-brown markings; distance of tarsi of prothoracic legs from apex of tibiae equal to 1-1/7 times maximum width of tibiae; apical portion of tibiae of prothoracic legs curved upward (Fig. 61); pattern of dark brown markings on abdominal terga as in Fig. 38 ..... *H. cahabensis* new species

Coxae of prothoracic legs without spot; vertex and thoracic nota without markings; distance of tarsi of prothoracic legs from apex of tibiae aproximately 2/3 maximum width of tibiae; apical portion of tibiae of prothoracic legs straight (Fig. 62); abdominal terga with faint narrow brown markings (Fig. 36) or without markings ..... *H. dolani*

Subgenus Homoeoneuria s.s. Eaton (1881)

Imago. — Length: ♂ body 8.0-10.0 mm, wing 6.0-10.0 mm, caudal filaments 7.0-11.0 mm; ♀ body 9.0-11.0 mm, wing 7.0-9.0 mm, cerci 2.0-3.0 mm, terminal filament 1.0-3.5 mm. Male genitalia: styliger bar well developed (Fig. 9, 11); penial arms well developed (Fig. 9, 11); penial process absent (Fig. 9, 11). Female sternum 7 with shallow, broad posteromedian emargination (Fig. 8); female sternum 9 posteromedially extended, pointed or minutely cleft apically (Fig. 8).

Egg. — Chorion covered with reticulated fiber coils (Fig. 69), attachment structures lettuce-shaped with 2 to 3 slender stalks (Fig. 70).

Type species. — *Homoeoneuria (H.) salviniae* Eaton.

Discussion. — *Homoeoneuria* s.s. presently consists of five species which are disjunctly distributed in Central and North America. The characters above distinguish it from the subgenus *Notochora*.

Homoeoneuria (Homoeoneuria) ammophila (Spieth)

Fig. 15, 35, 51, 60, 64

Oligoneuria ammophila Spieth 1937:139; 1838:1; Burks 1953:80.

Homoeoneuria ammophila Edmunds and Allen 1957:318; Edmunds, Berner and Traver 1958:375.

Male Imago (in alcohol). — Length: body 9.5-10.0 mm; fore wings 10.0-11.0 mm; caudal filaments 10.0-11.0 mm. Head dark brown, venter pale yellow. Antennae brown. Basal 1/2 of ocelli dark brown, remainder pale white. Eyes grayish-black. Thorax: dark brown, membranous areas pale yellow, posterolateral corners of mesoscutellum dark smoky brown; pronotum with prominent posterolateral and posteromedian pale yellow spots, posteromedian spot anteriorly extended almost entire pronotal length, larger than posterolateral spots (Fig. 6). Wings: membrane of fore and hind wings grayish-white; longitudinal veins of fore and hind wings pale yellow. Legs: coxae and trochanters brown, darker at margins, remaining segments pale yellow, progressively paler distally. Abdomen: terga brownish-yellow, tergum 1 darker; terga 1-9 with moderately broad dark brown markings near posterior margins, progressively more widespread posteriorly (Fig. 35) except tergum 1 with brown markings on posterior 1/2 of segment. Sterna brownish-yellow, anterolateral corners and sternum 1 darker; basal 1/3 of sternum 9 with brown markings, margins dark shiny brown, metallic on posterior margin; sterna 2-8 with median longitudinal translucent pale yellow line, progressively narrows posteriorly with brown-rimmed translucent pale yellow lateral streaks. Genitalia: penes pale yellow except lateral processes brown; shape of penes as in Fig. 13, 14 of Edmunds *et al.* (1958), lateral view as in Fig. 15. Caudal filaments: pale white; light brown setae on articulations.

Female Imago. — Unknown.

Mature nymph (in alcohol). — Length: body 8.0-9.5 mm; caudal filaments 1.7-2.1 mm. Head yellow; vertex with reddish-brown markings extended between eyes (Fig. 51). Lateral ocelli white, inner 1/2 dark brown; median ocellus white, faintly suffused with dark brown. Eyes grayish-black. Antennae yellow, pedicel glabrous. Mouthparts: mandibular prosthecae similar to Fig. 47; galea-lacinia of maxillae with submarginal row of 13-15 long, spinous setae; posterior margin of superlingua strongly curved; segment 1 of labial palpi approximately 4/5 length of segment 2. Thorax: yellow; pronotum with thin streak of reddish-brown band near posterior margin (Fig. 51) and anterior margin of fore wing pads. Legs pale yellow. Prothoracic legs: coxae without spot; tibiae moderately bowed (Fig. 60), maximum width approximately 5/6 maximum width of femora; distance of tarsi from apex of tibiae approximately 3/4 maximum width of tibiae; apical portion of tibiae slightly projected downward. Mesothoracic legs: tarsal claws approximately 1/3 length of tarsi and 3/5 length of tarsal claws of metathoracic legs. Metathoracic legs: tarsal claws (Fig. 64) 1-1/8 length of tarsi. Abdomen: terga and sterna yellow; terga 1-9 with moderately broad dark brown markings near posterior margin as in imagos (Fig. 35). Caudal filaments: pale yellow, setae pale yellow.

Geographical Distribution. — (Fig. 76). *Homoeoneuria ammophila* is known to occur in Indiana, Illinois (Spieth, 1937; Burks, 1953) and Kansas (Edmunds, *et al.* 1958).

Type Deposition. — Holotype (nymph) is deposited in AMNH collection. Nymphal paratypes are deposited in AMNH, CNC and CU collections.

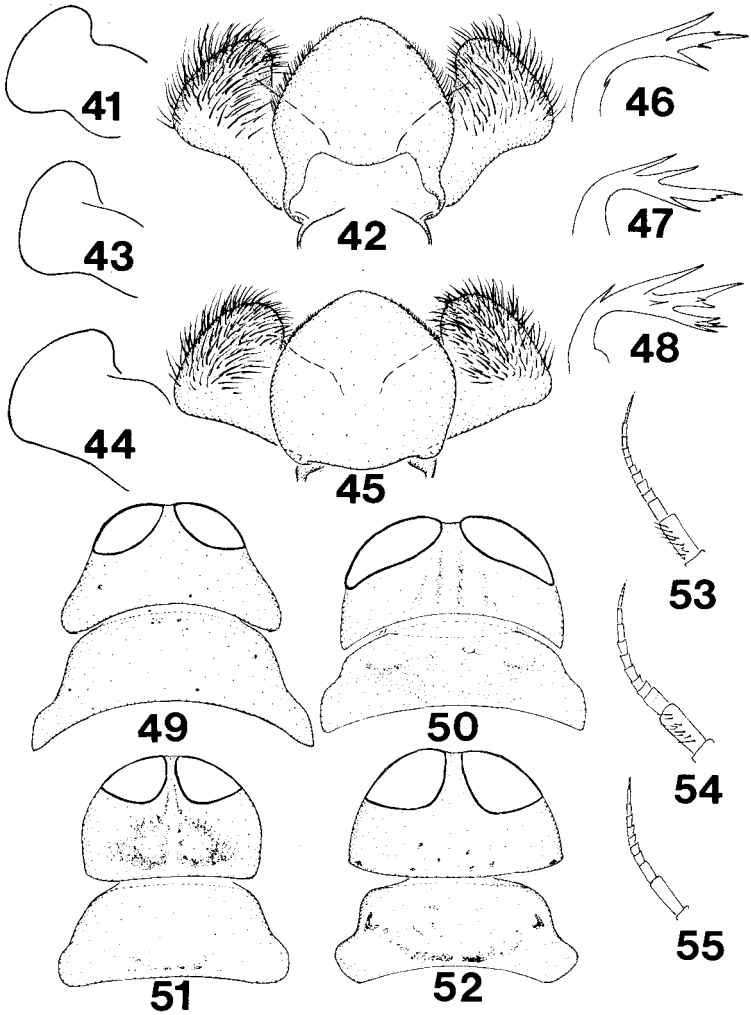
Discussion. — *Homoeoneuria ammophila* was first described by Spieth (1937) in *Oligoneuria* from a last instar nymph but was subsequently transferred to *Homoeoneuria* by Edmunds and Allen

(1957). Edmunds, Berner and Traver (1958) tentatively described the adults of *H. ammophila* from two male imagos collected from the Kansas River, Kansas. Although Edmunds *et al.* (1958) were uncertain about the association of the nymphs and adult of the species, we are convinced that the decision was correct.

Homoeoneuria ammophila can be distinguished from all other species of the genus by the following combination of characters. In the imagos: (1) posteromedian pale yellow spot of pronotum is extended anteriorly almost the entire pronotal length and is distinctly larger than the posterolateral spots (Fig. 6); (2) abdominal terga are yellow and terga 1-9 have moderately broad dark brown markings near posterior margin (Fig. 35); and (3) shape of penes is as in Fig. 15, and Fig. 13, 14 of Edmunds *et al.* (1958). In the nymph: (1) vertex has irregular reddish-brown markings extended between eyes (Fig. 51); (2) antennal pedicels are glabrous (Fig. 55); (3) galea-lacinia of maxillae have a submarginal row of 13-15 long and spinous setae; (4) prothoracic coxae have no spots; (5) prothoracic tibiae are slightly bowed (Fig. 60) with a maximum width of 5/6 maximum width of femora; and (6) abdominal terga have moderately broad dark reddish-brown markings (Fig. 35).

Homoeoneuria ammophila appears most closely related to *H. cahabensis* and *H. dolani* but can be distinguished from them by any of the following characters. In the imagos: (1) abdominal terga are yellow and terga 1-9 have moderately broad dark brown markings (Fig. 35); and (2) shape of penes is as in Fig. 15, and Fig. 13, 14 of Edmunds *et al.* (1958). In the nymph: (1) vertex has irregular reddish-brown markings extended between eyes (Fig. 51); (2) galea-lacinia of maxillae have a submarginal row of 13-15 long and spinous setae; and (3) abdominal terga have moderately broad dark brown markings similar to Fig. 35.

Biology. — The biology of *H. ammophila* is unknown. Nymphs have been collected in June and July (Spieth 1937; Burks, 1953). Spieth (1937) collected a last instar nymph in July and adults were collected in August (M.V. Peters) from Kansas River 1/4 mi. SE Bonner Springs, Wyandotte Co., Kansas. Males of *Homoeoneuria* sp. were observed flying at dusk in the evening (McCafferty in Edmunds *et al.* 1976). The species was probably *H. ammophila* based on its geographical distribution.



FIGURES 41-55. Mature nymph of *Homoeoneuria* (s.s.) [41-45, hypopharynx (or outline of left lobe of superlingua of hypopharynx); 46-48, prostheca of mandible; 49-52, head and pronotum; 53-55, antennae]: 41, 46, 49, 53, *H. alleni* (New Mexico); 50, *H. alleni* (Utah); 42, 46, 54, *H. salviniae;* 43, 51, *H. ammophila;* 44, 47, 52, 55, *H. cahabensis;* 45, 48, *H. dolani.*

Homoeoneuria (Homoeoneuria) dolani Edmunds, Berner & Traver

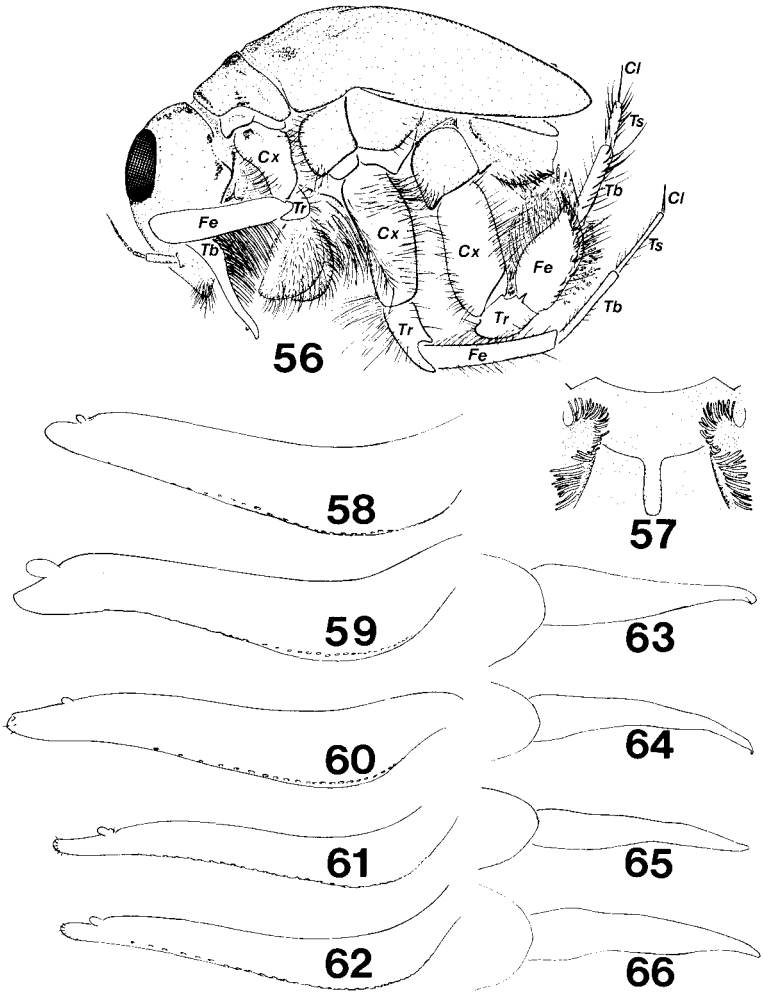
Fig. 21-22, 36, 45, 48, 62, 66

Homoeoneuria dolani Edmunds, Berner & Traver 1958:378.

Male Imago (in alcohol). — Length: body 8.0-9.0 mm; fore wings 9.0-10.0 mm; caudal filaments 10.0-11.0 mm. Head dark brown, venter pale yellow. Antennae brown. Basal 1/2 of ocelli brown, remainder pale white. Eyes grayish-yellow. Thorax: dark brown except membranous areas pale yellow: pronotum with prominent posterolateral and posteromedian pale yellow spots, posteromedian spot extended almost entire pronotal length, and larger than posterolateral spots (Fig. 6). Wings: membrane of fore and hind wings purplish-blue in fresh specimens, purplish-brown in preserved; longitudinal veins of fore and hind wings brown. Legs: coxae and trochanters brown, darker at margins, remaining segments pale yellow, progressively paler distally. Abdomen: terga brown, slightly darker on margins; terga without or with very narrow reddish-brown markings (Fig. 36). Sterna light brown, sternum 1 darker; basal 1/3 to 1/2 of sternum 9 with faint brown markings, margin dark shiny brown, metallic brown on posterior margin; sterna 1-8 with median longitudinal pale yellow line, progressively narrows posteriorly with translucent brownish lateral streaks. Genitalia: penes pale yellow, lateral process dark brown; shape of penes as in Fig. 4 of Edmunds *et al.* (1958); lateral view of extruded ejaculatory ducts of penes as in Fig. 21-22. Caudal filaments: white, dark brown at extreme base; yellowish-brown setae on articulations.

Female Imago (in alcohol). — Length: body 9.0-10.0 mm; fore wings 7.0-8.0 mm; cerci 2.0-3.0 mm; terminal filament 1.6-2.5 mm. Color of head, antennae and ocelli as in male imago. Eyes grayish-black. Thorax: color of nota, pleura and sterna as in male imago except mostly paler; posterolateral and posteromedian pale yellow spots on pronotum smaller than male imago. Wings: color of membrane and veins as in male imago. Legs: coxae brown, except margins and remaining segments shriveled, pale white. Abdomen: color of terga and sterna as in male imago except sternum 9 without brown markings; submedian streaks on sterna not as pronounced as in male imago. Caudal filaments: brown.

Mature Nymph (in alcohol). - Length: body 9.0-12.0 mm; caudal filaments 2.2-2.5 mm. Head pale yellow. Lateral ocelli white, inner 1/2 pale gray; median ocellus grayish-black. Eyes grayish-black. Antennae pale yellow; pedicel glabrous. Mouthparts: mandibular prosthecae as in Fig. 48: galea-lacinia of maxillae with submarginal row of 18-22 long, spinous setae; posterior margin of superlingua slightly curved (Fig. 45); segment 1 of labial palpi approximately 2/3 length of segment 2. Thorax: pale yellow. Legs pale yellow. Prothoracic legs: coxae without spot; tibiae strongly bowed (Fig. 62), maximum width approximately 2/3 maximum width of femora; distance of tarsi from apex of tibiae approximately 2/3 maximum width of tibiae; apical portion of tibiae straight. Mesothoracic legs: tarsal claws approximately 1/4 length of tarsi and 1/2 length of tarsal claws of metathoracic legs. Metathoracic legs: tarsal claws (Fig. 66) 6/7 length of tarsi. Abdomen: terga and sterna pale yellow; terga without markings or with very narrow faint reddish-brown markings near posterior margin as in imagos (Fig. 36). Caudal filaments: cerci pale yellow, terminal filament transulcent white; setae pale yellow.



FIGURES 56-66. Mature nymph of *Homoeoneuria* (s.s.) 56, lateral view of head and thorax of *H. cahabensis* (abbreviations: Cx, coxa; Tr, trochanter; Fe, femur; Tb, tibia; Ts, tarsus; Cl, tarsal claw). 57, ventral view of abdominal sternum 1 of *H. dolani*. 58-66, tibia and remnant of tarsus of prothoracic leg (Fig. 58-62) and tarsal claw of metathoracic leg (Fig. 63-66): 58, *H. salviniae;* 59, 63, *H. alleni;* 60, 64, *H. ammophila;* 61, 65, *H. cahabensis;* 62, 66, *H. dolani*.

Geographical Distribution. — (Fig. 76). *Homoeoneuria dolani* is known to occur from the sandy rivers of Georgia, South Carolina (Edmunds *et al.,* 1958) and Florida. Specimens from Florida have been collected from the following localities: Santa Rosa Co., Blackwater River at Deaton Bridge 3.5 mi. N. Harold, 14/5-VIII-1967, W.L. & J.G. Peters, & P.T.P. Tsui, nymphs and adults (FAMU); Okaloosa Co., Shoal River on HWY 393 at Dorcas, 18-V-1967, G. Cooper, J. Jones & W.L. & J.G. Peters, nymphs (FAMU); 29-VIII-1967, W.L. & J.G. Peters & P.T.P. Tsui, nymphs (FAMU).

Type Deposition. — Holotype (♂ imago) and allotype (♀ imago) are depopsited in UU collections. Adult and nymphal paratypes are deposited in ANSP, UF & UU collections.

Discussion. — *Homoeoneuria dolani* was described by Edmunds *et al.* (1958) from male and female imagos, and nymphs. Additional specimens including a good series of reared adults from Florida merit a redescription of the species.

Both imagos and nymphs of *H. dolani* exhibit variations in markings on the abdominal terga. Most imagos and nymphs available to us have no markings on the abdominal terga while a few have very narrow reddish-brown markings near the posterior margin of terga 2-9 (Fig. 36). Such variation occurs through out the distributional range of the species.

Homoeoneuria dolani can be distinguished from all other species of the genus by the following combination of characters. In the imagos: (1) posteromedian pale yellow spot on pronotum is extended anteriorly to almost entire pronotal length and is distinctly larger than the posterolateral spots (Fig. 6); (2) abdominal terga are brown and terga 2-9 either have a very narrow reddish-brown marking near the posterior margin (Fig. 36) or no markings; and (3) shape of penes is as in Fig. 4 of Edmunds *et al.* (1958) and extruded ejaculatory ducts are shown in Fig. 21-22. In the nymph: (1) vertex and pronotum have no markings; (2) antennal pedicels are glabrous (Fig. 55); (3) galea-lacinia of maxillae have a submarginal row of 18-22 long and spinous setae; (4) prothoracic coxae lack spot; (5) prothoracic tibiae are strongly bowed (Fig. 62) with a maximum width of approximately 2/3 of maximum width of femora; and (5) abdominal terga 1-9 either have very narrow reddish-brown markings near posterior margin (Fig. 36) or no markings.

Homoeoneuria dolani appears most closely related to *H. cahabensis* but can be distinguished from it by any of the following characters. In the imagos: (1) abdominal terga are brown, and terga 2-9 either have very narrow reddish-brown markings near posterior margin (Fig. 36) or no markings; (2) shape of penes is as in Fig. 4 of Edmunds *et al.* (1958) and lateral view of extruded ejaculatory ducts is shown in Fig. 21-22. In the nymph: (1) vertex and pronotum lack markings; (2) prothoracic coxae lack spot; (3) abdominal terga are brown and terga 2-9 either have very narrow reddish-brown markings near the posterior margin or no markings; and (4) setae of caudal filaments are unicolorous pale yellow.

Biology. — *Homoeoneuria dolani* is one of the strictly sand-dwelling mayfly species occurring in the Blackwater River, Florida. The other two species are *Dolania americana* Edmunds & Traver and *Pseudiron meridionalis* Traver. The nymphal habits of these three species vary greatly as nymphs of *H. dolani* are non-predaceous while *D. americana* and *P. meridionalis* are predaceous. Nymphs of *H. dolani* are shallow burrowers, *D. americana* are deep burrowers while those of *P. meridionalis* are non-burrowers.

Nymphs of *H. dolani* are found in shifting sand, mostly in deep areas of the river. Burrowing behavior of nymphs is as discussed in *H. cahabensis.* Gut contents of nymphs included a mixture of sand and particulate organic matter.

Except for the dates of collection of the nymphs and adults, knowledge of the seasonal distribution of *H. dolani* is very limited. In the Savannah River, nymphs have been collected from June to September and adults from August to October. Mature nymphal exuviae have been collected as late as November. In the Blackwater River, nymphs were collected from May to October and the adults in late July to August.

Adults were observed swarming in midmorning (1000 to 1200h.) cruising about 1 m above the water. Based on several days of observations during emergence period in the Blackwater River, swarming seemed to take place only in full sunlight.

Five dissected mature female nymphs indicate a mean of 315 eggs (range: 270-365) per individual.

Homoeoneuria (Homoeoneuria) cahabensis Pescador & Peters

new speices

Fig. 6, 9, 11-12, 16-20, 37-38, 44, 47, 52, 55, 56, 61, 65

Homoeoneuria sp. Edmunds, Berner & Traver 1953:380.

Male Imago (in alcohol). — Length: body 9.0-10.0 mm; fore wings 7.0-8.0 mm; caudal filaments 7.0-8.0 mm. Head dark smoky brown, venter pale yellow. Antennae dark reddish-brown. Basal 1/2 of ocelli dark smoky brown, remainder pale white. Eyes grayish-yellow. Thorax: dark smoky brown, membranous areas pale yellow; pronotum with prominent posterolateral and posteromedian pale yellow spots, posteromedian spot extended almost entire pronotal length and larger than posterolateral spots (Fig. 6). Wings: membrane of fore and hind wings bright metallic blue in fresh specimens, bluish-brown in preserved specimens; longitudinal veins of fore and hind wings bluish-brown. Legs: coxae, trochanters, margins of claws smoky brown, remaining segments brownish-yellow. Abdomen: terga smoky brown, darker at lateral margins, terga 1-9 with narrow dark brown markings near posterior margins, progressively more widespread on terga 4-9 (Fig. 37). Sterna light smoky brown, sternum 1 darker, basal 1/2-2/3 of sternum 9 with brown markings, margins dark shiny brown, metallic brown on posterior margin; sterna 1-8 with median longitudinal translucent pale yellow line, progressively narrowed posteriorly with translucent pale lateral streaks. Genitalia: penes pale yellow, outer sclerotized sheath brown; shape of penes as in Fig. 9, 11-12; lateral view of sequentially extruded ejaculatory ducts of penes as in Fig. 16-18, ventral view Fig. 19-20. Caudal filaments: cerci pinkish-white; terminal filament darker, progressively paler distally, dark brown at extreme base; shiny brown setae on articulations.

Female Imago (in alcohol). — Length: body 10.0-11.0 mm; fore wings 8.0-9.0 mm; cerci 2.5-3.0 mm; terminal filament 1.9-2.5 mm. Color of head, antennae and ocelli as in male imago. Eyes grayish-black. Thorax: color of nota, pleura and sterna as in male imago; irregular pale yellow spot between coxae of metathoracic legs much larger than in male imago. Wings: color of membrane and veins of fore and hind wings as in male imago. Legs: coxae and extreme base of trochanters smoky brown, remaining segments shriveled, pale yellow. Abdomen: color of terga and sterna light smoky brown, markings as in male except submedian spots on sterna and brown markings on sternum 9 not as pronounced. Caudal filaments: smoky brown.

Mature Nymph (in alcohol). — Length: 7.0-10.7 mm; caudal filaments 2.0-2.6 mm. Head pale yellow; vertex with small circular reddish-brown markings (Fig. 52). Lateral ocelli white, inner 1/2 dark brown; median ocellus grayish-black. Eyes grayish-black. Antennae pale yellow; pedicel glabrous (Fig. 55). Mouthparts: mandibular prosthecae similar to Fig. 47; galea-licinia of maxillae with a submarginal row of 23-24 spinous setae; posterior margin of superlingua slightly curved (Fig. 44); segment 1 of labial palpi approximately 2/3 length of segment 2. Thorax: pale yellow; pronotum and mesonotum with prominent broken transverse reddish-brown band (Fig. 52). Legs pale yellow. Prothoracic legs: coxae with reddish-brown basal spot (Fig. 56); tibiae strongly bowed (Fig. 61), maximum width approximately 3/4

maximum width of femora; distance of tarsi from apex of tibiae approximately equal to 1-1/7 times maximum width of tibiae; apical portion of tibiae curved upward. Mesothoracic legs: tarsal claws approximately 1/4 length of tarsi and 1/2 length of tarsal claws of metathoracic legs. Metathoracic legs: tarsal claws (Fig. 65) 3/4 length of tarsi. Abdomen: terga and sterna pale yellow, markings as in imagos (Fig. 38). Caudal filaments: cerci pale yellow, terminal filament white; setae on articulations pale yellow, base reddish-brown.

Geographical Distribution. — (Fig. 76). *Homoeoneuria cahabensis* occurs in Alabama and Mississippi. Alabama: Holotype, male imago; Perry Co., Cahaba River, Barton Beach, 1 mi E Marion Fish Hatchery, 28/30-VI-1977, M.L. Pescador and R.W. Flowers; allotype, female imago, same data as in holotype. Paratypes. Alabama: 10 male and 14 female imagos, 70 nymphs, same data as in holotype; 7 male and 10 female imagos, 10 nymphs, Perry Co., Cahaba River off state Hwy 183, 27/28-VI-1968, W.L. & J.G. Peters, M.L. Pescador, P.T.P. Tsui and M. Makinde. Mississippi: 3 nymphs, Franklin Co., Homochitto River at U.S. Hwy 98, 5-VI-1956, C.D. Hynes and L. Berner; 20 nymphs, Franklin Co., Homochitto River, 4-1/2 mi. SE Bude, 2-IX-1972, P.H. Carlson.

Type Deposition. — The nymphs and adults were associated by rearing. All types are preserved in alcohol. Holotype, allotype and nine male and 13 female imaginal, and 41 nymphal paratypes are deposited in the FAMU collection. Three male and four female imaginal, and 12 nymphal paratypes are deposited in the UF collection. Five male and 7 female imaginal and 30 nymphal paratypes are deposited in the UU collection. Fifteen and 10 nymphal paratypes are deposited in the CU and PHC collections respectively.

Etymology. — The species is named after the Cahaba River.

Discussion. — *Homoeoneuria cahabensis* represents the *Homoeoneuria* sp. nymphs from the Homochitto River, Alabama that Edmunds, Berner and Traver (1958) did not assign to any particular species. The external morphology and color of the nymphs are similar to those collected from Cahaba River, Alabama where adult specimens were obtained and the two populations are considered conspecific.

The nymphs of *Homoeoneuria cahabensis* vary in degree of reddish-brown markings of the vertex and pronotum. Some nymphs have pronounced reddish-brown markings while others are not as pronounced. This variation occurs throughout the distribution of the species although the latter appear to be more common among the Homochitto River collection. Likewise the mean body length of mature nymphs from the Homochitto River are smaller [9.10 mm (range: 7.8-10.3 mm), compared to 9.95 mm (range: 9.2-10.7 mm)] in Cahaba River.

Homoeoneuria cahabensis can be distinguished from other species of the genus by the following combination of characters. In the imagos: (1) posteromedian pale yellow spot on the pronotum is anteriorly extended to almost entire pronotal length and is distinctly larger than the posterolateral spots (Fig. 6); (2) abdominal terga are smoky brown, and terga 1-9 have narrow dark brown markings near posterior margin (Fig. 37); and (3) shape of penes is as in Fig. 9, 11-12, 16 and lateral view of extruded ejaculatory ducts are shown in Fig. 17-20. In the nymph: (1) vertex and pronotum have reddish-brown markings (Fig. 52); (2) antennal pedicels are glabrous (Fig. 55); (3) galea-lacinia of maxillae has a submarginal row of 23-25 long and spinous setae; (4) prothoracic coxae have a reddish-brown spot near base; (5) prothoracic tibiae are strongly bowed (Fig. 61) with a maximum width of approximately 3/4 of maximum width of femora; and (6) abdominal terga 1-9 have narrow dark brown markings near the posterior margin as in the imagos (Fig. 38).

Homoeoneuria cahabensis appears most closely related to *H. dolani* but can be distinguished from it by any of the following characters. In the imagos: (1) abdominal terga are smoky brown and terga 1-9 have narrow dark brown markings near the posterior margin (Fig. 37); and (2) shape of penes is as in Fig. 9, 11-12. In the nymph: (1) vertex and pronotum have reddish-brown markings (Fig. 52); (2) prothoracic coxae have a reddish-brown spot near base (Fig. 56); (3) abdominal terga 1-9 have narrow dark brown markings near the posterior margin (Fig. 38); and (4) setae of caudal filaments are pale yellow with reddish-brown base.

Biology. — In the Cahaba River, the nymphs were collected in loose shifting sand bottoms near the edge of the river at a depth of 0.6-1.3 m in moderately fast flowing current. To determine the position of the nymphs in the substratum, some were transported and released in shallower and clearer stretches of the river. The nymphs were observed partially buried leaving the head and caudal filaments exposed, thus forming a broad U-shaped position. Such orientation is accomplished by the scouring motion of the mesothoracic and metathoracic legs in a sidewise fashion. As soon as the nymph is anchored to the substratum, the prothoracic legs

are projected forward with the tibiae almost at right angle to the femora and the long plumose hair placed lateroventral to the mouthparts. Such orientation of the prothoracic legs and the placement of the long plumose hairs, and the unique structures of the mouthparts form an efficient food filtering device for the nymphs. Gut contents of the nymphs include a mixture of sand and particulate organic matter.

Emergence of the adults in the Cahaba River has been recorded on June 27-28, 1968, and June 28-30, 1977. Based on the size of the wing pads of the nymphs collected in the area in June, emergence appears to extend through July and perhaps until August. In the Homochitto River, however, emergence appears to occur later, as several nymphs that were collected in the early part of September were still immature. A small swarm of imagos were observed in the Cahaba River on June 27 and 28, 1968 from 0730 to 0930 h. The water temperature at this time was 30°C with clear skies. Seventeen imagos were collected from the swarm, 9 females and 8 males, which is almost a 1:1 ratio.

In 1977, 35 mature nymphs were collected and reared in the laboratory at a water temperature of 28-30°C. Of the 24 imagos which emerged, five emerged between 1100 and 1200hr, and 19 emerged between 1200 and 1300hr. Emergence in the laboratory therefore occurred 3-4 hours later than the swarms observed in the field.

The duration of the subimaginal stage is very brief. Four individuals were observed and the time from emergence to shedding of the subimaginal skin was 30, 50, 60, and 62 seconds respectively.

The subimagos float on the surface of the water until they molt to imagos. Some subimagos were observed to use the nymphal skin as a raft or foothold while on the surface of the water. Unlike most mayflies in which the entire subimaginal exuviae are shed during the final molt, *Homoeoneuria* does not shed the wing covering, hence, the imaginal wings are semi-transparent with microsetae (Fig. 71-72).

Five dissected mature female nymphs indicate a mean number of 303.5 eggs (range 255-352).

Homoeoneuria (Homoeoneuria) alleni Pescador & Peters new species

Fig. 40, 49, 50, 53, 59, 63

Male Imago. — Unknown.

Female Imago. — Unknown.

Mature Nymph (in alcohol). — Length: body 10.0-12.0 mm; caudal filaments 2.5-3.0 mm. Head pale yellow, a narrow transverse purplish-brown band below eyes, connecting lateral ocelli; vertex washed with purplish-brown (Fig. 50). Lateral and median ocelli grayish-white, inner 1/2 black. Antennae pale yellow; pedicel with short, thick setae (Fig. 53). Mouthparts: mandibular prosthecae similar to Fig. 46; galea-licinia of maxillae with a submarginal row of 19-23 long, spinous setae; posterior margins of superlingua strongly curved (Fig. 41); segment 1 of labial palpi approximately 5/9 length of segment 2. Thorax: pale yellow, nota faintly washed with purplish-brown, slightly more pronounced on pronotum (Fig. 50). Legs pale yellow. Prothoracic legs: coxae without spot; tibiae moderately bowed (Fig. 59), maximum width approximately 9/10 maximum width of femora; distance of tarsi from apex of tibiae approximately 1/5 maximum width of tibiae; apical portion of tibiae straight to slightly curved downward. Mesothoracic legs: tarsal claws approximately 2/7 maximum length of tarsi and approximately 1/2-3/4 length of tarsal claws of metathoracic legs. Metathoracic legs: tarsal claws (Fig. 63) equal to 1-1/10 length of tarsi. Abdomen: terga and sterna pale yellow, posterior 1/2 of terga 1-9 with purplish-brown markings (Fig. 40). Caudal filaments: pale yellow; setae pale yellow, base purplish brown.

Geographical Distribution. — (Fig. 76). *Homoeoneuria alleni* is known to occur in Mexico, New Mexico, and Utah. New Mexico: Holotype, male nymph, Rio Grande, Las Cruces, 19-VII-1977, elevation 3,600′ (1100 m), R.K. Allen; Paratypes, New Mexico: 13 nymphs same data as holotype. Mexico: 1 nymph, Chihuahua, small stream 17 mi. W. Cuauhtemoc on Hwy 16, 13-VIII-1977, elev. 7,300′ (2225 m), R.K. Allen. Utah: 2 nymphs, Kane Co., Escalante Riv., 1 mi. upstream from mouth, 19-VIII-1958, G.G. Musser and G.R. Smith; 1 nymph Grand Co., Colorado River, Westwater Canyon, 19-VIII-1976, W. Reichert.

Type Deposition. — All types are preserved in alcohol. Holotype and 6 nymphal paratypes are deposited in the CAS collection. Six nymphal paratypes are deposited each in the FAMU and UU collections. One nymphal paratype is deposited in the BYU collection.

Etymology. — The species is named for Dr. Richard K. Allen, collector of the holotype, in honor of his significant contribution to the study of Ephemeroptera.

Discussion. — The nymphs of *H. alleni* exhibit a few color and morphological variations. The nymphs from Utah appear to lack color markings on the vertex and thoracic nota (Fig. 49) while those from Mexico and New Mexico have purplish-brown markings (Fig. 50). Some nymphs from New Mexico have prothoracic tarsi more

than 1/2 the maximum length of tibial portion distal to the tarsi whereas, others have about 1/3.

Homoeoneuria alleni can be distinguished from the other species of the genus by the following combination of characters. In the nymphs: (1) vertex and pronotum are washed with purplish-brown; (2) antennal pedicels have short thick setae (Fig. 53); (3) galea-lacinia of maxillae has a submarginal row of 19-23 long and spinous setae; (4) prothoracic coxae lack spot; (5) prothoracic tibiae are moderately bowed (Fig. 59) with a maximum width of approximately 9/10 of the maximum width of femora; and (6) abdominal terga 1-9 have pronounced purplish-brown markings (Fig. 40).

Based on the nymph, *H. alleni* appears most closely related to *H. salviniae* but can be distinguished from it by any of the following characters: (1) distance of tarsi of prothoracic legs from apex of tibiae is approximately 1/5 of maximum width of tibiae; and (2) abdominal terga 1-9 have pronounced purplish-brown markings near posterior margins (Fig. 40).

Biology. — Except for the dates of nymphal collections, the biology of *H. alleni* is unknown. The nymphs were collected in August and none had black wing pads.

Homoeoneuria (Homoeoneuria) salviniae Eaton

Fig. 39, 42, 46, 54, 58

Homoeoneuria salviniae Eaton 1883:36; Allen and Cohen 1977:399

Male Imago. — Unknown.

Female Imago (in alcohol). — Length: body 8.0-12.0 mm; caudal filaments 2.5-3.5 mm. Head black, venter pale yellow. Wings: membrane of fore and hind wings transparent, faintly smoky changing to a very light purplish-bronze; veins of fore and hind wings opaque and bordered narrowly with light brown. Legs: coxae of prothoracic, mesothoracic, and metathoracic legs castaneous, trochanters fuscous, remainder of legs pale fuscous and rather castaneous, trochanters fuscous, remainder of legs pale fuscous and rather shrivelled. Abdomen: terga fuscous becoming paler along the median line, with paired fuscous submedian markings; a large basal pair of submedian markings on segment 2, slightly divergent apically, followed by a pair of short transverse spots, one on each side; tergum 3 with the basal pair of spots each narrower about 3 times as long as broad, each followed by a transverse spot; terga 4-7 with elongate parallel or divergent spots each followed by two small spots; terga 8 and 9 with very reduced spots. Sterna fuscous yellow. Caudal filaments: fuscous.

Mature Nymph (in alcohol). — Length: body 9.0-11.0 mm; caudal filaments 2.7-3.0 mm. Head pale yellow. Lateral and median ocelli grayish-yellow, basal margins reddish-brown. Antennae pale yellow; pedicel with short, thick setae (Fig. 54). Mouthparts: mandibular prosthecae similar to Fig. 46; galea-lacinia of maxillae with submarginal row of 18-20 long, spinous setae; posterior margin of superlingua strongly curved (Fig. 41-42); segment 1 of labial palpi approximately 5/7 length of segment 2. Thorax: pale yellow. Legs pale yellow. Prothoracic legs: coxae without spot; tibiae moderately bowed (Fig. 58), maximum width equal to maximum width of femora; distance of tarsi from apex of tibiae slightly less than 1/2 maximum width of femora; apical portion of tibiae straight. Mesothoracic legs: tarsal claws slightly less than 1/3 maximum length of tarsi and approximately 2/3 length of tarsal claws of metathoracic legs. Metathoracic legs: tarsal claws equal length with tarsi. Abdomen: terga and sterna pale yellow; terga 4-9 with a dark brown spot near posterolateral corners, progressively larger posteriorly and faintly connected with brown transverse line (Fig. 39). Caudal filaments: pale yellow.

Geographical Distribution. — (Fig. 76). *Homoeoneuria salviniae* is known to occur in Guatemala (Eaton, 1881) and Mexico. Mexico: 6 nymphs, Chiapas, Rio Leventa, 10 mi. E Cintalapa on Hwy 190, 20-VIII-1966, R.K. Allen (CAS).

Type Deposition. — Lectotype (female imago) is deposited in BMNH collection.

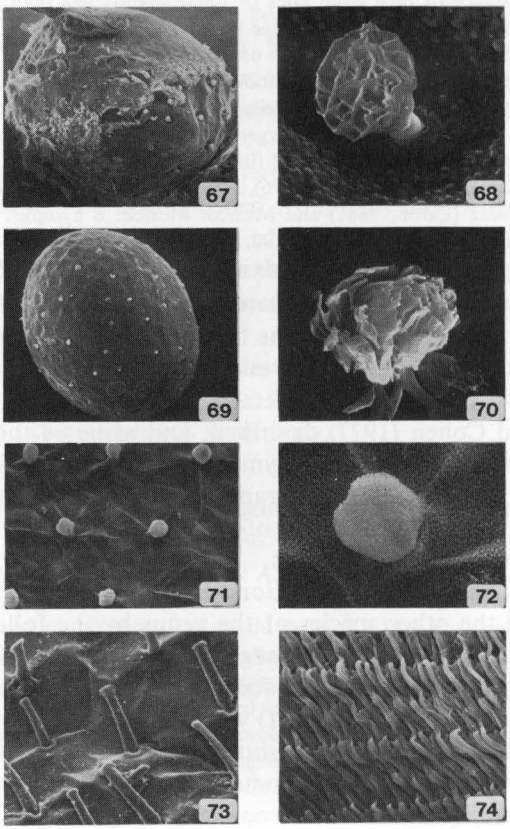
Discussion. — Adult specimens were not available to us, therefore the redescription of the female imago is a compilation of the description of Eaton (1883) and notes made by Kimmins (pers. comm. 1967) from the female lectotype.

Allen and Cohen (1977) described, and assigned the specimens from Chiapas, Mexico as the nymph of *H. salviniae*. Such assignment was based on the geographic proximity of the nymphal population to the type locality of the species, and the geographic isolation from the other species.

Based on the above description, *H. salviniae* can be differentiated from the other species of the genus by the following combination of characters. In the imago: (1) pronotal pale yellow spots are apparently absent; and (2) abdominal terga are fuscous, paler along median. In the nymph: (1) vertex and pronotum lack markings; (2) antennal pedicels have short thick hairs (Fig. 54); (3) galea-lacinia of maxillae have a submarginal row of 18-20 long and spinous setae; (4) prothoracic coxae lack spots; (5) prothoracic tibiae are moderately bowed (Fig. 58) with 9/10 maximum width of femora; and (6) abdominal terga 4-9 have a dark brown spot near the posterolateral corners and are progressively larger posteriorly and faintly connected with a brown transverse line (Fig. 39).

Based on nymphs, it appears that *H. salviniae* is closely related to

H. alleni but can be distinguished from it by any of the following characters: (1) distance of tarsi of prothoracic legs from apex of tibiae is slightly less than 1/2 maximum width of tibiae; and (2) abdominal terga 4-9 have dark brown spots near the posterolateral



FIGURES 67-74. Scanning electron microphotographs of *Homoeoneuria*. 67-68, *H. (Notochora) fittkaui:* 67, egg; 68, detail of attachment structure of egg. 69-74, *H.* (s.s.) *cahabensis:* 69, egg; 70, detail of attachment structure of egg; 71-72, papilla-like setae on wing of female imago; 73, setae on abdominal terga of nymph; 74, setae on dorsal surface of paraglossa of nymph.

corners and are progressively larger posteriorly and faintly connected by a thin transverse brown line (Fig. 39).

Biology. — The biology of *H. salviniae* is unknown. Eaton (1883) remarked that adults were collected early in the morning floating dead on surface of the stream. Recently, Allen and Cohen (1977) collected the nymphs in Chiapas, Mexico during the third week of July but none had black wing pads.

Subgenus NOTOCHORA Pescador and Peters, new subgenus

Imago. — Length: ♂ body 7.0 mm, caudal filaments 6.5 mm; ♀ body 6.8-7.0 mm, cerci 2.0 mm, terminal filament 1.2 mm. Male genitalia: Styliger plate weakly developed; penial arms weakly developed; penes with finger-like processes (Fig. 10, 14). Female sternum 7 with deep, narrow posteromedian constriction (Fig. 7); female sternum 9 posteromedially extended, apically pointed (Fig. 7).

Egg. — Chorion covered with granulate setae; attachment structures cauliflower-shaped with broad single stalk (Fig. 67-68).

Etymology. — notos, Gr., meaning south; Choros, Gr., meaning country; masculine.

Type species. — *Homoeoneuria (N). fittkaui* Pescador and Peters, new species.

Discussion. — *Notochora* is monotypic and is known only from northern Brazil. The characters above distinguish if from *Homoeoneuria* s.s. The wings of *Notochora* specimens that are available are damaged that it was impossible to reconstruct the wing venation. The nymphs are unknown.

Homoeoneuria (Notochora) fittkaui Pescador and Peters, new species

Fig. 5, 10, 13-14, 34

Male Imago (in alcohol). — Length: body 7.0 mm. Head brown, venter pale yellow. Antennae brown. Ocelli and eyes shriveled (color determination impossible). Thorax: brown, membranous areas pale yellow; pronotum with prominent posterolateral and posteromedian pale yellow spots, posteromedian spot much smaller anteriorly, extended approximately 1/2 maximum pronotal length and subequal width to posterolateral spots (Fig. 5). Wings: membrane of fore and hind wings pale yellow in preserved specimens; longitudinal veins of fore and hind wings light brown. Legs: light brown, margins and prothoracic legs darker, ventral surface of femora, tibiae and tarsi of mesothoracic and metathoracic legs pale yellow. Abdomen: terga and sterna brownish-yellow, margins and tergum 10 darker; terga no markings (Fig. 34). Sterna 1-8 with median longitudinal translucent pale yellow line, progressively narrows posteriorly. Genitalia: penes yellow except lateral processes

brown; shape of penes as in Fig. 10, 13-14. Caudal filaments: pale white; pale yellow setae on articulations.

Female Imago (in alcohol). — Length: body 7.0 mm; wings 6.8-7.0 mm; cerci 2.0 mm; median filament 1.2 mm. Color of head and antennae as in male imago. Ocelli pale white, base brown. Eyes, grayish-black. Thorax: color and markings of nota, pleura and sterna as in male imago except metasternum hyaline; pale yellow spots on pronotum not as pronounced. Wings: color of membrane and veins as in male. Legs: coxae and trochanters brown, remaining segments shriveled, pale yellow. Abdomen: color of terga and sterna as in male except segment 10 with same color as other segments. Caudal filaments: pale yellow, progressively paler distally.

Nymph. — Unknown.

Geographical Distribution. — (Fig. 76). Holotype male imago, Brazil: Amazonas State, Río Negro about 30 km below Barcelos, 7-11-1962, E.J. Fittkau. Paratypes, Brazil: 3 female imagos, same data as holotype.

Type Distribution. — All types are preserved in alcohol. Holotype and one female imaginal paratype are deposited in the INPA collection. Two female imaginal paratypes deposited in the UU collection.

Etymology. — *Homoeoneuria (Notochora) fittkaui* is named for Dr. E.J. Fittkau, Zoologische Sammlung des Bayerischen Staates, München, Germany, for collecting the specimens.

Discussion. — *Homoeoneuria fittkaui* can be distinguished from the other species of the genus by the following combination of characters. In the imagos: (1) posteromedian pale yellow spot of pronotum is subequal to posterolateral spots (Fig. 5); (2) abdominal terga have no markings (Fig. 34); and (3) shape of penes is as in Fig. 10, 13-14.

Biology. — Except for the collection of imagos in February, biology of *H. fittkaui* is unknown.

Homoeoneuria sp.

This nymphal exuvium collected from Kearney, Nebraska, is one of the specimens Edmunds et al. (1958) did not assign to any particular species. Presence of setae on the antennal pedicel and almost equal width of tibiae and femora of the prothoracic legs suggest the specimen probably belongs to the *alleni-salviniae* group. Other characters to correctly identify it to species are missing. Another unidentified nymph from Guadalupe River, Texas reported by Edmunds *et al.* (1958) was not available to us for study. Attempts to locate the specimens were unsuccessful.

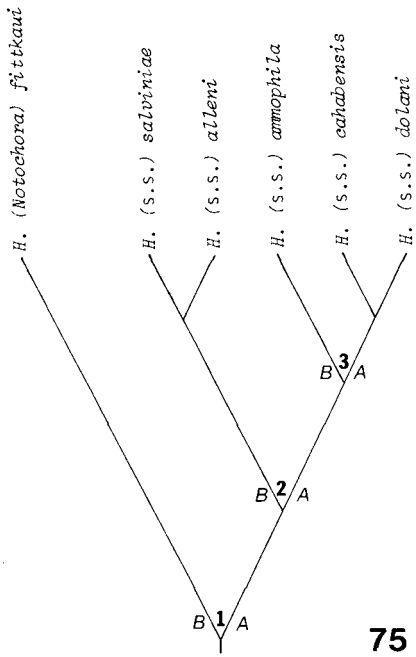


FIGURE 75. Phylogenetic diagram of *Homoeoneuria*.

PHYLOGENETIC RELATIONSHIPS AND ZOOGEOGRAPHY

Nymphs and imagos of *Homoeoneuria* possess a number of distinctive external morphological characters which when analyzed enable interpretations of the probable phylogeny of the group. The common derivation of character states is based on the concept that ancestral character states are generally widespread in the genus and often the family and order. Following this line of thought, we speculate that the ancestor of *Homoeoneuria* probably possessed the following combination of characters. In the imagos: (1) bars of the male styliger plate were weakly developed (Fig. 13); (2) penes had no finger-like processes (Fig. 12); (3) female sternum 7 had

shallow and broad posteromedian emargination (Fig. 8); and (4) male and female imagos had pronounced color markings on the abdominal terga (Fig. 40). In the nymph: (1) antennal pedicel was glabrous (Fig. 55); (2) tibiae of prothoracic legs were slightly bowed, and slightly narrower or as broad as the femora (Fig. 58); (3) tarsi of the prothoracic legs were close to the apex of the tibiae (Fig. 58-60); (4) galea-laciniae of the maxillae had a submarginal row of several spinous setae; (5) posterior margin of superlingua of the hypopharynx was strongly curved (Fig. 41-42); and (6) abdominal terga had pronounced color markings (Fig. 40).

Figure 75 depicts the phylogeny of *Homoeoneuria* species. The sequence of branching is determined by shared possession of derived character states. Table 1 shows the different phyletic lineages and corresponding character states used to interpret the phylogeny.

Furcation 1 represents the common ancestral derivation of subgenera *Homoeoneuria* s.s. and *Notochora*. Within the subgenus *Homoeoneuria* s.s. (lineage 1A) there has been the development of a pronounced styliger bar, reduction of the posteromedian emargination of female abdominal sternum 7 (Fig. 8; Table 1), and complete lack of accessory finger-like processes of the penes which are found in *Notochora* (lineage 1B) (Fig. 14).

Lineage 2A which is represented by *H. ammophila, H. cahabensis* and *H. dolani* has nymphs that retained the primitive glabrous antennal pedicel (Fig. 55) but have derived narrow prothoracic tibiae and distantly located prothoracic tarsi (Fig. 60-62; Table 1). Lineage 2B has derived setae of antennal pedicel (Fig. 53-54) (*H. salviniae* and *H. alleni*) but the primitive character states of the prothoracic tibiae and tarsi are retained. Imagos of lineage 2B are known only from female specimens which were not available to us for study. Therefore only the nymphs were analyzed.

Lineage 3A is represented by *H. cahabanensis* and *H. dolani,* and lineage 3B by *H. ammophila*. Evolutionary changes on abdominal markings of both nymphs and imagos, curvature of the hypopharyngeal superlinguae and width of prothoracic tibiae (Table 1) suggest an interesting evolutionary trend that occurred between these two lineages. A phenocline ranging from a broad markings in *H. ammophila* (Fig. 35) to intermediate in *H. cahabanensis* (Fig. 37-38) and very narrow markings (Fig. 36) to

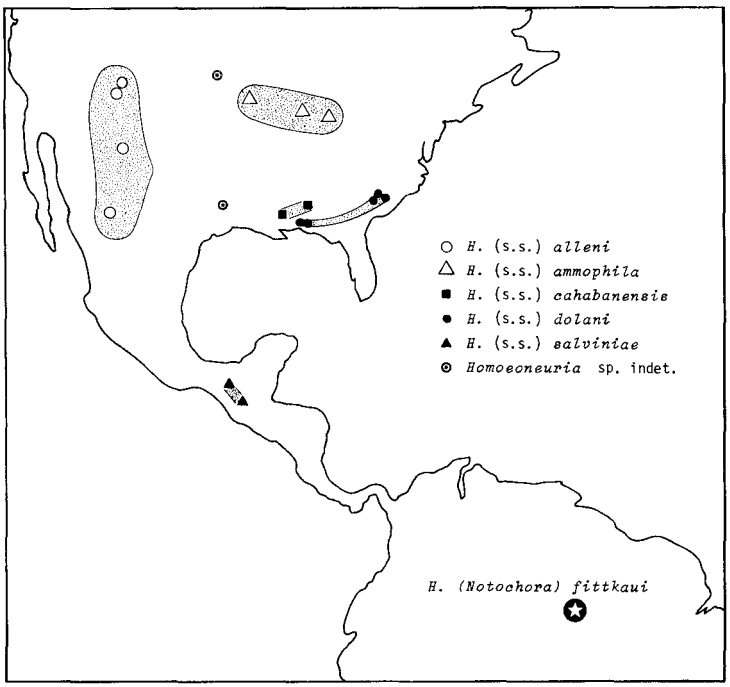


FIGURE 76. Geographical distribution of *Homoeoneuria*.

absent in *H. dolani* suggests an evolutionary trend towards gradual loss of markings. Additionally, progressive narrowing of the nymphal prothoracic tibiae shows similar phenoclinal pattern in that nymphs of *H. ammophila* (Fig. 60) have comparatively broader prothoracic tibiae than *H. cahabensis* and *H. dolani*, the last usually having the narrowest (Table 1). Differences in curvature of the posterior margin of the hypopharyngeal superlingua further complement the evolutionary pattern shown by abdominal marking and prothoracic tibiae with *H. ammophila* having moderately curved hypopharyngeal superlingua (Fig. 43) and slightly curved in both *H. cahabensis* and *H. dolani* (Fig. 44-45). Available data indicate that *H. cahabensis* and *H. dolani* possess more derived character states than *H. ammophila*. Between the

TABLE 1. Character States of Figure 75. D, derived; P, primitive.

Furcation 1	*A*	*B*
Styliger bar	(D) well developed (Fig. 11)	(P) weakly developed (Fig. 13)
Penes	(P) without processes (Fig. 12)	(D) with finger-like processes (Fig. 14)
Sternum 7	(D) with shallow and broad posteromedian emargination (Fig. 8)	(P) with deep & narrow posteromedian emargination (Fig. 7)
Furcation 2	*A*	*B*
Antennal pedicel	(P) glabrous (Fig. 55)	(D) with short and thick setae (Fig. 53-54)
Comparative width of tibiae and femora of prothoracic legs	(D) tibiae 2/3-5/6 maximum width of femora	(P) tibiae 9/10 to equal maximum width of femora
Tarsi of prothoracic legs	(D) located from apex of tibiae at approximate distance of 2/3 to 1-1/2 maximum width of tibiae (Fig. 60-62)	(P) located from apex of tibiae at approximate distance of 1/5 to 1/2 maximum width of tibiae (Fig. 58-59)
Furcation 3	*A*	*B*
Abdominal markings	(D) none to narrow (Fig. 36-38)	(P) moderately broad (Fig. 35)
Number of submarginal spinous setae of galea-lacinia of maxillae	(P) >15	(D) <15
Posterior margin of hypopharyngeal superlingua	(D) slightly curved (Fig. 44)	(P) moderately curved (Fig. 43)
Comparative width of tibiae and femora of prothoracic legs	(D) 2/3 to 3/4 width of femora	(P) 5/6 width of femora

sister species *H. cahabensis* and *H. dolani,* the latter possesses more derived character states.

The genus *Homoeoneuria* exhibits a North American and northern South American distribution (Fig. 76). When species distributions are superimposed on the proposed phylogeny, some inferences can be drawn concerning the distributional pattern. One species, *H. fittkaui,* is confined to northern South America while two sister species, *H. salviniae* and *H. alleni,* occur in Central America, the latter being found also as far west as Utah (Fig. 76). *Homoeoneuria ammophila* is presently known in the midwestern United States, and two closely related species, *H. cahabensis* and *H. dolani,* are confined in the southeastern United States (Fig. 76).

Although the possibility remains that this disjunct distributional pattern of *Homoeoneuria* is an artifact of insufficient collections, other organisms exhibit similar distributional patterns. Some fishes such as the poeciliid, *Gambusia affinis,* has a disjunct Middle and North American distribution (Rosen and Bailey, 1963) similar to the North and Central American species of *Homoeoneuria*. In a paper on vicariant patterns and historical biogeography, Rosen (1978) advanced excellent arguments concerning the North and Middle American distribution of two poeciliid genera *Heterandria* and *Xiphophorus*. Axelrod (1975), Martin and Harrell (1975), and Dott and Batten (1976) proposed geological explanations for the present disjunction of the once continuous distributional pattern of the flora and fauna of North and Central America.

A comprehensive documentation of the ecology and biology of *Homoeoneuria* species is necessary to have better in-depth analysis of historical biogeography.

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