

A REDESCRIPTION AND PHYLOGENETIC RELATIONSHIPS OF NESOPHLEBIA
(EPHEMEROPTERA, LEPTOPHLEBIIDAE, ATALOPHLEBIINAE)

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Abstract. The unique genus Nesophlebia is known only from the island of Madagascar / Malgasy Republic/. The female imago and nymph of N. adusta are described for the first time and additional characters are given for the male imago. Nesophlebia is most closely related to Maheathraulius from the Seychelles. The phylogenetic relationships of these two genera center around the Penaphlebia lineage.

Taxonomy, nymph, Penaphlebia-, Miroculis- Atalonella lineages

Peters and Edmunds (1964) established Nesophlebia for N. adusta which they described from one male imago collected at Perinet (= Andasibe), Malgasy Republic; legs were broken off and missing from the holotype. Recently one of us (GFE) collected additional material of N. adusta from near the type locality. In this paper, we complete the description of the male imago and describe the female imago for the first time. Morphological terms and procedures used in this paper are as given in Peters, Peters and Edmunds (1978).

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Nesophlebia Peters and Edmunds, 1964
(Figs. 1-6, 11-17, 20-23, 28-32)

Nesophlebia Peters and Edmunds, 1964: 248; Demoulin 1970: 121.

Imago. Legs: ratios of segments of male fore legs, 0.68:1.00 (2.50 mm):0.04:0.48:0.40:0.32:0.20; claws of a pair similar, both apically hooked with an opposing hook (Fig. 4)/remainder of male as in Peters and Edmunds (1964)/. Eyes of female separated on meson of head by a length 4 times maximum width of an eye. Egg guide or ovipositor of female extended to posterior margin of abdominal segment 10 (Fig. 11) and composed of posterior portion of sternum 7 and anterior portion of sternum 8. Ninth sternum of female entire and blunt apically (Fig. 12).

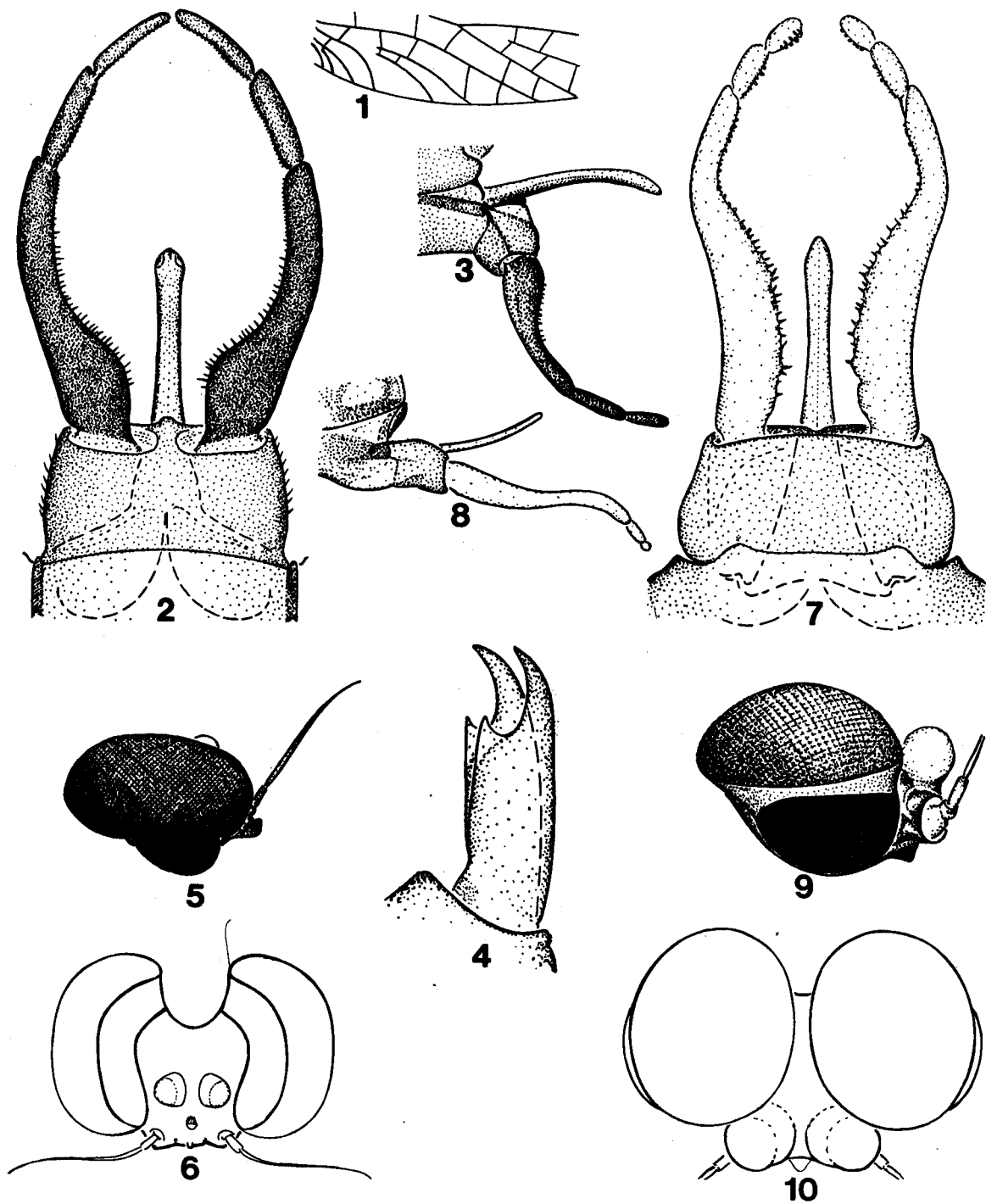
Mature nymph. Head prognathous. Antennae 1 1/2 to 2 times maximum length of head. Mouthparts (Figs. 14 - 17, 28 - 32): dorsal hair of labrum as in Fig. 30, submedian and anterior areas of hair ventrally; anteromedian emargination deeply cleft, width of cleft narrow, cleft with 5 small rounded denticles (Fig. 31). Clypeus as in Fig. 30. Left mandible as in Fig. 28. Lingua of hypopharynx with well developed lateral processes, paired submedian row of long hair on internal dorsal surface, submedian lobes with short hair apically, anterior margin of lingua deeply cleft; superlingua as in Fig. 32, with a row of hair along anterior margin, lateral margins blunt. Segment 2 of maxillary palpi a little longer than length of segment 1, segment 3 of palpi (Fig. 14) a little longer than 1/2 length of segment 2, triangular; hair on maxillae as in Fig. 14. Labium as in Fig. 15; segment 2 of palpi a little longer than segment 1; segment 3 of palpi (Fig. 17) a little longer than 1/2 length of segment 2, triangular; glossae curved over ventrally (Fig. 16), glossae ventral to paraglossae. Legs (Figs. 20 - 23): outer margin of femora indented near apex so tibiae can draw partially into femora (Fig. 20); apex of claws hooked and narrow, denticles on claws progressively larger apically (Fig. 23). Gills (Fig. 13): gills on segment 2 - 7 alike; each gill with a single lamella, each gill long, slender and deeply forked; main trunk of tracheae forked near fork of lamella and each branch along median line of each portion of lamella, tracheal branches absent; main trunk of tracheae darkly pigmented. Posterolateral spines on abdominal segments 4 - 9, spines progressively larger posteriorly. Terminal filament a little longer than cerci.

Type species. Nesophlebia adusta Peters and Edmunds, 1964.

Nesophlebia adusta Peters and Edmunds, 1964

Male imago (in alcohol). /See description of male imago in Peters and Edmunds (1964)/. Legs light chestnut brown, apex of meso- and metathoracic femora darker.

Female imago (in alcohol). Eyes black. Head chestnut



Figs. 1 - 10, male imago: 1 - 6 - Nesophlebia adusta, 7 - 10 - Maheathraulus scotti. 1 - cubital area of fore wing, variation; 2 - 3, 7 - 8 - ventral and lateral views of genitalia; 4 - fore claw; 5 - 6, 9 - 10 - lateral view and dorsal outline of eyes.

brown, carinae darker. Antennae light chestnut brown. Thorax light chestnut brown, area around base of prothoracic legs, lateral margins of pronotum, and base of fore wings washed with blackish-brown. Color and markings of legs as in male imago. Wings: color as in male imago except membrane of fore wings

uniformly light brown. Abdomen: light chestnut brown, darker marks on terga as in male imago, except more extensive on terga 1 - 2 and 7 - 8. Ovipositor or egg guide chestnut brown. Caudal filaments light brown.

Mature nymph (in alcohol). Head light brown, venter paler. Thorax light brown, venter paler, markings as in male and female imagos. Legs light brown with blackish-brown markings on femora and tibiae as in Fig. 20. Abdomen: light brown, venter paler; darker marks on terga as in male and female imagos, except all marks less distinct. Membrane of gills light grey, tracheae black. Caudal filaments light brown.

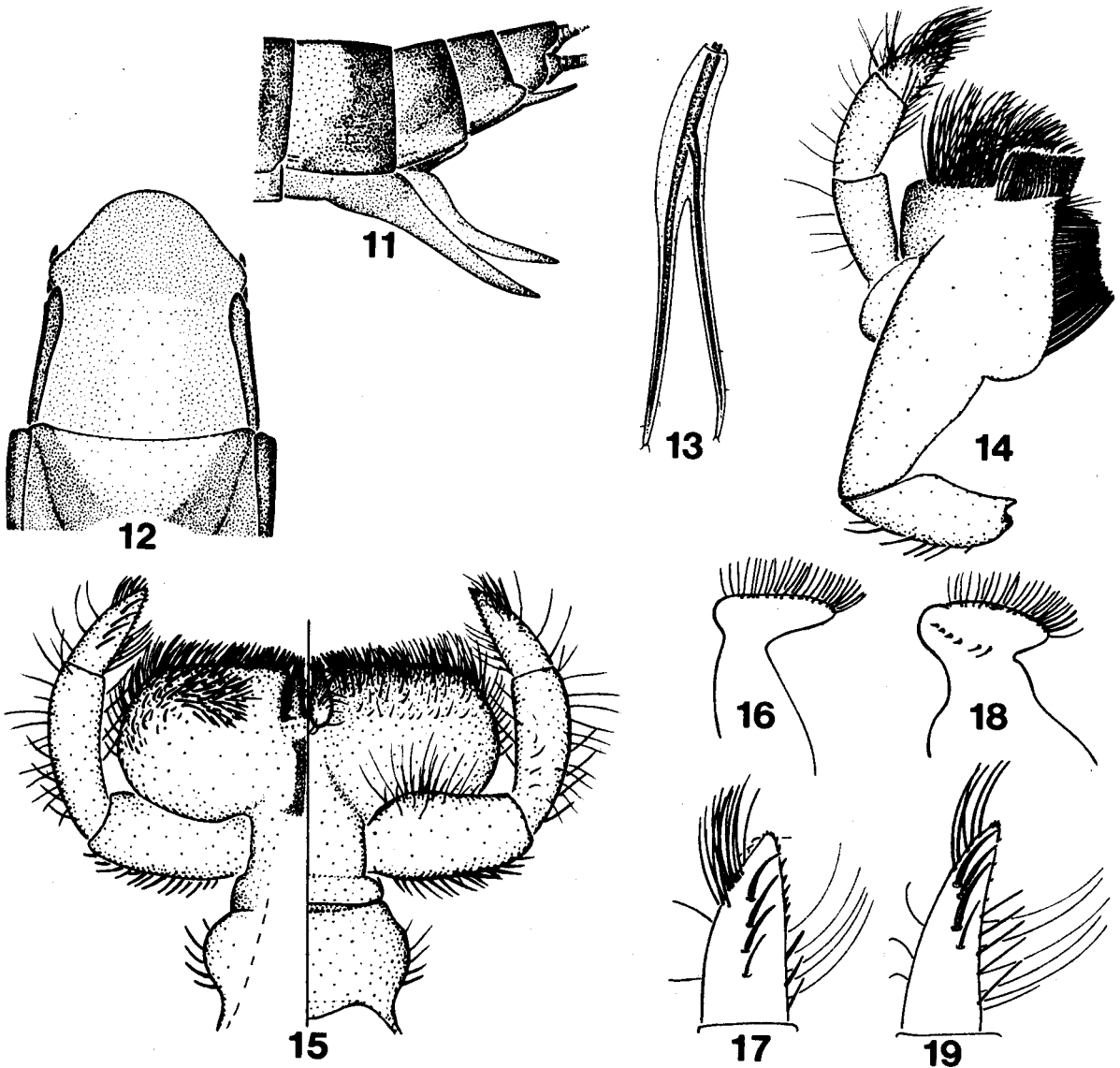
Additional specimens. All specimens collected from the Malgasy Republic by G. F. Edmunds, Jr., C. H. Edmunds and F. Emmanuel. One male imago, 1 female imago, 2 nymphs, Province Tamatava (East), Anevoka Riv., 15 km E. Perinet (= Andasibe), 11-10-71; 1 nymph, Province Tamatava (East), Amboasary Riv., Perinet (= Andasibe), 11-10-71. All specimens are in alcohol. One male imago, 1 female imago and 1 nymph deposited in the collections of University of Utah and 2 nymphs deposited in the collections of Florida A&M University. Association of the nymph with the male and female imagos is by the abdominal color pattern and the size of the developing hind wings on specimens collected from the same locality.

Biology. Imagos of Nesophlebia were collected flying along the banks of the Anevoka River at 1000 hrs. The river is fast flowing and about 7 meters wide at the collection site. Bottom substrate consists of large rocks to gravel.

DISCUSSION

Nesophlebia can be distinguished from all other genera of the Leptophlebiidae by the following combination of characters. In imagos: (1) hind wings are very small with only one longitudinal vein present /Figs. 29 - 30 in Peters and Edmunds (1964)/, (2) claws of a pair are similar and each is apically hooked with an opposing hook (Fig. 4), (3) upper portion of male eyes is reniform /Figs. 5 - 6 and Fig. 62 in Peters and Edmunds (1964)/, and (4) female possesses an egg guide or ovipositor which extends to posterior margin of abdominal segment 10 (Fig. 11). In the nymph: (1) glossae of labium are curved over ventrally (Figs. 15 - 16), (2) inner margin of segment 3 of labial palpi possesses a row of small denticle like setae (Figs. 15, 17), (3) abdominal gills occur on segments 2 - 7 and all gills are deeply forked (Fig. 13), (4) denticles on claws are progressively larger apically (Fig. 23), and (5) posterolateral spines occur on abdominal segments 4 - 9.

Nesophlebia appears to be most closely related to Maheathraululus Peters, Gillies and Edmunds which occurs only in the Seychelles. However, Nesophlebia can be distinguished from Maheathraululus by the following combination of characters. In the imagos, by the characters that are given above to distinguish Nesophlebia from all genera of the Leptophlebiidae. In the



Figs. 11 - 12, female imago of Nesophlebia adusta: 11 - lateral view of abdominal segments 7 - 10; 12 - sterna 8 - 9; Figs. 13 - 19 mature nymph: 13 - 17 - N. adusta, 18 - 19 - Maheathraulus scotti. 13 - gill 4; 14 - ventral view of right maxilla; 15 - labium /venter on right, dorsum on left/; 16, 18 - lateral view of glossa /venter on right/; 17, 19 - dorsum of 3rd segment of labial palpi.

nymph: (1) abdominal gills occur on segments 2 - 7 and all gills are deeply forked (Fig. 13), (2) anteromedian emargination of labrum is deeply cleft with 5 small rounded denticles (Fig. 31), (3) segment 3 of labial palpi is a little longer than 1/2 length of segment 2 (Fig. 15), (4) posterolateral spines occur on abdominal segments 4 - 9, and (5) denticles on claws are progressively larger apically (Fig. 23).

Several figures of Maheathraulus and Nesophlebia (Figs. 2 - 3, 5 - 10, 18 - 19, 24 - 27) were redrawn for this paper to include details not given in other publications (Peters, Gillies and Edmunds 1964; Peters and Edmunds 1964, 1970). The

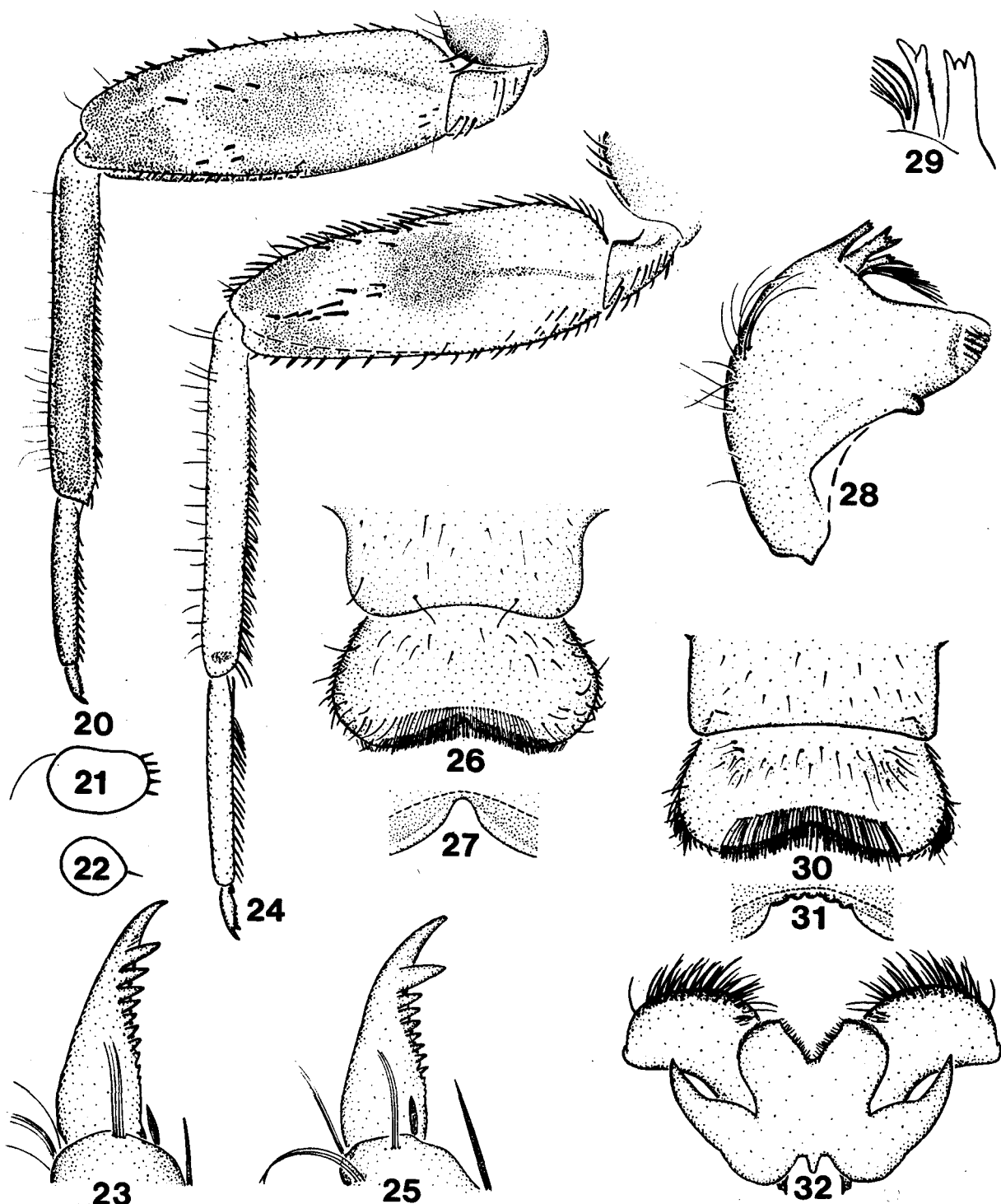
nymphal claw of Maheathraulius was originally made from a specimen with broken denticles and relative size of denticles was estimated; based on intact material, the apical denticle is much larger than the other denticles (Fig. 25). In Nesophlebia ICu₁ of the fore wings was correctly figured as attached to CuA by a cross vein, but the holotype from which the figure was drawn seems to be an atypical specimen; in all additional material, ICu₁ is free at the base as shown in Fig. 1.

The female imagos of Nesophlebia and Maheathraulius both possess a long ovipositor or egg guide; however, the morphology of the two structures is entirely different. In Maheathraulius, the ovipositor is composed of the posterior portion of sternum 7 and in cross section the sclerite curves around to form a tubular ovipositor. In Nesophlebia, the ovipositor is composed of the posterior portion of sternum 7 and the anterior portion of sternum 8. In this case, the posterior portion of sternum 7 forms the ventral half of the ovipositor while the anterior portion of sternum 8 forms the dorsal half of the ovipositor (Fig. 11).

Well developed ovipositors or egg guides are known in several major phyletic lineages in the Leptophlebiidae and the structure is of variable morphology. Illustrated examples include Peters (1971) for Hagenulus Eaton, Towns and Peters (1979) for Isothraulius Towns and Peters, and Peters and Edmunds (1970) for Habrophlebia Eaton, Habrophlebiodes Ulmer, and Megaglena Peters and Edmunds. Thus the ovipositor or egg guide has apparently developed independently several times within the Leptophlebiidae. Its function is unknown and no field observation have been published, although Berner (1950) gave laboratory observations for Habrophlebiodes brunneipennis Berner. Berner (pers. commun.) suggests that the ovipositor helps the female deposit eggs singly or in a small batches as the ovipositor touches the water and Edward L. Smith (pers. commun.) suggests that it is used to break the surface tension of the water.

After study of the Eastern Hemisphere Leptophlebiidae (excluding genera from Australia and New Zealand), Peters and Edmunds (1970) suggested that Nesophlebia, Maheathraulius and Hagenulodes Ulmer were closely related as a derivative of the Thraulius-group genera. This relationship was proposed based on a single character - the two long intercalaries in the cubital area of the fore wings. Subsequent studies of leptophlebiid genera in South America (Pescador and Peters 1980, Savage and Peters 1982) and New Zealand (Towns and Peters 1980) have distinguished several other lineages, and relationships of many of the Ethiopian and Oriental genera can now be clarified. Hagenulodes appears to be closely allied to the Meridialaris lineage of Pescador and Peters (1980) and shares all derived character states used to define that lineage, except short scattered spines occur on the basal and medial margins of the labial submentum (postmentum) in Hagenulodes.

Nesophlebia and Maheathraulius appear to be closely related



Figs. 20 - 32, mature nymph: 20 - 23, 28 - 32 - *Nesophlebia adusta*, 24 - 27 - *Maheathraulus scotti*. 20, 24 - fore leg; 23, 25 - fore claw; 21, 22 - cross section of tibia and tarsus; 26 - 27, 30 - 31 - clypeus and labrum with detail of anteromedian emargination; 28 - left mandible; 29 - detail of incisors of right mandible; 32 - hypopharynx.

based on the derived character states of fused slender penes, entire female ninth sternum, deeply forked and slender abdominal gills, and the shape of the labrum.

Nesophlebia and Maheathraulius appear to center around the Penaphlebia lineage based on derived character states given by Savage and Peters (1982) to separate the Hapsiphlebia lineage from the Penaphlebia lineage. The Penaphlebia lineage was originally defined by Pescador and Peters (1980) and includes Penaphlebia Peters and Edmunds, Massartella Lestage, and unnamed genera from Australia. Later Savage and Peters (1982) further defined the lineage. Based on the character states for lineages given by Savage and Peters (1982), the Penaphlebia lineage is defined by the one derived character state "maxillary palpal segment 2 with pectinate setae on inner margin". While Nesophlebia possesses this derived state, Maheathraulius does not.

An analysis of all character states for furcation 3 in Savage and Peters (1980) indicates Nesophlebia and Maheathraulius are intermediate in character states between the Penaphlebia lineage and the Miroculis-Atalonella lineages. Both genera possess five derived character states common to the Miroculis and Atalonella lineages. These five states are: long setae on subimaginal wings (character 1), fore wings with less than 25 costal cross veins (character 2), lateral margins of clypeus curved (character 4), setae on outer margin of labrum (character 5), and a reduced number of hairs on the outer margin of the mandibles (character 6). Further, Maheathraulius possesses two additional derived character states common to the Miroculis and Atalonella lineages. These two states are the hair-like setae on the inner margin of segment 3 of the labial palpi (character 8) and the enlarged apical denticle on the claws (character 9).

Only one derived character state (pectinate setae on maxillary palpi) would place Nesophlebia in the Penaphlebia lineage, while five derived character states would align Nesophlebia with the Miroculis-Atalonella lineages; Maheathraulius shares seven derived character states with the Miroculis-Atalonella lineages. Based on the analysis of furcation 3, both genera are more derived than the Penaphlebia lineage.

An analysis of all character states for furcation 4 in Savage and Peters (1982) to delineate the Miroculis and Atalonella lineages suggest that Nesophlebia and Maheathraulius are as derived as the Miroculis lineage. Neither genus possesses the derived character state that delineates the Atalonella lineage. Nesophlebia does share five derived (characters 1, 7, 8, 10, 11) and one ancestral (character 13) character states with the Miroculis lineage, but three character states (characters 4, 5, 9) are more derived in Nesophlebia than in the Miroculis lineage. Maheathraulius shares seven derived (characters 1, 2, 4, 5, 6, 7, 12) and one ancestral (character 13) character states with the Miroculis lineage and is more derived than the Miroculis lineage in one character state (character 9).

Until apparently related genera from Madagascar and Africa can be described and studied, a full character state analysis for Nesophlebia and Maheathraulius is not possible. Both genera

appear to center around the Penaphlebia lineage either as a derived group in the Ethiopian Region or as a subgroup of the Miroculis lineage. As more genera studied, the presently defined lineages will be reevaluated to distinguish broadened generic lineages.

This is the first record from the Ethiopian Region of genera centering around the Penaphlebia and Miroculis lineages. Previously, the Penaphlebia lineage was known only from southern South America and Australia, and recent research suggests the lineage does not occur in New Zealand or New Caledonia. The Miroculis lineage is currently known only from northern South America.

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