A NEW GENUS AND SPECIES OF LEPTOPHLEBIIDAE: ATALOPHLEBIINAE FROM THE CELEBES (SULAWESI) (EPHEMEROPTERA)

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ABSTRACT

Sulawesia a new genus of the Leptophlebiidae: Atalophlebiinae is established based on the adults and nymph of a new species, *S. haema* from the Celebes (Sulawesi). *Sulawesia* belongs to the Atalophlebioides lineage and is closely related to genera in Australia. The zoogeography of *Sulawesia* is discussed.

INTRODUCTION

Large collections of Ephemeroptera from the Celebes (Sulawesi) have recently become available. Among the specimens are adults and nymphs of a new genus of Leptophlebiidae: Atalophlebiinae which is of phylogenetic and zoogeographic importance.

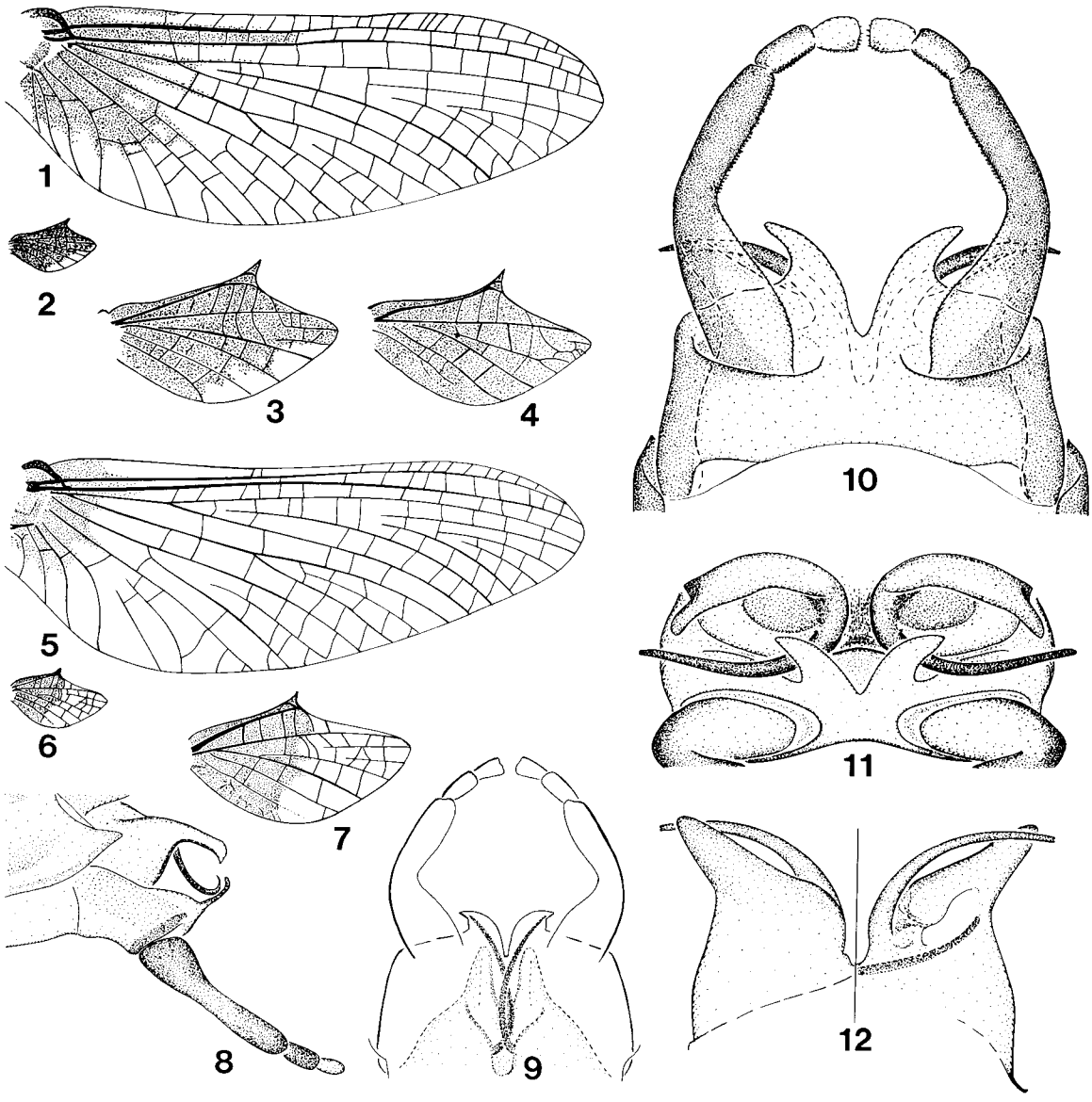
This paper in part is based on material collected during Project Wallace, sponsored by the Royal Entomological Society of London and the Indonesian Institute of Sciences. Descriptions of Project Wallace and its study sites are given in Knight (1983) and Dudgeon (1986).

Terminology and procedures used in the descriptions follow those of Peters, Peters and Edmunds (1978). Abbreviations used in the collection localities and deposition of types are: Sulawesi Utara Province (SUP), Sulawesi Tengah Province (STP), Sulawesi Selatan Province (SSP), John T. Polhemus (JTP), Dan A. Polhemus (DAP), David Dudgeon (DD), Jan van Tol (JT). British Museum (Natural History), London [BM(NH)], Florida A&M University, Tallahassee (FAMU), Museum Bogoriense, Bogor, Indonesia (MBB), Rijksmuseum van Natuurlijke Historie, Leiden (RNH), University of Hong Kong (HK), United States National Museum Natural History, Washington, D.C. (USNM), and University of Utah, Salt Lake City (UU).

SULAWESIA, new genus
(Figs 1-34)

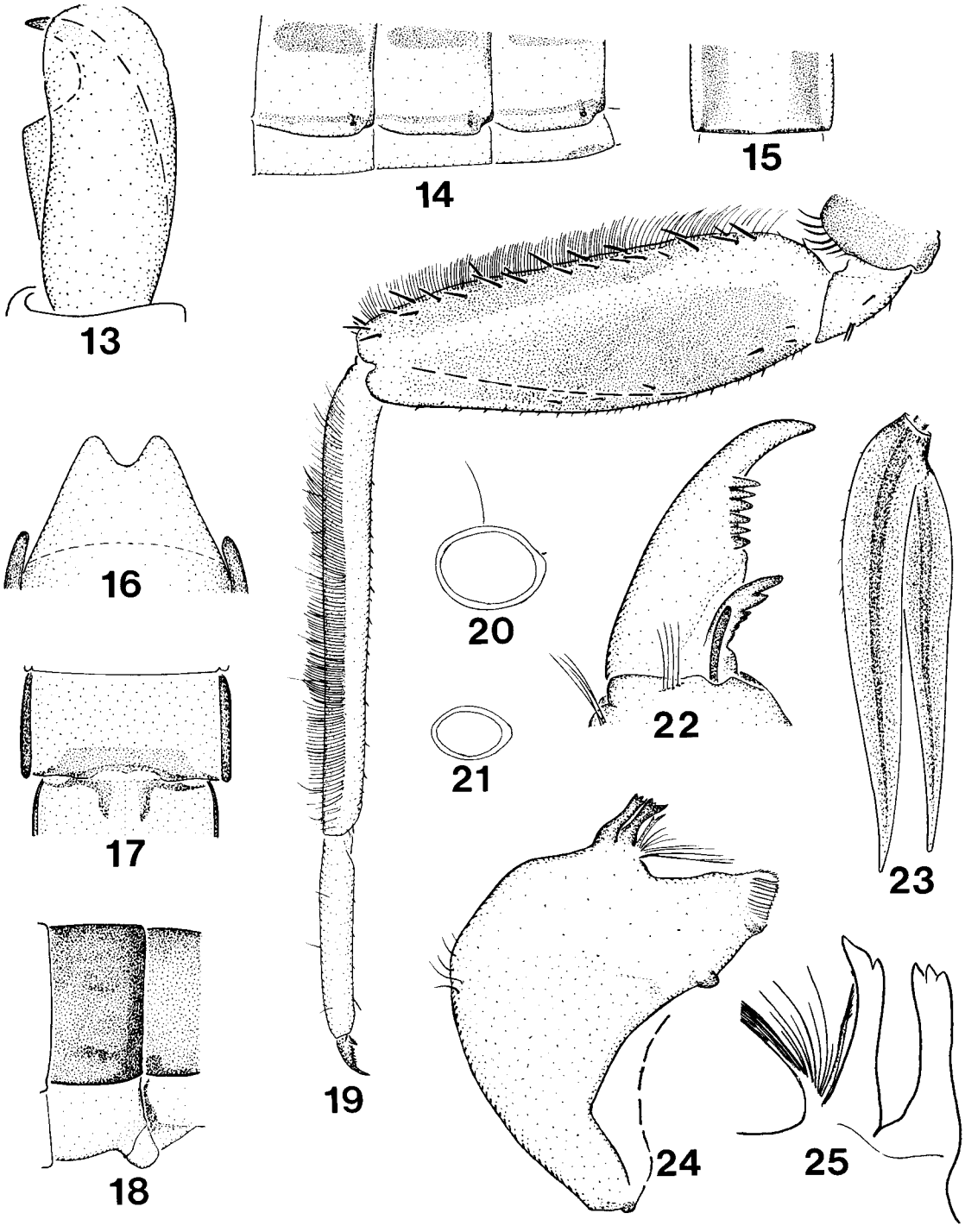
Imago. Length of male: body, 6.2–7.0 mm; fore wings, 6.7–7.2 mm. Length of female: body, 5.7–9.5 mm; fore wings, 7.9–10.0 mm. Eyes of male meet on meson of head, dorsally upper portion circular shaped, lower portion of eyes 3/4 length of upper portion; eyes of female separated on meson of head by a length 3 times as great as maximum width of an eye. Wings (Figs 1–7): maximum width of male fore wings a little less than 1/3 maximum length of fore wings; maximum width of female fore wings a little more than 1/3 maximum length; vein Rs of fore wings forked less than 1/3 of distance from base to margin; vein MA forked 1/2 to a little more than 1/2 of distance from base to margin, fork symmetrical; vein MP2 attached at base to veins MP1 and CuA with a cross vein (Fig. 1) to vein MP appears assymetrically forked (Fig. 5), attachment of vein MP2 to MP1 a little less than 1/2 of distance from base to margin, base of vein MP2 equidistant from MP2

I.C. Campbell (ed.) Mayflies and Stoneflies, 327–335.

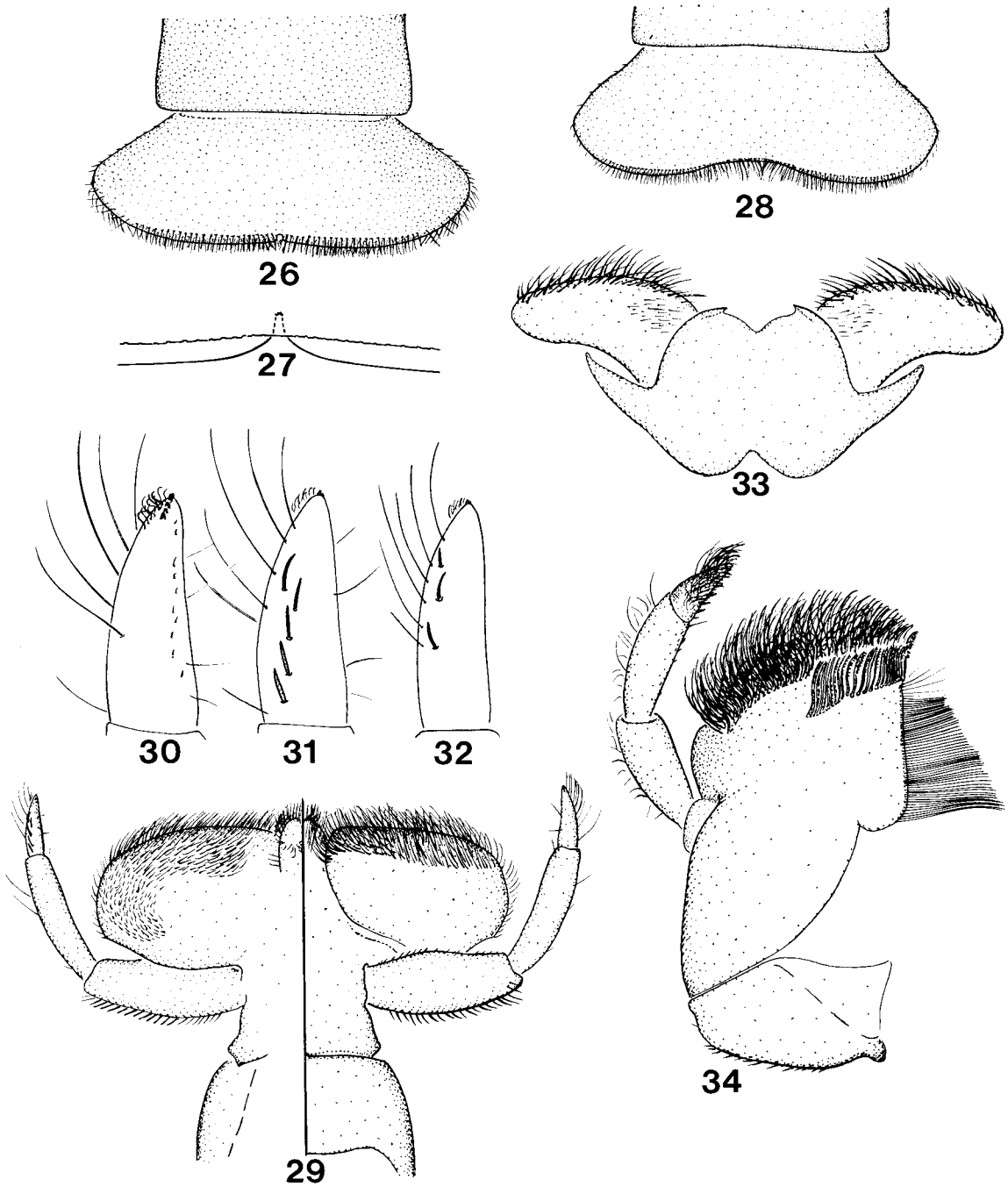


Figs 1–12. Sulawesia imagos. Figs 1–7, wings: 1–3, fore wing, hind wing, hind wing enlarged, *S. haema* male; 4, hind wing enlarged, *S. haema* female; 5–7, fore wing, hind wing, hind wing enlarged, *Sulawesia* sp. female. Figs 8–12, genitalia of *S. haema* male: 8, lateral; 9, ventral, alternate position of penes; 10, ventral; 11, posterior; 12, penes (dorsum on left, venter on right).

and CuA; CuA area and cross veins as in Fig. 1, 5. Costal margin of hind wings with a well developed costal projection (Fig. 2–4, 6–7), apex of projection acute and located 1/2 to little more than 1/2 distance from base of wings; apex of wings acute; cross veins as in Fig. 2–4, 6–7. Legs: ratios of segments in male fore legs, 0.71: 1.00 (2.10 mm): 0.05: 0.33: 0.29: 0.14: 0.10. Claws of a pair dissimilar, one apically hooked (Fig. 13), other obtuse, pad-like. Male genitalia (Figs 8–12): segment 2 of forceps a little longer in length than segment 3, segment 2 of forceps 1/5 length of segment 1; apex of segment 3 blunt; base of forceps broad, forceps bent inwardly near middle of segment 1; length of styliger plate along median line (excluding dorsomedial projection) 1/2 maximum width, apex of styliger plate broadly expanded dorsal to forceps (Figs 8–11), expansion deeply cleft medially and apical inner margin of each lobe with a broad acute projection;



Figs 13–25. Sulawesia. Figs 13–18, imagos: 13, fore claw of male; 14, abdominal segments 5–7, male, lateral; 15, tergum 6 of male; 16, 9th sternum of female; 17–18, ventral and lateral views of segments 7 and anterior 8 of female abdomen. Fig.s 19-25 mature nymph: 19, fore leg; 20–21, cross sections of tibia and tarsus; 22, fore claw; 23, abdominal gill 4; 24, left mandible; 25, incisor of right mandible.



Figs 16–24. Sulawesia mature nymph: Figs 26-28, labrum with detail of anteromedian margin; 29–32, labium with ventral (30) and dorsal (31-32) detail of 3rd labial palp; 33, hypopharynx; 34, maxilla. Figs 26–27, 32–34, *S. haema*; 28–31, *Sulawesia* sp. Dorsum of labium on left; venter on right.

penes broad, penis lobes divided almost to base of penes, each penis lobe with a broad apical extension laterally projected at a 45° angle, extension curved ventrally, median base of each extension with a long, well developed spine, spine curved dorsally toward apex of extension (Figs 8, 11–12). Ninth sternum of female cleft apically (Fig. 16); posterior margin of sternum 7 and an-

terior margin of sternum 8 as in Fig. 17–18, sternum 8 with anterolateral sclerotized areas and median ridge. Terminal filament 1 1/2 times as long as cerci.

Mature nymph. Head prognathous. Antennae 1 1/2 times maximum length of head. Mouthparts (Figs 24–34): dorsal hair on labrum as in Figs 26, 28; anterosubmedian and anterior areas of hair ventrally; anterior margin with a small to large, V-shaped, median cleft, cleft dorsally hooded (Fig. 27). Clypeus as in Fig. 26. Left mandible as in Fig. 25. Lingua of hypopharynx with well developed lateral processes, paired submedian row of long hair on internal dorsal surface, apex of submedian lobes with short spines and a rack-like process (Fig. 33), anterior margin cleft; superlingua as in Fig. 33 with a row of hair along anterior margin, lateral margins rounded. Segment 2 of maxillary palpi a little longer to equal length of segment 1, segment 3 a little less than 1/2 to 2/3 length of segment 2, triangular; a V-shaped ridge near the ventral, inner anterolateral margin on maxillae; hair on maxillae as in Fig. 34. Labium as in Fig. 29–32; segment 2 of palpi a little less than length of segment 1; segment 3 of palpi a little less than 1/3 to 2/5 length of segment 2, triangular; paraglossae ventral to glossae. Legs (Figs 19–22): maximum width of tibiae 1 1/2 times maximum width of tarsi, tibiae oval in cross section (Fig. 20); outer margin of femora indented near apex so tibiae can draw partially into femora (Fig. 19); apex of claws hooked and narrow, apical half of claws with a row of denticles, denticles progressively larger apically, base of claws with a large denticle giving appearance of a second claw, basal denticle with 2–3 smaller, widely based denticles. Gills (Fig. 23): gills on segments 1–7 alike; gills deeply forked and 2 portions of lamellae basally overlap, each portion long, slender and smoothly tapered to apex; main trunk of tracheae forked near base of gills and each branch along median line of each portion of lamellae; main trunk darkly pigmented, membrane of lamellae darkly pigmented. Posterolateral spines on abdominal segments 3–9, spines progressively larger posteriorly. Terminal filament longer than cerci.

ETYMOLOGY. Sulawesi, the Indonesian name of the island also called the Celebes.

TYPE SPECIES. *Sulawesia haema*, new species.

Sulawesia haema, new species

(Figs 1–4, 8–27, 32–34)

Male imago (in alcohol). Upper portion of eyes brown, lower portion brownish-black. Head brown, carinae darker. Antennae pale. Thorax brown, sutures paler, carinae darker especially in pleurae, pronotum heavily washed with darker brown, mesonotum dark brown. Coxae brown, heavily washed with darker brown; trochanters, femora, and tibiae of prothoracic legs brown, heavily washed with darker brown, remainder of legs pale, except tarsal segment 5 and claws washed lightly with darker brown; trochanters, femora, and tibiae of mesothoracic and metathoracic legs brown, heavily washed with darker brown, especially along carinae, remainder of legs brown, except tarsal segments 1 and 2 pale. Wings (Figs 1–3): longitudinal and cross veins of fore wings light brown, darker in apical half of wings; membrane of fore wings hyaline, except apical 1/3 of cells C and Sc translucent whitish, basal half of cell Sc and basal area of wings brown as in Fig. 1; longitudinal and cross veins and membrane of hind wings dark brown, except hyaline along outer margin of wings as in Figs 2–3. Abdomen: segments 1–7 translucent, light brown, segments 8 and 9 opaque, light brown; terga 1–9 with a narrow, dark brown, transverse line; tergum 1 with lateral 1/4 washed heavily in dark brown; terga 3–9 with wide, submedian, longitudinal, dark bars as in Figs 14–15, bars indistinct on tergum 3; spiracles and tracheae washed with dark brown; ganglia on sterna 6–7 lightly washed with dark brown. Genitalia (Fig. 10): light brown except long curved spine on penes darker, forceps segment 1 and outer margin of forceps segments 2 and 3 heavily washed with dark brown. Caudal filaments light brown, except basal 4 segments darker, remainder of segments with darker annulations at articulations.

Female imago (in alcohol): Eyes black. Head dark brown, carinae blackish-brown. Antennae pale. Thorax dark brown, sutures paler, carinae blackish-brown, pronotum heavily washed with blackish-brown. Legs dark brown, heavily washed with blackish-brown, except apex of tibiae, tarsi and claws pale. Wings: longitudinal and cross veins dark brown, cross veins paler posterior to cell R1; membrane of fore wings hyaline, except basal half of cell Sc and basal area of wings reddish-brown (as in Fig. 1); longitudinal and cross veins and membrane of hind wings dark brown (Fig. 4). Abdomen: brown, terga uniformly washed with blackish-brown except terga 2-7 with a narrow pale longitudinal, median line extending entire length of each tergum; spiracles and tracheae washed with blackish-brown (Fig. 18). Caudal filaments brown, paler near apex.

Mature nymph (in alcohol). Head brown, venter pale. Thorax: brown, venter pale, blackish-brown marks as in male and female imagos. Legs: brown, dorsal surface of coxae, trochanters and femora lightly washed with blackish-brown. Abdomen: brown, venter pale, blackish-brown color marks as in male and female imagos, except median tergal line wider in female nymph than in female imago. Gills (Fig. 23): membrane grayish-black, tracheae black. Caudal filaments brown, except setae of male nymph darker.

MATERIAL EXAMINED. Holotype ♂ imago, INDONESIA, Celebes (Sulawesi), SUP, Toraut Riv., Dumoga-Bone Nat. Park, 211 m, 0°34′N, 123°54′E, 3-IX-85, DAP; allotype ♀ imago, same data as for holotype; paratypes: 29 ♂♂, 1 ♀, 2 ♂ subimagos, 3 ♀ subimagos, 11 nymphs, same data as for holotype; 12 ♂♂, 37 nymphs, SUP, Tumpah Riv., Dumoga-Bone Nat. Park, 222 m, 0°34′N, 123°54′E, 4-IX-85, JTP & DAP; 5 nymphs, SUP, trib. of Tumpah Riv., Dumoga-Bone Nat. Park, 235 m, 0°35′N, 123°54′E, 5-IX-85, JTP & DAP;17 nymphs, SUP, Tumpah Riv., Dumoga-Bone Nat. Park, 250 m, 0°35′N, 123°53′E, 5-IX-85, JTP & DAP; 64 ♀♀, 52 nymphs, STP, stream at Lindu Foot Path, Lore Lindu Nat. Park, 830 m, 5-X-85, JTP & DAP; 1 nymph, SUP, Metalanga Riv., 5 km S of Doloduo, 7-IX-85, JTP & DAP; 22 nymphs, STP, stream 10 km SE of Kamarora, Lore Lindu Nat. Park, 850 m, 8-X-85, JTP & DAP; 3 nymphs, SUP, swift clear stream nr. S end of Lake Mala, 1000 m, 10-IX-85, JTP & DAP; 5 ♂♂, 1 ♀, 1 ♂ subimago, SUP, Tumpah Riv., Dumoga-Bone Nat. Park, at light, 5-VIII-85, DD; 2 ♂♂, 1 ♀ subimago, SUP, Toraut Riv., Dumoga-Bone Nat. Park, at light, 15-VIII-85, DD; 37 nymphs, SUP, Tumpah Riv., nr. Edward's subcamp, Dumoga-Bone Nat. Park, *ca* 600 m, UTM = WL 9365, 29-30-IV-85, JT; 4 nymphs, SUP, Tumpah Riv, nr. base camp, Dumago-Bone Nat. Park, 0°34′N, 123°54′E, 18-IV-85, JT; 1 ♂, SUP, Toraut Riv. nr. base camp, Dumoga-Bone Nat. Park, 24-V-85, JT; 35 nymphs, SUP, Tumpah Riv. between Waterfall Creek and confl. with Toraut Riv., Dumoga-Bone Nat. Park, 0°34′N, 123°54′E, 22-IV-21-V-85, JT; 4 nymphs, SUP, Waterfall Creek, Dumoga-Bone Nat. Park, O°35′N, 123°54′E, 23-IV-85, JT; 21 nymphs, STP, Palu, 50 km SE of Lore Lindu Nat. Park, nr. Dongi Dongi Shelter, 950 m, UTM = SJ86, 4-9-XII-85, JT; 8 nymphs, Palu, 65 km SSE of Lore Lindu Nat. Park, Marena shelter, 600 m, UTM = SJ62, 15-XII-85, JT; and 20 nymphs, Palu Riv., 65 km SSE of Lore Lindu Nat. Park, Morena shelter, 700 m, UTM = SJ63, 17-XII-85, JT. All types are in alcohol. Association of the nymphs and male and female imagos is by the color pattern in the wings of specimens collected at the same locality. Types are deposited in the following collections: holotype, allotype, 5 ♂ imaginal paratypes, 7 ♀ imaginal paratypes and 15 nymphal paratypes in USNM; 5 ♂ imaginal paratypes, 8 ♀ imaginal paratypes and 15 nymphal paratypes in MBB, BM(NH), and HK; 14 ♂ imaginal paratypes, 2 ♀ subimaginal paratypes, 17 ♀ imaginal paratypes, 2 ♂ subimaginal paratypes and 44 nymphal paratypes in FAMU; 14 ♂ imaginal paratypes, 1 ♂ subimaginal paratype, 17 ♀ imaginal paratypes, 2 ♀ subimaginal paratypes and 44 nymphal paratypes in UU; and all paratypes collected by JT in RNH. The basal color pattern on the fore wings of both males and females is less extensive

in a few specimens from any given locality. Further, the apex of the female hind wings is hyaline in a few specimens at a given locality.

The position of penes of the male genitalia shown in Figs 8, 10–12 occurs in 3 subimagos and 35 of 49 imagos examined. However, the lateral lobes are sometimes parallel with the lateral spines overlapping (Fig. 9). In 14 cases, the penes were in this position or intermediate between the common position (Figs 10–12) and the position of Fig. 9.

The nymphs of *S. haema* inhabit small rocky streams (3–5 m wide) to large rocky rivers (up to 50 m wide) in forested areas. Nymphs have been collected from elevations of 211 m to 1,000 m in late April to mid December, while adults have been collected from early August to early October.

An apparent second species of *Sulawesia* is represented in our collections from southern Celebes (Sulawesi). Localities for these specimens are: 28 nymphs, SSP, Marana Riv., nr. Camba, 50 km E of Maros, 450 m, 14-X-85, JTP & DAP; 12 nymphs, SSP, trib. of Djene Berang, E of Ujung Pandong, QK91, 22-VI-85, JT; and 15 nymphs, 1 ♀, SSP, stream nr. Malino, N of Lompobattang, 800–1,000 m, 5°15′S, 119°51′E, 20-VI-85, JT. The nymphs of this species are large and generally darker than *S. haema*, and the basal color pattern in the membrane of the fore and hind wing pads is less extensive, especially in male nymphs. Further, the shape of the anteromedian cleft of the labrum is broader (Fig. 28), and there are more spines on the dorsal surface of segment 3 of the labial palpi (Figs 29, 31). The one female of this species differs from the female of *S. haema* in the following characters: (1) greater size with fore wings 10.0 mm and body 9.5 mm, (2) generally a red-brown color over all body parts, (3) basal color pattern in the membrane of the fore and hind wings less extensive (Fig. 5), (4) vein MP of the fore wings apparently asymmetrically forked (Fig. 5), and (5) costal projection of the hind wings near middle of wing (Figs 6, 7). Except for the greater size and the medial position of the costal projection of the hind wings, these characters also appear as variants in *S. haema*. We will not describe and name this second species until the male imago is known, but the species is included in the generic description. All specimens of this second species collected by JTP & DAP are deposited in the collections of FAMU, while those collected by JT are deposited in the collections of RNH.

Etymology. haima, G., meaning blood, in allusion to the coloration in the wings.

DISCUSSION

Sulawesia can be distinguished from all other genera of the Leptophlebiidae by the following combination of characters. In the imagos: (1) veins Rs and MP of fore wings are forked about equidistant from base of wings (Figs 1, 5); (2) costal margin of the hind wings has a well developed costal projection (Figs 2–4, 6, 7); (3) claws of a pair are dissimilar, one apically hooked and other obtuse, pad-like (Fig. 13); (4) apex of styliger plate of male is broadly expanded dorsal to forceps (Figs 9–11); and (5) penes of male genitalia have paired, median, long, well developed spines that curve dorsally to apex of penes (Figs 8, 10–12). In the nymph: (1) anterior margin of labrum has a small to large, V-shaped, median cleft that is hooded dorsally (Figs 26–28); (2) base of claws has a large denticle giving appearance of a second claw; basal denticle has widely based denticles (Fig. 22); (3) abdominal gills are deeply forked and 2 portions of lamellae basally overlap (Fig. 23); and (4) main trunk of tracheae of abdominal gills do not branch in each gill portion (Fig. 23). *Sulawesia* is a member of the *Atalophlebioides* lineage as defined by Towns and Peters (1980) [equivalent to the *Meridialaris* lineage as defined by Pescador and Peters (1980)] and is based on the following derived character states: (1) labrum has an anteromedian cleft that is dorsally hooded (Figs 26–28); (2) lateral margins of the submentum lack setae (Fig. 29); and (3) lateral margins of the clypeus are divergent apically (Fig. 26).

Sulawesia appears to be most closely related to a group of Australian members of the *Atalophleb-*

ioides lineage, especially *Kirrara amenia* Harker, as evidenced by the following derived character states: (1) outer margin of mandibles has only a small tuft of hairs (Fig. 24); (2) outer margin of mandibles is indented near base of outer incisor (Fig. 24); (3) inner margin of segment 3 of maxillary palpi has a row of long spines (Fig. 34); and (4) abdominal gills are slender (Fig. 23). However, *Sulawesia* can be distinguished from the Australian representatives in the adults and nymphs by the combination of characters given above.

The adults of *Sulawesia* appear to be closely related to *Petersula* from Sri Lanka and southern India as evidenced by two derived character states: (1) veins Rs and MP of the fore wings are forked about equidistant from the base (Figs 1, 5); and (2) the cubital area of the fore wings has two relatively short intercalaries of about equal length (Figs 1, 5). However, based on a study of all genera in the *Atalophlebioides* lineage, these two character states are convergent between *Sulawesia* and *Petersula* and *Petersula* is most closely related to representatives of the *Atalophlebioides* lineage in southern India, Sri Lanka and Madagascar.

Sulawesia is the first genus recorded from the mayfly fauna of the Celebes with close affinities to genera in Australia. One of us (GFE with D.A. Polhemus) is currently studying the zoogeographical composition of the mayfly fauna of the Celebes: except for *Sulawesia,* the entire fauna appears to be Oriental in origin and shows strong affinities with genera occurring in Thailand, the Malay Peninsula, Borneo, and the Philippines. Some of the more widespread genera, for example *Prosopistoma,* occur in Africa, Madagascar, Europe, Sri Lanka, the Malay Peninsula, the Philippines, Java, Sumatra, New Guinea, the Solomon Islands, and Australia. However, the mayfly fauna of the Celebes lacks a considerable number of genera found west of Wallace's original line in Borneo, Java, Sumatra and the Southeast Asian mainland.

Based on phylogenetic studies, *Sulawesia* is a member of an ancient Gondwanian lineage which is widespread throughout Australia, New Zealand, South America, Madagascar, Sri Lanka, and southern India. *Sulawesia* appears to belong to a group of genera found in southern South America, New Zealand and Australia rather than being Lemurian (Madagascar, Sri Lanka and India) in origin as discussed by Mackerras (1970) for some Tabanidae. The *Atalophlebioides* lineage has not been recorded from Southeast Asia or Borneo and *Sulawesia* was not recorded by Ulmer (1939, 1940) from the Sunda Islands, nor is it present in our unpublished records from any of the Sunda Islands, Southeast Asia or New Guinea. The absence of the *Atalophlebioides* complex in Southeast Asia between southern India and the Celebes is curious. Considerable mayfly material is available to us from New Guinea and the relationships of the known fauna are entirely Oriental, with a few genera extending to Australia but not New Caledonia or New Zealand. The occurence of a member of the *Atalophlebioides* lineage in such isolation from the rest of the complex suggests a long distance dispersal. We cannot rule out extinction elsewhere in the area or the failure to collect the genus or its relative in some other areas where it may occur, but this seems unlikely. The only other biogeographically disjunct mayfly pattern in the area is *Ephemerellina (Austremerella)* which occurs in southeastern Queensland, Australia, while its apparently closest relative (*Ephemerellina* s.l.) occurs in China (Kiangsi and Yunnan Provinces) and South Africa (Allen 1965).

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