

## Reevaluation of the Genera *Compsoeuria* Eaton and *Trichogenia* Braasch & Soldán (Ephemeroptera: Heptageniidae)

J.M. WEBB<sup>1</sup>, D. BRAASCH<sup>2</sup> & W.P. MCCAFERTY<sup>3</sup>

<sup>1</sup>Department of Entomology, Purdue University, West Lafayette, Indiana 47907-2089, USA.  
E-mail: jmw975@yahoo.com

<sup>2</sup>Dipl.-Biologe, Kantstrasse 5, 14471 Potsdam, Germany. E-mail: h.braasch@t-online.de

<sup>3</sup>Department of Entomology, Purdue University, West Lafayette, Indiana 47907-2089, USA.  
E-mail: mccaffer@purdue.edu

### Abstract

*Compsoeuria* Eaton (Ephemeroptera: Heptageniidae) has been placed in both the Heptageniinae Needham tribes Compsoeuriini Wang & McCafferty and Ecdyonurini Ulmer by different mayfly workers. In order to clarify the phylogenetic position of the genus, we examined adult material of its type species (*C. spectabilis* Eaton), larvae originally described as *C. spectabilis*, and material of potentially related species. We determined that the larva originally described as *C. spectabilis* was incorrectly associated with adults and is actually a species of *Trichogenia* Braasch & Soldán. Herein we name this species *Trichogenia ulmeri* N.SP. Braasch & Webb. The adults of *C. spectabilis* possess Ecdyonurinae characters and therefore *Compsoeuria* and Compsoeuriini are transferred to Ecdyonurinae. In order to maintain the stability of genera within Heptageniinae, we establish Trichogeniini Webb & McCafferty N.TRIB. *Compsoeuriella* Ulmer and *Notonurus* Crass are confirmed to be synonyms of *Compsoeuria*. *Heptagenia lieftincki* Ulmer is shown to be a member of *Compsoeuria* [= *Compsoeuria lieftincki* (Ulmer) N.COMB.]. *Compsoeuria* is also shown to be distinct from *Thalerosphyrus* Eaton and several species previously placed in *Thalerosphyrus* are moved to *Compsoeuria*, for example *T. josettae* [= *Compsoeuria josettae* (Sartori & Elouard) N.COMB.]. The southeast Asian genus *Trichogenia* is reviewed; *Trichogenia hubleyi* Webb & McCafferty N.SP. is described from larvae from Celebes and Borneo, Indonesia; and *Heptagenia nasuta* Ulmer is provisionally transferred to *Trichogenia* [= *Trichogenia nasuta* (Ulmer) N.COMB.]

**Keywords:** Ephemeroptera; Heptageniidae; Ecdyonurinae; Heptageniinae; *Trichogenia*; *Compsoeuria*; *Compsoeuriella*; *Thalerosphyrus*; systematics; new species

## Introduction

Heptageniidae (Ephemeroptera) is widespread and abundant throughout North America, Europe, Africa and Asia, and three subfamilies are currently recognized: Ecdyonurinae Ulmer, Heptageniinae Needham, and Rhithrogeniinae Lestage (Wang and McCafferty 2004). While most heptageniid genera are easily placed in a subfamily, the placement of the genus *Compsoeuria* Eaton has been uncertain. For example, Braasch (1990) stated that *Compsoeuria* belonged to Ecdyonurinae, while Kluge (2004) placed *Compsoeuria* as *incertae sedis* within the Heptageniidae. Based on the described larval characteristics (Ulmer 1939: 675), however, *Compsoeuria* would belong in the Heptageniinae tribe Compsoeuriini Wang & McCafferty (Wang and McCafferty 2004).

In order to clarify the phylogenetic relationships and generic concept of *Compsoeuria*, we examined material of *C. spectabilis* Eaton, 1881, the type species of the genus, as well as material of potentially related genera. We found that the confusion surrounding *C. spectabilis* stems from the incorrect assignment of larvae to the species by Ulmer (1939). According to the higher classification of Wang and McCafferty (2004), the adults of *C. spectabilis* are clearly Ecdyonurinae, and the larvae Ulmer (1939) described as *C. spectabilis* are clearly Heptageniinae (more precisely an unnamed species of *Trichogenia* Braasch & Soldán). In this paper, we update the classification of *Compsoeuria*; confirm generic equivalences with *Compsoeuria*; distinguish between *Compsoeuria* and *Thalerosphyrus* Eaton; provide a new name for the *Trichogenia* species previously known as the larvae of *C. spectabilis* (Ulmer 1939); describe an additional species of *Trichogenia* from Celebes and Borneo, Indonesia; and provide a key to the species of *Trichogenia* larvae. Abbreviations used in the material examined include: FAMU (Florida A&M University collection), PERC (Purdue Entomological Research Collection), ROM (Royal Ontario Museum), and ZMUH (Zoologisches Institut und Zoologisches Museum der Universität Hamburg).

## *Compsoeuria* Eaton

*Compsoeuria* Eaton, 1881: 23

*Compsoeuriella* Ulmer, 1939: 563; (syn.) Braasch and Soldán, 1986a: 46

*Cosmetogenia* Eaton, 1883: 18 (obj. syn.)

*Notonurus* Crass, 1947: 126; (syn.) Gillies, 1963: 232

Wang and McCafferty (2004) placed *Compsoeuria* as the sister group of *Trichogenia* in the Heptageniinae tribe Compsoeuriini because larvae described as *C. spectabilis* by Ulmer (1939) have a row of setae on the ventral surface of the maxillae, triangular glossae, no distinct dorsal apical projection on the femora, two rows of setae on the lateral margin of the mandibles, and a wide labrum. Male adults of *C. spectabilis*, however, possess

Ecdyonurinae characters such as parallel-sided medial margins of the mesothoracic furcasternum as well as forewings with a reduced number of crossveins. Because Ulmer (1939) did not rear any larvae of *C. spectabilis*, Jensen (1972), Braasch and Soldán (1986a), and Edmunds and Polhemus (1990) viewed this association with caution. We found Ulmer's (1939) association to be incorrect because forewings dissected out of a mature larva similar to that described by Ulmer (1939) have numerous crossveins and are shaped differently than those of adults of *C. spectabilis*, and also have other Heptageniinae characters noted above. Therefore, the true larva of *C. spectabilis* is still unknown. The larva described by Ulmer (1939) as *C. spectabilis* is an unnamed species of *Trichogenia* which is further discussed under that genus (see below).

Based on the evidence provided above, *Compsoeuria* can no longer be included in the Heptageniinae and is placed in Ecdyonurinae, with the name Compsoeuriini accompanying its type genus to Ecdyonurinae. The potential relationships of *Compsoeuria* to other Ecdyonurinae are discussed below. The phylogenetic concept of the Heptageniinae clade defined by larval characters that Wang and McCafferty (2004) named Compsoeuriini remains the same; however, this concept is now relevant only to the genus *Trichogenia*. Given the constraints of a strict phylogenetic classification, we must establish a new tribe, Trichogeniini Webb & McCafferty **N.TRIB.**, allowing each of the additional eight Heptageniinae genera to retain their generic status.

Braasch and Soldán (1986a) noted that adults of *Compsoeuriella thienemanni* Ulmer, 1939, the type species of *Compsoeuriella* Ulmer, were congeneric with *C. spectabilis* adults and synonymized *Compsoeuriella* with *Compsoeuria*. Wang and McCafferty (2004) did not recognize this synonymy because they believed *Compsoeuria* to be a member of the Heptageniinae, and placed *Compsoeuriella* as a junior synonym of *Thalerosphyrus* instead, based on the shared possession of long, pointed supracoxal sclerites in the larvae. Examination of larvae and males of several species of *Thalerosphyrus* and *Compsoeuriella* indicates, however, that the two are distinct. The penes of *Compsoeuriella* are slightly expanded laterally, are only partially fused medially, have distinct dorsal sclerites both apically and laterally, and have ventral and dorsolateral spines. The penes of *Thalerosphyrus* are not expanded laterally, are fused medially for most of their length, do not have ventral or dorsolateral spines (small dorsolateral spines may be present in some species), and do not have as well-developed apical sclerites. Additionally, the forewings of the two genera differ in that those of *Compsoeuriella* tend to have a reduced number of crossveins and a slightly sigmoidal bend in the costa and subcosta, whereas those of *Thalerosphyrus* have numerous crossveins and a straight costa and subcosta. The legs of *Compsoeuriella* have numerous black spots that are not present in *Thalerosphyrus*. The larvae of *Thalerosphyrus* and *Compsoeuriella* also differ in many characters. *Thalerosphyrus* larvae, for example, have well developed posterolateral spines on the abdomen, simple setae on the inner surface of the hindtibiae, slight posterolateral extensions of pronotum, distinct thickening of the

anterior margin of the head capsule, do not possess any black spotting on the head capsule or femora, and the glossae are subquadrate and laterally expanded. *Compsoeuriella* larvae, on the other hand, generally have shorter posterolateral spines on the abdominal segments, have fimbriate setae on the inner surface of the hindtibiae, generally lack posterolateral expansions on the pronotum, do not have the anterior margin of the head capsule thickened, usually have conspicuous black spots on the head capsule and/or femora, and the glossae are narrow and pointed apically. For these reasons, we no longer recognize any synonymy of *Compsoeuriella* with *Thalerosphyrus* and because all of the adult characters of *Compsoeuriella* are present in *Compsoeuria*, we recognize the previous synonymy of *Compsoeuriella* with *Compsoeuria*. All African species transferred to *Thalerosphyrus* by McCafferty (2003) are recombined with *Compsoeuria*.

The phylogenetic position of *Compsoeuria* (and Compsoeuriini) within the Ecdyonurinae is unclear. The possession of ventral spines on the penes, the general shape and the sclerotization of the penes, and the possession of black spotting on the head capsule indicate *Compsoeuria* may be related to members of the tribe Leucrocutini Wang & McCafferty. However, unlike other members of the Leucrocutini, the apical setae on the ventral side of the galealaciniae are simple rather than fimbriate, and the distal dentisetae on the maxillae are branched rather than simple, indicating a closer relationship to the Notacanthurini Wang & McCafferty and Atopopini Wang & McCafferty. The long supracoxal sclerites of the larvae are similar to those found in most *Thalerosphyrus* (a member of Atopopini) but we believe this to be a case of convergence as *Compsoeuria* lacks apomorphies of the Atopopini such as a thickened anterior margin of the larval head capsule. In most males of Atopopini, the first foretarsal segment is greater than 0.5X the length of the second segment; in *Compsoeuria*, the length varies from 0.3-1.0X the length of the second segment.

We presently consider *Compsoeuria* to include the following species:

***Compsoeuria bequaerti* (Navás) AFROTROPICAL**

- Adenophlebia bequaerti* Navás, 1930: 316 (orig.)  
*Adenophlebia eatoni* Navás, 1931a: 271; (syn.) Demoulin, 1956: 45  
*Adenophlebia inflexa* Navás, 1932: 285; (syn.) Demoulin, 1956: 45  
*Notonurus cooperi* Crass, 1947: 127; (syn.) Demoulin, 1970: 97  
*Compsoeuriella cooperi*; (comb.) Gillies, 1963: 232  
*Compsoeuriella bequaerti*; (comb.) Gillies, 1963: 232  
*Notonurus bequaerti*; (comb.) Demoulin, 1956: 45  
*Compsoeuria bequaerti*; (comb.) Braasch and Soldán, 1986a: 46  
*Thalerosphyrus bequaerti*; (comb.) McCafferty, 2003: 792

***Compsoeuria cingulata* (Navás) ORIENTAL**

- Thalerosphyrus cingulatus* Navás, 1933: 18 (orig.)  
*Compsoeuria cingulata*; (comb.) Braasch and Soldán, 1986a: 46

***Compsoeuria diehli* Braasch & Soldán ORIENTAL***Compsoeuria diehli* Braasch & Soldán, 1986a: 48 (orig.)***Compsoeuria flowersi* Braasch & Soldán ORIENTAL***Compsoeuria flowersi* Braasch & Soldán, 1986b: 59 (orig.)***Compsoeuria josettae* (Sartori & Elouard) N.COMB. AFROTROPICAL***Thalerosphyrus josettae* Sartori & Elouard, 1996: 125 (orig.)***Compsoeuria lieftincki* (Ulmer) N.COMB. ORIENTAL***Heptagenia lieftincki* Ulmer, 1939: 571 (orig.)***Compsoeuria njalensis* (Kimmins) AFROTROPICAL***Afronurus njalensis* Kimmins, 1937: 433 (orig.)*Compsoeuriella njalensis*; (comb.) Gillies, 1963: 232*Compsoeuria njalensis*; (comb.) Braasch and Soldán, 1986a: 46*Thalerosphyrus njalensis*; (comb.) McCafferty, 2003: 792***Compsoeuria sinuosa* (Navás) AFROTROPICAL***Adenophlebia sinuosus* Navás, 1931b: 109 (orig.)*Notonurus sinuosus*; (comb.) Demoulin, 1970: 98*Compsoeuria sinuosa*; (comb.) Braasch and Soldán, 1986a: 46*Ecdyonurus sinuosus*; (comb.) Kluge, 1988: 298*Thalerosphyrus longinosi* McCafferty, 2003: 792 (unnecessary name change)***Compsoeuria spectabilis* Eaton ORIENTAL***Compsoeuria spectabilis* Eaton, 1881: 23 (orig.)***Compsoeuria thienemanni* (Ulmer) ORIENTAL***Compsoeuriella thienemanni* Ulmer, 1939: 564 (orig.)*Compsoeuria thienemanni*; (comb.) Braasch and Soldán, 1986a: 46*Thalerosphyrus thienemanni*; (comb.) Wang and McCafferty, 2004: 17***Compsoeuria tortinervis* (Navás) AFROTROPICAL***Adenophlebia tortinervis* Navás, 1930: 317 (orig.)*Notonurus tortinervis*; (comb.) Demoulin, 1956: 48*Compsoeuriella tortinervis*; (comb.) Gillies, 1963: 232*Compsoeuria tortinervis*; (comb.) Braasch and Soldán, 1986a: 46*Thalerosphyrus tortinervis*; (comb.) McCafferty, 2003: 792

*Thalerosphyrus* is restricted presently to *T. bishopi* Braasch & Soldán, 1986a; *T. determinatus* (Walker, 1853); *T. flowersi* Venkataraman & Sivaramakrishnan, 1987; *T. sinuosus* (Navás, 1933); *T. sumatranus* (Ulmer, 1939); *T. torridus* (Walker, 1853); and *T. vietnamensis* (Dang, 1967). While *T. ethiopicus* Soldán, 1977, and *T. separatus* Nguyen & Bae, 2004 are likely members of *Afronurus* Lestage we are retaining them in

*Thalerosphyrus* until we can examine specimens. Similarly, *Thalerosphyrus melli* Ulmer, 1925, is probably a member of *Epeorus* Eaton, but we have not examined specimens to confirm this and we are therefore retaining it in *Thalerosphyrus* for the time being.

**Material examined.** *Compsoeuria flowersi*, 2♂, Indonesia, Java, GC Crampton [PERC]. *C. lieftincki*, 2♂ syntypes, Indonesia, West Java, 150m, Djasinga, Tjibarangbang Fluss, abends an der Lampe im Flussbett, 6-VII-1935, Lieftinck [FAMU]. *C. njalensis*, 5♂ 2♀, South Africa, no other data [PERC]; 1♂, South Africa, Skandinawiedrift, 30-III-1965 [PERC]. *C. spp.* 1♂, India, Kalia (Kerala), 7-I-1962, F. Schmid [PERC]; 1♂, Madagascar, Majunga Prov, 25km SW Ambalanjankomby, XI-1962, ED Cashatt [PERC]; 1♂ 5♀, South Africa, Vaal R at Skandinawiedrift, 30-III-1965, 28-IV-1965, 10-IV-1969, HJ Schoonbee [PERC]; 1♂, Sri Lanka, Sabaragamuwa Prov, Helihul-Oya, 1-III-1962 [PERC]; 1♂, Sri Lanka, Sabaragamuwa Prov, Rakwana, 27-II-1962 [PERC]. *C. spectabilis*, 3♂, Indonesia, W Java, Buitenzorg (now Bogor), 13-II-1932, VII-1932, Lieftinck [PERC]. *C. thienemanni*, 3♂, Malaysia, Sabah, Mansuncun R NE of Kota Kinabalu, 18-VIII-1972, WL and JG Peters [PERC]; 26♂ 11♀, Vietnam, Gia Lai, An Khe District, Cha R 3km E Buoenloy, 25-VI-1996, B Hubley, DC Currie, J Swann ROM 961090 [ROM]. *C. tortinervis?*, 1♂, B Congo, 9mi NW of Bunyakiri, 8-IX-1957 [PERC].

### *Trichogenia* Braasch & Soldán

As indicated above, the larva Ulmer (1939:675) described as *C. spectabilis* is actually an unnamed species of *Trichogenia* [= *Trichogenia ulmeri* N.SP.]. Wang and McCafferty (2004) considered Ulmer's *Compsoeuria* to belong to a different genus than *Trichogenia* based on differences in mouthpart morphology. However, examination of a new species described below and *T. ulmeri* shows that these two species are fundamentally the same as *T. maxillaris* Braasch and Soldán, 1988 and differ in only a few characters. Therefore, we place them all in *Trichogenia*.

Adult males have not been associated with any larvae of *Trichogenia*. However, it is highly probable that *Heptagenia nasuta* Ulmer, 1939, known only from adults from Indonesia, is *Trichogenia* (Braasch and Soldán 1988) based on the following: i) the only confirmed larvae of the subfamily Heptageniinae known from southeast Asia are *Trichogenia*; ii) *H. nasuta* is the only adult of the subfamily Heptageniinae known from southeast Asia; iii) wings dissected from wingpads of mature *Trichogenia* larvae have a slight violet tinge, similar to *H. nasuta* (Braasch and Soldán 1988). For these reasons we provisionally transfer *H. nasuta* to *Trichogenia* [= *Trichogenia nasuta* (Ulmer) N.COMB.].

**Diagnosis:** Larvae of *Trichogenia* can be differentiated from those of all other genera of Heptageniidae by the following combination of characters: i) ventral side of maxillae with setae in a row; ii) tergum with branched robust setae and many long, fine setae; iii) lamellae of gills 1 reduced; iv) lamellae of at least gills 2-4 long, narrow, and pointed

apically; v) apex of femora without dorsal projection.

At this time we do not have material available to provide characters for separating adult males of *Trichogenia* from other Heptageniinae genera. The long pair of ventral spines on the penes shown in Figures 156 and 157 by Ulmer (1939:569) in combination with the violet coloration in the wings may be diagnostic.

**Species included:** *Trichogenia maxillaris*, *T. nasuta* N.COMB., *T. hubleyi* N.SP., *T. ulmeri* N.SP.

### ***Trichogenia hubleyi* Webb & McCafferty N.SP.**

**Larval description:** Head capsule subrectangular (Fig. 1), with numerous fine and sparse branched, robust setae dorsally. Labrum (Fig. 2) much wider than long, dorsally with numerous long, fine setae, ventrally with median row of short, robust setae and many long, fine setae laterally. Mandibles (Figs 3 and 4) with dense patch of setae on lateral margin at base of outer canines, lateral margin with row of long setae on apical half and patch of setae dorsally on basal portion. Hypopharynx (Fig. 5) with lateral margins of superlingua subparallel; lingua with median U-shaped notch bordered by pair of apicolateral processes. Maxillae (Fig 6) ventrally with row of fimbriate setae, dorsally with lateral row of long, fine setae; apical margin of galealacinae with nine comb setae; first segment of palp with numerous long, fine setae; second segment with long, fine setae laterally, bare medially; third segment small, sharp. Glossae broadly rounded apically, numerous robust setae ventrally; dorsal surface of last segment of palps with row of fine setae stopping at medial margin (Fig 7). Thorax dorsally with numerous fine setae, sparse ginkgo-shaped robust setae; pronotum with pair of small, spicule-covered protuberances; meso- and metathoracic supracoxal sclerites long, sharp, projecting dorsally (Fig. 8). Forefemora dorsally with row of long, fine setae and numerous long, robust setae; anterior surface with spatulate setae and long, fine setae; ventral margin with numerous short, robust setae and short, fine setae. Foretibiae with sparse row of fine setae on posterior margin; lateral ridge with row of spatulate setae; anterior margin with numerous short, robust setae; entire surface of tibiae covered with fine setae. Foretarsi covered with fine setae, laterally with several spatulate setae. Mid- and hindlegs similar to forelegs but with more numerous robust setae; femora with anterior face with robust setae all of approximately same size and shape (Fig. 9). Abdomen dorsally with numerous fine setae and branched robust setae (Fig. 10); posterior margins of terga with sharp spines. Gills 1–7 with numerous long fibrils, lamellae with long, fine setae; lamellae of gills 1 small; lamellae of gills 2–4 long and narrow; lamellae of gills 5–7 rounded, with short apical point. Caudal filaments with short spines at intersegmental margins; median caudal filament with long, fine setae on both sides of joints; cerci with long, fine setae medially.

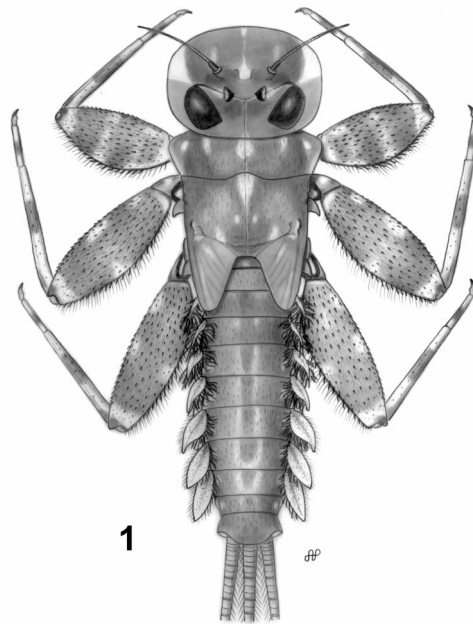
**Adult:** Unknown.

**Etymology:** The specific epithet is in honor of Brad Hubley of the Royal Ontario

Museum, Canada, who has provided us with numerous southeast Asian specimens.

**Diagnosis:** *Trichogenia hubleyi* can be differentiated from congeners by the following combination of characteristics: i) well-developed comb setae on the anterior margin of the galealacinae; ii) long supracoxal spines on the meso- and metathorax; iii) anterior surface of femora with setae all of same size; iv) abdominal terga with numerous branched, robust setae scattered over entire surface.

**Material examined:** HOLOTYPE: 1 larva, Indonesia, Celebes, Sulawesi Utara Province, swift clear stream nr S end of L Mara, 10-IX-1985, JT & DA Polhemus [PERC] PARATYPES: 17 larvae (parts of one slide-mounted), same data as holotype [PERC].



**FIGURE 1.** *Trichogenia hubleyi*. Dorsal habitus.

### ***Trichogenia maxillaris* Braasch & Soldán**

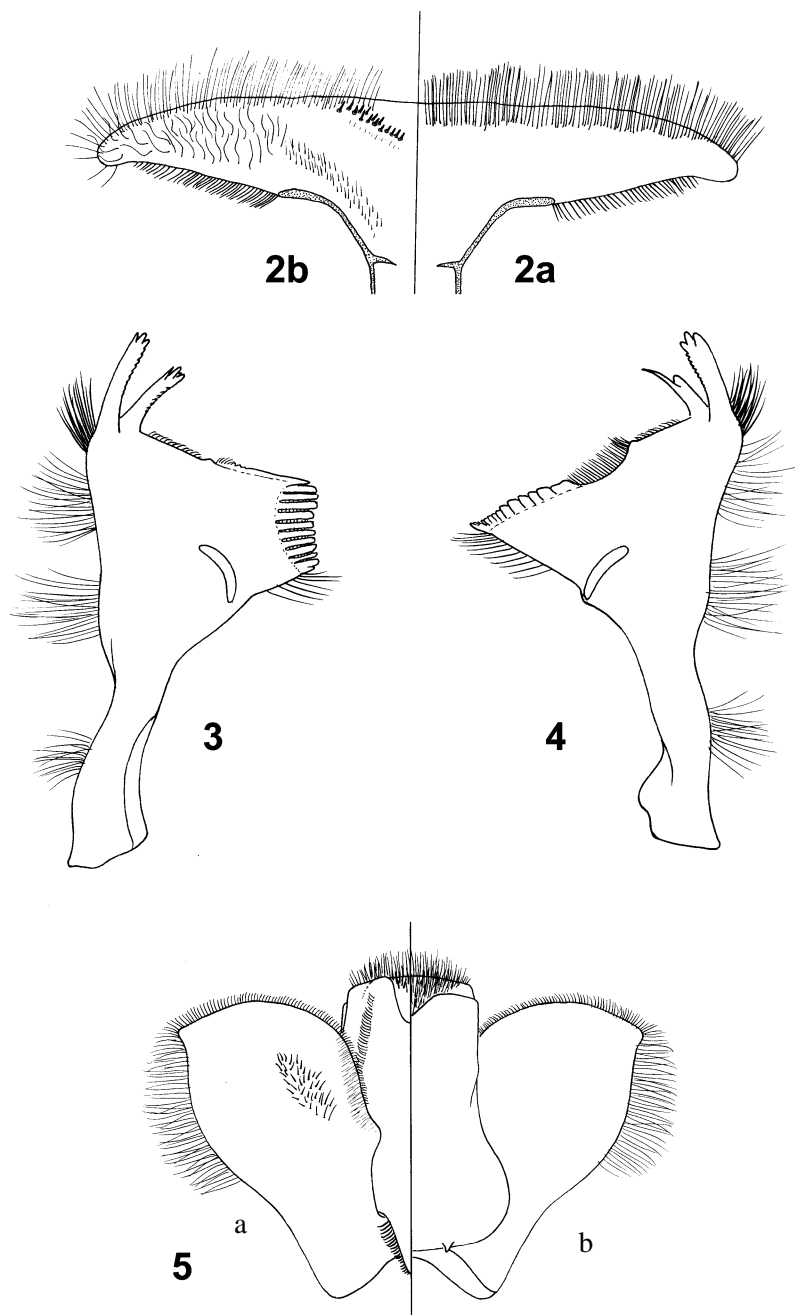
*Trichogenia maxillaris* Braasch & Soldán, 1988: 120 (orig.)

*Heptagenia maxillaris*; (comb.) Kluge, 2004: 173

The larva of this species was adequately described by Braasch and Soldán (1988). The adults are unknown.

**Diagnosis:** *Trichogenia maxillaris* can be differentiated from congeners by the following combination of characteristics: i) supracoxal sclerites blunt; ii) absence of comb setae on apical margin of maxillae; iii) hypopharynx apically divergent (Fig. 11); iv) ventral surface of terminal segment of labial palp with long row of setae extending to posteromedial margin (Fig. 12).

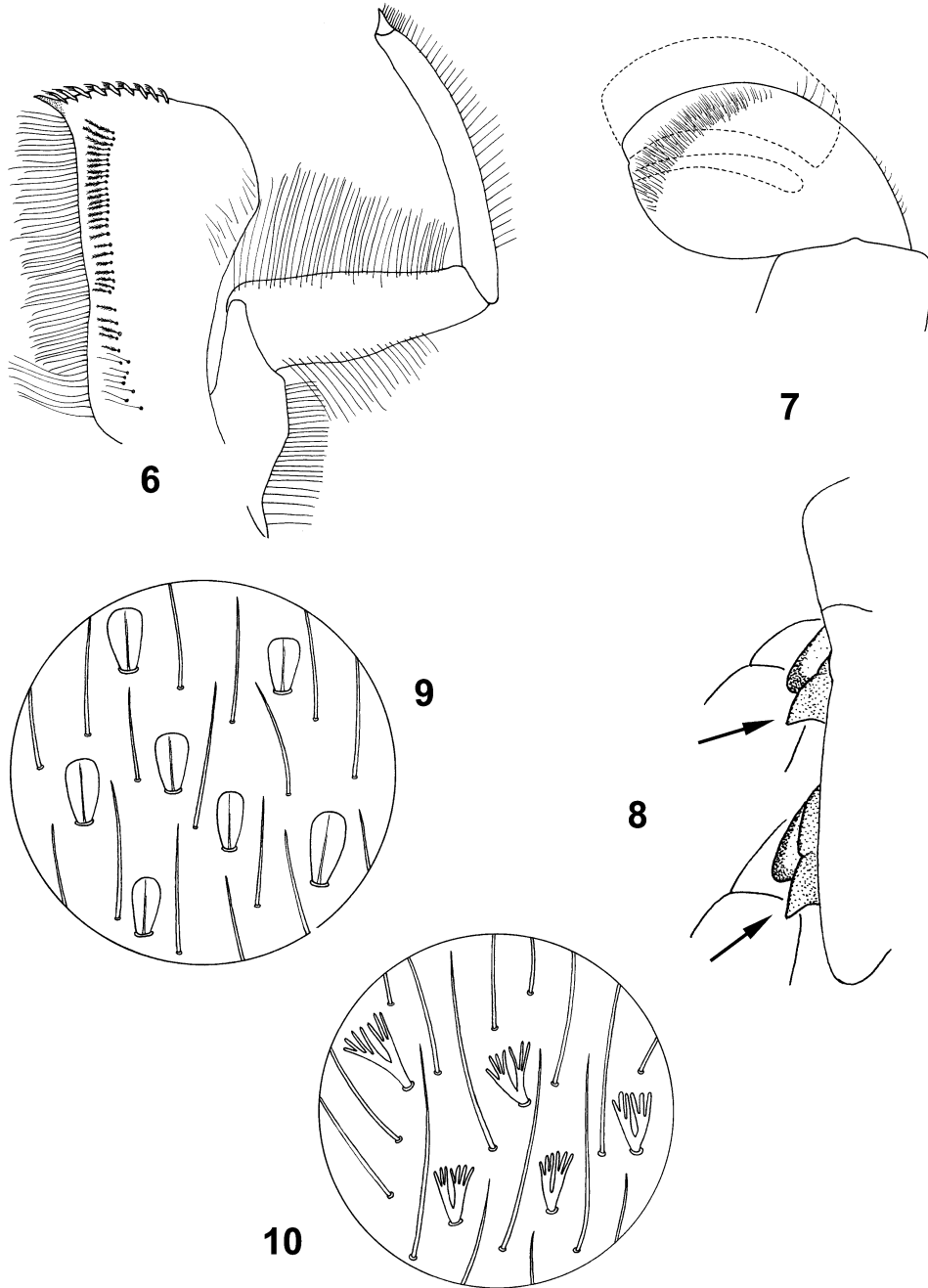




**FIGURE 2–5.** *Trichogenia hubleyi*. **2**, labrum: a. dorsal b. ventral; **3**, left mandible; **4**, right mandible; **5**, hypopharynx: a. dorsal b. ventral.

**Material Examined:** THAILAND: 1 larva, Chiangmai Prov, small stream and waterfalls, Doi Sutep, W of Chiangmai, 19-XI-1964, WL and JG Peters [PERC]; VIETNAM: 1 larva, Vihm Phú: Tam Dao Hill Stn, lower waterfall of stream flowing through town, 11-V-1996, B Hubley and DC Darling, ROM 961029 [ROM]; 1 larva, Gai

Lai: An Keh Dist, 10 km NW Buoenloy, small stream 1km on trail past Cha R,  
1°rainforest edge, 27-VI-1996, B Hubley, ROM 961099 [ROM].



**FIGURE 6–10.** *Trichogenia hubleyi*. **6**, maxilla: ventral; **7**, labial palp: dorsal view of terminal segment; **8**, supracoxal sclerites (indicated by arrows); **9**, hindfemur: setae on middle section of anterior face; **10**, tergum V: setae.

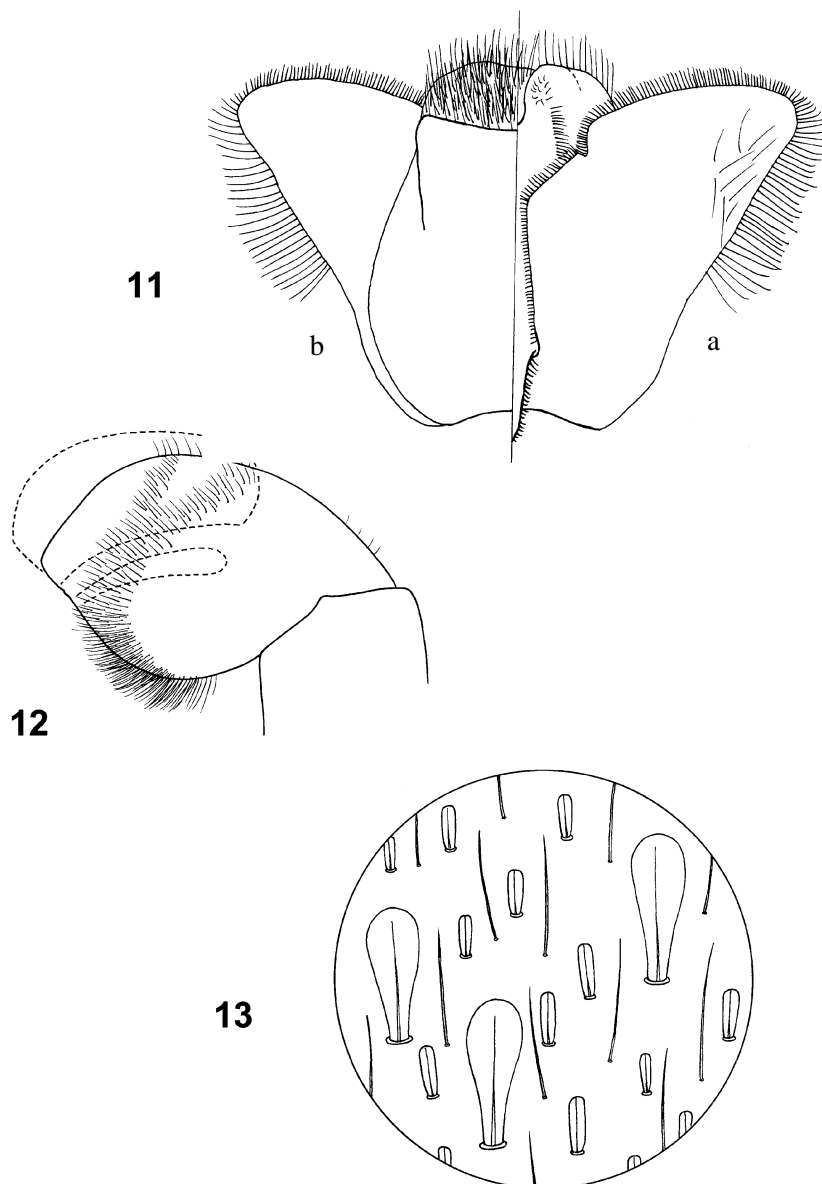


FIGURE 11–13. 11–12, *T. maxillaris*, 11, hypopharynx: a. dorsal b. ventral; 12, labial palp: dorsal view of terminal segment. 13, *T. ulmeri*, hind femur: setae on middle section of anterior face.

***Trichogenia nasuta* (Ulmer) N.COMB.**

*Heptagenia nasuta* Ulmer, 1939: 567 (orig.)

Ulmer (1939) described *Heptagenia nasuta* from adult males and females. The larva is unknown.

***Trichogenia ulmeri* Braasch & Webb N.SP.***Compsoneuria spectabilis* Eaton (larva nec adult); (misid.) Ulmer, 1939:675**Larval Description:** see Ulmer (1939).**Adult:** unknown.**Etymology:** The specific epithet is in honor of the late Georg Ulmer.**Diagnosis:** *Trichogenia ulmeri* can be differentiated from congeners by the following combination of characteristics: i) anterior surface of femora with both long and short robust setae (Fig. 13); ii) presence of comb setae on apical margin of maxillae; iii) long supracoxal spines on the meso- and metathorax; iii) abdominal terga with sparse branched, robust setae, most occurring near posterior margin.**Material Examined:** HOLOTYPE: 1 larva, Indonesia, Sumatra, Ranau, Urwaldbach, R25c, 29-I-1929, Thienemann [ZMUH]. PARATYPES: INDONESIA: 1 larva, same data as holotype [ZMUH]; 2 larvae, Indonesia, E. Kalimantan, Long Tua, Tua cr, 3°10'N 115°47'E, 440m, 7-IV-1994, B Hubley, IIS 940541 [ROM].**Key to the Species of *Trichogenia* larvae**

- 1 Gill lamellae 2–7 long, narrow and sharply pointed; base of outer canines of mandibles without dense lateral brush of setae; supracoxal sclerites short; distribution Thailand, Vietnam ..... *T. maxillaris*
- Gill lamellae 5–7 rounded with pointed apex; base of outer canines of mandibles with dense lateral brush of setae; supracoxal sclerites long and pointed; distribution Indonesia ..... 2
- 2 Anterior surface of femora with setae all of approximately same size and shape (Fig. 9); abdominal terga with numerous, many-branched robust setae (Fig. 10); distribution Celebes ..... *T. hubleyi*
- Anterior surface of femora with some robust setae distinctly larger than others (Fig. 13); abdominal terga with few branched robust setae, generally found only near posterior margins; distribution Sumatra, Borneo ..... *T. ulmeri*

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