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## The concept of *Compsoeuria* Eaton, 1881 revisited in light of historical and new material from the Sunda Islands (Ephemeroptera: Heptageniidae: Ecdyonurinae)

MICHEL SARTORI<sup>1,2</sup>

<sup>1</sup>Museum of Zoology, Palais de Rumine, Place Riponne 6, CH-1005 Lausanne, Switzerland. E-mail : [michel.sartori@vd.ch](mailto:michel.sartori@vd.ch)

<sup>2</sup>Zoologisches Museum und Biozentrum Grindel, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany.

E-mail: [michel.sartori@uni-hamburg.de](mailto:michel.sartori@uni-hamburg.de)

### Abstract

Based on re-examination of material belonging to the Museum of Zoology, Hamburg University, Germany, especially Georg Ulmer's collection, as well as newly collected specimens from the Sunda Islands, the genuine concept of *Compsoeuria* Eaton, 1881 is revised. The genus has had as junior synonyms *Compsoeuriella* Ulmer, 1939 (Oriental) and *Notonurus* Crass, 1947 (Afrotropical). A recent molecular study removed *Notonurus* from this synonymy. The type species of *Compsoeuria*, *Compsoeuria spectabilis* Eaton, 1881, is redescribed. A lectotype male imago is designated for *Compsoeuriella thienemanni* Ulmer, 1939, type species of *Compsoeuriella*. Based on egg morphology, nymphal stages of both *Compsoeuria* and *Compsoeuriella* are unequivocally attributed. The nymph of *Compsoeuria spectabilis* is described and corresponds in part to what Ulmer (1939) described as the nymph of *Compsoeuriella thienemanni*. The latter nymph is also redescribed from material collected recently in Sumatra. Due to the important number of morphological differences between these two species, *Compsoeuriella* **stat. prop.** is removed from its synonymy with *Compsoeuria*. Besides *C. thienemanni*, the genus *Compsoeuriella* encompasses *C. langensis* (Braasch & Boonsoong, 2010) **comb. nov.** from Thailand and *C. tagbanua* (Braasch & Freitag, 2008) **comb. nov.** from the Philippines (Palawan), which is partially redescribed. All other species under the combined concept of *Compsoeuria/Compsoeuriella* are mentioned and their generic placements are discussed. The new combination *Afronurus taipokauensis* (Tong & Dudgeon, 2003) **comb. nov.** from Hong Kong, China is proposed.

**Key words:** *Compsoeuriella*, *Notonurus*, *Afronurus*, Indonesia, Java, Sumatra, new combination, Georg Ulmer

### Introduction

*Compsoeuria* Eaton, 1881 was established for the species *C. spectabilis* Eaton, 1881 on the basis of male and female imagos from Lahat, Sumatra. The genus was characterized by the few crossveins in the forewing that are arranged in a peculiar manner; the given name means literally “the one with elegant veins”. In his later monograph (Eaton 1885), the same author confirmed the diagnosis and provided a drawing of the wings, the male genitalia, as well as the legs of the female imago (Eaton 1885: plate XXIII, fig. 42; plate XXIV, fig. 42). The species was later mentioned by Klapálek (1905) also from Buitenzorg, Java and without further information except that the wing venation is typical for the genus. Ulmer (1924) redescribed and illustrated *C. spectabilis* based on new material mainly also coming from Buitenzorg, Java (now called Bogor). He also associated with this species two male subimagos coming from Sumatra.

In his monumental work devoted to the mayflies of the Sunda Islands, Ulmer (1939) mentioned again *C. spectabilis* as the sole known species of the genus, which he characterized by the especially short segment 1 of the fore tarsi of the male imago, and by the short hind tarsi of the female imago. As new material, he mentioned one pinned female and several male and female imagos in ethanol coming from Buitenzorg. He then described the new genus and new species *Compsoeuriella thienemanni* Ulmer, 1939, based on both male and female imagos from Java and Sumatra, and he noted a close relationship to *C. spectabilis*, especially concerning the wing venation, but

differing by the proportion of the segments of the tarsi in both sexes. In the same work, Ulmer proposed the description of the nymph of both species.

Crass (1947) subsequently established the genus *Notonurus* Crass, 1947 for a peculiar species from South Africa, *N. cooperi* Crass, 1947. Gillies (1963) doubted the validity of the genus *Notonurus* because of its strong similarities with the aforementioned Oriental genus *Compsoeuriella* Ulmer, 1939, especially wing venation, genitalia, male fore tarsi proportions and proposed the synonymy between both genera. He went one step further about twenty years later (Gillies 1984) when comparing the nymphs of *N. njalensis* and *C. thienemanni* and stated that both *Compsoeuriella* and *Notonurus* possess suprcoxal spurs and so are the same genus. Since that time, the synonymy has been widely accepted by mayfly workers.

In 1986, Braasch & Soldán published two important works (Braasch & Soldán 1986a,b). In the first one, they described in great detail Ulmer's species under the name "*Compsoeuriella thienemanni* Ulmer (?)", both in the adult and nymphal stages, from material collected in South Vietnam. Association between adults and nymphs was based on their being taken from the same place. They illustrated genitalia with the presence of titillators. The associated nymph presents a strong coloration pattern on the anterior margin of the head, with 4–6 white dots, and gills with pointed apices. In the same work, Braasch & Soldán (1986a) claimed that the differences between the genera *Compsoeuriella* and *Compsoeuriella* were not reliable based on the male fore tarsus proportions, the only reliable character to separate both genera according to Ulmer (1939) himself. To support this assumption, they described a new species from Sumatra named *Compsoeuriella diehli* Braasch & Soldán, 1986a which exhibits male fore tarsus proportion intermediate between *C. spectabilis* and *C. thienemanni*, and declared *Compsoeuriella* to be a subjective junior synonym of *Compsoeuriella*. They also justified this synonymy against the view of Tshernova (1974) who proposed a key to male imagos of Heptageniidae of the world. She separated the genera *Compsoeuriella* from *Compsoeuriella* by the absence of genital titillators in the former and the presence of such structures in the latter. Concerning the nymphs, Braasch & Soldán (1986a) argued that the nymph described by Ulmer (1939) under the name *C. spectabilis* was wrongly associated because the adult of *C. spectabilis* clearly belongs to the subfamily Ecdyonurinae, whereas the nymph characteristics are of the Heptageniinae type. Finally, Braasch & Soldán (1986a) put in doubt also the association of the adult and nymph of *C. thienemanni*, because the nymph they described is completely different from the one by Ulmer, and they claimed that the nymph should belong to a new genus. Remarkably, they disregarded the fact that Ulmer's association was made by rearing.

In a subsequent paper (Braasch & Soldán 1986b), the same authors proposed a revision of the genus *Compsoeuriella*, which include Ulmer's material deposited in the ZMH. They listed diagnostic features for the genus, among which they stated that the male genitalia have strongly arched and divergent titillators. They illustrated the genitalia of *C. spectabilis* and *C. thienemanni* (without interrogation mark this time, thereby implying confidence in their specific assignment of material), together with those of a new species from Sumatra named *C. flowersi* Braasch & Soldán, 1986b and known from adults only.

The situation remained as described above until Wang & McCafferty (2004) published their revision of the Heptageniidae of the world. They claimed that the synonymy between *Compsoeuriella* and *Compsoeuriella* was wrong, because, based on the nymph, *Compsoeuriella* is a Heptageniinae and *Compsoeuriella* an Ecdyonurinae. They redefined *Compsoeuriella* and put *Compsoeuriella* in synonymy with another genus, *Thalerosphyrus* Eaton, 1881, which nymphs also possess supra coxal spurs. Obviously the authors did not pay attention to Braasch & Soldán (1986a) remark (the article was written in German) about the mis-association made by Ulmer between the adult and the nymph. Two years after these nomenclatorial changes, Webb *et al.* (2006) stated that the nymph of *C. spectabilis* does not belong to the same species as the adult, and the association is erroneous! The nymph was redescribed as *Trichogenia ulmeri* Braasch & Webb, 2006 and belongs to Heptageniinae. Consequently *Compsoeuriella* is withdrawn from its synonymy with *Thalerosphyrus* and put again in synonymy with *Compsoeuriella*, which is an Ecdyonurinae, as stated 20 years earlier by Braasch & Soldán (1986a).

In a recent paper, Vuataz *et al.* (2013) investigated the phylogeny and biogeography of Heptageniidae in Madagascar. They used molecular tools (mitochondrial and nuclear genes) to assess the origin and diversification of this fauna, and comparative material from Africa, and Southeast Asia, all belonging to the subfamily Ecdyonurinae. Among their findings, they showed that all Malagasy species were closely related and formed a monophyletic group related to the African *Compsoeuriella*. Moreover, they found an autapomorphy for the Madagascar + Africa lineage, compared to Oriental *Compsoeuriella*: the setae on the maxillae are long and simple compared to the much shorter and fimbriate setae of the Oriental lineage. Consequently, they reinstalled the genus

*Notonurus* for all Afrotropical *Compsoeuria* species, removing it from Gillies synonymy with *Compsoeuriella* (and so with *Compsoeuria*).

The current concept of *Compsoeuria* has been shaped over the years by the work of Braasch and collaborators: Adults with few crossveins in the forewing, with compact genitalia bearing titillators, and nymphs with contrasted color patterns, especially on the head and the legs, bearing acute supracoxal spurs.

But some important questions are still unsolved, or some facts are at least intriguing.

There is no evidence at all that the association of *Compsoeuria* adults and nymphs proposed by Braasch is correct. In fact, although the genus *Compsoeuria* with *C. spectabilis* as the type species was described from Sumatra and Java, although two other species have been described from Sumatra (*C. diehli* and *C. flowersi*), not a single nymph has been described from the Sunda Islands, except *Compsoeuriella thienemanni* of course. The closest nymphs known are from Philippines (*C. tagbanua* Braasch & Freitag, 2008) or Thailand (*C. langensis* Braasch & Boonsoong, 2010). There is another species of *Compsoeuria* that has been described at all stages and association made by rearing: *C. taipokauensis* Tong & Dudgeon, 2003 from Hong Kong. Unfortunately, the description does not mention important characters on male and nymphal stages, but Wang & McCafferty (2004) removed it anyway from the genus *Compsoeuria* to the genus *Ecdyonurus*. In conclusion, the true nymph of *C. spectabilis* stills need to be described and its association with adults proved with solid arguments.

What is the true nymph of *C. thienemanni* whatever its generic assignment? Are Braasch & Soldán (1986a) correct when they state that their nymphs from Vietnam belong to this species, or is Ulmer (1939) right with his association made by a rearing? The two nymphal descriptions differ too much for representing the same species. Moreover, Ulmer's description of *C. thienemanni* is precise enough to say that he could not be wrong when, for instance, he draws the head (Ulmer 1939: fig. 440) with contrasted patterns and white spots on the anterior margin, which is typical of *Compsoeuria* sensu Braasch & Soldán (1986a; 1986b), but on the same plate (Ulmer 1939: figs. 442–445), draws gills with obtuse apex, and mostly blackish (“die Farbe der Lamellen ist schwärzlichgrau”, Ulmer 1939, p. 675), a character found in no other *Compsoeuria* nymph described.

What is the exact genital structure of *Compsoeuria*, and more precisely, does *Compsoeuria* possess titillators or not? When illustrating male genitalia of *C. spectabilis*, neither Eaton (1885) nor Ulmer (1924) have drawn structure which could be interpreted as titillators. Is Tshernova (1974) right when she separates *Compsoeuriella (thienemanni)* by the presence of titillators, which are lacking in *Compsoeuria (spectabilis)*? Is the redescription proposed by Braasch & Soldán (1986b) of the genitalia of *C. spectabilis* correct and does this species in fact possess titillators which have been overlooked by former authors? Unfortunately, the type specimens of *C. spectabilis* are lost, being not in Naturalis in Leyden where it was supposed to be located (Eaton 1885, p. 275); the single specimen still there is a male imago without abdomen collected in 1932 in West Java (W. Hogenes, in litt.). It is also absent from the collections of the Natural History Museum in London where Eaton's collection is housed (Kimmins 1960).

Based on the study of Ulmer's original material, as well as specimens recently collected from the Sunda Islands, a new analysis of the problem is proposed.

## Material and methods

Drawings were made with the help of a camera lucida or pictures taken from stereomicroscope Leica M205C or Keyence digital microscope and microscope Olympus BX51 or Zeiss Axioscop 2. Final digital drawings were performed on Adobe Illustrator CS6 according to Coleman (2003; 2006; 2009). Setae and scale libraries were made available thanks to C.O. Coleman and R.W. Holzenthal. For scanning electronic microscope (SEM) pictures, the nymphal structures were dehydrated, critical point dried, and then platinum coated or carbon coated, and observed either under a LEO 1525 or a FEI Quanta 250 at 5.00kV. Final plates were assembled in Adobe Photoshop CS6. Material is deposited in the following institutions: Zoologisches Museum, Universität Hamburg, Germany [ZMH]; Musée cantonal de zoologie, Lausanne, Switzerland [MZL]; Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences), Museum of Zoology, Bogor, Indonesia [LIPI].

**Ontogenic stage association.** Among the new material (see below) are several specimens belonging to putative *Compsoeuria/Compsoeuriella* nymphs, among which one mature female nymph of each form. It is well known that oogenesis in mayflies is completed at the last nymphal instar (Soldán 1979), i.e. the egg chorionic

structures are comparable to what can be found in the subimaginal or imaginal stages. Taxonomic usefulness of these structures has been shown in numerous examples, especially in Heptageniidae (Belfiore *et al.* 2003; Gaino & Mazzini 1987;1988; Haybach 2008; Klonowska-Olejnik 1997). Thus, the association of immature and adult stages has been done through the egg chorionic structure.

### ***Compsoneturia* Eaton, 1881**

*Compsoneturia* Eaton, 1881, Ent. Mon. Mag. 18 : p.23

*Compsoneturia* Eaton, 1885, Trans. Linn. Soc. Lond. 2 : p. 275, plates 23 and 24 (42)

*Compsoneturia* Ulmer, 1924, Treubia 6 : p. 86, figures 53A, 55–58 (pro parte non female in figures 53B and 54)

*Compsoneturia* Ulmer 1939, Arch Hydrobiol. Suppl. 16 : p. 562 (pro parte)

**nec** *Compsoneturia* Braasch & Soldán 1986 Reichenbachia 24: p. 59 et auct seq.

**Diagnosis. Imago.** Forewing (Figs 1, 22) crossveins generally reduced in number, comprised between 45 –65, trimmed with violet or brown especially in the costal and subcostal fields. Costal and subcostal fields with few crossveins (< 12), at least two rows of crossveins in the radial field and one crossing the radial-median fields. Male foreleg with first tarsal segment reduced in length, ca 4 times shorter than the second one (Figs 3, 4). Styliger plate straight or slightly convex, last two segments of the gonopods subequal in length (Figs 6, 23). Male genitalia with inner median titillators, penis lobes with apical, subapical and basal spines; lateral sclerite broad and basal sclerite weakly developed (Figs 7, 24).

**Nymph.** Head unicolorous, not thickened, with sometimes lateral markings but without whitish spots on the fore margin (Figs 79–80). Distal dentisetae on maxillae with inner one entire and outer one fringed (Figs 43–44). Scattered setae on the maxillae fimbriate (Figs 45–46). Labial glossae rhomboid with outer margin convex (Fig. 12). Supracoxal spurs present but rounded or bluntly developed (Figs 79–80). Spines on the upper face of femora rounded or truncate (Figs 14, 62). Inner margin of femora without long and thin setae (Figs 13, 61). Gills generally tinted with greyish-purple (Figs 16–18, 79–80). All gills with fibrillous and plate like structures, except gill VII only plate-like. Hind tibiae with two rows of fine setae (Figs 13, 15, 61). Tarsal claw with 3–4 subapical teeth. Caudal filaments with whorls of spine like setae on each segment, without long and thin setae.

**Eggs.** Chorion covered by polygonal ridges; one pole with KCT's larger than those in equatorial area; micropyle with double margin (Figs 20–21).

#### **Species included.**

*Compsoneturia spectabilis* Eaton, 1881 (imagos, nymphs): Java, Sumatra

*Compsoneturia lieftincki* (Ulmer, 1939) (imagos): Java

**Discussion.** At the imaginal stage, the combination of the forewing crossveins, the male foretarsi proportions and genitalia will distinguish the genus from all its relatives. At the nymphal stage, *Compsoneturia* is distinguished from its relatives by the shape of the supracoxal spurs, by the presence of two rows of setae on the hind tibiae, by the shape of the outer distal dentiseta, and by the shape and coloration of the gills. Using the key provided by Webb & McCafferty (2008), *Compsoneturia* will key out at couplet 15 leading to “*Afronurus* in part”.

### ***Compsoneturia spectabilis* Eaton, 1881**

*Compsoneturiella thienemanni* Ulmer, 1939, Arch. Hydrobiol. Suppl. 16, p. 672, nymph (pro parte)

*Compsoneturiella thienemanni* Gillies, 1984, Proc. 4<sup>th</sup> Int. Conf. Ephemeroptera, p. 21, nymph

**nec** *Compsoneturia thienemanni* Braasch & Soldán, 1986, Reichenbachia 24(3), p. 41, adult, nymph

#### **Material examined.** Specimens in ethanol

1 male imago, Buitenzorg, 13.2.32. Lieftinck leg. [ZMH]

1 male (one fore- and one hind legs on slide) and 1 female imagos, Buitenzorg, XI. 1919, Karny leg. [ZMH]

1 female subimago, Buitenzorg, VII. 1929, Lampe, Thienemann leg. [ZMH]

2 female imago and 1 male subimago, Buitenzorg, I. 1929, Lampe, Thienemann leg. [ZMH]

4 nymphs (two mounted on slides), Indonesia, Java, Buitenzorg [Bogor], in Tjiliwung [Ciliwung] River, 25.V.1929, FB3, Prof. Thienemann leg [ZMH, MZL] (sub. nom. *C. thienemanni*)



4 nymphs, Indonesia, West Java, Fish ponds south of the Puntjak pass, 13.IX.1928, B13, Prof. Thienemann leg [ZMH] (sub. nom. *C. thienemanni*)

1 nymph, Indonesia, West Java, Buitenzorg, Pakantjilan River, 16.IX.1928, B7, Prof. Thienemann leg [ZMH] (sub. nom. *C. thienemanni*)

8 nymphs (one mounted on slide), Indonesia, Sumatra Barat, Ombilin River, Talawi, 277 m., 00° 34.147'S 100° 43.543'E, 8.XI.2011, UN4, M. Balke leg [MZL, ZMH, LIPI]

1 nymph, Indonesia, Sumatra Barat, stream near Lubuk Sikaping, 440 m., 0° 10.839'S 100° 08.533'E, 29.IX.2009, SUM12, M. Balke & D. Amran leg. [MZL]

**Pinned specimen.** One male imago, Buitenzorg, Java. K. Kraepelin leg. 24.II–12.III.1904

**Comments on the material examined of *C. spectabilis*.** The pinned specimen is the one observed and mentioned by Klapálek (1905, p. 107) and illustrated by Ulmer (1924, fig. 53A, fig. 55C). In figure 53A the segment V of Klapálek's specimen does not possess a sagittal dark banding, i.e. these marks are present only on segments III–IV and VI–VII. This drawing is thus an interpretation by Ulmer (1924, p. 86): “auf Tergit V manchmal undeutlich oder fehlend”.

Genitalia and legs of the 1919 male imago have been illustrated by Ulmer (1924, figs 56–58); the attribution of the specimen to coll. Jacobson in the legends is a probable mistake since the original label bears the name of Karny.

**Sequence data.** One specimen has been used for the study by Vuataz et al. (2013) under the name “Heptageniidae 2” in figures and “Heptageniidae sp. 2” in table S1, with one mitochondrial (CO1) and two nuclear genes (H3, wg) sequenced. Access numbers in GenBank are for CO1: HF536606, for wg: HF536599, for H3: HF536592.

**Description.** *Male imago description based on the 1932 specimen.* General coloration faded, with legs yellowish, thorax and compound eyes brownish-orange, wings translucent, costal and subcostal fields milky, abdomen translucent with ventral nerve cord whitish, gonopods yellowish, cerci whitish, some junctions between segments lightly tinted in orange, suggesting cerci originally banded with darker color.

**Measurements:** Body length: ca 6.5 mm; Forewing length: 6.9 mm; Gonopods length: 0.9 mm; Cerci length: ca. 14 mm

**Head:** Compound eyes large, meeting in middle at distance equal to distance between lateral ocelli; lateral ocelli two times larger than front one. Frons translucent with well-marked carina.

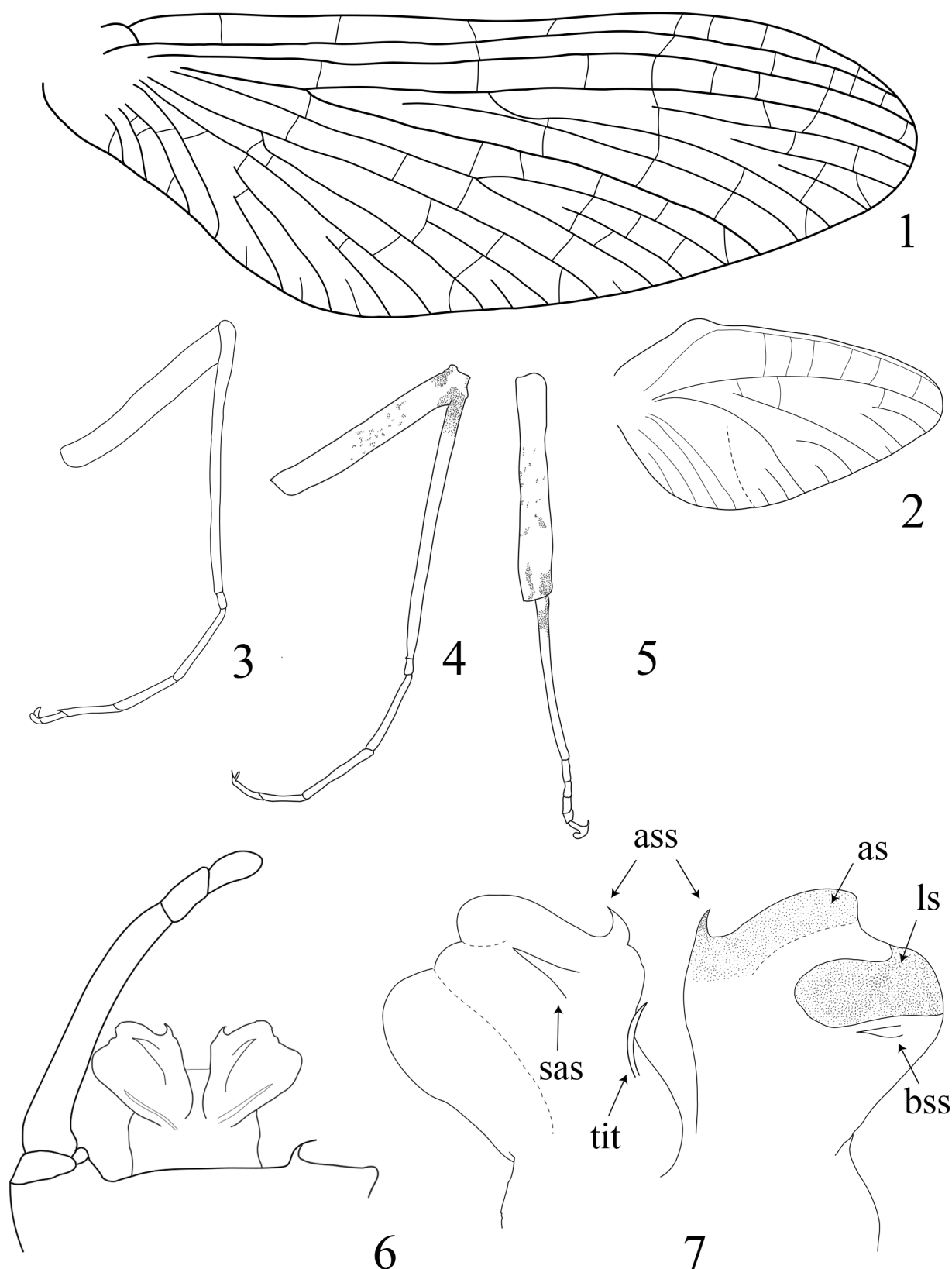
**Thorax:** Transversal suture on mesothorax present but barely visible; medial depression of furcasternum of mesothorax subparallel. Forewing (Fig. 1) with few crossveins, arranged roughly in several rows; costal field with ca. 10 crossveins, subcostal field with only 6; hindwing as in Fig. 2. Foreleg (Fig. 3) with tibia ca 1.3x length of femur, and tarsi subequal or slightly longer than tibia; tarsal segment 1 very short, 4.5x shorter than second; segment 3 and 4 subequal, 0.8x length of segment 2, segment 5 0.5x length of segment 4; tarsal claw dissimilar, one obtuse, one hooked. Hind leg with tibia subequal to femur, tarsi shorter than tibia, tarsal segments 1 and 2 subequal, segment 4 the shortest, segments 3 and 5 subequal and slightly shorter than segments 1 and 2.

**Abdomen (genitalia):** styliger plate (Fig. 6) almost straight, slightly emarginated adjacent to bases of gonopods.; basal segment rounded, 2x longer than wide; segment 1 short and broad, segments 3 and 4 subequal in length, together about  $\frac{1}{3}$  length of segment 2; segment 2 with small rounded inner projection at base. Penis lobes separated by V shape in ventral view (Fig. 7) and U shape in dorsal view; lobes expanded laterally; apical sclerite long, extending to half length of lobe, with distinct subapical spine; base of apical sclerite tinted in orange brown, suggesting strong chitinization. In dorsal view, lateral sclerite broad and rounded, not constricted at apex, basal sclerite weakly developed, with small and acute spine directed inwards on outer margin. Titillators small but present, visible in ventral view, but barely visible in dorsal view.

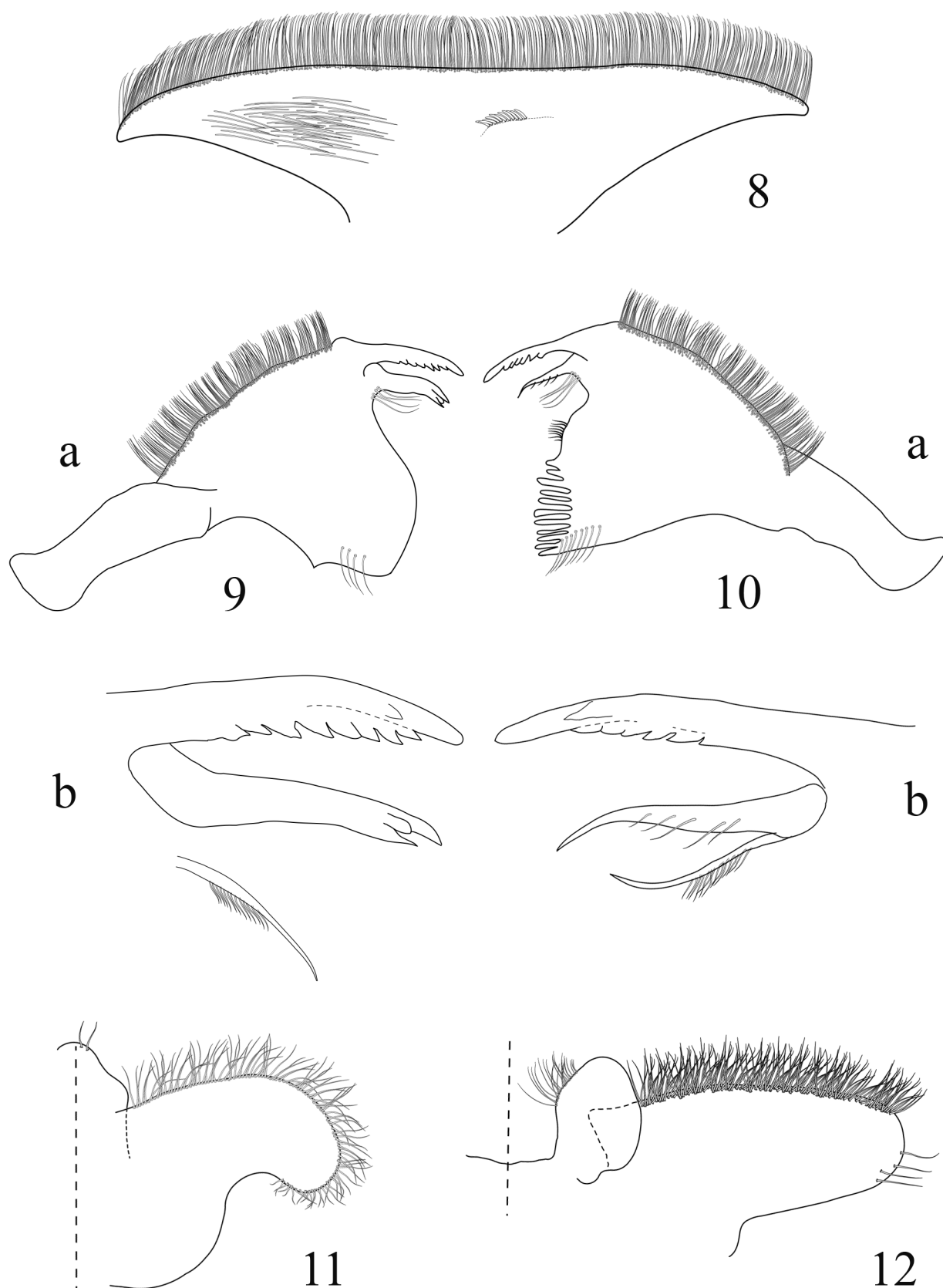
**Nymph.** (Note: The nymph of *C. spectabilis* has been described by Ulmer (1939) under the name *Componeuriella thienemanni* (figs 442–454). It is redescribed here anyway for comparative purposes.)

**Size:** body length between 5.7 and 7.9 mm.

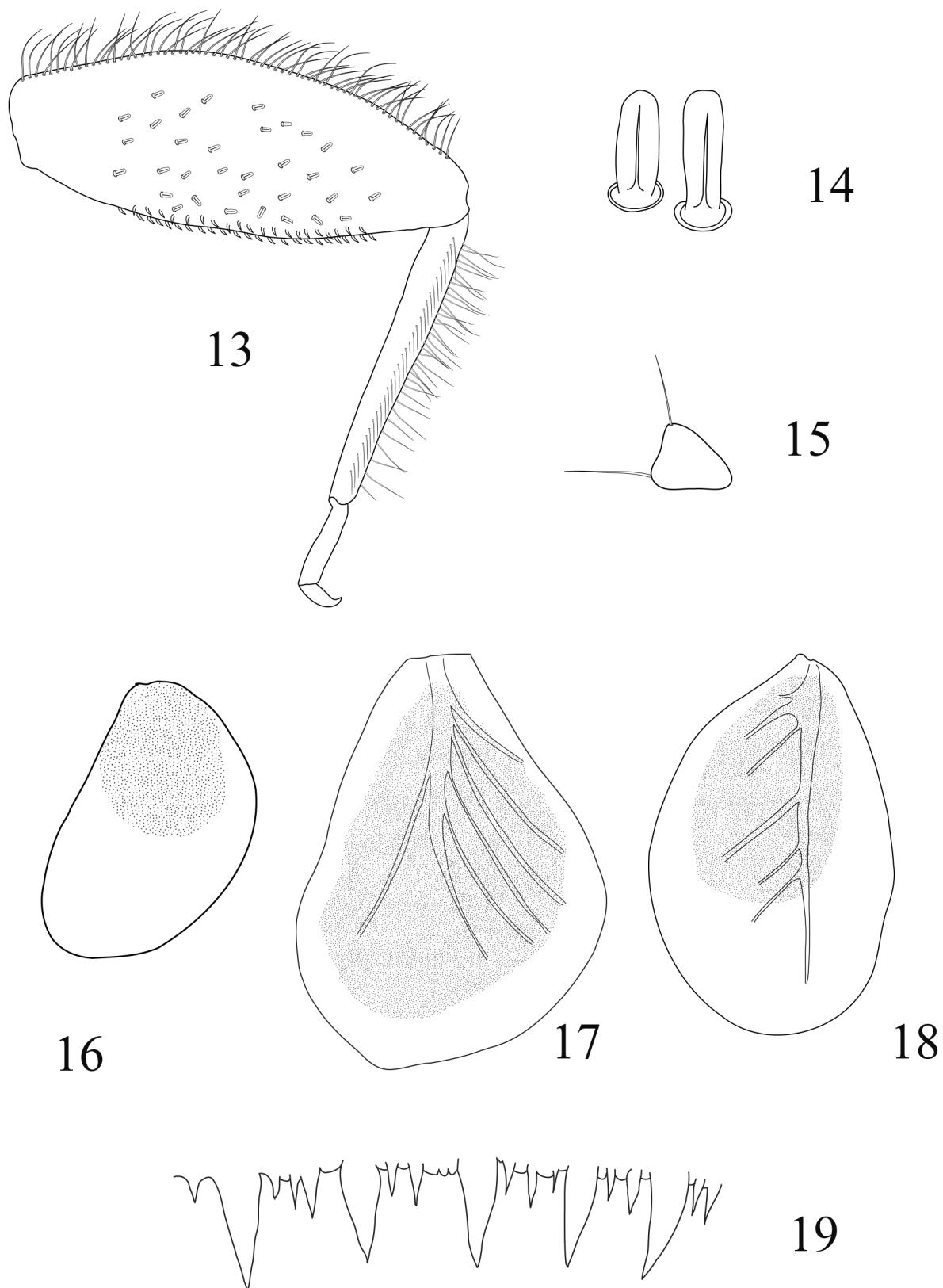
**Coloration (Fig. 79):** head uniformly dark brown, except white spot around ocelli and transverse white line starting from lateral ocelli and reaching margin of head in front of compound eyes in perpendicular orientation; prothorax medium brown with two whitish spots, one proximal, one distal, on median part of each hemi-thorax, sometimes linked together with light line; dorsal face of femora greyish brown, with three elongated maculae on outer margin, sometimes less visible on inner margin, apices of femora and tibiae dark brown, tibiae uniformly



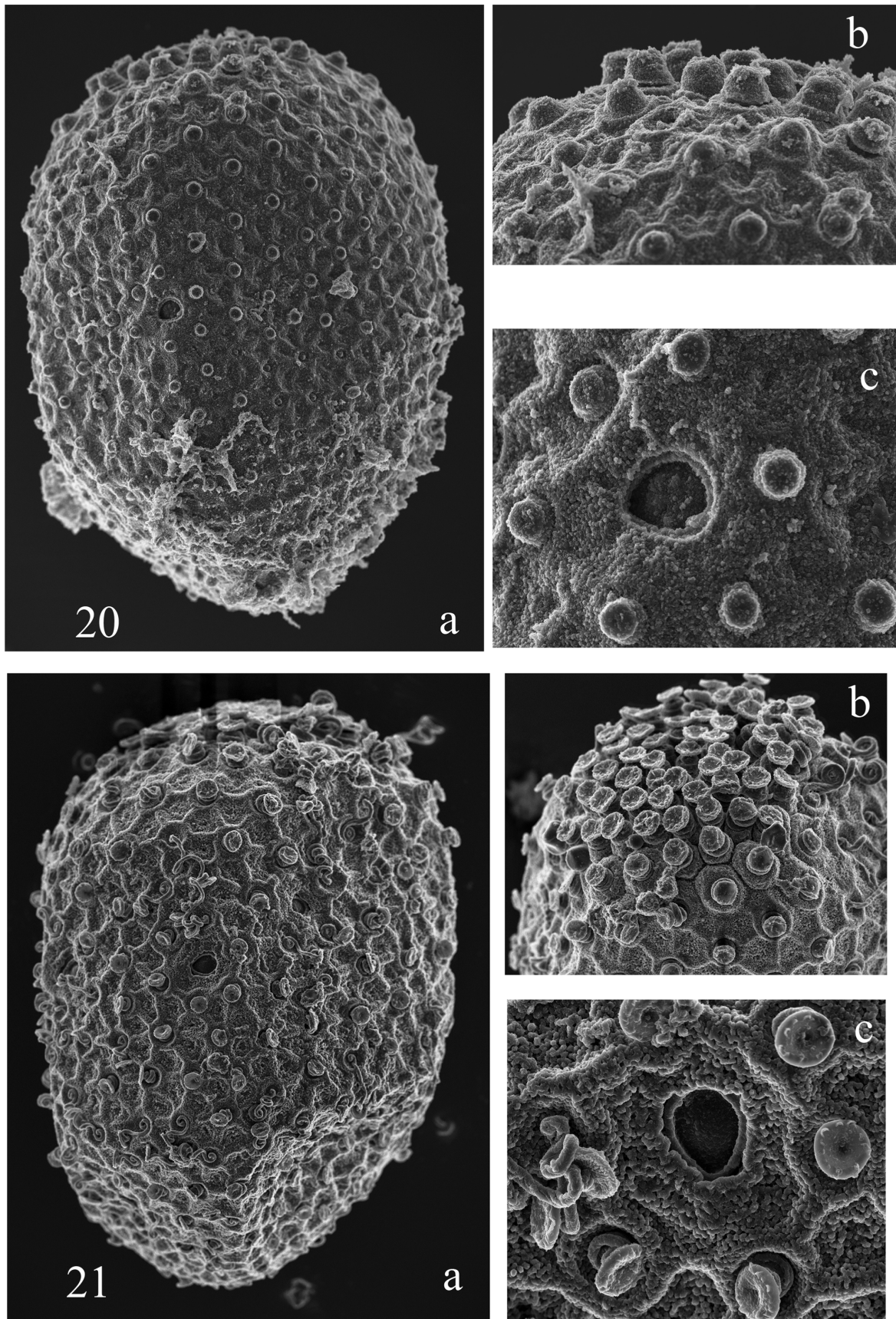
**FIGURES 1–7.** *Compsooneuria spectabilis* Eaton, male imago. Fig. 1 : Forewing; Fig. 2: Hindwing; Fig.3: Foreleg; Figs 4–5: Fore- and hindlegs of a 1919 specimen mounted on slide by Ulmer; Fig. 6: Genitalia; Fig. 7: Penis structure in ventral (left) and dorsal (right) view. Abbreviations: as: apical sclerite; ass: spine on the apical sclerite; bss: basal sclerite spine; ls: lateral sclerite; sas: subapical spine; tit: titillator



**FIGURES 8–12.** *Compsoeura spectabilis*, nymphal mouthparts. Fig. 8: Labrum, with structure on the dorsal face (left) and ventral face (right); Fig. 9: Right mandible; Fig. 10: Left mandible; a: general view, b: details of the incisors; Fig. 11: Hypopharynx (left side); Fig. 12: Labium (left side).



**FIGURES 13–19.** *Compsooneuria spectabilis*, thoracic and abdominal parts. Fig. 13: Hind leg; Fig. 14: Bristles on the upper face of hind femora; Fig. 15: Schematic cross section of the tibia and the respective position of the two rows of setae; Fig. 16: Gill I (only the plate drawn); Fig. 17: Gill V (only the plate drawn); Fig. 18: Gill VII; Fig. 19: Posterior margin of tergite IV.



**FIGURES 20–21.** SEM pictures of eggs extracted from a female imago (Fig. 20) and from mature nymph (Fig. 21) of *Componeuria spectabilis*. Fig. 20: Female imago from Java, Buitenzorg, XI. 1919, Karny leg; Fig. 21: Female nymph (UN4) from Sumatra, Ombilin River, Talawi, 8.XI.2011, Balke leg.; a: egg in toto; b: detail of the pole; c: micropyle and detail of the chorionic structure.

medium brown, sometimes slightly banded; abdominal tergites medium brown, with markings, as follows: segments III, IV, VI and VII with double sagittal blackish line crossing whole segment, on segment V, diffuse yellowish macula in middle, on segments VIII and IX, elongate transverse yellowish macula crossed in middle by sagittal dark brown line, sometimes incomplete; posterior margin of tergites II–VII with blackish line enlarging when reaching sides; abdominal sternites uniformly whitish; cerci medium brown with dark brown banding every two segments.

*Head:* Labrum (Fig. 8) greatly extended laterally, with narrow tips slightly turned posteriorly; anterior margin almost straight, covered by numerous long and simple setae; ventral surface with row of small stout setae; dorsal surface with scattered long and simple setae directed medially. Mandibles strongly arched, both with lateral margin covered with several rows of long and thin setae; right mandible (Fig. 9) with outer incisor saw-like on its inner margin, composed of ca. 9 teeth, and with subapical tooth in ventral position; inner incisor trifid; presence of 4 fimbriate setae below incisors and 4 long and simple setae below mola; left mandible (Fig. 10) with outer incisor saw-like on its inner margin, composed of ca. 6 teeth, and with subapical tooth in ventral position; inner incisor slender and pointed, bearing 4–5 setae-like structures arising from ventral face; 4 fimbriate setae present below incisors, followed by tuft of short setae above mola, and 8 long and simple setae below mola. Maxillae with row of ca. 13 comb-shaped setae on anterior margin, medial comb-shaped setae bearing 12–13 teeth (Fig. 47); ventral surface of galea covered by scattered fimbriate setae (Figs 45–46); proximal dentiseta bifid and fimbriate, first (outer) distal one fimbriate, second (inner) distal one entire (Figs 43–44). Hypopharynx (Fig. 11) with well-developed superlinguae, densely covered with long and simple setae on lateral margin, ending below rounded apex of lobes; lingua with tuft of small setae. Labium (Fig. 12) characterized by well-separated glossae, somewhat rhomboid; paraglossae very large, and extending laterally, more than two times longer than wide.

*Thorax:* Leg ornamentation rather similar among fore-, mid- and hindlegs. Supracoxal spurs weakly developed on forelegs, apparent on mid- and hindlegs, rounded apically. Hindleg (Figs 13, 60) with femur bearing row of long and simple setae on its outer margin; inner margin with row of stout spines directed toward apex, and an incomplete submarginal row of stout spines; bristles on upper face of femora elongated (Figs 14, 62), with rounded apex; tibiae each with two rows of long and very thin setae, one on outer margin, one on lateral ridge (Figs 13, 61); inner margin with only 5–6 short spines regularly arranged. Tarsal claw hooked, with 3–4 subapical denticles (Fig. 63).

*Abdomen:* Posterolateral projections weakly developed on segments I–IV, more pronounced on segments V–IX. Gills broadly oval (Figs 16–18), fibrillate part well-developed on gills I–VI, absent on gill VII; plate gills with tracheation barely visible, strongly colored with purple gray on most of plate, except in apical region and close to margins. Posterior margin of tergites (Fig. 19) with few but very large spines, with 2–3 intercalary small pointed spines. Cerci with whorl of stout and pointed setae on each segment.

*Eggs* (from mature nymph and female): Size: 115–130  $\mu\text{m}$  x 80–95  $\mu\text{m}$ ; chorion smoothly granulated, covered by polygonal ridges (Fig. 21a), and KCTs arranged in polygonal mesh with ridges joining them. KCTs on one pole regularly arranged and three times larger than those on other part of egg (Fig. 21b). Micropyles located in equatorial area, with prominent double margins (Fig. 21c).

**Discussion.** The specimens housed in ZMH completely fit the diagnosis proposed by Eaton (1885) and Ulmer (1924), especially concerning wing venation and leg proportions. Fig. 1 of the forewing is almost identical to Fig. 55A in Ulmer (1924) of a female imago also from Buitenzorg. Figs 3 and 4 of the legs are identical to those proposed by Ulmer (1924) in Fig. 58 for another male imago from Buitenzorg. Genitalia are basically comparable in the general shape; Ulmer's drawing (Ulmer 1924, Fig. 56) exhibits the characteristic apical sclerite, although he did not draw the spine in ventral view, but mentioned it in the text and illustrated it in lateral view (Ulmer 1924, Fig. 57B). Major differences between the two drawings are the stem of the lobes which are clearly convex in our specimen but concave in Ulmer's drawing, and the shape of the styliger plate which is not flat but concave with a pointed process in the middle.

As the specimen drawn by Ulmer (1924, Figs 56–58) is also deposited in the collections of ZMH, it has been re-studied and a complementary description and interpretation is given. The contour of the genitalia of the 1919 specimen in ventral and dorsal view is in accordance with Ulmer's drawing, except the stem of the penis which is clearly convex. The shape of the styliger plate is undoubtedly different but results of a partial drying of the specimen which has folded the plate, hence making this "pointed process" apparent but not real. The basal segments of the gonopods are not in the same plane as the styliger because of the folding. Penis lobes are somewhat

distorted and the lateral sclerites are not well visible but the two small spines at the base of the sclerites are noticeable as are those of the apical sclerites in lateral view (Ulmer 1924, Fig. 57B). Therefore, there is no clear difference between these two specimens, taking into account that the 1919 specimen is less well preserved than the 1932 one.

The major difference is the presence of concealed and hard to see titillators in *C. spectabilis*, as well as the presence of subapical spines on the ventral side of the penis lobes; these two structures were evidently overlooked by Ulmer (1924) in his redescription.

The slide preparation of fore- and hind legs made by Ulmer is presented in Figs 4 and 5. Foreleg (Fig. 4) with coloration patterns very characteristic; the dorsal face of the femur is covered by small and dark maculae in the distal part; apex of the femur with two dark maculae near the inner and the outer margins; proximal part of the tibia dark brown, becoming lighter distally on a short distance; apex of tibia medium brown, as are the distal outer part of each tarsal segments. Hindleg (Fig. 5) with coloration patterns as in the foreleg.

There is a third male imago available in the ZMH collections, pinned and mentioned by Klapálek (1905), and also coming from Buitenzorg. The observation of the genitalia is difficult because of the twisted gonopods, but the general shape is in accordance with the two others, the apical sclerite with the median spine is present, the lateral sclerite has the same shape, but the minute spine at the base of the sclerite cannot be seen. Wing venation is in agreement with the one of the described specimen. This specimen is therefore also considered as belonging to *C. spectabilis*. It is the only one that gives an idea of the color patterns of the thorax and the abdomen.

The nymph of *C. spectabilis* described here is the only one known to belong to the genus *Compsoeuria* at the moment (but see discussion, and Fig. 80). The generic diagnosis therefore applies to the species *C. spectabilis*.

### ***Compsoeuria lieftincki* (Ulmer, 1939)**

*Heptagenia lieftincki* Ulmer, 1939, Arch. Hydrobiol. Suppl. 16, p. 571, male and female imagos

*Compsoeuria lieftincki* Webb et al., 2006, Zootaxa 1335, p. 59

**Material examined.** Two males and one female syntypes with subimaginal exuviae, Indonesia, West Java, Djasinga, Tjibarangbang River, 150m., caught at light in the evening above the river, 6.VII.1935, Lieftinck leg [ZMH].

**Description.** *Male imago.* (Note: Only significant characters are mentioned here; for a complete description see Ulmer 1939).

All specimens faded. Forewings translucent, except costal and subcostal fields milky. Hindwings entirely colored in light brown, color presumably more pronounced on fresh material.

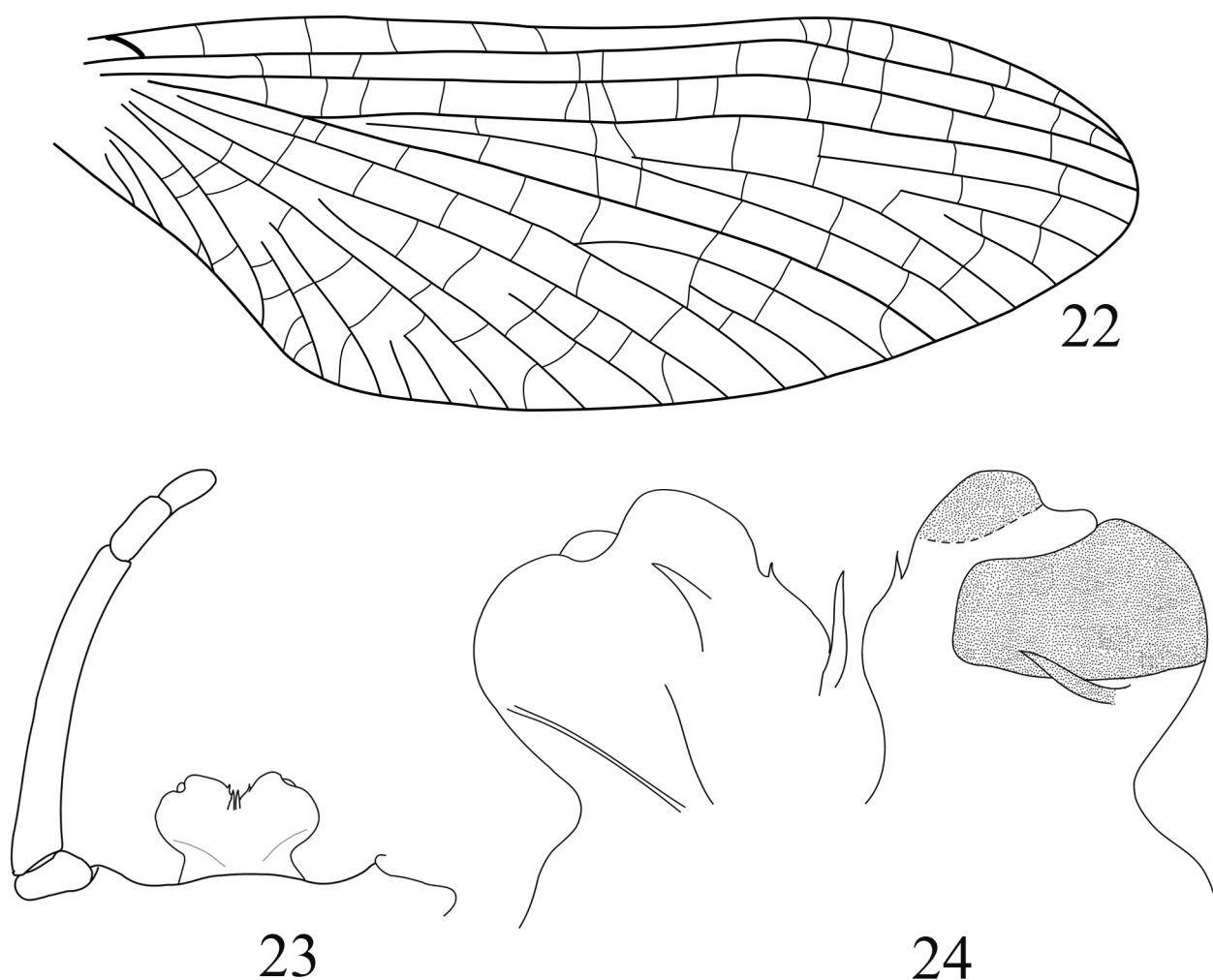
Foreleg similar to *C. spectabilis*, with first segment of tarsus very short (Ulmer, 1939, fig. 160).

Forewing (Fig. 22) with 12 crossveins in costal and subcostal fields; row of crossveins readily apparent in middle of radial-median field, crossveins on distal part of radial field less distinct. Overall number of crossveins greater than number in other species (> 90).

Gonopods, styliiger plate and genitalia characteristic of genus (Fig. 23). Penis lobes (Fig. 24) with small apical spine at base of well-developed apical sclerite, protruding outwards slightly, giving apex of lobe more concave appearance than found in other species; subapical spine and titillators slender; basal sclerite not easily observed, with only acute and long spine visible; lateral sclerite broad and quadrate.

Nymphal stage unknown.

**Discussion.** Ulmer (1939) described this species in the genus *Heptagenia* Walsh, 1863, because the first segment of the hind tarsus is not longer than the second. As illustrated by Ulmer (1939, fig. 161), this first segment is subequal in length to the second one in *H. lieftincki*. The presence of a transverse suture on the mesonotum, together with the median depression of the furcaterum of mesothorax subparallel clearly indicates that *C. lieftincki* belongs to the subfamily Ecdyonurinae and therefore cannot be a member of the Heptageniinae where belongs the genus *Heptagenia*. Consequently, the combination proposed by Webb et al. (2006) is followed here. *Compsoeuria lieftincki* possesses genitalia in accordance with the actual concept of *Compsoeuria*, but the forewing venation is intriguing since it possesses many more crossveins than in *C. spectabilis*. *Compsoeuria lieftincki* exhibits few crossveins in the costal and subcostal fields, as in *C. spectabilis*, together with rows of crossveins in the radial and median fields, together with the reduced first tarsal segment of the forelegs.



**FIGURES 22–24.** *Componeuria lieftincki* (Ulmer), male imago. Fig. 22: Forewing; Fig. 23: Genitalia; Fig. 24: Penis structure in ventral (left) and dorsal (right) view.

The female of *C. lieftincki* described by Ulmer (1939, p. 573) does not belong to the same species or even genus as the male mentioned here, because of the wing venation with numerous crossveins in the costal and subcostal fields and the hind leg proportions, the latter being already mentioned by Ulmer (1939, p.574) as something strange (“auffällig”).

### General considerations on the genus *Componeuria* and other species

The two species mentioned above are the only ones considered here as belonging to the genus *Componeuria* with certainty. The genus seems limited to some Sunda Islands such as Java and Sumatra. It is also presents on Sulawesi (young nymphs in MZL collections, fig. 80) and may represent what Edmunds & Polhemus (1990) mentioned from Celebes as “*Afronurus*-ally”. At the moment, there is no evidence of the presence of the genus in Borneo.

The species described by Navás as *Thalerosphyrus cingulatus* (Navás, 1933) has been transferred to the genus *Componeuria* by Braasch & Soldán (1986a), which is in accordance with their concept of *Componeuria*. The wing venation illustrated by the author (Navás 1933, fig. 33) could be of a *Componeuria* species. The genitalia are not illustrated or described at all, and the foreleg tarsus is described as segment I slightly longer than the second (“*articulo primo tarsorum paulo longiore secundo*”), which is a condition never found in *Componeuria*/*Componeuriella*. It is therefore possible that the author overlooked the small first tarsal segment and compared the second and the third, which are generally subequal. The final attribution of this species to *Componeuria* needs further study.



Based on some special characters, it is possible that the species described as *Componeuria* (*Siamoneuria*) *kovaci* by Braasch (2006) from northern Thailand belongs to the genus *Componeuria*. Braasch (2006) erected the subgenus *Siamoneuria* for a peculiar species which male imago has the first segment of the fore tarsus short, but which penis lobes lack apical spines, and with nymphs with uniform color of the head, supracoxal spurs rounded, and glossae rounded among others. Later, Braasch & Boonsoong (2010) stated that this species could not belong to the genus *Componeuria* because the nymph lacks the typical combination of characters such as long, sharply pointed supracoxal spurs, spotting on the head capsule and narrow, apically pointed glossae, and declared the species *incertae sedis*. As we have demonstrated above, none of the nymphs of the true *Componeuria* possess such characters. The final attribution of this species needs further studies anyway.

Finally, it is most probable that some of the ca. 40 Southeast Asian species described under the generic name *Afromurus* Lestage, 1924, belong in fact to the genus *Componeuria*. For instance, the species *A. freitagi* (Braasch, 2011), described at the nymphal stage only from the Philippines, presents several characters of the genus *Componeuria*: supracoxal spurs rounded, gills with tracheation weakly marked, with lamellae tinted and oval. Unfortunately, there is no information about the detailed structure of the legs and maxillae, thus making the exact assignment of this species impossible without a revision of the material.

### ***Componeuriella* Ulmer, 1939 stat. prop.**

*Componeuriella* Ulmer 1939, Arch Hydrobiol. Suppl. 16 : p. 563 (adults), p. 672 (nymphs pro parte)

*Componeuria* Braasch & Soldán 1986 Reichenbachia 24: p. 59 et auct seq.

**Diagnosis.** Imago. Overall number of crossveins in the forewing reduced in number compared to other Heptageniidae, except other members of the tribe Componeuriini (*Componeuria* and *Notonurus*). Cross veins in the costal and subcostal fields, sometimes also in the radial and median fields, trimmed with violet or brown. Costal and subcostal fields with numerous crossveins (> 15), no rows of crossveins visible in the radial-median fields, sometimes present at apex of the radial field (Fig. 25). Male foreleg with first tarsal segment slightly shorter than the second one (Figs 26–27). Styli plate faintly convex (Fig. 28). Last segment of the gonopods generally smaller than the previous one. Male genitalia with median titillators, penis lobes with apical, subapical and basal spines (Fig. 29). Lateral sclerite narrow, and basal sclerite well-developed.

Nymph. Head not thickened, dark with whitish spots near the anterior margin (Figs 81–82). Distal dentisetae on maxillae with inner and outer one simple (Figs 48–51). Labial glossae conical with concave outer margin apically (Figs 35, 68, 72, 75). Scattered setae on the maxillae generally fimbriate (Figs 52–53). Supracoxal spurs well developed, sharply acute and often pointed (Figs 81–82). Spines on the upper face of femora pointed, or at least with strongly convergent margins (Figs 37, 66, 69). Inner margin of femora with long and thin setae (Figs 36, 65). Gills generally whitish with well visible tracheation (Figs 38–39). All gills with fibrillose and plate like structures, except gill VII only plate-like. Hind tibiae with one row of fine setae on the outer margin (Figs 36, 65). Tarsal claw with 0–2 subapical teeth. Caudal filaments with whorls of spine like setae on each segment, without long and thin setae.

Eggs. Chorion covered by flat, fibrillose and rounded structures; on each pole, KCT's around two times the size of the others; micropyle with single margin (Figs 41–42; Boonsoong & Braasch 2013, fig. 7A–B).

### **Species included:**

*Componeuriella thienemanni* Ulmer, 1939 (imagos, nymphs): Sumatra, Java

*Componeuriella* sp. 1 (imagos, nymphs): Vietnam, Thailand

*Componeuriella langensis* (Braasch & Boonsoong, 2010) (imagos, nymphs): Thailand **comb. nov.**

*Componeuriella tagbanua* (Braasch & Freitag, 2008) (imagos, nymphs): Philippines (Palawan) **comb. nov.**

**Discussion.** As already mentioned, the genus *Componeuriella* corresponds to the concept of *Componeuria* by Braasch & Soldán (1986b) and subsequent authors.

At the nymphal stage, *Componeuriella* is distinguished from its relatives by the contrasted color pattern of the cephalic capsule, with at least 4 whitish dots close to the anterior margin, the acute supracoxal spurs, the presence of long and thin setae on the inner margin of the femora, the bristles on the upper face of femora pointed or at least

with margins clearly convergent, the outer distal dentisetæ of the maxillæ entire, and by the presence of a single row of setæ on the hind tibiae.

At the imaginal stage, the combination of the number of forewing crossveins in the costal and subcostal fields, the male foretarsi proportions and genitalia will distinguish the genus from *Compsoeuriella*, but differences with *Notonurus* were not found.

The eggs of *Compsoeuriella* differ from those of *Compsoeuriella* by the arrangement of the chorion and the margin of the micropyle. To our knowledge, no eggs of *Notonurus* are presently described.

Within the tribe Compsoeuriini, *Compsoeuriella* share several features with the Afrotropical genus *Notonurus* in the nymphal stage, including the overall color pattern of the head and the pointed supracoxal spurs. *Compsoeuriella*, however, typically has fimbriate scattered setæ of the maxillæ together with entire distal dentisetæ (Figs. 48–53) whereas those of *Notonurus* have simple scattered setæ on the maxillæ and numerous distal dentisetæ (Figs 55–58).

### ***Compsoeuriella thienemanni* Ulmer, 1939**

*Compsoeuriella thienemanni* Ulmer 1939, Arch Hydrobiol. Suppl. 16 : p. 563 (adults), p. 672 (nymphs pro parte)

**nec** *Compsoeuriella thienemanni* Braasch & Soldán, 1986, Reichenbachia 24(3), p. 41 (adult, nymph)

**nec** *Compsoeuriella thienemanni* Boonsoong & Braasch, 2013, Zookeys 272, p.75 (nymph)

**Material examined.** Specimens in ethanol.

1 female imago, Sumatra, Wai Lima, Lampongs, XI–XII. 1921. Karny leg. [ZMH]

2 male imagos (fore- and hind legs mounted on slide), 1 male subimago, Sumatra, Lake Singkarak, III.1929, Lampe, Prof. Thienemann leg. [ZMH]

1 male subimago (with corresponding nymphal exuvia on slide), Sumatra, shore of the Lake Singkarak, 23.II.1929, F3e, Prof. Thienemann leg [ZMH]

4 nymphs (one mounted on slide), Indonesia, West Java, Fish ponds south of the Puntjak pass, 13.IX.1928, B13, Prof. Thienemann leg [ZMH, MZL]

1 nymph, Indonesia, West-Java, Buitenzorg, lateral branch of the Tjiliwung River, IX. 1928, B3, Prof. Thienemann leg [ZMH]

3 nymphs (two mounted on slides), Indonesia, Sumatra Barat, Harau Canyon, stream, 540m, 0° 04.428'S 100° 38.002'E, 27.IX.2009, SUM09/UN11, M. Balke & D. Amran leg. [ZMH, MZL]

1 nymph, Indonesia, Sumatra Barat, Sawahlunto, Sikalang, 200m, 0° 37.678'S 100° 46.314'E, 21.IX.2009, SUM01, M. Balke & D. Amran leg. [LIPI]

Pinned specimen. 1 female imago, E. Jacobson, Toentang Java, Oct. 1910 [ZMH] (sub. nom *C. spectabilis*)

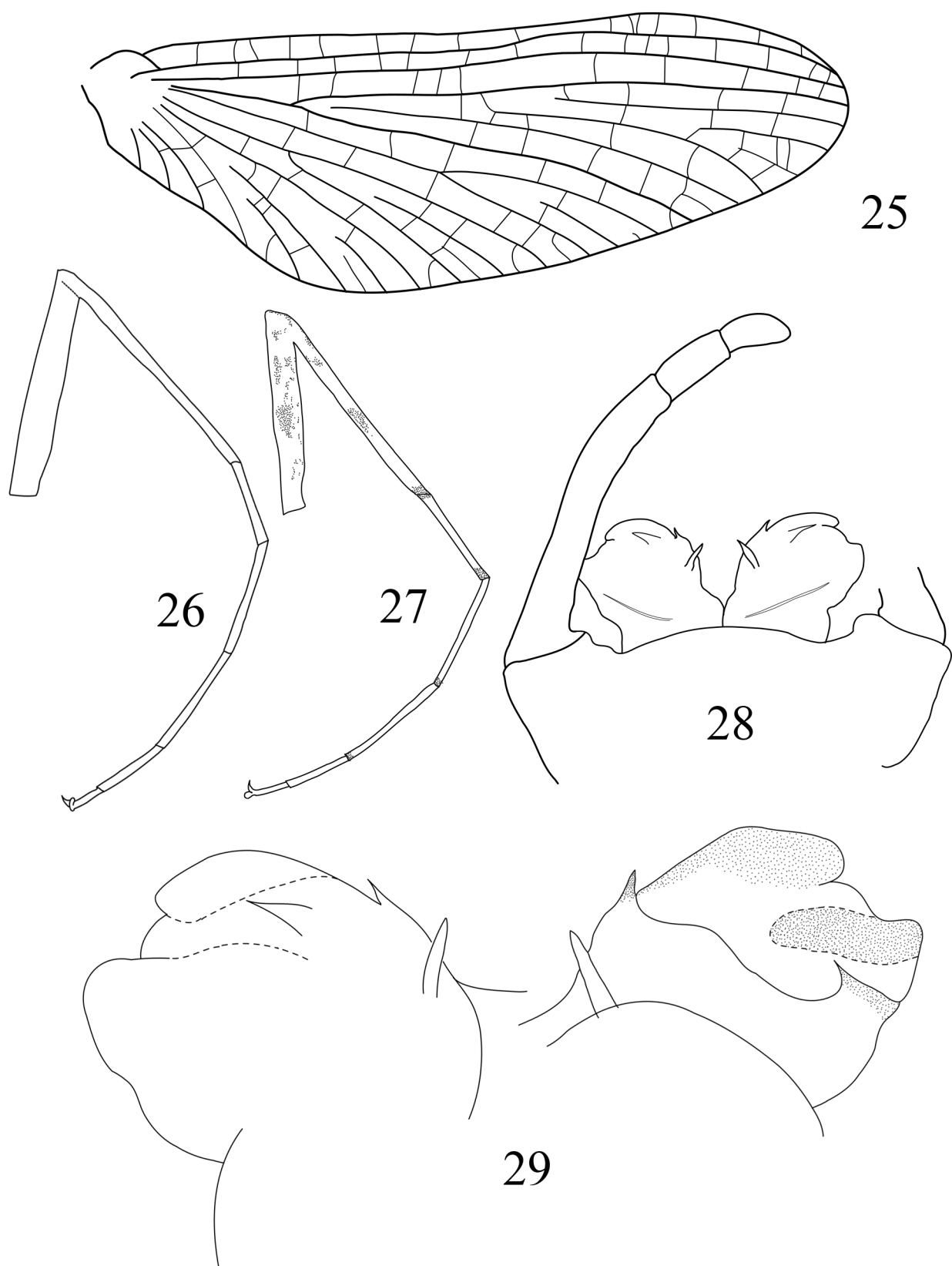
**Lectotype designation.** Ulmer did not designate a holotype for *Compsoeuriella thienemanni*, although he mentioned that the type was a male imago; therefore all the original material constitutes the type series and consequently all specimens are syntypes. In the ZMH collections catalogue, under this species name, appears the mention of a holotype male imago. This information is also available in Weidner (1964). This terminology cannot be accepted because the “holotype” has not been designated by Ulmer and cannot be ascertained by the presence of a single specimen (see also Recommendation 73F. Avoidance of assumption of holotype, ICZN, 1999). Weidner (1962; 1964) also used the term “paratypoides” which should correspond to our actual concept of “paratypes”. Finally Ulmer himself brought some confusion; when describing the nymph of *C. thienemanni*, he mentioned in the material examined the four nymphs belonging to the species *C. spectabilis* (see above), with the following comment in bracket “darunter das typische Stück”, which means “among which the typical one”. This cannot be taken into account for the designation of a type specimen, and this is not a nomenclatorial act according to the Code.

As obviously all the specimens examined by Ulmer under the name *Compsoeuriella thienemanni* encompass more than one species, a lectotype is designated among them, which is the best preserved male imago, with dissected genitalia, and which bears the following labels:

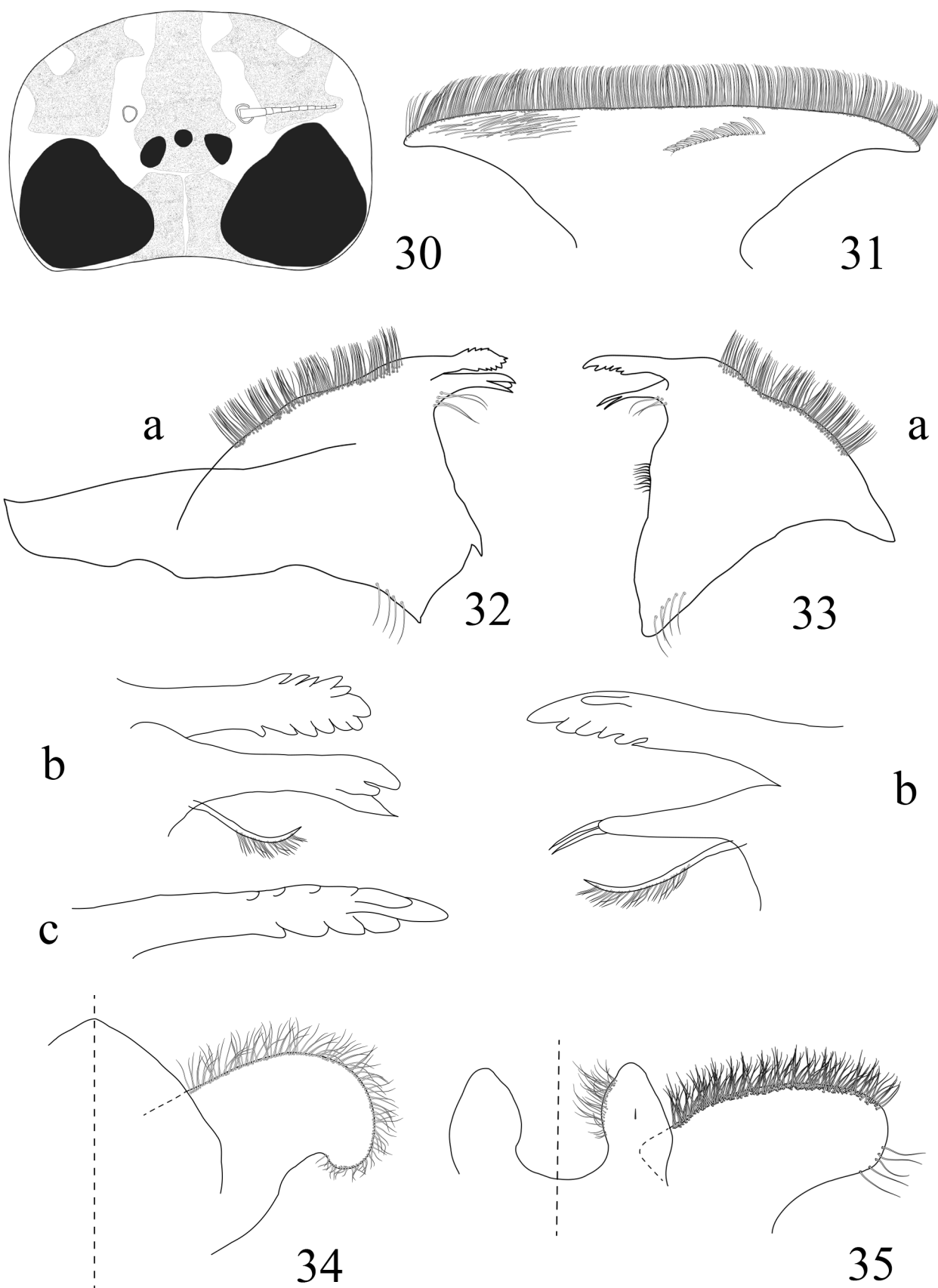
i) Zool Mus. Hamburg—Coll. G. Ulmer—Eing Nr. 6–1963

ii) *Compsoeuriella* Thienemanni Ulm.

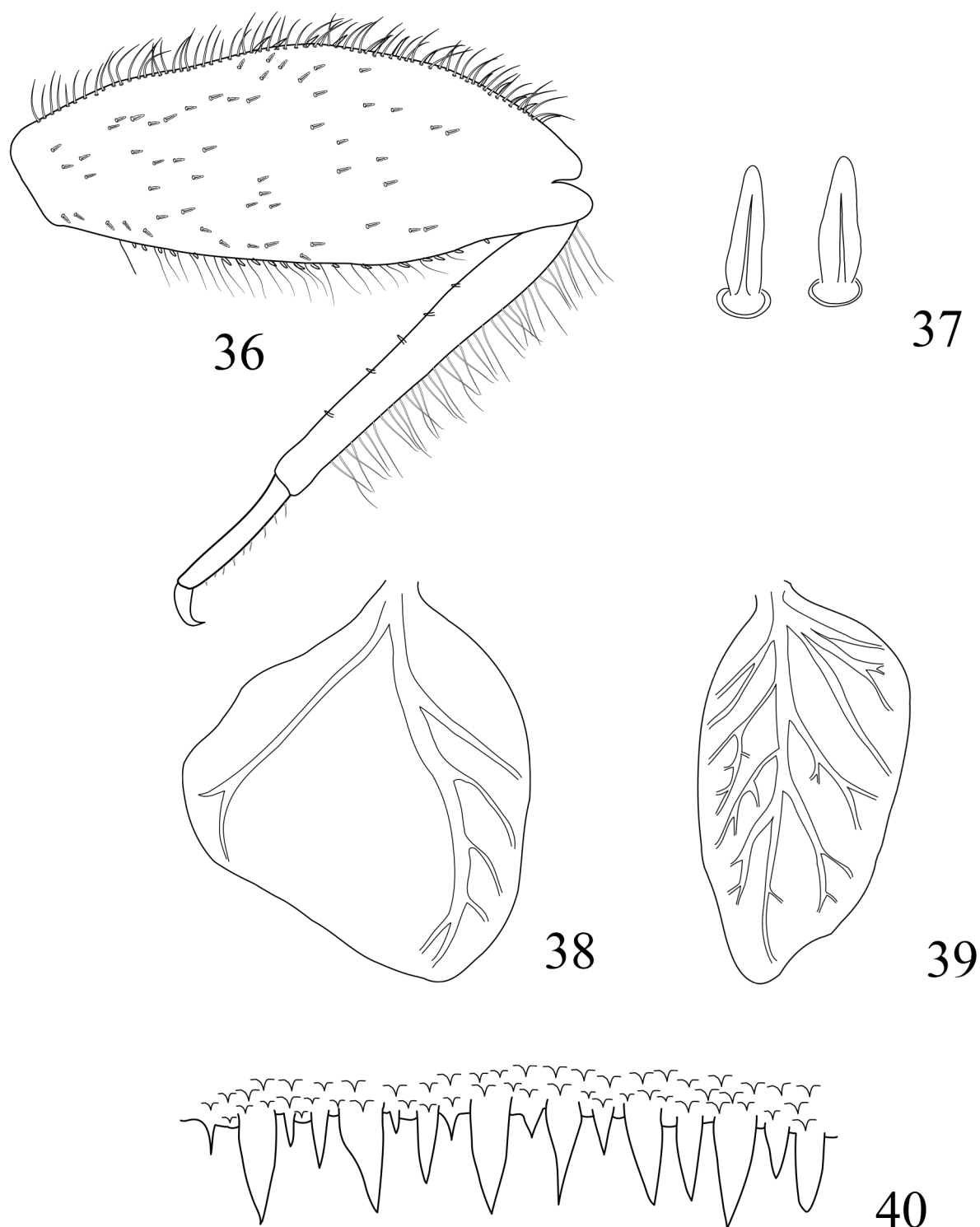
iii) Singkarak, Lampe III. 29;



**FIGURES 25–29.** *Componeuriella thienemanni* Ulmer, male imago lectotype. Fig. 25: Forewing; Fig. 26: Foreleg; Fig. 27: Foreleg of a (para ?) lectotype mounted on slide by Ulmer; Fig. 28: Genitalia; Fig. 29: Penis structure in ventral (left) and dorsal (right) view.



**FIGURES 30–35.** *Compsoeuriella thienemanni*, nymphal mouthparts. Fig. 30: Dorsal view of the head; Fig. 31: Labrum, with structure on the dorsal face (left) and ventral face (right); Fig. 32: Right mandible; Fig. 33: Left mandible; a: general view, b: details of the incisors. c: detail of the right incisor of another specimen; Fig. 34: Hypopharynx (left side); Fig. 35: Labium (left side).



**FIGURES 36–40.** *Compsoneriella thienemanni*, thoracic and abdominal parts. Fig. 36: Hind leg; Fig. 37: Bristles on the upper face of hind femora; Fig. 38: Gill V (only the plate drawn); Fig. 39: Gill VII; Fig. 40: posterior margin of tergite IV.

iii) *Compsoneriella thienemanni* Ulmer, 1939 LECTOTYPUS ♂, M. Sartori des., 2013

The type locality is therefore restricted to Singkarak, Sumatra, Indonesia (articles 73.2.3 and 76.2, ICZN, 1999).

**Description.** *Male imago (lectotype).* Coloration faded, legs yellowish, thorax and compound eyes brownish-orange, wings translucent, costal and subcostal fields milky in distal part, abdomen translucent, except segments VII–X yellowish, with ventral nerve cord whitish, gonopods yellowish, cerci whitish, some junctions between

segments lightly tinted in orange in proximal part, suggesting cerci originally banded with darker color on ca. one-third of their length.

*Measurements:* Body length: ca. 6.6 mm; Forewing length: 6.3 mm; Gonopods length: 0.8 mm; Cerci length: ca. 10 mm but probably broken at apex.

*Head:* Compound eyes large, meeting in middle at distance superior to distance between lateral ocelli; lateral ocelli two times larger than median ocellus. Frons translucent with well-marked carina.

*Thorax:* Transversal suture on mesothorax present; medial depression of furcasternum of mesothorax subparallel. Forewing (Fig. 25) with numerous crossveins, those of costal and subcostal fields tinted with orange (blackish originally?); no rows of crossveins visible. Foreleg (Fig. 26) with tibia slightly longer than femur, and tarsi 1.75x longer than tibia; tarsal segment 2 and 3 subequal in length, segment 1 shorter, ca. 0.7x length of segment 2, segment 4 0.55x length of segment 3 and segment 5 0.5x length of segment 4; tarsal claws dissimilar, one obtuse, one hooked. Hind leg with tibia shorter than femur, tarsi subequal length of tibia, tarsal segments 1 longest, segments 2, 3 and 5 subequal, only slightly shorter than segment 1, segment 4 shortest.

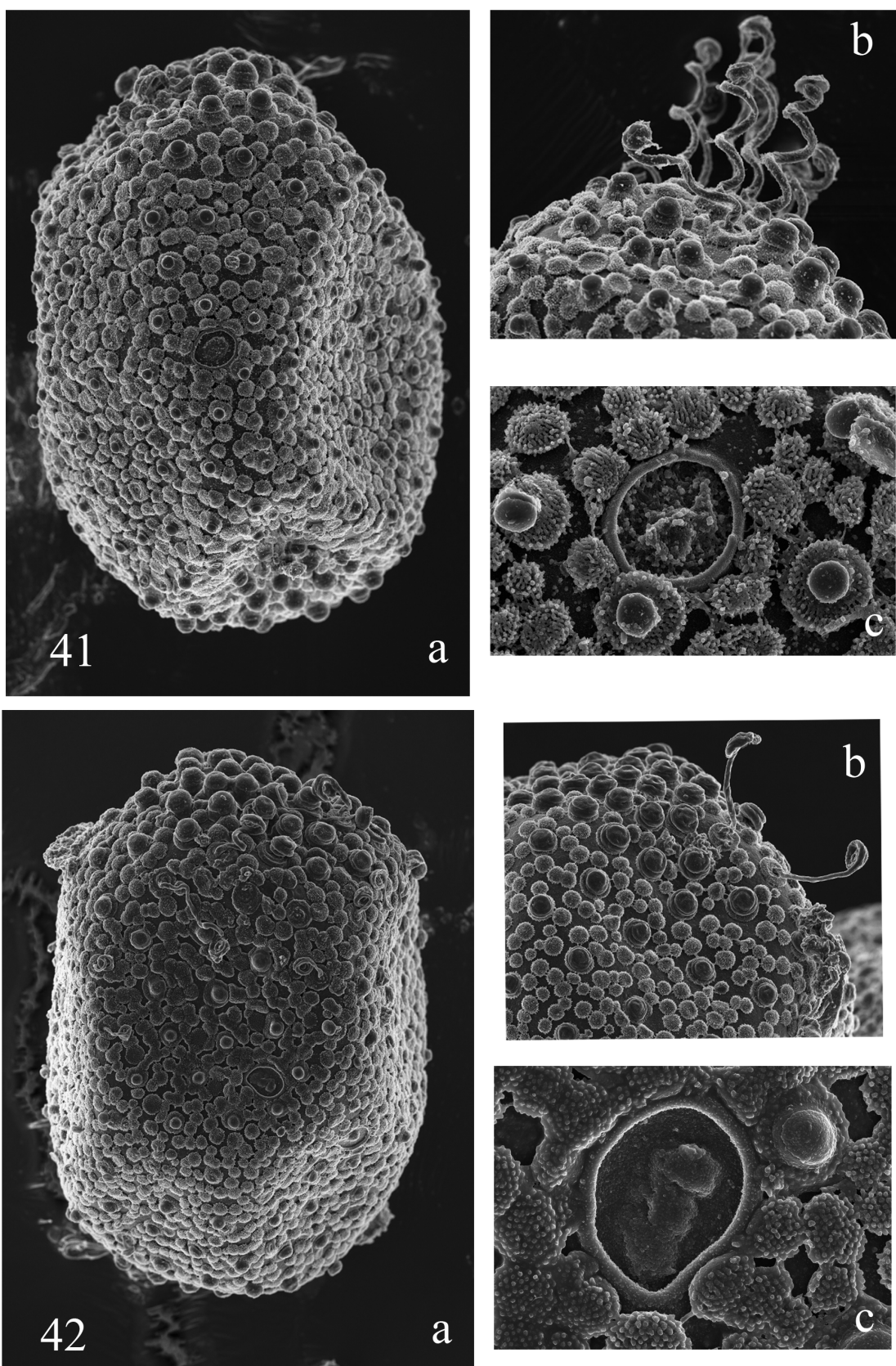
*Abdomen (genitalia):* styliger plate (Fig. 28) slightly convex; basal segment rounded, 2x longer than wide, with inner corner well-marked; segment 1 short and broad, segment 4 slightly shorter than segment 3, together between  $\frac{1}{2}$  and  $\frac{1}{3}$  length of segment 2. Penis lobes stocky. In ventral view (Fig. 29, left), apical sclerite reaching half of lobe width, with distinct basal spine; well-developed subapical spine present below apical sclerite; on inner face of lobes, two stout and pointed titillators. In dorsal view (Fig. 29, right), lateral sclerite narrow and constricted at apex, basal sclerite strongly developed and bearing on outer margin one small and acute spine directed inwards.

*Nymph. Size:* body length up to 7mm and 8 mm in male and female nymphs respectively.

*Coloration (Fig. 81):* overall medium brown with yellowish brown markings. Head (Fig. 30) with lateral margin yellowish and 4 rounded spots near anterior margin, median spots apparently extend backward in yellowish band through antennae and to anterior margin of compound eyes. Femora also contrasted, yellowish with two brownish maculae longitudinal to outer margin and two to inner margin, base of stout bristles on upper face strongly colored in dark brown; tibiae whitish with three ringed brownish maculae, largest macula in middle of tibia, others present in proximal and distal positions. Prothorax greyish brown with two diagonal elongated yellowish bands on each side, mesothorax with two blackish maculae situated medially and close to prothorax. Abdominal tergites with much contrasted patterns: tergite III with two median and longitudinal black thick lines, tergite IV with triangular black lines not reaching posterior margin of segment, tergite V with small triangular black lines on proximal fourth of segment, tergite VI with blackish lines faded in background, but with two rounded yellowish anterior dots, tergite VII broadly similar to tergite IV, tergites VIII and IX dark brown with two small yellowish dots in middle of segment, tergite X medium brown with two large yellowish maculae in middle of segment, reaching anterior margin. Cerci light brown, banded with dark brown segments.

All patterns slightly variable from one individual to another, with respect to size and intensity of maculae, black lines and spots.

*Head:* Labrum (Fig. 31) greatly extended laterally, with narrow tips; anterior margin almost straight, covered by numerous long and simple setae; dorsal surface with long row of small stout setae; ventral surface with scattered long and simple setae directed toward middle of labrum and concentrated near anterior margin. Mandibles strongly arched, both with lateral margin covered with several rows of long and thin setae; right mandible (Fig. 32) with outer incisor saw-like on both margins (those on outer margin often difficult to see on microscopic slides, Fig. 32c), composed of ca. 6 teeth, inner incisor trifold (Fig. 32b); presence of 4 fimbriate setae below incisors and 4 long and simple setae below mola (Fig. 32a); left mandible with outer incisor saw-like on its inner margin, composed of ca. 6 teeth, and with subapical tooth in ventral position; inner incisor slender and pointed, bearing 2 setae-like structures in apical position (Fig. 33b); 3 fimbriate setae present below incisors, followed by tuft of short setae above mola, and 5 long and simple setae below mola (Fig. 33a). Maxillae with row of ca. 12 comb-shaped setae on anterior margin, medial ones bearing 7–9 teeth (Fig. 54); ventral surface of galea covered by scattered long fimbriate setae (Figs 52–53); proximal dentisetula bifid and fimbriate, with two distal dentisetulae simple (Figs 48–51). Hypopharynx (Fig. 34) with well-developed superlinguae, densely covered with long and simple setae on lateral margin, ending below rounded apex of lobes; lingua without or with few short setae arranged in tuft. Labium (Fig. 35) with glossae somewhat slender and with inner margin slightly concave before apex, inner margin covered with dense simple setae, outer margin with fimbriate setae, dorsal face with single pointed bristle; paraglossae large and extending laterally, two times longer than wide.



**FIGURES 41–42.** SEM pictures of eggs extracted from a female imago (Fig. 41) and from a mature nymph (Fig. 42) of *Componeuriella thienemanni*. Fig. 41: Female imago from Sumatra, Wai Lima, Lampongs, XI–XII. 1921, Karny leg; Fig. 42: Female nymph (UN11) from Sumatra, Harau Canyon, 27.IX.2009, Balke leg; a: egg in toto; b: detail of the pole; c: micropyle and detail of the chorionic structure.

**Thorax:** Leg ornamentation rather similar between all three pairs, except forefemora lack row of stout spines on inner margin. Supracoxal spurs strongly developed, especially on mid- and hindlegs, acute apically. Hindleg (Figs 36, 64) with femur bearing row of long and simple setae on its outer margin, together with stout spines on distal half; inner margin with row of stout spines directed toward apex, row of long and very thin setae and incomplete submarginal row of stout spines (Fig. 36); bristles on upper face of femora elongated, with lateral margins clearly convergent, with rounded apex (Figs 37, 66); tibiae (Fig. 65) each with one row of long and very thin setae on outer margin; inner margin with only 5–6 short spines regularly arranged. Tarsal claw (Fig. 67) hooked, with no subapical denticles.

**Abdomen:** Posterolateral projections weakly developed on segments I–III, more pronounced on segments IV–IX. Gills (Fig. 38) broadly oval or rounded and asymmetrical, fibrillate part well developed on gills I–VI, absent on gill VII; plate gills with tracheation apparent, gill VII (Fig. 39) more elongated than others, with inner margin concave near apex. Posterior margin of tergites (Fig. 40) with row of large and pointed spines, together with intercalary small and medium ones; several rows of microdenticles apparent. Cerci with whorl of stout and pointed setae on each segment.

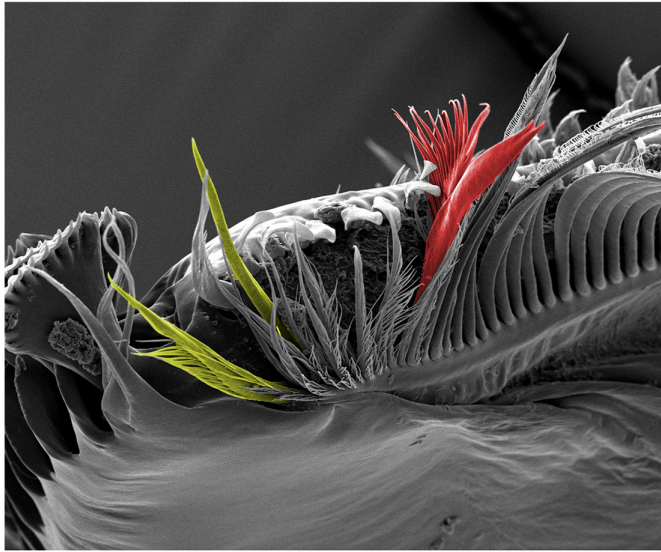
**Eggs** (from mature nymph and female): Size: 110–125  $\mu\text{m}$  x 85–100  $\mu\text{m}$ . Chorion covered with flat, fibrillose and rounded structures (Figs 41a, 42a), some bearing KCTs; on each pole, KCTs around two times size of KCTs located elsewhere (Figs 41b, 42b); micropyle with single margin (Figs 41c, 42c).

**Discussion.** The lectotype description fits the diagnosis proposed by Ulmer (1939), but there are some intriguing points. The first one concerns the forewing venation. When describing its new genus *Compsoneriella*, Ulmer stated that the wing venation was very close to the one of *Compsoneria* (...“ganz ähnlich wie bei *Compsoneria* Etn”), a statement not correct when comparing our Figs 1 and 8, with Ulmer’s (1939) fig. 143 and Ulmer’s (1924) fig. 55. In *C. thienemanni*, the arrangement and number of crossveins are quite different than in *C. spectabilis*. The “rows” of crossveins are absent, and the crossveins are more numerous than in the previous species, especially in the costal and subcostal fields. An answer to this “paradox” can be found in his 1924 paper. When redescribing *C. spectabilis*, he illustrated the forewing (Ulmer 1924, fig. 54) and the abdomen in lateral view (Ulmer 1924, fig. 53B) of a pinned female imago (coll. Jacobson), mentioning that this female possesses different abdominal color patterns as well as different wing venation, but Ulmer considered them as intraspecific variation. When making the diagnosis of the genus *Compsoneriella* (Ulmer 1939, p. 563), he wrote that the wing venation of the new genus is similar to the one of this female from 1924 (“wie bei der von mir in Treubia, 6, 1924, f. 53b, 54 abgebildeten dunkleren Form (Tuntang, Java) der *C. spectabilis* Etn”). This female possesses numerous crossveins, more than 15 in the costal field and more than 12 in the subcostal one, and the general pattern is similar to the lectotype of *Compsoneriella thienemanni*. One can therefore conclude that this female was misidentified by Ulmer, and rather than being a variation of *C. spectabilis*, constitute a female imago of *C. thienemanni*.

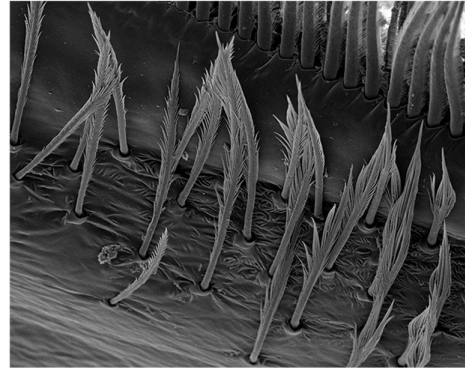
The foreleg proportions illustrated in my Fig. 26 are a little bit different from the drawing made by Ulmer (1939, fig. 140) as well as his description, and this can be due to some distortion in the drawing since it has been done with the leg attached to the body, and therefore all pieces not always in the same plane. Fig. 27 presents the leg of a specimen on Ulmer’s slide, which can belong to the lectotype or to the other male imago, and which kept its original coloration. In this figure, the leg proportions are more in accordance with Ulmer’s description, except that tarsal segment 3 is longer than the first one, whereas Ulmer stated that they are of the same length. The coloration of the leg is as follow: on the dorsal face of the femur, the same small blackish maculae as in *C. spectabilis* can be found; on the ventral side there are three large dark spots, one apical, one subapical and one in the middle of the femur; tibia is ringed by three maculae, one apical, one in the middle and one subproximal; distal part of the tarsal segments tinted in blackish, the coloration fading towards the apex of the tarsus to become light brown on segment 4.

Major differences have to be found on the genitalia. Ulmer’s drawings (1939, figs. 145–149) did not mention any spines or sclerotized structures, but the general shape is in accordance with the drawings. These genital structures are difficult to represent because the penis is thick due to a very developed basal sclerite on dorsal side, and the structures not easy to see. Anyway, penis lobes bear a spine of the apical sclerite together with subapical spine below the apical sclerite, an inner spine on the basal sclerite, and titillators. Although broadly similar, genitalia of *C. thienemanni* differ from those of *C. spectabilis* in several respects; the basal sclerite is much more developed and the basal spine is small, the lateral sclerite is narrower, the apical spine is less developed and the titillators are much more developed than in *C. spectabilis*.

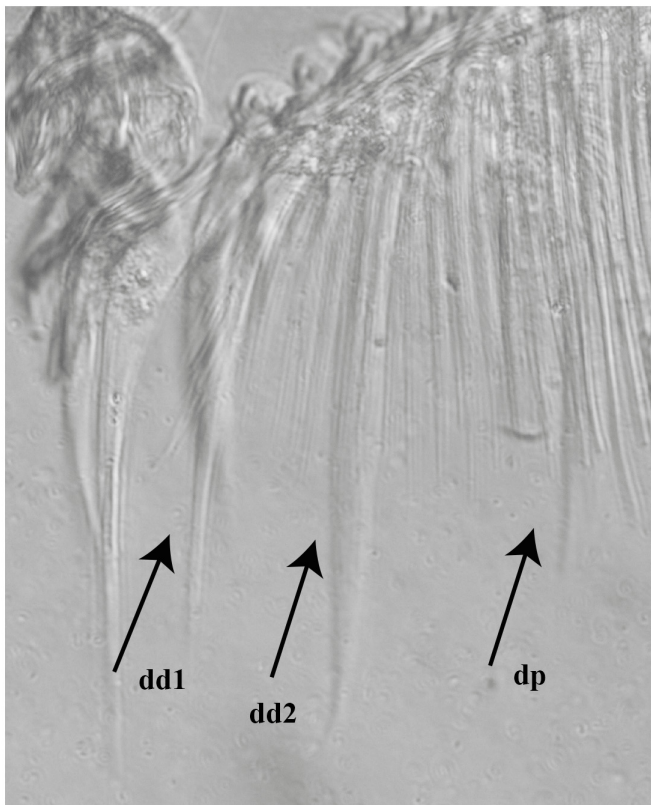




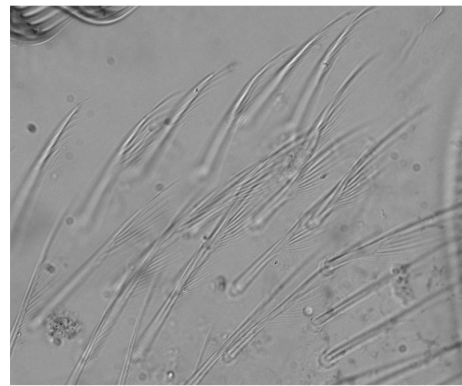
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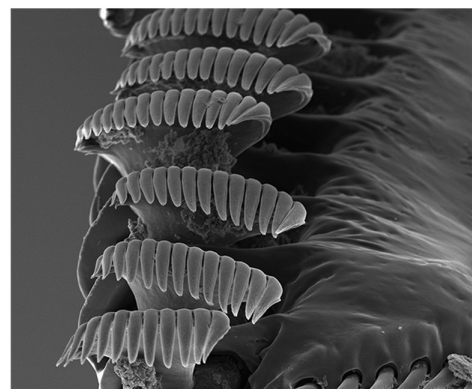
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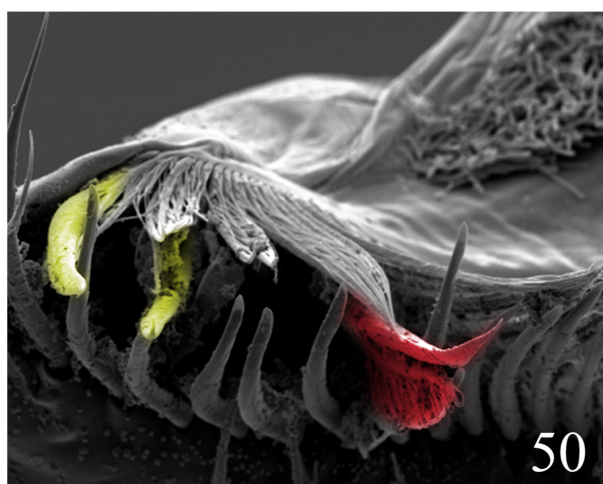
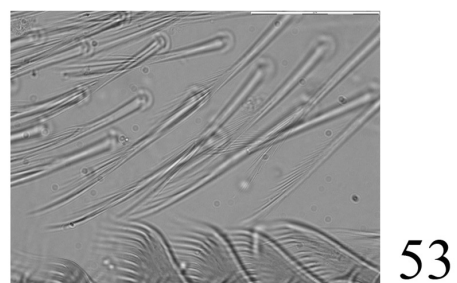
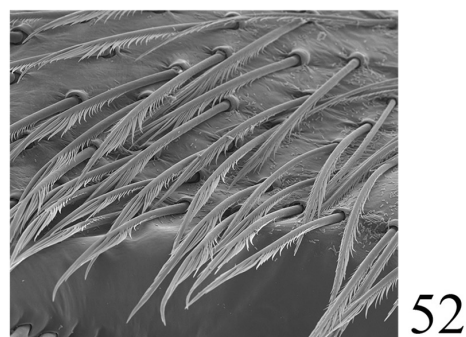
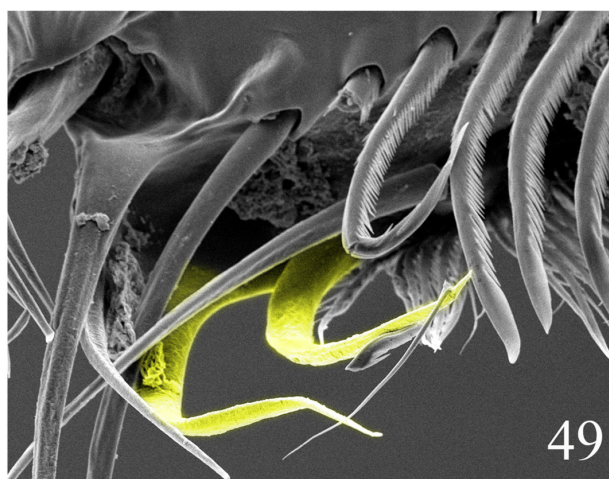
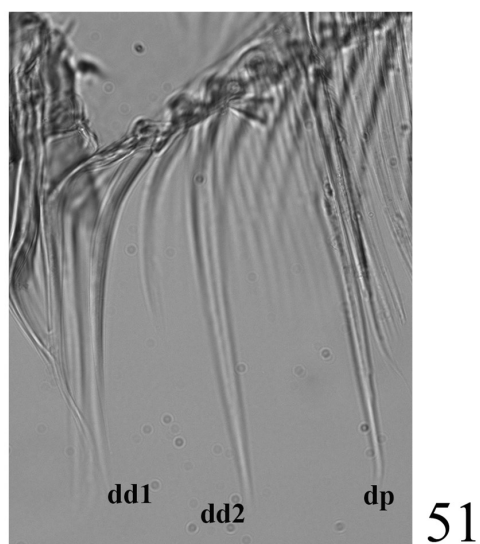
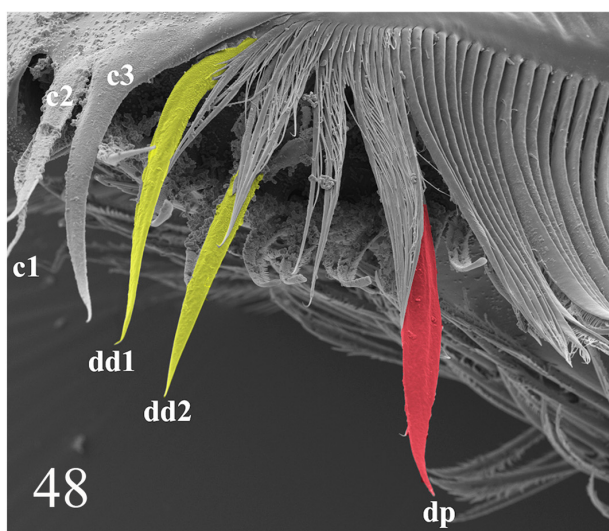


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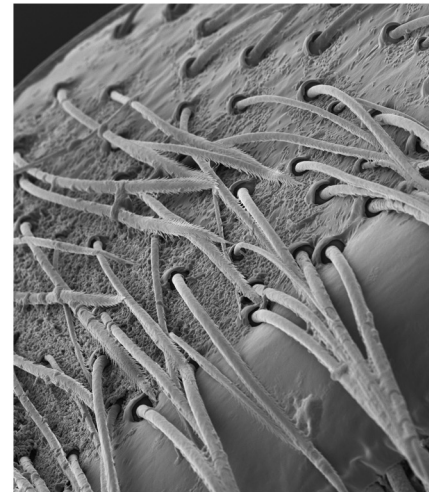
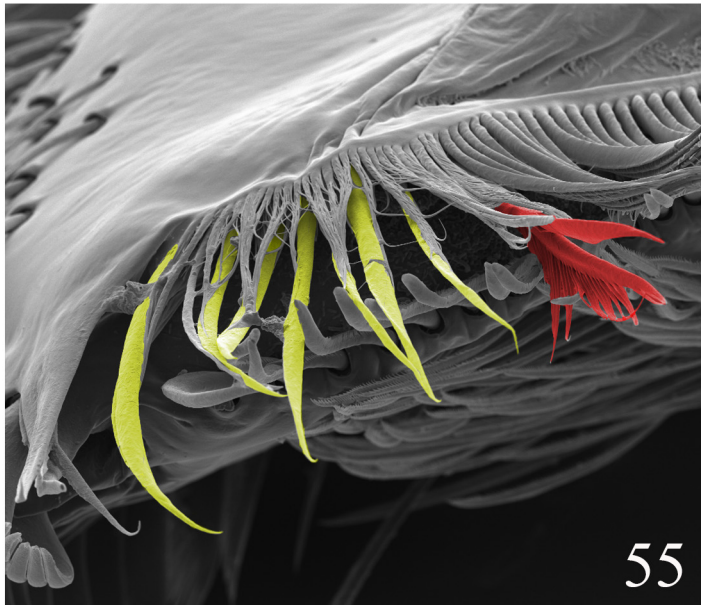
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**FIGURES 43–47.** Nymphal maxillae details of *Compsoneturia spectabilis*. Fig. 43: SEM view of the dentisetae, proximal dentiseta in red, distal dentisetae in yellow, with first one fimbriate; Fig 44: Same view in optical microscope; Fig. 45: SEM view of fimbriate scattered setae on the ventral face of the galea; Fig. 46: Same view in optical microscope; Fig. 47: SEM view of the comb-shape setae on the crown of the galea; abbreviations: dp: proximal dentiseta, dd1, first distal dentiseta, dd2 second distal dentiseta.

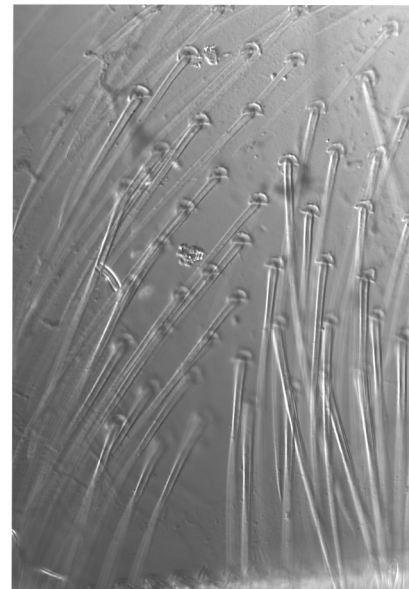
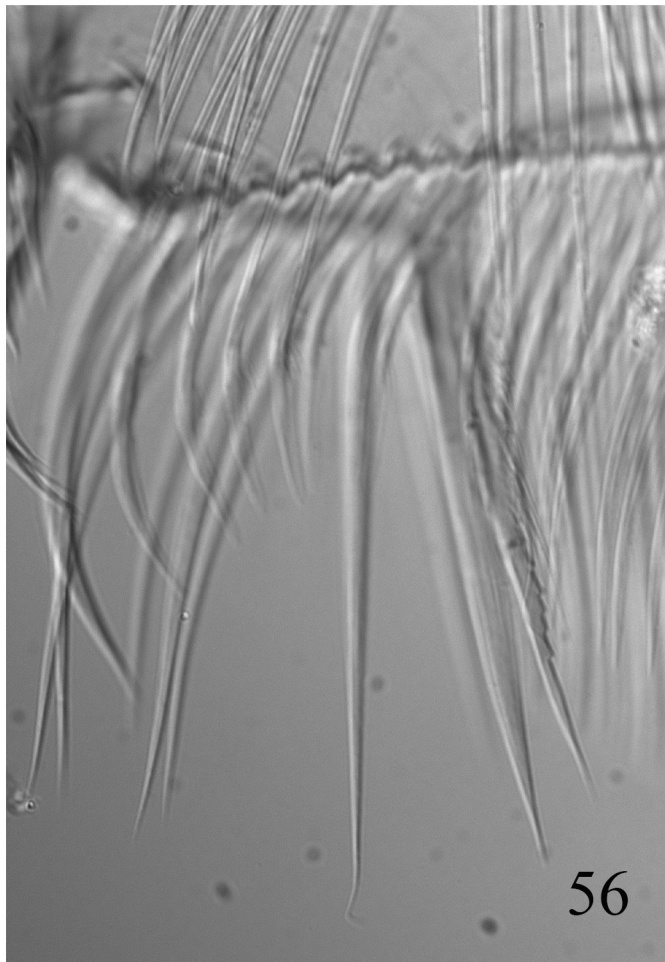


**FIGURES 48–54.** Nymphal maxillae details of *Compsoeuriella thienemanni*. Fig. 48: SEM view of the dentisetae, proximal dentiseta in red, distal dentisetae in yellow, with first one entire; Figs 49–50: Different angle views of the dentisetae in SEM, to show the outer distal dentiseta always entire; Fig. 51: Same view in optical microscope; Fig. 52: SEM view of fimbriate scattered setae on the ventral face of the galea; Fig. 53: Same view in optical microscope; Fig. 54: SEM view of the comb-shape setae on the crown of the galea; abbreviations: dp: proximal dentiseta, dd1, first distal dentiseta, dd2, second distal dentiseta.

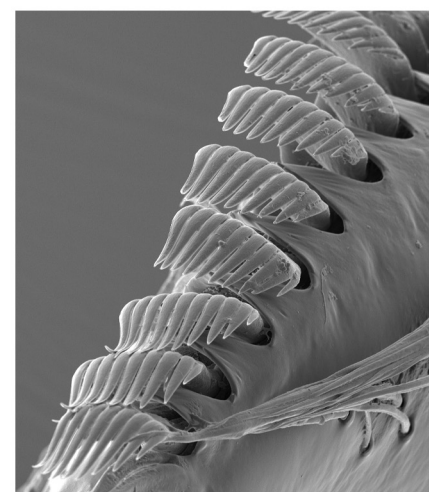




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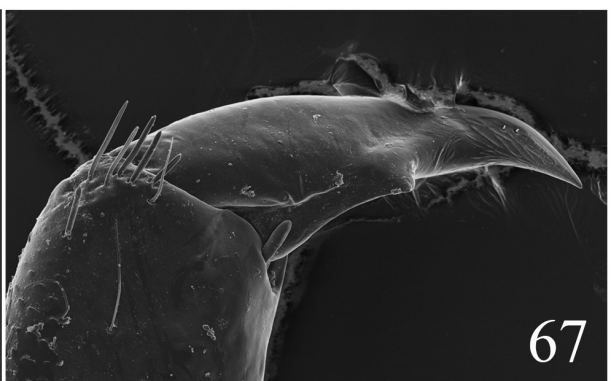
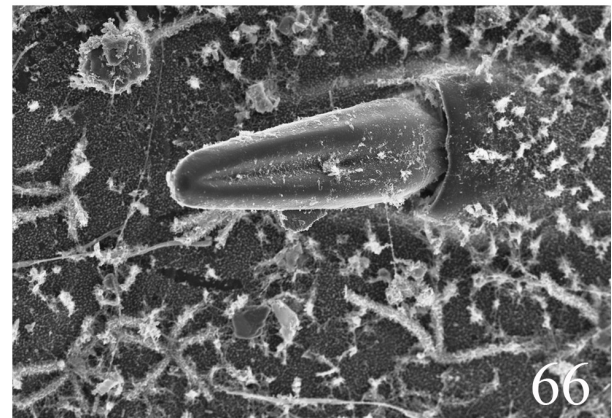
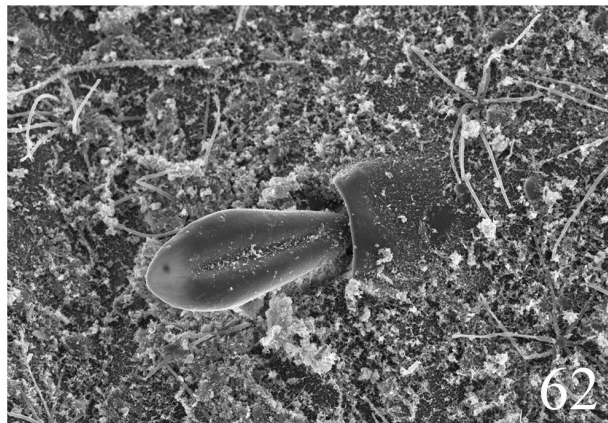
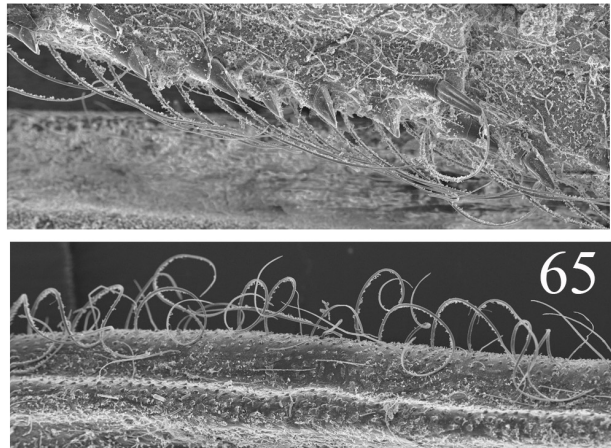
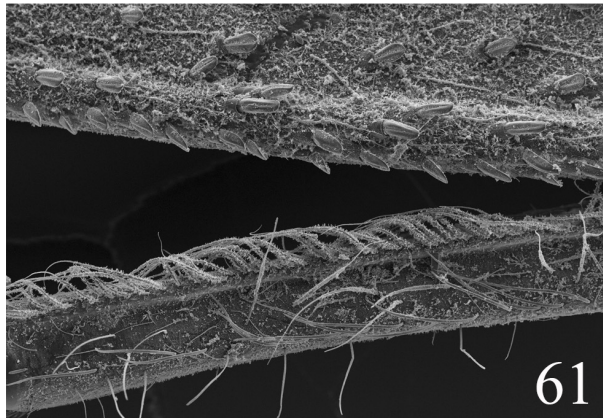
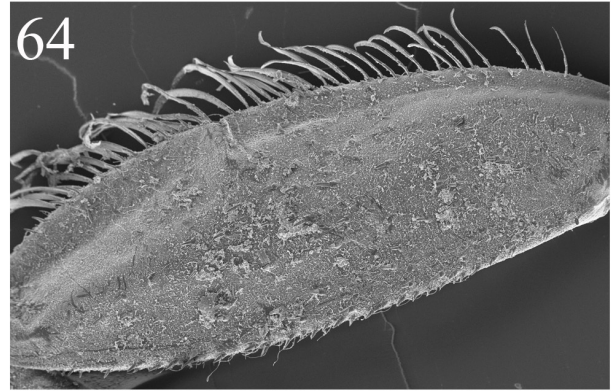
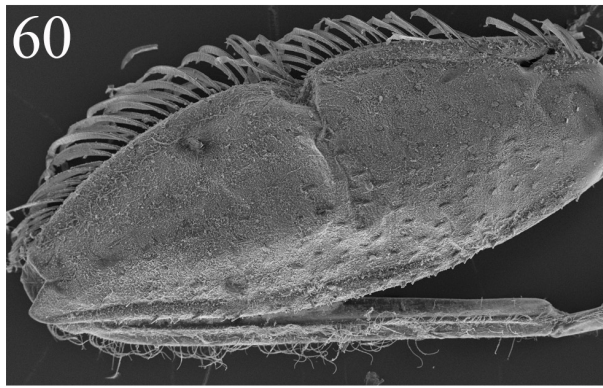
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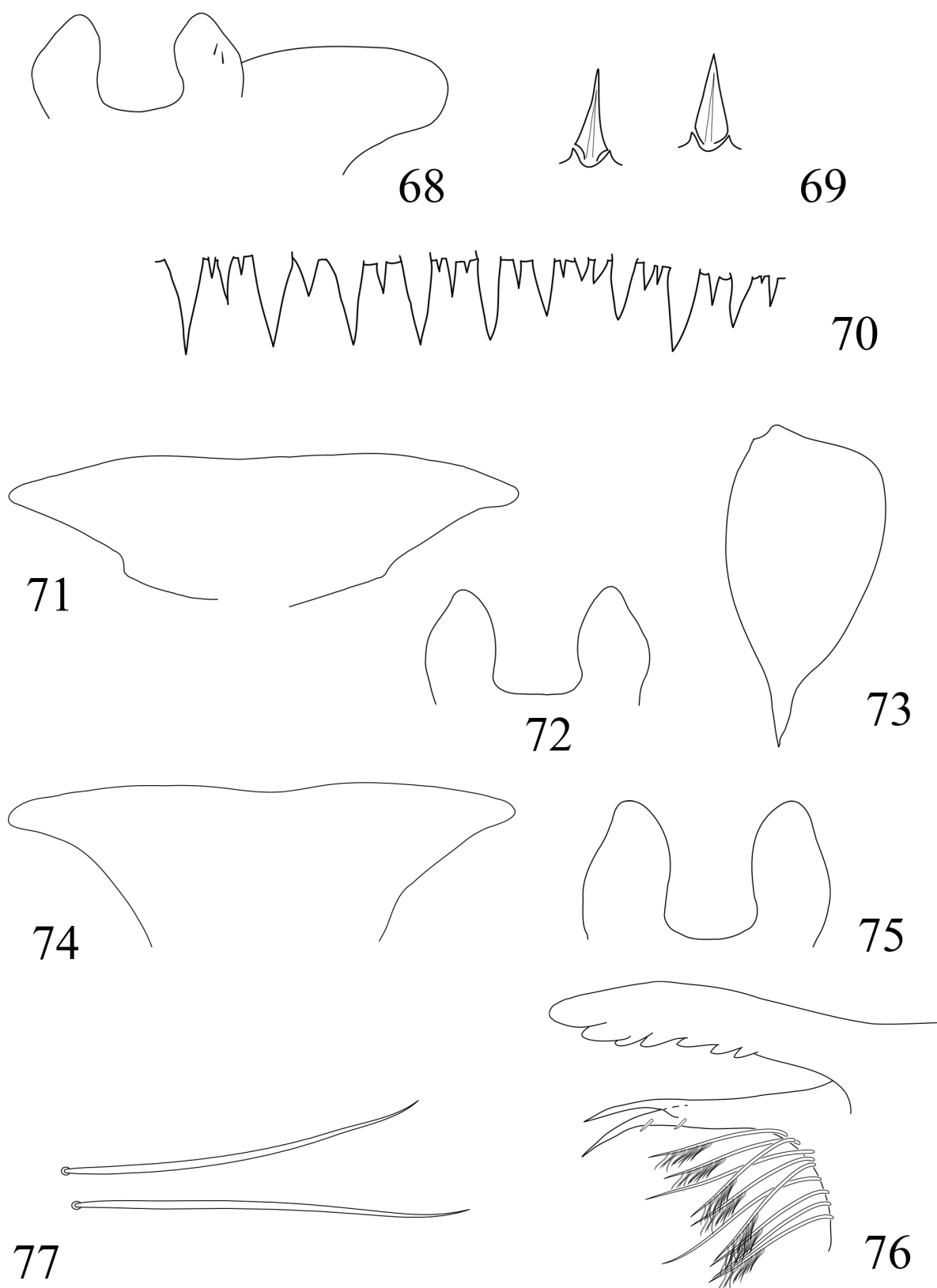
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**FIGURES 55–59.** Nymphal maxillae details of *Notonurus* sp. from Madagascar. Fig. 55: SEM view of the dentisetae, proximal dentiseta in red, distal dentisetae in yellow; Fig. 56: Same view in optical microscope; Fig. 57: SEM view of scattered setae on the ventral face of the galea; Fig. 58: Same view in optical microscope; Fig. 59: SEM view of the comb-shape setae on the crown of the galea.

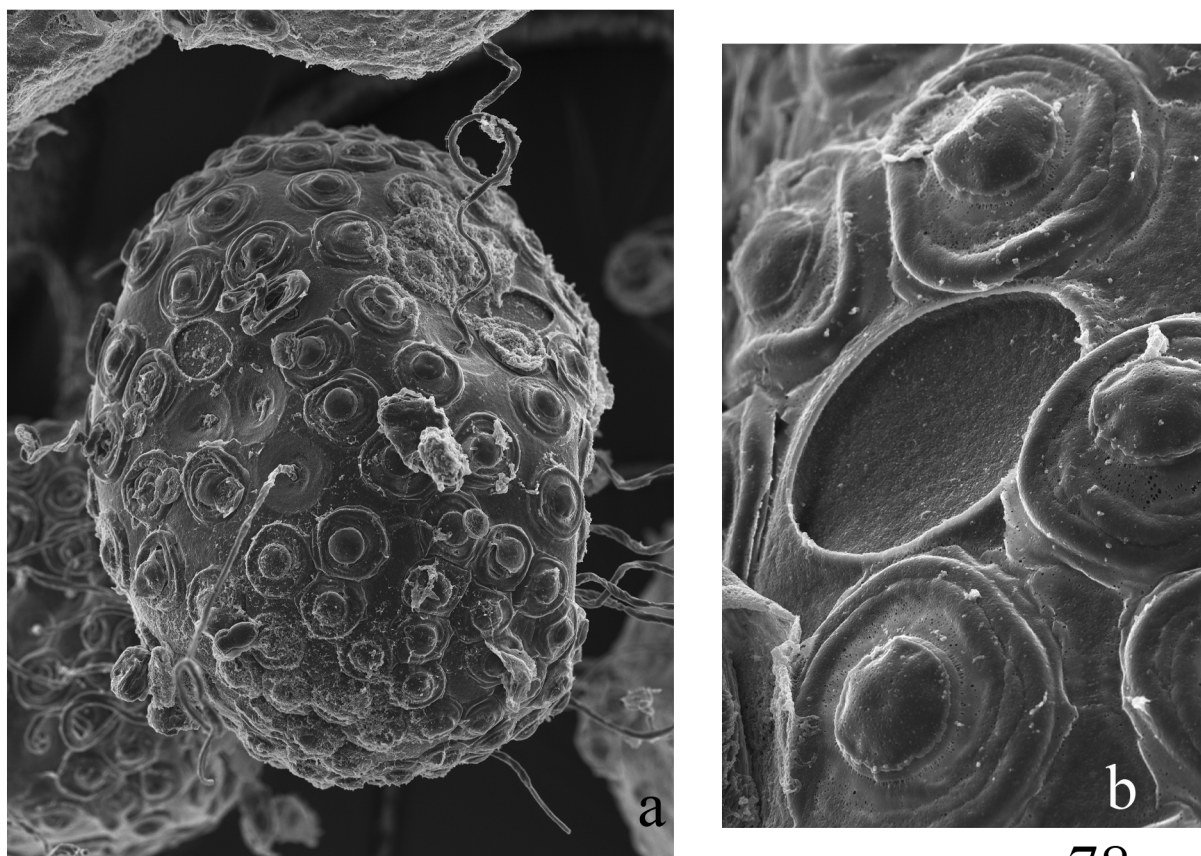




**FIGURES 60–67.** Nymphal leg structures of *Compsoeura spectabilis* (Figs 60–63) and *Compsoeuriella thienemanni* (Figs 64–67) with SEM. Figs 60 and 64: Dorsal view of the hind leg; Figs 61 and 65: Detail view of the posterior margin of the hind femur and the hind tibia; Figs 62 and 66: Bristle on the upper face of femora; Figs 63 and 67: Tarsal claw.



**FIGURES 68–77.** *Componeuriella* spp, nymphal structures. Figs 68–70 : *Componeuriella* sp. 1 from Thailand. Fig. 68: Outline of the labium (left side paraglossa only drawn); Fig. 69: Bristles on the upper face of hind femora; Fig. 70: Posterior margin of tergite IV. Figs 71–73: *Componeuriella langensis*. Fig. 71: Outline of the labrum ; Fig. 72: Outline of the glossae; Fig. 73: Outline of gill VII. Figs 74–77: *Componeuriella tagbanua*. Fig. 74: Outline of the labrum; Fig. 75: Outline of the glossae; Fig. 76: Detail of the left mandible; Fig. 77: Scattered setae on the ventral side of the galea.



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**FIGURE 78.** SEM pictures of eggs extracted from a mature nymph of *Afronurus taipokauensis* comb. nov. from Hong Kong, China; a: egg in toto; b: micropyle and detail of the chorionic structure.

One misinterpretation by Ulmer needs to be corrected. When describing the maxillae, he mentioned that the crown of the galea bears two rows of comb-shape setae (Ulmer 1939, fig. 453e); in fact the mounted nymph was about to molt, and what Ulmer interpreted as a second row is in fact the row of the next molt. The nymph of *C. thienemanni* described here is very closely related to the one illustrated by Braasch & Soldán (1986a) under the name *Compsoeuria thienemanni* (?) from Vietnam, and reported later on also from Thailand (Braasch & Boonsoong 2010). In peculiar the abdominal patterns are almost identical between insular and continental populations (see Braasch & Soldán 1986a, fig. 14.5 and Boonsoong & Braasch 2013, fig. 31). Anyway, both are distinct species, as demonstrated below.

*Compsoeurietta thienemanni* occurs in Java and Sumatra; there is no evidence at the moment that the species inhabits other islands. The pinned specimens reported by Ulmer (1939, p.566) from Borneo (Nanga Serawai, 12-18.XI.1924, Prof. Winkler leg) could not be related to *C. thienemanni*, although probably belonging to the genus *Compsoeurietta* (see below).

### ***Compsoeurietta* sp. 1**

*Compsoeuria thienemanni* Boonsoong & Braasch, 2013, Zookeys 272, p.75 (nymph)

? *Compsoeuria thienemanni* Braasch & Soldán, 1986, Reichenbachia 24(3), p. 41 (adult, nymph)

**Material examined.** 2 nymphs, Thailand, Chiangmai Province, near Hot, Mae Nam Chaem, 200 m., 18° 12' 07.54" N, 98° 36' 32.85" E, IV. 2003, D. Braasch leg. [MZL]

**Discussion.** The Thai material differs from *C. thienemanni* by the following characters: maxilla with 8–9 comb-shape setae on the crown, instead of 12 in *C. thienemanni*; glossae (Fig. 68) of the labium more conical,



dorsal face with two spines instead of one; bristles on the upper face of femora clearly pointed (Fig. 69), posterior margin of the abdominal tergites without rows of microdenticles (Fig. 70), apex of gill VII clearly pointed instead of rounded. As in *C. thienemanni*, the tarsal claw bears no subapical teeth. The Vietnamese material present similar characters, but in the absence of material in hand, it cannot be ascertained that both populations belong to the same species. Anyway, this Thai species needs to be redescribed and named on the basis of a much more abundant material than covered here (Boonsoong & Sartori, in prep.).

***Componeuriella langensis* (Braasch & Boonsoong, 2010) comb. nov.**

*Componeuria langensis* Braasch & Boonsoong, 2010, Zootaxa 2610, p. 7 (adult, nymph)

**Material examined.** 2 nymphs, Thailand, Mae Hong Son Province, Soppong, Nam Lang River, 605 m., 19° 34.447' N, 98° 16.727' E, 3–25. IV. 2003, D. Braasch leg. [MZL]

**Discussion.** The species has been adequately described by Braasch & Boonsoong (2010), and differs from the two previous ones by its labrum less expended laterally (Fig. 71), by the shape of the glossae, with inner margin regularly convex and outer margin slightly concave (Fig. 72), the inner margin of the fore femora with a row of spines and fine and long setae, the presence of microdenticles on the posterior margin of the abdominal tergites, and by the presence of 2 subapical teeth on the tarsal claw. Contrary to what has been previously illustrated (Braasch & Boonsoong 2010: Fig. 45), gill VII is not obtusely rounded but is apically narrowly pointed (Fig. 73). Finally the overall body coloration and pattern is not as contrasted as in the previous species.

***Componeuriella tagbanua* (Braasch & Freitag 2008) comb. nov.**

*Componeuria tagbanua* Braasch & Freitag, 2008, Dtsch. Entomol. Z. 55(1), p. 119, (adult, nymph)

**Material examined.** 2 nymphs, Philippines, Palawan, Mun. Narra, Estrella Falls, 7 km N. Narra, Taritien River, in forest, 100–200 m., 9° 18' N, 118° 23' E, 5.IV.1992, M. Zerning leg. [MZL]

The nymph of this species has been incompletely described, and some important characters have not been mentioned or drawn. A complementary description is given below.

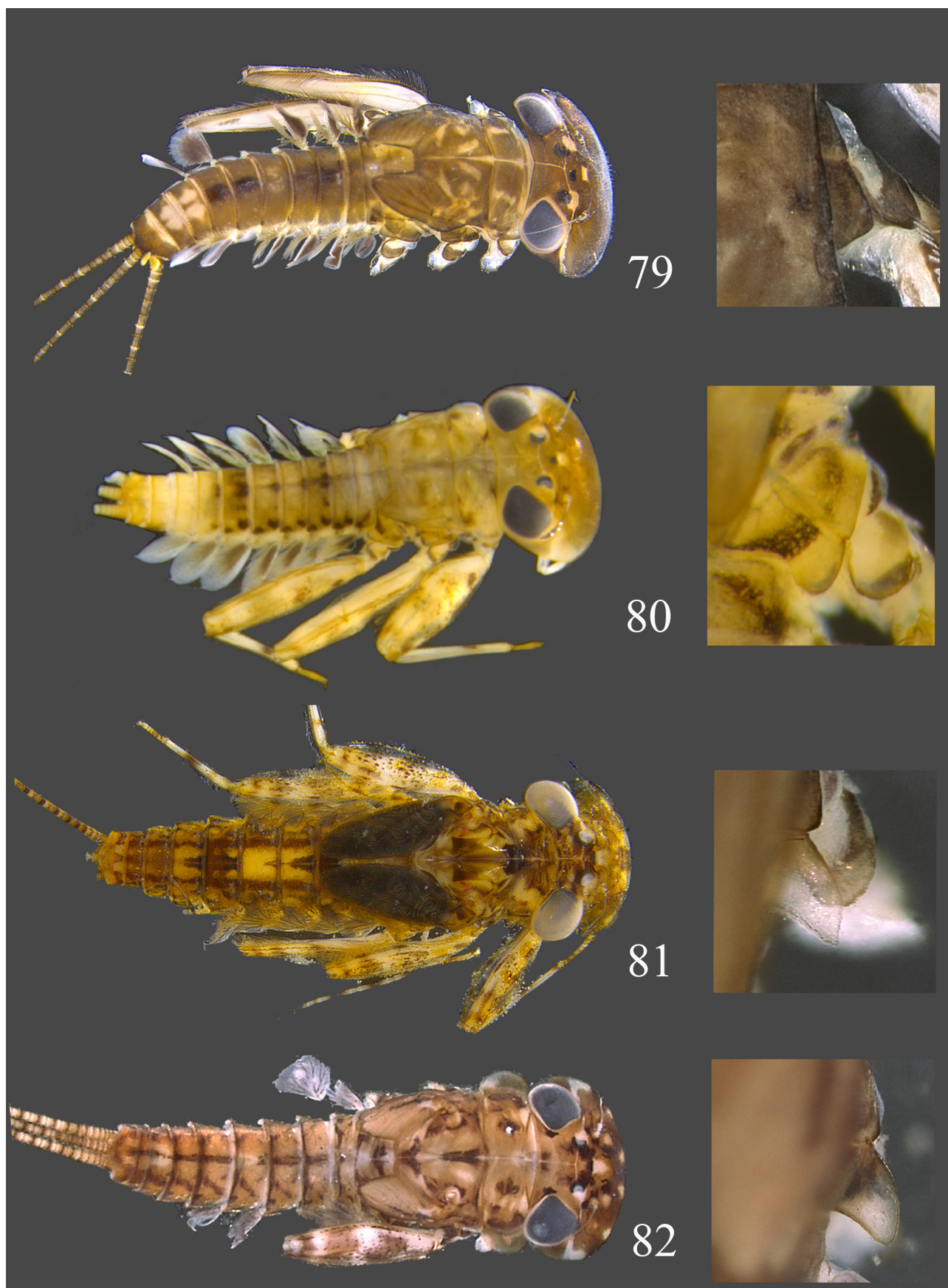
**Complementary description.** *Coloration:* see Fig. 82.

*Head:* Labrum (Fig. 74) moderately extended laterally, with narrow tips; anterior margin slightly concave, covered by numerous long and simple setae. Mandibles with 10–11 fimbriate or simple setae below inner incisor (Fig. 76); right mandible with 5 long and simple setae below mola; left mandible with inner incisor slender and bifid, with some minute teeth (Fig. 76); 6 long and simple setae below mola. Maxillae each with row of ca. 9 comb-shaped setae on anterior margin, medial comb-shaped setae with 11–12 teeth each; ventral surface of galea covered by scattered long and simple setae (Fig. 77); proximal dentisetula bifid and fimbriate, two distal dentisetulae simple. Hypopharynx with well-developed superlinguae, densely covered with long and simple setae on lateral margins, ending at tip of rounded apex of each lobe. Labium (Fig. 75) with glossae with inner margin regularly convex and outer margin slightly concave.

*Thorax:* Hindleg with femur similar to other species, but tibia with row of submarginal bristles close to inner margin. Tarsal claw with 2 subapical teeth.

*Abdomen:* Posterior margin of tergites with row of large and pointed spines, together with intercalary small ones; several rows of microdenticles apparent.

**Discussion.** The nymph of *C. tagbanua* fits the present concept of *Componeuriella* with one major exception: the scattered setae on the galea are not fimbriate but simple, such as those found in the Afrotropical genus *Notonurus*. At the moment, it is considered as a case of convergence. Besides this, *C. tagbanua* does possess the characteristic dentisetulae typical for *Componeuriella*, and all other characters. In addition to the scattered setae of the galea, this species differs from all others by the high number of setae below the inner incisor of the mandibles.



**FIGURES 79–82.** General overview of the nymphs, with emphasize on their supracoxal spurs (midleg). Fig. 79: *Componeuria spectabilis*; Fig. 80: *Componeuria* sp. from Sulawesi; Fig. 81: *Componeuriella thienemanni*; Fig. 82: *Componeuriella tagbanua*.



## General considerations on the genus *Compsoeuriella* and other species

*Compsoeuriella* is distributed throughout Southeast Asia, the Philippines and some of the Sunda Islands. It is also reported (under the name *Compsoeuria*) from Malaysian Peninsula, Borneo and Sulawesi (Edmunds & Polhemus, 1990). The presence of the genus *Compsoeuriella* in Borneo is based only on a report from male imagos from Sabah (Webb et al. 2006) and of the male and female imagos attributed by Ulmer to *C. thienemanni*. These specimens certainly belong to *Compsoeuriella* based on the wing venation, but cannot be attributed to *C. thienemanni* since the abdominal patterns are quite different. Not a single nymph or other complementary material has been presented from this island. The exact situation of *Compsoeuriella* in Borneo therefore needs further investigations.

In addition to Borneo, the status of *Compsoeuriella* in Sulawesi needs further investigations. Edmunds & Polhemus (1990) mentioned that *Compsoeuriella* (sub nom. *Compsoeuria*) is widespread and abundant in Sulawesi. Some very young nymphs (coll. M. Balke) were observed which unfortunately do not allow an accurate description.

Some described species cannot reliably be attributed to *Compsoeuriella* at the moment. *Compsoeuria diehli* Braasch & Soldán, 1986 is described based on male imagos from Northern Sumatra; the illustrated wing venation is in accordance with the one of a *Compsoeuriella* species for the costal and subcostal fields, but presents four rows of crossveins which could indicate its placement in the genus *Compsoeuria*. The illustrated genitalia are on the other hand very close to those of *C. thienemanni*, and it is also possible that *C. diehli* should be its junior synonym. More material, especially nymphs are needed.

*Compsoeuria flowersi* Braasch & Soldán, 1986b is also problematic. Described in a subsequent paper (Braasch & Soldán 1986b), following the description of *C. diehli* (Braasch & Soldán 1986a), this species comes from the same place as *C. diehli*, and is also only known from male imagos, which present peculiar genitalia with a very developed and detached apical sclerite. This species was not compared to *C. diehli* and could represent in fact the same species. The peculiar genitalia illustrated (Braasch & Soldán 1986b, figs 10–11) are different from those illustrated with gonopods and styliger plate in fig. 1, and could result from a drawing of genitalia mounted on slide preparation. As for *C. diehli*, complementary information is much needed before any definitive attribution of this species can be proposed.

The species *Compsoeuria cabayuganensis* Braasch & Freitag, 2008 was described as the type species of the new subgenus *Palawaneuria* from Palawan Island, Philippines. This species is only known at the imaginal stages, and present very peculiar male genitalia with a long penis stem, and no spines on the lobes. Later on, Braasch (2011) put this species in *incertae sedis* until the nymphal stage is known.

*Compsoeuria perakensis* was described by Braasch & Boonsoong (2010) from Northern Malaysia, based on two male imagos. This species presents genitalia without spines on the ventral side of the lobes, or on the apical or basal sclerites. The forewing has very few crossveins, fewer than in *Compsoeuria*, especially in the radial field. This species is considered as *incertae sedis* at the moment until complementary information can be provided.

Finally Tong & Dudgeon (2003) described *Compsoeuria taipokauensis* from Hong Kong, China, at all stages. The authors did not mention which generic characters they used to place this species in *Compsoeuria*. Wang & McCafferty (2004) displaced the species to the genus *Ecdyonurus* based on the original description. Thanks to the courtesy of Dr. Xiaoli Tong, male imagos and nymphs of this species were investigated. Both stages present no affinities with *Compsoeuriini*, and therefore the species does not belong to *Compsoeuriella* or *Compsoeuria*. The overall morphology presents more affinities with the genus *Afronurus* than with *Ecdyonurus*. The egg morphology especially, with the chorionic surface entirely covered with large KCTs (Fig. 78a), is rather similar to what can be found in *Afronurus zebratus* (Hagen, 1864) or *Afronurus kugleri* Demoulin, 1973 (Gaino et al. 1987; Gaino & Mazzini 1987; Sartori 1992). The micropyle area is extremely wide and open (Fig. 78b). This species is therefore considered provisionally as *Afronurus taipokauensis* (Tong & Dudgeon, 2003) **comb. nov.**

## Conclusion

The complicated situation in which the taxonomy of the tribe *Compsoeuriini* has been put is unfortunately due to Ulmer. As it has been already demonstrated by earlier workers, his associations between alate and nymphal stages,

as well as between male and female imagos, were often too speculative and incorrect, and based on similar color patterns or the same sampling location. The tribe Compsoneriini was created by Wang & McCafferty (2004) in the subfamily Heptageniinae to accommodate the genera *Compsoneria* and *Trichogenia*. Webb et al. (2006) removed the tribe from this subfamily to incorporate it in the Ecdyonurinae with the sole genus *Compsoneria* as affiliate. Morphological characters of the tribe include the presence of ventral spines on the penis lobes, the general shape of the genitalia and the possession of black spotting on the head capsule.

The tribe Compsoneriini as redefined here encompasses three genera at the moment: *Compsoneria*, *Compsoneriella* and *Notonurus*. They are characterized by the reduced number of crossveins in the forewing, the general shape of the genitalia with ventral, apical and basal spines, the presence of supracoxal spurs in the nymph, and the distal dentisetae of the maxilla which are branched. The genus which exhibits the most primitive characters is *Notonurus* from the Afrotropics, such as the spotted cephalic capsule, and the distal dentisetae composed of several branches (Figs 55–56); on the contrary, the simple scattered setae on the maxillae (Figs 57–58) is considered as an autapomorphy of the genus, because most of all related genera in the subfamily Ecdyonurinae possess fimbriate setae. The adult morphology is very close to the one of *Compsoneriella*, especially forewing venation, foreleg proportion and general outlook of the genitalia (Crass 1947; Kimmins 1937; Schoonbee 1967). The presence of supracoxal spurs is not a unique characteristic of Compsoneriini, because the same happens in the genera *Thalerosphyrus* (Ecdyonurinae) and *Trichogenia* (Heptageniinae). *Compsoneriella* and *Compsoneria* shares the presence of scattered fimbriate setae on the maxillae (with the notable exception of *Compsoneriella tagbanua*), and the distal dentisetae composed of two branches, the more distal one entire in *Compsoneriella* whereas it is fimbriate in *Compsoneria*. Other differences between both genera have been put in advance earlier. *Compsoneria* presents the most derived morphology compared to the two other genera, with reduced supracoxal spurs, reduced forewing venation, and the presence of two rows of setae on the hind tibiae.

The presence of the tribe Compsoneriini in the Afrotropical (Africa and Madagascar) and Oriental Realms may indicate an African origin for the lineage, with a subsequent diversification in Asia through the drift of the Deccan Plate. The Afrotropical ancestors of *Notonurus* are at the origin of a lineage which spread and diversified in Southeast Asia (*Compsoneriella*), and developed in apotypic genus on some islands (*Compsoneria*). To know if this pattern is the same also for the genus *Afronurus* needs further investigations.

## Acknowledgments

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