The species of Thalerosphyrus Eaton, 1881 (Insecta, Ephemeroptera, Heptageniidae, Ecdyonurinae) in Java and Sumatra, with some comments on the diversity of the genus in the Oriental Realm

Michel Sartori¹,²

¹ Zoologisches Museum und Biozentrum Grindel, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany
² Museum of Zoology, Palais de Rumine, Place Riponne 6, CH-1005 Lausanne, Switzerland

Corresponding author: Michel Sartori (michel.sartori@uni-hamburg.de)

Academic editor: E. Dominguez | Received 15 May 2014 | Accepted 13 June 2014 | Published 25 June 2014

http://zoobank.org/9B2AB654-B7BD-4831-AD36-E78C981520CE

Citation: Sartori M (2014) The species of Thalerosphyrus Eaton, 1881 (Insecta, Ephemeroptera, Heptageniidae, Ecdyonurinae) in Java and Sumatra, with some comments on the diversity of the genus in the Oriental Realm. ZooKeys 420: 19–39. doi: 10.3897/zookeys.420.7904

Abstract

Three species belonging to the genus Thalerosphyrus Eaton, 1881 are reported from Java and Sumatra. The nymphs of Th. determinatus (Walker, 1853) from Java, Th. sinuosus (Navás, 1933) from Java and Sumatra and Th. lamuriensis Sartori, 2014 from Sumatra are redescribed. The egg morphology of the three species is also presented for the first time. A key to the nymphs is proposed. General considerations on the composition of the genus Thalerosphyrus in the Oriental Realm are given. The distribution of the genus is greatly expended, and currently ranges over the Himalaya and Sumbawa in the Sunda Islands.

Keywords

Thalerosphyrus determinatus, Thalerosphyrus sinuosus, Thalerosphyrus lamuriensis, Ecdyonurus sumatranus, distribution, Bali, Sumbawa, nymph, eggs, SEM

Introduction

The genus Thalerosphyrus was created by Eaton (1881) to accommodate the species Bae-
tis ? determinata Walker, 1853 described on the basis of a single male imago from Java. Later on (Eaton 1885), the same author added also Baetis ? torrida Walker, 1853 known
by a single female imago from the Philippines. *Th. determinatus* was recorded later by Ulmer (1913) also from Java, and redescribed in detail, with abdominal patterns, coloration and drawing of the genitalia. Another species was described from Java by Navás under the name *Ecdyonurus ? sinuosus* Navás, 1933 on the basis of a single female imago, and then transferred to the genus *Thalerosphyrus* by Ulmer (1939) who described the male imago and reported the species also from Sumatra. In the same work (Ulmer 1939), the author described *Th. determinatus* and *Th. sinuosus* in the nymphaL stage. Dang (1967) created the genus *Ecdyonuroides* for a peculiar nymph he collected in Vietnam (*E. vietnamensis*) which possesses extremely well developed posterolateral expansions on the abdomen. He recognized the similarity with a nymph described by Ulmer (1939) under the name *Ecdyonurus sumatranus* and designated Ulmer’s species at the type species of his new genus. Later on, Braasch and Soldán (1984) put *Ecdyonuroides* in synonymy with *Thalerosphyrus* on the basis of a rearing of *E. vietnamensis* nymph which gave a male imago with *Thalerosphyrus* characters and proposed the new combination *Th. vietnamensis*. In the following years, two other *Thalerosphyrus* species were described: *Th. bishopi* (Braasch & Soldán, 1986b) from West Malaysia, and *Th. flowersi* (Venkataraman & Sivaramakrishnan, 1987) from southern India, both at the adult and nymphaL stages.

Braasch and Soldán (1986a) described a new genus (*Asionurus*) from Vietnam and showed that the nymph described by Ulmer (1939) under the name *Th. sinuosus* was incorrectly associated with adults of this species and that the nymph actually belonged to this new genus and therefore proposed to call this taxon *Asionurus ulmeri*. Wang and McCafferty (2004) suggested that the nymph described by Ulmer (1939) as *Th. determinatus* was wrongly associated and should be the nymph of *Th. sinuosus* according to abdominal patterns.

The concept of the genus *Thalerosphyrus* is far from being clear, because the type material of the type species, *Th. determinatus* is in bad state, missing all legs but one as well as the abdomen (hence the genitalia) (Kimmins 1960). The uncertainties about the actual status of the genus *Thalerosphyrus* let Kluge (2004) to consider it as *incertae sedis*, referring only to the nymphs of *Th. sumatranus, Th. vietnamensis* and *Th. flowersi* as belonging to his non ranking taxon *Ecdyonuroides/g(1)* characterized by their developed posterolateral expansions of the abdomen.

When revising Ulmer’s collection in the Zoologisches Museum in Hamburg, Sartori (2014d) restudied the type material of *Ecdyonurus sumatranus* Ulmer, 1939 and showed that the holotype belonged to the genus *Rhithrogena* Eaton, 1881, and thus put *Ecdyonuroides* Dang, 1967 in synonymy with *Rhithrogena* and proposed a new name for the nymph as *Th. lamuriensis*.

Within the ongoing revision of Ulmer’s collection (Sartori 2014a; b; c; d), we have reinvestigated all material of *Thalerosphyrus* deposited in the Museum of Zoology in Hamburg. Despite the above mentioned uncertainties, we follow the *Thalerosphyrus* concept proposed by Ulmer (1913; 1924; 1939) because his redescriptions of *Th. determinatus* is in accordance with Eaton’s (1885) diagnosis, especially body and wing lengths and hind leg ratios. The nymphs of the species found in Java and Sumatra are described based on this historical material as well as on specimens recently collected.
**Material and methods**

Original material studied here is deposited in the following institutions:

| Institution | Location |
|-------------|----------|
| ZMH         | Zoologisches Museum und Biozentrum Grindel, Hamburg, Germany |
| MZL         | Musée cantonal de zoologie, Lausanne, Switzerland |
| LIPI        | Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences), Museum of Zoology, Bogor, Indonesia |

In the absence of adequate life stages to link nymph and adults as previously proposed by Sartori (2014a; c; d), eggs were extracted from either female imago or sub-imago for *Th. determinatus* and *Th. sinuosus* because no mature female nymphs were available, and from a mature female nymph for *Th. lamuriensis* as no alate stage of this species are known for sure.

Ontogenetic stage association relies thus on the following assumptions; three nymphal forms present together with three different egg morphologies, one species found only on Java, one on Java and Sumatra and the latter only on Sumatra.

Drawings were made with the help of a camera lucida taken from stereomicroscope Leica DM 750 and pictures from microscope Zeiss Axioscop 2 or Visionary Digital Passport II. Final digital drawings were performed on Adobe Illustrator CS6. For scanning electronic microscope (SEM) pictures, the eggs were dehydrated, carbon coated, and observed under a LEO 1525 at 5.00 kV; maxillae were dehydrated, critical point dried, and then platinum coated, and observed under a FEI Quanta 250 at 5.00 kV. Final plates were assembled in Adobe Photoshop CS6.

**Results**

*Thalerosphyrus* Eaton, 1881

**Nymphal diagnosis.** Medium to large Heptageniidae (up to 20 mm) with contrasting color patterns.

Head broad and thickened anteriorly (Figs 2, 5, 8); labrum (Figs 16–17) small, wider than long, without conspicuous median incision; mandibles (Figs 18–19) with outer margin covered with numerous thin setae, outer and inner incisors subequal in length, outer one saw-like on both sides, inner one trifid, left mandible with tuft of setae above mola; maxillae with 3-segmented palp, ventral surface of galea-lacinia covered with numerous long setae (Fig. 25), which appear entire in optical microscope, but are slightly feathered in SEM, crown of the galea-lacinia with 20–25 comb-shape setae, median ones bearing 12–17 teeth (Fig. 26), distal dentisetae bifid and fimbriate, as the proximal one (Figs 23–24); hypopharynx with robust lingua and well developed super-linguae bend backwards (Figs 27–28); labium with rhomboid glossae (Figs 20–22), paraglossae regularly curved, apex not bend backwards and moderately expended laterally.
Figures 1–3. *Thalerosphyrus determinatus* (Walker, 1853). 1 Habitus in dorsal view 2 Habitus in ventral view 3 Detail of abdominal segments VI–IX in ventral view.

Thorax with pronotum slightly to greatly enlarged laterally; supracoxal spurs acute and well developed especially on mid- and hind legs; femora rather similar between the three pairs of legs, row of stout and pointed bristles on inner and outer margins, no thin setae present; outer margin of fore tibia with few thin setae on proximal fourth, mid tibia with a row of thin setae on outer margin almost to tarsi, hind tibia (Figs 30,
The species of Thalerosphyrus Eaton, 1881...

32, 34) with two rows of thin setae, one on the outer margin, one in submarginal position, spine-like bristles absent or present.

Abdomen with posterolateral projection generally greatly enlarged from segment III to VII or VIII (Figs 3, 6, 9); posterior margin of tergites (Figs 35–37) with large and pointed teeth, microdenticles present and generally numerous; all gills asymmetrical (Figs 38–49), gills I–VI with plate-like and extremely developed fibrillose parts, gill VII only plate-like; terminal filament well developed, cerci whitish with more or less enlarged brown bands; segments with whorls of stout and pointed setae.

Discussion. The scattered setae on the ventral surface of the maxilla indicate clearly that Thalerosphyrus belong to the subfamily Ecdyonurinae. The presence of acute supracoxal spurs, the anterior margin of the head thickened and generally well developed posterolateral projections of the abdomen are discriminating characters according to Webb and McCafferty (2008). To these we can add the shape of the gills II–V (VI) strongly asymmetrical and wider than long, with fibrillose part well developed. In the Oriental Realm, Thalerosphyrus could be confused with Compsoneuriella Ulmer, 1939 because of the acute supracoxal spurs, but is easily told by the much more developed posterolateral projections of the abdomen, the higher number of comb-like setae on the crown of the galea-lacinia, the shape of the gills which are never so wide in Compsoneuriella, and by the shape of the distal dentisetae, which are simple and not fimbriate in Compsoneuriella (Sartori 2014c).

Species included. Thalerosphyrus determinatus (Walker, 1853): Java
Thalerosphyrus sinuosus (Navás, 1933): Java, Sumatra
Thalerosphyrus vietnamensis (Dang, 1967): Vietnam
Thalerosphyrus bishopi Braasch & Soldán, 1986: West-Malaysia
Thalerosphyrus flowersi Venkataraman & Sivamarakrishnan, 1987: South India
Thalerosphyrus lamuriensis Sartori, 2014: Sumatra

The species described by Ulmer (1926) as Thalerosphyrus melli from China has been recently assigned to another genus as Epeorus melli (Ulmer) by Zhou et al. (2007); the species Th. torridus (Walker, 1853) described based on a single female imago from the Philippines most probably belong to the genus Afronurus (Braasch 2011); the species Th. separatus Nguyen & Bae, 2004 and Th. ethiopicus Soldán, 1977 described from Vietnam and Sudan respectively, have been suggested to be also members of the genus Afronurus by Webb et al. (2006).

Distribution. The genus Thalerosphyrus is endemic to the Oriental Realm. It is known from India, through Southeast Asia (Thailand, Vietnam, West Malaysia), up to Sumbawa in the Sunda Islands (see below), suggesting, as for Rhithrogena (Sartori 2014d), that the Wallace line is not a barrier to the dispersal of some Ephemeroptera. The genus is however not currently reported from Sulawesi (Edmunds and Polhemus 1990). According to Braasch (2011), Thalerosphyrus is also not recorded from the Philippines, and its presence on the island of Borneo is only based on few data and no named species are known (Braasch 2011); in the MZL collections is a single nymph (Sabah, Mesilau River, 8 km north of Kundessan, 2100 m, 1.VIII.1985, J.T. & D.A. Polhemus leg) which is clearly related to Th. lamuriensis, but complementary material is needed before any definitive answer can be found. In the MZL collections is also
Figures 4–6. *Thalerosphyrus sinuosus* (Navás, 1933). 4 Habitus in dorsal view 5 Habitus in ventral view 6 Detail of abdominal segments VI–IX in ventral view.

deposited a single nymph from Nepal (Nawakot & Sindhu Districts, Patibhanjyang Village, elev. ca 6000', 10.IX.1968, C. Wiens leg) which expands the distribution of the genus to the Himalaya.
Thalerosphyrus determinatus (Walker, 1853)

Material examined. 2 nymphs, Java, Dieng plateau, stream Seraju (D13), ca 1950 m a.s.l., 5.VI.1929, Prof. Thienemann leg. [ZMH] ; 1 nymph entirely mounted on microscopic slide, Java, Gedeh Panggerango, Tjisarua, 1050 m, 10.VIII.1930, Dr. Lieftrinck leg [ZMH]; Inymph, Java, Java Barat Province, rocky stream at Cibodas (CL 2186), 1300 m, 3.XI.1985, J.T. & D.A. Polhemus leg [MZL]; 1 nymph, Bali, Baturiti, Desa Antapan, 815 m, 8°19.34’S, 115°11.61’E, 9.X.2009 (BLI005), M. Balke & D. Amran leg [MZL]; 1 nymph, Sumbawa, Nusa Tenggara Barat Province, Madsewu River, 2 km above Badindi, 61 km NW of Bima (CL 2174), 750 m, 20.X.1985, J.T. & D.A. Polhemus leg [MZL].

Eggs extracted from a female imago (caught together with a male imago) and identified by Ulmer as *Th. determinatus*: West Java, Tjibodas, Tjiwalen Bridge, 1400 m, 4.IX.1932, Dr Lieftinck leg [ZMH].

Description of the nymph. Body size: up to at least 14.5 mm (not full grown nymph).

Coloration pattern: see Figs 1–2.

**Head.** Labrum moderately expended laterally, less than 4 times larger than long, with rounded apexes (as in Fig. 16); dorsal surface and anterior margin covered with long and thin setae; ventral surface with a median arch of less than 10 strong and pointed setae. Crown of the galea-lacinia of the maxillae composed of ca. 25 comb-shape setae, the median ones bearing 12–15 teeth. Right mandible with 5–6 bifid and fimbriate setae below the inner incisor and ca. 10 long simple and thin setae below the mola; left mandible with 8–9 simple and fimbriate setae below the inner incisor and ca. 9–10 long simple and thin setae below the mola. Hypopharynx with robust lingua bearing a tuft of small setae, superlinguae densely covered with long and thin setae replaced before the apex by very small setae up to the lower part of the superlinguae (Fig. 27). Labium with glossae rhomboid, slightly concave on their outer margin near apex (Fig. 20), dorsal surface with three stout setae and numerous thin and simple setae.

**Thorax.** Pronotum weakly expended laterally (Fig. 1). Femora with submarginal rows of pointed bristles on the inner and outer margins, increasing in numbers from the fore to the hind leg. Bristles on the upper face of hind femora arrow-shaped, clearly pointed (Fig. 29). Hind tibia (Fig. 30) without any bristles in outer marginal or submarginal position. Tarsal claw with 2–3 teeth.

**Abdomen.** Posterolateral expansions not developed on segments I–II, increasing in size from segment III to VII where it may reach the middle of segment VIII, shorter on segment VIII (Fig. 3) and comparable proportionally to those of segments V–VI. Gill I (Fig. 38) with elongated and rounded plate, ca 2.5× longer than wide; gill IV strongly asymmetrical (Fig. 39), wider than long, gill VI and VII oval and asymmetrical with obtuse apex (Figs 40–41). Posterior margin of tergites with irregular pointed teeth, and numerous microdenticles (Fig. 35). Cerci rather unicolor medium brown, some segments darker in the proximal half.
Figures 7–9. *Thalerosphyrus lamuriensis* Sartori, 2014. 7 Habitus in dorsal view 8 Habitus in ventral view 9 Detail of abdominal segments VI–IX in ventral view.

**Description of the eggs.** Size: ca 120 µm × 75 µm; chorion regularly covered by small KCT’S, (1.0–1.5 µm), a little bit larger at poles (Fig. 10), and by microgranules (< 0.3 µm); margin of micropyle irregular and formed by microgranules (Fig. 11).
Discussion. The abdominal pattern of the nymph is the one which is the closest to the one of the male imago redescribed by Ulmer (1924). According to Wang and McCafferty (2004) and our own observations (see below), the illustration of the abdominal patterns of the nymph (Ulmer 1939, fig. 402) as *Th. determinatus* does not belong to this species, nor do any of Ulmer’s, other drawings.

The species may be easily recognized from its relatives mainly by the weak postero-lateral expansions of the abdomen, and the absence of bristles on the outer margin of the hind tibiae.

*Th. determinatus* as defined here is the less common species found in the investigated area. However it is reported from Bali and Sumbawa for the first time. The species is absent from Sumatra and seems to live in middle to high altitudes, based on the few available data.

*Thalerosphyrus sinuosus* (Navás, 1933)

*Thalerosphyrus determinatus* Ulmer, 1939, (nymph, pro parte)

**Material examined.** 4 nymphs, two partially mounted on two microscopic slides, Sumatra, Singkarak, stream at Subanpass (F20), 1000 m, 4.III.1929, Prof. Thiemenmann leg [ZMH]; 1 nymph, Sumatra, Tjurup, Kali Dzernih, forested stream (M9), 7.V.1929, Prof. Thienenmann leg [ZMH]; 1 nymph, Sumatra, Ranau, stream in primary forest (R25c), 29.I.1929, Prof. Thienenmann leg [ZMH]; 2 nymphs, one partially mounted on a microscopic slide, Java, Gurung Ungaran, XII. 1909, Jacobson leg [ZMH]; 1 nymph, Java, Kali Tjiwalen near Tjibodas, 1350 m, in mosses and dead leaves (FY7f), 10.VII.1929, Prof. Feuerborn leg [ZMH]; 1 nymph, West Java, stream in Tjibodas, under the “mountain garden” (FY14c), 15.VII.1929, Prof. Feuerborn leg [ZMH]. [All specimens sub. nom *Thalerosphyrus determinatus* det. Ulmer].

10 nymphs, Java Tengah, Wonosobo-Kertek village road, creek, 800 m, 7°21.68’S, 109°55.67’E, 10.X.2011 (JVA011), M. Balke leg. [LIPI, MZL]; 2 nymphs, Sumatra Barat, Sijunjung / Muara area, forest, 488 m, 00°40.10’S, 101°07.26’E, 10.XI.2011 (UN7), M. Balke leg [MZL]; 7 nymphs, one entirely mounted on a microscopic slide, Sumatra Barat, Universitas Andalas campus, forest stream, 360 m, 00°54.67’S, 100°28.38’E, 8.XI.2011 (UN1), M. Balke leg [MZL]; 2 nymphs, Sumatra Barat, Lubukbargalung, Lubuk Paraku River, 50 km south Solok, 420 m, 100°32.50’E, 0°56.75’S, 25.V.2010 (SU5), J.-M. Elouard leg [MZL].

Eggs extracted from a female imago: Java, Buitenzorg, 13.II.1932, Dr Lieftinck leg [ZMH], and from a female subimago: Western Sumatra, Danau di Atas, stream near the road, 1000–1100 m (FF20e), 16.III.1929, Prof. Feuerborn leg [ZMH] and identified by Ulmer as *Th. sinuosus*.

**Sequence data.** One specimen from Sumatra (SU5) and one from Java (JVA011) have been used for the study by Vuataz et al. (2013) under the name “*Thalerosphyrus*” in figures and “*Thalerosphyrus sp.*” in table S1, with voucher numbers “340SuTh” and
“346JaTh” respectively, with one or two mitochondrial (CO1, 16S) and two to four nuclear genes (28S, H3, wg, EF-1α) sequenced. Access numbers in GenBank are:
The species of Thalerosphyrus Eaton, 1881...

| Voucher # | CO1 | 16S | 28S | H3 | wg | EF-1α |
|-----------|-----|-----|-----|----|----|-------|
| 340 SuTh  | HE651394 | HE651430 | HE651453 | HE651512 | HE651485 | HE651535 |
| 346JaTh   | HF536601 |               |       | HF536587 | HF536594 |       |

**Description of the nymph.** Body size: up to at least 10.5 mm (not full grown nymph).

**Coloration pattern:** see Figs 4–5.

**Head.** Labrum slightly expended laterally, ca 3.5 times larger than long, with rounded apexes (Fig. 16); dorsal surface and anterior margin covered with long and thin setae; ventral surface with a median arch of ca 10 strong and pointed setae. Crown of the galea-lacinia of the maxillae composed of ca 25 comb-shape setae, the median ones bearing 12–15 teeth (Fig. 26). Right mandible with 7–8 fimbriate setae below the inner incisor and ca. 5–6 long simple and thin setae below the mola; left mandible with 10–11 simple and fimbriate setae below the inner incisor and ca. 8–9 long simple and thin setae below the mola. Hypopharynx with robust lingua bearing a tuft of small setae, superlinguae densely covered with long and thin setae replaced before the apex by very small setae up to the lower part of the superlinguae. Labium with glossae rhomboid, slightly concave on their inner margin near apex (Fig. 21), dorsal surface with three stout setae and numerous thin and simple setae.

**Thorax.** Pronotum slightly expended laterally and posteriorly (Fig. 4). Femora with submarginal rows of pointed bristles on the inner and outer margins, increasing in numbers from the fore to the hind leg. Bristles on the upper face of hind femora arrow-shaped, clearly pointed (Fig. 31). Hind tibia with a row of 6–7 arrow-shaped bristles in submarginal position (Fig. 32). Tarsal claw with 2–3 teeth.

**Abdomen.** Posterolateral expansions not developed on segment I, weakly developed on segment II, strongly developed on segment III and increasing in size up to VII where they may be as long as segment VIII, shorter on segment VIII and smaller proportionally to those of segments III (Fig. 6). Gill I with elongated and rounded plate, less than two times longer than wide (Fig. 42); gill III–VI strongly asymmetrical, wider than long (Figs 43–44), gill VII oval and asymmetrical with inner concave margin near apex (Fig. 45). Posterior margin of tergites with irregular pointed teeth, and numerous microdenticles (Fig. 36). Cerci whitish in proximal part, with dark brown segment every two or three, distal part more uniformly medium brown.

**Description of the eggs.** Size: ca 130–140 µm × 85–90 µm; chorion regularly covered by small KCT’S, (1.5–2.0 µm), a little bit larger at poles (Fig. 12), and by mesogranules (1.0 µm); margin of micropyle smooth and entire (Fig. 13).

**Discussion.** The nymph mentioned here includes what Ulmer (1939) described as the nymph of *Th. determinatus*; the material is composed of three slides made by Ulmer himself and most of the drawings (Ulmer 1939, figs 403–418) were based on them. It appears that Ulmer confused the two species, and this is also because he made no slide preparation of the true *Th. determinatus*. *Th. sinuosus* as defined here is closely related to *Th. determinatus*, but can be easily separated by the shape of the posterolateral expansions of the abdomen, the shape of the gills, the shape of the glossae, and by the presence of arrow-shaped bristles on the hind tibiae.
Figures 16–22. Mouthparts structure of *Th. determinatus* (20), *Th. sinuosus* (16, 21) and *Th. lamuriensis* (17, 18, 19, 22). 16–17 Hemi-labrum 18 Left mandible 19 Right mandible 20–22 Labial glossa.

The eggs of *Th. sinuosus* differ from those of *Th. determinatus* by the margin of the micropyle and by the presence of mesogranules on the chorion.

*Th. sinuosus* is present on Java and Sumatra. We cannot confirm the occurrence of the species outside these two islands, although based on egg morphology, and some
The species of \textit{Thalerosphyrus Eaton, 1881}...

The species could be present in Thailand, but supplementary description of the nymph is needed.

\textit{Thalerosphyrus lamuriensis} Sartori, 2014

\textit{Ecdyonurus sumatranus} Ulmer, 1939, (nymph, not female adult)
\textit{Thalerosphyrus determinatus} Ulmer, 1939, (nymph, pro parte)
\textit{Thalerosphyrus sumatranus} Braasch & Soldan, 1984 (nymph)

\textbf{Material examined.} Besides the type material mentioned in Sartori (2014d), the following specimens have been examined.

\textbf{Figures 23–26.} SEM (23, 25, 26) and optic (24) pictures of maxillar structure. 23–24 Dentisetae of \textit{Th. lamuriensis} dp: proximal dentisetae, dd distal dentisetae 25 Scattered setae on the ventral face of the galea-lacinia of \textit{Th. sinuosus} 26 Comb-shape setae on the crown of the galea-lacinia of \textit{Th. sinuosus}.  
1 nymph, Sumatra, Singkarak, stream at Subanpass (F19), 1000 m, 4.III.1929, Prof. Thienemann leg [ZMH]; 3 nymph, one partially mounted on microscopic slide, Sumatra, Toba area, stream south of Balige (FT13), 8.IV.1929, Prof. Feuerborn leg [ZMH]; 2 nymphs, Sumatra, Toba area, Balige, stream at ca 1100 m (T13), 5.IV.1929, Prof. Feuerborn leg [ZMH] [All specimens sub. nom Thalerosphyrus determinatus det. Ulmer].

1 nymph, Sumatra Utara Province, swift stream 20 km East of Parlilitan (CL 2192), 1070 m, 10.XI.1985, J.T. & D.A. Polhemus leg [MZL]; 2 nymphs, Sumatra Barat, Tarusan, upstream Tarusan, 10 m, 100°29.84'E 1°13.61'S, 24.V.2010 (SU3), J.-M. Elouard leg [MZL]; 2 nymphs, Sumatra Barat, Kotobarapak, upstream Kototbarapack, 100 m, 100°32.08'E, 1°13.78'S, 24.V.2010 (SU4), J.-M. Elouard leg [MZL]; 4 nymphs, Sumatra Barat, Lubukbargalung, Lubuk Paraku River, 50 km south Solok, 420 m, 100°32.50'E, 0°56.75'S, 25.V.2010 (SU5), J.-M. Elouard leg [MZL].

Eggs extracted from the mature female nymph mentioned above from Polhemus collected specimens.

Sequence data. Three specimens (SU3, SU4, SU5) have been used for the study by Vuataz et al. (2013) under the name “Thalerosphyrus” in figures and “Thalerosphyrus sp.” in table S1, with voucher numbers “319SuTh”, “317SuTh” and “339SuTh” respectively, with one or two mitochondrial (CO1, 16S) and two to four nuclear genes (28S, H3, wg, EF-1α) sequenced. Access numbers in GenBank are:

| Voucher # | CO1   | 16S  | 28S  | H3    | wg    | EF-1α  |
|-----------|-------|------|------|-------|-------|--------|
| 319SuTh   | HE651389 |      |      |       |       |        |
| 317SuTh   | HE651388 | HE651425 | HE651450 | HE651508 | HE651480 | HE651532 |
| 339SuTh   | HE651393 | HE651429 |      | HE651511 | HE651484 | HE651534 |

Description of the nymph. Body size: up to 21 mm (full grown female nymph).

Coloration pattern: see Figs 7–8.

Head. Labrum greatly expended laterally, ca 4 times larger than long, with narrow and somewhat acute apexes (Fig. 17); dorsal surface and anterior margin covered with long and thin setae; ventral surface with a long median arch of ca. 20 strong and pointed setae ending close to the anterior margin. Crown of the galea-lacinia of the maxillae composed of ca. 20 comb-shape setae, the median ones bearing 12–14 teeth. Right mandible (Fig. 19) with 11–12 fimbriate setae below the inner incisor and 5 long simple and thin setae below the mola; left mandible (Fig. 18) with 8–9 fimbriate setae below the inner incisor and ca. 8–9 long simple and thin setae below the mola. Hypopharynx with robust lingua bearing a tuft of small setae, superlinguae densely covered with long and thin setae up to the lower part of the superlinguae (Fig. 28). Labium with glossae rhomboid, clearly concave on their inner and outer margins near apex (Fig. 22), dorsal surface with numerous stout setae and numerous thin and simple setae.

Thorax. Pronotum greatly expended laterally and posteriorly (Fig. 7). Femora with submarginal rows of pointed bristles on the inner and outer margins, only slightly increasing in numbers from the fore to the hind leg. Bristles on the upper face of
The species of Thalerosphyrus Eaton, 1881...

Figures 27–34. Mouthpart (27–28) and thoracic (29–34) structures of *Th. determinatus* (27, 29, 30), *Th. sinuosus* (31, 32) and *Th. lamuriensis* (28, 33, 34). 27–28 Apex of superlingua of hypopharynx 29, 31, 33 Bristles on the dorsal face of hind femur 30, 32, 34 Outer margin of hind tibia.

hind femora with subparallel or slightly convergent margins, apex rounded or truncate (Fig. 33). Outer margin of hind tibia with a row of 12–15 pointed bristles in marginal or submarginal position (Fig. 34). Tarsal claw with 3–4 teeth.

*Abdomen.* Posterolateral expansions not developed on segments I–II, moderately developed on segment III and strongly increasing in size up to VIII where they may
Figures 35–37. Posterior margin of abdominal tergite IV. 35 *Th. determinatus* 36 *Th. sinuosus* 37 *Th. lamuriensis.*
The species of Thalerosphyrus Eaton, 1881...

Figures 38–49. Gills of *Th. determinatus* (38–41), *Th. sinuosus* (42–45) and *Th. lamuriensis* (46–49). 38, 42, 46 Gill I 39, 43, 47 Gill IV 40, 44, 48 Gill VI 41, 45, 49 Gill VII.

be longer than segment IX (Fig. 9). Gill I with asymmetrical elongated and rounded plate, less than two times longer than wide (Fig. 46); gill III–VI strongly asymmetrical, wider than long (Figs 47–48), gill VII oval and asymmetrical with slightly pointed apex (Fig. 49). Posterior margin of tergites with long and pointed teeth regularly alter-
nating with two small ones, and few microdenticles (Fig. 37). Cerci whitish with 3–4 dark brown bands increasing in size towards the apex.

**Description of the eggs.** Size: ca 140–150 µm × 85–90 µm; chorion regularly covered by pedunculate KCT’S, (1.0–1.5 µm), a little bit larger at poles (Fig. 14), no micro- or mesogranules present; margin of micropyle edged, as formed by fused peduncles (Fig. 15).

**Discussion.** A major surprise was to find nymphs of *Th. lamuriensis* among the material identified by Ulmer (1939) as *Th. determinatus*, because he described this nymph based on a single specimen under the name *Ecdyonurus sumatranus* (Ulmer, 1939, see Sartori 2014d for a complete development of this case). *Th. lamuriensis* clearly differs from the two previous species by several characters, such as the posterolateral expansions of the abdomen reaching their largest size on segment VIII (compared to segment VII in *Th. determinatus* and *Th. sinuosus*), by the setation of the hypopharynx with long setae up to the concave margin of the superlinguae, the shape of the pronotum, the shape of the bristles on the upper face of hind femora, and the ornamentation of the hind tibiae. Together with *Th. vietnamensis* Dang, 1967, *Th. bishopi* Braasch & Soldán, 1986 and *Th. flowersi* Venkataraman & Sivamarakrishnan, 1987, *Th. lamuriensis* constitutes a group called by Kluge (2004) Ecdyonuroides/g(1) and characterized by “posterolateral projections […] on segments VI–VIII very long and pointed, exceeding segment length”. The three above mentioned species are incompletely described, but *Th. lamuriensis* differs from them apparently by the shape of the bristles on the upper face of femora, by the shape of the first gill and by the coloration of the abdomen (Braasch and Soldán 1984).

*Th. lamuriensis* possesses anyway far more characters in common with *Th. determinatus* and *Th. sinuosus* than the observed (although quite obvious) differences, and there is no reason on this basis to propose other generic rearrangement for Ecdyonuroides/g(1).

Eggs of *Th. lamuriensis* are very peculiar with pedunculate KCT’S, which distinguish them from the two other species.

*Th. lamuriensis* is the most abundant *Thalerosphyrus* species in Sumatra, and seems widespread throughout the island. In several places, it has been found together with *Th. sinuosus*.

**Key to the *Thalerosphyrus* nymphs occurring on Java and Sumatra**

1. Posterolateral expansions on the abdomen greatly enlarged (Fig. 8), reaching their maximum on segment VIII; protonum greatly enlarged laterally (Fig. 7); bristles on the dorsal face of hind femora truncate or rounded at apex (Fig. 33); hypopharynx with outer margin of superlinguae evenly covered with long setae (Fig. 28) ........................................*Th. lamuriensis*  

   – Posterolateral expansions of the abdomen more or less developed, those of segment VIII always shorter than those of segment VII (Figs 3, 6); prono-
The species of Thalerosphyrus Eaton, 1881...

tum moderately enlarged laterally; bristles on the dorsal face of hind femora arrow-shaped (Figs 29, 31); hypopharynx with outer margin of superlinguae covered with long setae ending at apex by minute setae (Fig. 27) .................. 2

2 Hind tibia with only two rows of thin setae (Fig. 30); posterolateral expansions of the abdomen weakly developed (Fig. 3); gill I more than 2.5 times longer than wide (Fig. 38) ............................................... *Th. determinatus*

– Hind tibia with two rows of thin setae and a submarginal row of arrow-shape bristles (Fig. 32); posterolateral expansions of the abdomen strongly developed (Fig. 6); gill I less than 2 times longer than wide (Fig.42) ........... *Th. sinuosus*

Notes on the male imaginal stages

The ZMH collections housed few male imagos of Thalerosphyrus, namely a single male of *Th. determinatus* and two of *Th. sinuosus*. These have been described in details by Ulmer (1913; 1924; 1939). Both species differ by the shape of the genitalia, by the coloration of the abdomen and by the tarsal composition of the hind legs. The report and description by Ulmer (1924) in Sumatra (Gunung Dempu, 1400 m, VIII.1916, Jacobson leg) of a male imago of the Philippine species “Thalerosphyrus” torridus (Walker, 1853) has already been considered as highly dubious by Braasch (2011). This specimen anyway displays general characteristics of the genus Thalerosphyrus, but differs from *Th. determinatus* and *Th. sinuosus* by the shape of the genitalia, and the tarsal composition of the hind leg. It is possible and even probable that this specimen represents the male stage of the species *Th. lamuriensis*, but only in situ rearing may bring the definitive proof.

Acknowledgments

I am indebted to the staff of the Zoologisches Museum Universität Hamburg (ZMH) for allowing me to study Ulmer’s, collection, especially to Kai Schütte and Hossein Rajaei. My appreciation goes to Michael Balke (Munich) and Jean-Marc Elouard (Montpellier) for putting their collections at my disposal, and to Jeff Webb (Missoula, USA) for useful comments. Technical assistance with SEM pictures by Geneviève L’Eplattenier and Raphael Grand (MZL) and Renate Walter (ZMH) was essential and they are warmly thanked for their help.

References

Boonsoong B, Braasch D (2013) Heptageniidae (Insecta, Ephemeroptera) of Thailand. Zookeys 272: 61–93. doi: 10.3897/zookeys.272.3638

Braasch D (2011) New species of the family Heptageniidae (Ephemeroptera) from Borneo and the Philippines. Deutsche Entomologische Zeitschrift 58: 201–219. doi: 10.1002/mmnd.201100024
Braasch D, Soldán T (1984) Beitrag zur Kenntnis der Gattung *Thalerosphyrus* Eaton, 1881 im Hinblick auf die Gattung *Ecdyonuroides* Thanh, 1967. Reichenbachia Staatliches Museum für Tierkunde in Dresden 22: 201–206.

Braasch D, Soldán T (1986a) *Asionurus* n. gen., eine neue Gattung der Heptageniidae von Vietnam (Ephemeroptera). Reichenbachia Staatliches Museum für Tierkunde in Dresden 23: 155–159.

Braasch D, Soldán T (1986b) Die Heptageniidae des Gombak River in Malaysia (Ephemeroptera). Reichenbachia Staatliches Museum für Tierkunde in Dresden 24: 41–52.

Crass RS (1947) Mayflies (Ephemeroptera) collected by J. Omer-Cooper in the Eastern Cape Province, South Africa, with a description of a new genus and species (*Notonurus cooperi*). Proceedings of the Royal Entomological Society of London A, 12: 124–128.

Dang NT (1967) Cac loai va giong moi tim thay trong khu he dong vat khong xuong song nuoc ngot va nuoc lorien Bac Viet-nam. Sinh Vat Dia Hoc 6: 155–165.

Eaton AE (1881) An announcement of new genera of the Ephemeridae (continued). Entomologist Monthly Magazine 18: 21–27.

Eaton AE (1883–1888) A revisional monograph of recent Ephemeridae or mayflies. Transactions of the Linnean Society of London, 2nd Ser Zoology 2: 1–352.

Edmunds GF, Polhemus DA (1990) Zoogeographical patterns among mayflies (Ephemeroptera) in the Malay Archipelago, with special reference to Celebes. In: Knight WJ, Holloway JD (Eds) Insects and the rain forests of South East Asia (Wallacea). The Royal Entomological Society of London, London, 49–56.

Kimmins DE (1960) The Ephemeroptera types of species described by A.E. Eaton, R. McLachlan and F. Walker, with particular reference to those in the British Museum (Natural History). Bulletin of the British Museum (Natural History) Entomology 9: 269–318.

Klug NJ (2004) The phylogenetic system of Ephemeroptera. Kluwer Academic Publishers, Dordrecht, 442 pp. doi: 10.1007/978-94-007-0872-3

Navás L (1933) Insecta Orientalia Serie 12. Memorie della Pontificia Accademia delle Scienze nuovi Lincei 17: 75–108.

Nguyen VV, Bae YJ (2004) Two heptageniid mayfly species of *Thalerosphyrus* Eaton (Ephemeroptera: Heptageniidae) from Vietnam. The Korean Journal of Systematic Zoology 20: 215–223.

Sartori M (2014a) About the status of the enigmatic Oriental genus *Rhithrogeniella* Ulmer, 1939 (Ephemeroptera, Heptageniidae). Oriental Insects (submitted).

Sartori M (2014b) Complementary description of *Dudgeodes ulmeri* Sartori, 2008 and *Teloganopsis media* Ulmer, 1939 (Ephemeroptera: Teloganodidae, Ephemerellidae). Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg (in press).

Sartori M (2014c) The concept of *Compsoneuria* Eaton, 1881 revisited in light of historical and new material from the Sunda Islands (Ephemeroptera, Heptageniidae, Ecdyonurinae). Zootaxa (in press).

Sartori M (2014d) What is *Ecdyonurus sumatranus* Ulmer, 1939? A contribution to the knowledge of the genus *Rhithrogena* in the Oriental Region (Ephemeroptera, Heptageniidae). Zootaxa 3802(2): 193–208. doi: 10.11646/zootaxa.3802.2.3

Soldán T (1977) Three new species of mayflies (Ephemeroptera) from the mist oasis of Erkwit, Sudan. Acta Entomologica Bohemoslovaca 74: 289–294.
Ulmer G (1913) Ephemeriden aus Java, gesammelt von Edw. Jacobson. Notes from the Leyden Museum 35: 110–115.
Ulmer G (1924) Ephemeropteren von den Sunda-Inseln und den Philippinen. Treubia 6: 28–91.
Ulmer G (1926) Beiträge zur Fauna sinica. III. Trichopteren und Ephemeropteren. Archiv für Naturgeschichte, Abteilung A 91: 19–110.
Ulmer G (1939) Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. Archiv für Hydrobiologie 16: 443–692.
Venkataraman K, Sivaramakrishnan KG (1987) A new species of Thalerosphyrus from South India (Ephemeroptera: Heptageniidae). Current Science 56: 1126–1129.
Vuataz L, Sartori M, Gattolliat JL, Monaghan MT (2013) Endemism and diversification in freshwater insects of Madagascar revealed by coalescent and phylogenetic analysis of museum and field collections. Molecular Phylogenetics and Evolution 66: 979–991. doi: 10.1016/j.ympev.2012.12.003
Walker F (1853) Ephemeridae. List of the specimens of neuropterous insects in the collection of the British Museum. The Trustees, London, 533–585.
Wang T-Q, McCafferty WP (2004) Heptageniidae (Ephemeroptera) of the world. Part I: Phylogenetic higher classification. Transactions of the American Entomological Society 130: 11–45.
Webb JM, Braasch D, McCafferty WP (2006) Reevaluation of the genera Compsoneuria Eaton and Trichogenia Braasch & Soldán (Ephemeroptera: Heptageniidae). Zootaxa 1335: 55–68.
Webb JM, McCafferty WP (2008) Heptageniidae of the world. Part II: Key to the Genera. Canadian Journal of Arthropod Identification 7: 1–55. http://www.biology.ualberta.ca/bsc/ejournal/wm_07/wm_07.html
Zhou CF, Wang SL, Xie H (2007) The Nymph and Additional Imaginal Description of Epeorus melli new combination from China (Ephemeroptera: Heptageniidae). Zootaxa 1652: 49–55.