

Phylogeny of the genus *Teloganopsis* Ulmer, 1939 with a redescription of *Teloganopsis media* Ulmer, 1939 and the description of a new Oriental species (Ephemeroptera: Ephemerellidae)

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Teloganopsis puigae n. sp., a new species of Ephemerellidae from a Dipterocarpacea forest of Borneo, is described. *Teloganopsis* was considered as a monotypic genus for a long time, but a recent new systematic concept reveals that it encompasses 14 species. In order to know the phylogenetic position of *Teloganopsis puigae* n. sp. within the *Teloganopsis* genus, a cladistic analysis is also performed. *Teloganopsis maculocaudata* (Ikonov, 1961) is removed from synonymy with *T. mesoleuca* (Brauer, 1857).

Keywords: *Teloganopsis*; phylogeny; Ephemerellidae; oriental realm; Borneo

Introduction

The genus *Teloganopsis* Ulmer was described based on a single male imago and several larvae from Java and Sumatra (Ulmer 1939). Until recently, this genus was considered as monotypic, with *Teloganopsis media* Ulmer, 1939 as the only species known (Allen 1965, 1980, 1984; McCafferty and Wang 2000; Kluge 2004). An up to date reassessment of Ephemerellidae genera by Jacobus and McCafferty (2008) led to several important changes. *Teloganopsis* comprises 13 more species which were previously placed in different genera, including *Uracanthella* Belov, 1979; *Amurella* Kluge, 1997 and *Kangella* Sartori, 2004; all put into synonymy with *Teloganopsis* by Jacobus and McCafferty (2008). Consequently, the genus possesses a wide distribution, being present from the Holarctic to the Oriental Realms.

During a survey of benthic macroinvertebrates in a lowland Dipterocarpacea forest in Borneo (Derleth 2003), two ephemerellid species were found belonging to genera *Hyrtanella* Allen & Edmunds, 1976 and *Uracanthella* respectively (Sartori et al. 2003). Based on this material, Jacobus and Sartori (2004) described *Hyrtanella pascalae*, whereas Jacobus and McCafferty (2006) assigned *Uracanthella* nymphs to

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Teloganopsis media. More recently, we have studied again these specimens, including subimagines, and have found several discrepancies with the original description. In order to solve the taxonomic position of the *Teloganopsis* population from Borneo, a direct comparison with the type material was needed. Thanks to the courtesy of Dr. H. Dastych (Zoologisches Museum Hamburg, Germany) who gave us access to Ulmer's collection, we will redescribe the type material and compare it with our own material from Borneo. In order to evaluate the phylogenetic hypothesis proposed by Jacobus and McCafferty (2008) for the *Teloganopsis* lineage, we also performed a cladistic analysis with an original set of morphological characters of all stages.

Materials and methods

Taxonomic study

The type material of *Teloganopsis media* deposited in the Zoological Museum of Hamburg (Germany) is constituted by the following specimens:

- (A) Holotype: ♂ imago in ethanol, without locality, leg. Dr. Lieftinck; 1 ♂ subimaginal exuvia and 1 ♀ larval exuvia together in the same vial (see Ulmer 1939, pp. 631–632 for comments; this material has been reared in aquarium by Dr. Lieftinck, and comes most likely from Java)
 (B) Fy7e: 1 ♀ larva, West Java, Kali Tjiwalen bei Tjibodas, ca. 1370 m, 15°C. 10.VII.1929, Gesiebe von Moos und Laub, Prof. Feuerborn leg.
 (C) FM7: 1 ♂ larva, Süd Sumatra, in Musi bei Simpang, 6.V.1929. id. leg.

Specimens from Borneo were collected during 2000–2001 in several localities of a dipterocarp forest in the northeast of East Kalimantan (Malinau District, Indonesia) (Derleth 2003). Material examined consists of 7 ♂ subimagines, 8 ♀ subimagines, and 91 larvae collected by P. Derleth and collaborators. Several specimens from Borneo were studied by light and scanning electron microscopes (SEM). For light microscopy analysis, four larvae were dissected completely and mounted in permanent slides. For SEM analysis, heads of two larvae and eggs of three larvae and one subimago, removed directly from the abdomen, were treated following the air-drying method explained in Ubero-Pascal et al. (2005), although in this case, we used tetramethylxilane (TMS) as transition liquid and Pt-coating by a metal evaporator. Specimens were observed in a JEOL 6300 Scanning Electron Microscopy at Centre de Microscopie Électronique of Université de Lausanne.

Phylogenetic study

The material cited above and 14 other species have been used for our phylogenetic analysis. The same morphological study carried out for the specimens from Borneo was applied to *Quatica paradinasi* (González del Tánago & García de Jalón, 1983), *Q. ikononovi* (Puthz, 1971), *Ephemerella mucronata* (Bengtsson, 1909), *Teloganopsis albai* (González del Tánago & García de Jalón, 1983), *T. brocha* (Kang & Yang, 1995), *T. deficiens* (Morgan, 1911), *T. hispanica* (Eaton, 1887), *T. maculocaudata* (Ikononov, 1961) and *T. mesoleuca* (Brauer, 1857). These specimens are deposited in the Musée Cantonal de Zoologie Lausanne, Switzerland. In addition, morphological

features of *T. chinoi* (Gose, 1980), *T. gracilis* (Tshernova, 1952), *T. jinghongensis* (Xu, You & Hsü, 1984), *T. oriens* (Jacobus & McCafferty, 2006), and *T. punctisetae* (Matsumura, 1931) were obtained only from literature. We list below all species considered as operational taxonomic unit (OTU), indicating the sources of morphological data. OTU labels correspond to the specific epithets, except for Borneo species.

Operational taxonomic units (OTU)

media. Examined material as indicated above. Literature consulted: Ulmer (1939). Imago ♀ and egg unknown.

Borneo. Examined material as indicated above. Imago unknown.

brocha. 1 larva, Taiwan, Wufeng, Hsinch Hsien, (304 m), 1991.10.24 (I). S.C. Kang & H.C. Yang leg. Literature consulted: Kang and Yang (1995). Imago unknown.

albai. 2 ♂, 1 subimago ♀, 16 larvae, Spain, río Agueda/El Payo (E. Salamanca), alt. 700 m., 18–20.VIII.88, Landolt & Studemann leg. Literature consulted: González del Tánago and García de Jalón (1983); Studemann and Landolt (1997); Studemann et al. (1989, 1995).

deficiens. 3 ♂, 3 ♀ and eggs, reared, USA, PA: Chester Co. E Fk E Br White Clay, cr. 1 mi WNW of London Grove, elev. 375', 39°52'30" N, 75°47'31" W, WCC2, VI/30/1980, coll. and det. D. H. Funk; 5 larvae, Dir 83, voucher, USA, NY: Delaware Co. E Br Delaware, R. 2.7 mi WSW Sinophopple, elev. 1010', 42°01'30", 75°07'14" W, EBH5, VI/28/1983, det. D. H. Funk. Literature consulted: Morgan (1911); Studemann and Landolt (1997).

hispanica. 2 ♂ and 4 ♀, Spain, Río Lozoya/Los Cotos, Valdesquí, alt. 1800 m., 16.VII.86, 20–21h, Tomka, Landolt & Studemann leg.; 8 larvae, Spain, Río Francia/Miranda C. (E. Castilla y León), alt. 600 m., 14.IV.90, Landolt & Studemann leg.; Eggs from larva, Spain, Río Lozoya/Los Cotos, Valdesquí, alt. 1800 m., 14.VII.86, 20–21h, Tomka, Landolt & Studemann leg. Literature consulted: González del Tánago and García de Jalón (1983); Studemann and Tomka (1987); Studemann et al. (1995).

ikonomovi. 4 ♂ and 5 ♀, Spain, Río Trevélez, 1700 m., Sierra Nevada (Granada, E), 28.VII.1991, Lubini leg.; 4 larvae, Former Yugoslavia, Ibar/Zupce (Kosovo, Yu), alt. 1350 m., 13.VII.88, Landolt & Studemann leg. Literature consulted: Ikonov (1961: figures 6–9); Jacob (1993); Studemann et al. (1989, 1995); Ubero-Pascal and Puig (2009).

maculocaudata. 2 ♂, 1 subimago ♀, 4 larvae and eggs, Bulgaria, riv. Struma near Kulata, 25.VI.1978, T. Soldán leg.; 3 larvae, Former Yugoslavia, Fluss Bregalnica bei stip, Macedonien, 7.V.1953, P. Ikonov leg. Literature consulted: Ikonov (1961: figures 3–5); Soldán (1982).

mesoleuca. 4 ♂, 5 ♀, 17 larvae and eggs, France, Loire/Châtillon, Gien, 130 m. alt., (Loiret, F), 11.6.88, Landolt & Studemann leg. Literature consulted: Jacob (1993); Studemann and Landolt (1997); Studemann et al. (1995).

paradinasi. 1 ♂ and 1 ♀, Spain, Río Tera/Trefacio (E. Zamora), alt. 960 m., VII.86, Landolt & Studemann leg.; 15 larvae, eggs, Spain, Río Eresma/La Splaná (E. Segovia), alt. 1280 m., 14.VII.86, Landolt, Studemann & Tonka leg. Literature consulted: González del Tánago and García de Jalón (1983); Jacob (1993); Studemann and Landolt (1997); Studemann and Tomka (1987); Studemann et al. (1995).

chinoi. Literature consulted: Gose (1980: figure 25); Ishiwata (1987: figure 11a); Jacobus and McCafferty (2008). Imago and eggs unknown.

gracilis. Literature consulted: Jacobus and McCafferty (2008); Kluge (1997, 2004); Tshernova (1952: figures 79–82). Imago and eggs unknown.

jinghongensis. Literature consulted: Tong and Dudgeon (2000); Xu et al. (1984); Zhou et al. (2006). Eggs unknown.

oriens. Literature consulted: Jacobus and McCafferty (2006). Imago and eggs unknown.

punctisetae. Literature consulted: Belov (1979: p. 578); Imanishi (1937); Ishiwata (1987: figures 5–11); Tshernova (1952: figures 83–88); Tshernova et al. (1986: figure 61.1). Eggs unknown.

mucronata. 1 ♂, 1 ♀ and 4 larvae, Germany, Wutach/Achdorf, Baden-Württemberg, D., 700 m., 16.V.85, Hefti & Studemann leg. Literature consulted: Jacob (1993); Studemann et al. (1995).

We performed the cladistic analysis using PAUP. One OTU, *mucronata*, has been treated as an outgroup. The character states have been coded numerically, although missing or unknown data are indicated by a question mark (?) and inapplicable character states are indicated by a slash (/). The default settings have been used to run the analysis and all the character-states have been treated as unordered and having equal weight. A heuristic search was performed using parsimony as the optimal criterion. Starting tree(s) were obtained via stepwise addition and tree-bisection-reconnection (TBR) was used as a branch-swapping algorithm. Topological constraints were not enforced and trees were unrooted. The bootstrap method has also been used for measuring the strength of consensus tree nodes and it was applied with 100 replicates and 50% majority-rule as cut off.

Phylogenetic study of *Teloganopsis* lineage

Fifty-nine morphological characters from egg, larva and imago have been chosen for our phylogenetic analysis (Appendix 1). The data matrix is presented in Table 1. Our cladistic analysis produced 12 most parsimonious trees and the consensus tree has a length of 110 steps (Figure 1a). The phylogram is presented in Figure 1b. The analysis is supported by a high consistency index (CI) of 0.6273, and a low homoplasy index (HI) of 0.3727.

In none of the reconstructions the OTU Borneo is recovered as the sister taxon of *media*, suggesting it represents a new, yet undescribed species.

The tree topology led us to consider two monophyletic sister groups among the species studied, one is constituted by *paradinasi* and *ikonomovi* and other gathers the remaining species, which we name clade A. Both clades are strongly supported by the same consensus value (100) and bootstrap values of 81 and 61 respectively (Figure 1). Clade A and the *paradinasi-ikonomovi* group share four characters related to larvae (gills acuminate and ventral lobe of sixth gill bifurcate) and imago (penis lobes not separated at base and second segment of forceps broad at the base, although width decreases towards distal end (Figure 3e)).

Clade A is characterised by only one character: subapical denticle of claw as long as apical denticle (Figure 6t); although the phylogenetic relationships of some species are not completely solved at base. Within this group we can recognise a clear monophyletic clade B, strongly supported by both consensus (100) and bootstrap (78) values, which gathers the majority of species, whereas three other species (*gracilis*, *maculocaudata* and *mesoleuca*) have an uncertain phylogenetic position in the cladogram (Figure 1a). On the other hand, clade B is characterised by two unique features: apex of maxilla truncated (Figure 2c) and proximal surface of forefemur with 2–5 strong setae placed in a perpendicular row to the longitudinal axis of femur (Figures 6q–r). It is probable that the number of features characterising clade B will increase when imagines, eggs and larval maxilla morphology are described for *oriens* and *jinghongensis*.

At least two lineages can be recognised within this last monophyletic group, although as the previous clade, the phylogenetic relationships of all species included are not completely solved. The lineage most numerous (clade C) includes species from the Oriental and East Palearctic Realms: *media*, *brocha*, *punctisetae*, *chinoi* and

Table 1. Data matrix of character states coded for each species included in the cladistic analysis, based on characters listed in Appendix 1.

	Character states																														
OTU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>media</i>	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	1	0	0	0	1	1	1	2	0	0	1	1	1	
<i>Borneo</i>	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1	2	0	1	1	1	0	
<i>albai</i>	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0	
<i>hispanica</i>	0	0	0	0	0	0	1	3	0	0	1	0	0	1	1	0	0	1	0	0	0	1	1	0	0	0	1	1	1	1	
<i>deficiens</i>	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0	
<i>brocha</i>	0	0	1	1	1	1	1	2	0	1	1	1	/	/	1	1	1	1	0	0	1	1	1	1	2	0	0	1	1	0	
<i>maculocaudata</i>	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	
<i>mesoleuca</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	
<i>paradinasi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	0	
<i>jinghongensis</i>	1	0	0	0	0	0	1	?	?	?	1	0	0	?	?	0	0	1	?	0	0	?	0	1	1	0	0	1	1	0	
<i>punctisetae</i>	1	0	0	1	1	1	1	?	?	?	1	0	?	?	?	1	0	?	?	?	?	0	?	1	1	1	0	1	?	?	?
<i>oriens</i>	0	0	?	?	?	0	1	?	?	?	1	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	0	1	0	1	0
<i>mucronata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	
<i>ikonomovi</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	
<i>gracilis</i>	1	0	?	0	?	0	0	0	?	0	1	0	?	0	0	0	0	?	?	?	0	?	?	?	?	0	0	?	?	?	
<i>chinoi</i>	0	0	?	1	0	1	1	?	?	?	1	?	?	?	?	?	0	?	?	?	0	?	?	?	?	1	0	?	1	?	

(continued)

Table 1. (Continued).

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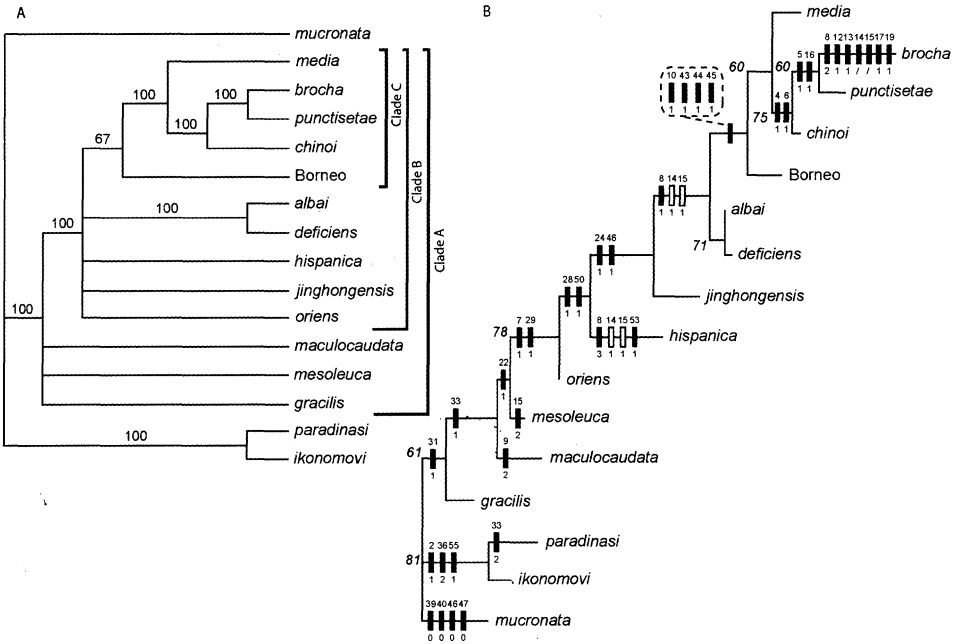


Figure 1. (a) Cladogram of the consensus tree. Consensus values are given above of each branch. (b) Phylogram of the consensus tree. Bootstrap values are indicated before of each node if > 50%. Characters that have changed only once are represented by black boxes; the number above the box corresponds to character as in Table 1 and the number below the box represents the character state.

the species from Borneo. This lineage is supported by four features: canine teeth of maxilla directed upwards (Figure 2d) and the morphology of costal projection and veins of hind wing (Figures 3c and f). Two others Oriental species, *jinghongensis* and *oriens*, are probably placed out of this lineage due to the lack of information on important character states, such as characters 14 and 15 (Figure 1b). The other lineage gathers two species from West Palearctic and Nearctic Realms, *albai* and *deficiens*, and it is strongly supported by both consensus (100) and bootstrap (71) values, but lacks specific characters.

Due to the uncertain phylogenetic position of several species within clade A, *gracilis*, *maculocaudata* and *mesoleuca* at base and *oriens*, *jinghongensis* and *hispanica* in the main monophyletic-clade, further studies would be necessary to reconstruct its phylogenetic relationships. The concept of *Teloganopsis* sensu Jacobus and McCafferty (2008) corresponds to our clade A. We follow this proposal at the moment, but the basal position and low consensus values of *gracilis* (type species of the genus *Amurella*) and *maculocaudata* and *mesoleuca* could indicate that they should be placed in other supraspecific ranking. The fact that *mesoleuca* and *maculocaudata*, considered up to now as synonyms, do not form a monophyletic group brings arguments to consider clade A as equal to the genus *Teloganopsis*.

Finally, the other sister group, *paradinasi-ikonomovi*, is characterised by three features related to larval and egg morphologies: the presence of tubercles and

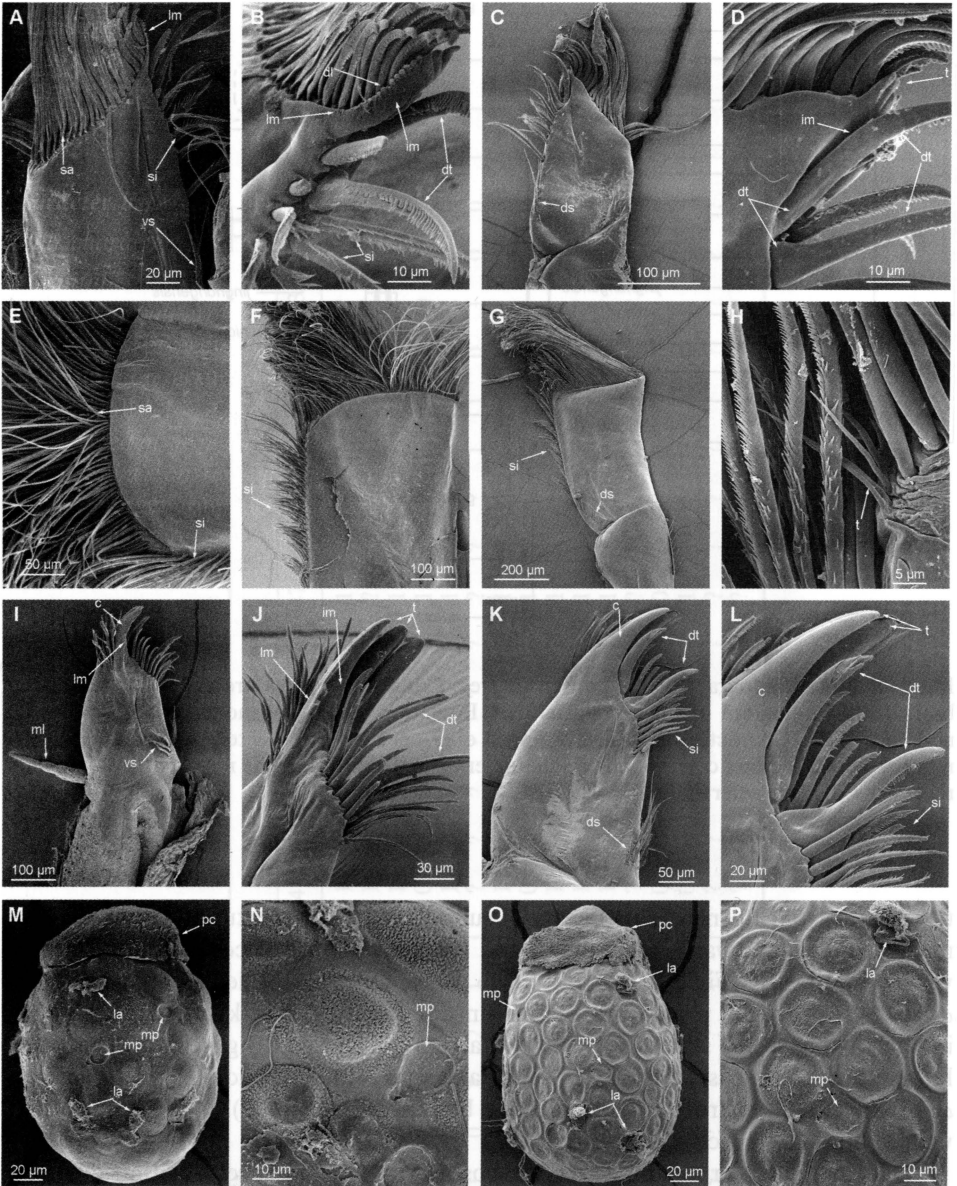


Figure 2. Maxillary characters used in phylogenetic analysis, (a–b) ventral view and (c–d) dorsal view in *Teloganopsis puigae* n. sp.; (e–f) ventral view and (g–h) dorsal view in *Teloganopsis brocha*; (i–j) ventral view and (k–l) dorsal view in *Quatica paradinassi*. (m–n) Egg morphology in *Teloganopsis maculocaudata* and (o–p) in *T. mesoleuca*. Abbreviations. c: maxillary canine; dl: denticles in lateral margin of canine; ds: dorsal setae at maxilla base; dt: dentisetae; im: inner margin of maxilla; la: lateral attachment structure; lm: lateral margin of canine; ml: maxillary palp; mp: micropyle; pc: polar cap; sa: setae in maxilla apex; si: setae in inner margin of maxilla; t: tooth of canine; vs: ventral setae at maxilla base.

star-like setae in the head (Studemann and Tomka 1987: figure 3) and furrows demarcating the mesh units of chorion sculpturing (Ubero-Pascal and Puig 2009: figure 7b). The strongest support of this clade led us to confirm that *paradinassi*

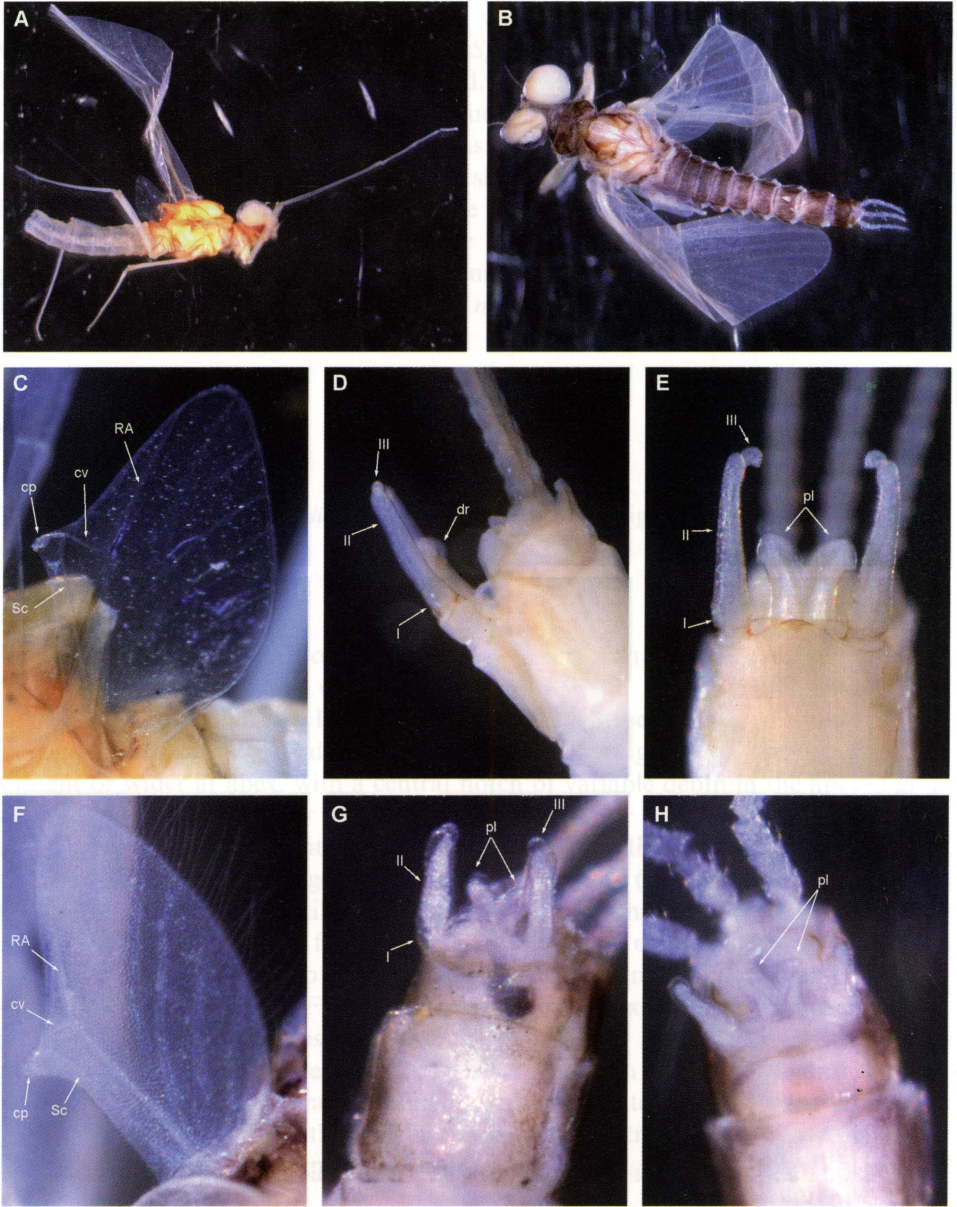


Figure 3. (a, c–e) Imago of *Teloganopsis media*, (a) ♂ habitus in lateral view; (c) hind wing; (d) genitalia in lateral view; (e) genitalia in ventral view. (b, g–h) Subimago of *Teloganopsis puigae* n. sp.; (b) ♂ habitus in dorsal view; (f) hind wing; (g–h) genitalia in ventral view. Abbreviations. I–III: segments of forceps; cp: costal projection; cv: cross-vein; dr: dorsal projection of penis lobe; pl: penis lobes; RA: radial vein; Sc: subcosta vein.

and *ikonomovi* form a monophyletic group corresponding to the genus *Quatica* Jacobus & McCafferty, 2008. Our results are in complete agreement with the phylogeny proposed by Jacobus and McCafferty (2008), although they also include three more species,

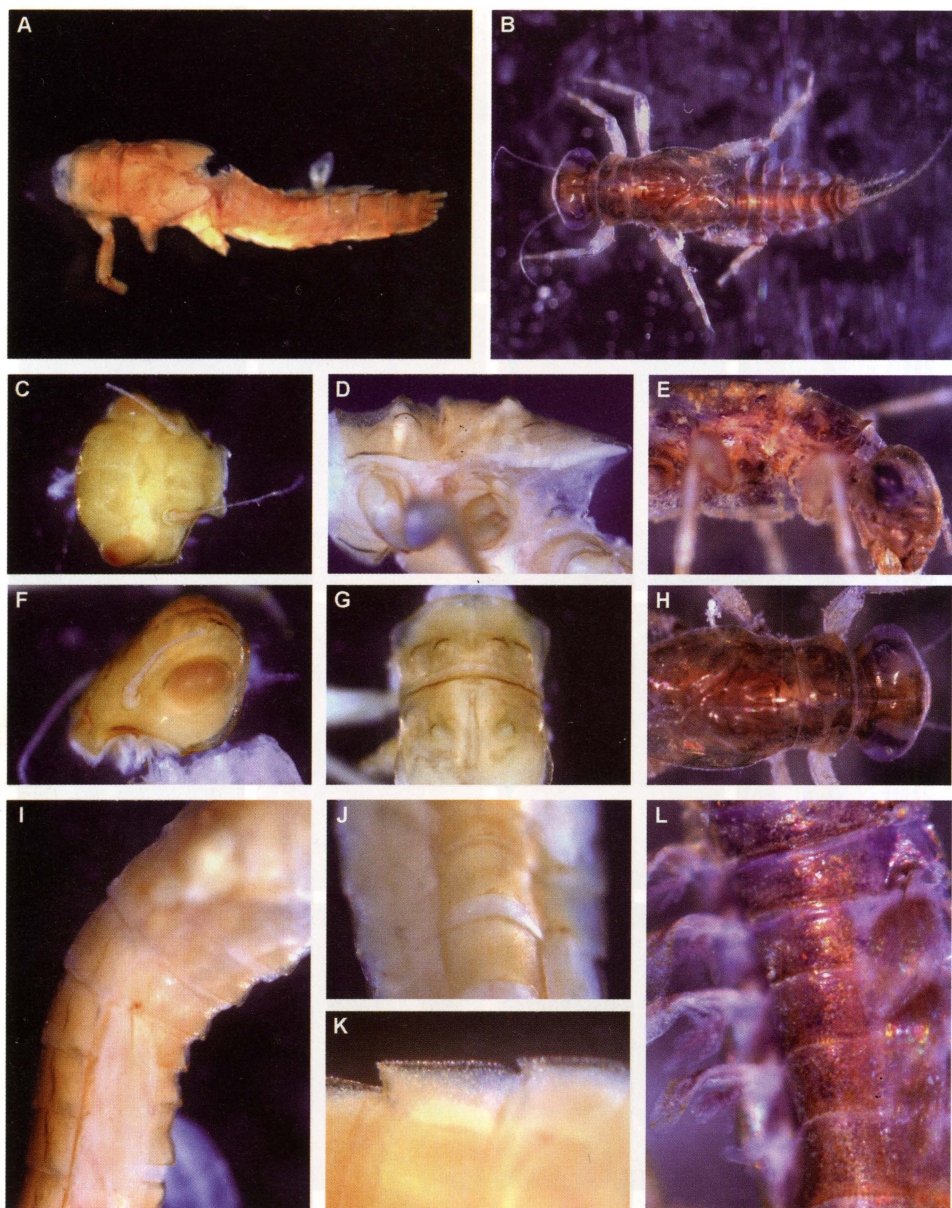


Figure 4. (a, c–d, f–g, i–k) *Teloganopsis media*, larva, (a) habitus in dorsal view; (c, f) head in frontal and lateral views; (d, g) thorax in lateral and dorsal views; (i–k) abdomen in lateral, dorsal and ventral views. (b, e, h, l) *Teloganopsis puigae* n. sp., larva (b) habitus in dorsal view; (e, h) thorax in lateral and dorsal view; (l) abdomen in dorsal view.

T. bauernfeindi (Thomas, Marie & Dia, 2000), *T. changbaishanensis* (Su & You, 1988) and *T. subsolana* (Allen, 1973), which were not treated in our phylogenetic analysis. As already said, this genus is not restricted to the Oriental Realm but it is also present in East and West Palearctic as well as North America. This kind of distribution is uncommon but not rare among present mayflies. Similar patterns can

be found in Heptageniidae (*Heptagenia* Walsh, 1863; *Rhithrogena* Eaton, 1881), Caenidae (*Cercobrachys* Soldán, 1986; *Sparbarus* Sun & McCafferty, 2008), in Leptophlebiidae (*Leptophlebia* Westwood, 1840) or Ameletidae (*Ameletus* Eaton, 1885). We are not in accordance with Studemann and Tomka (1989) and Jacobus and McCafferty (2008) when they consider *T. maculocaudata* as a subjective synonym of *T. mesoleuca*. We have shown important differences in larval, imaginal and egg characters such as: the number of canine teeth of maxilla, the shape of lateral margin on ventral side of maxilla canine, the apical shape of penis lobes, and above all the chorionic sculpturing of egg (Figures 2m–p). Based on this evidence, we propose *T. maculocaudata* to be reinstalled as *bona species*.

Systematic account

Teloganopsis Ulmer, 1939

Type species. *Teloganopsis media* Ulmer, 1939 by original designation.

Description

The following features complement the description given by Jacobus and McCafferty (2008). Imago with forewing slender and elliptic. Hind wing small, ca 1/5 of forewing length. Penis base straight and lobes separated at mid-length with divergent apex and dorsolaterally projected (Figures 3d, e); rarely penis straight or wider at apex, with a central notch of variable depth in the apex. Larva without tubercles, spines or complex setae (star-like or microtrichia-like) on head and abdominal tergites. Anterior face of forefemur with a row of long and stout setae perpendicularly arranged to the longitudinal axis (Figure 6q); rarely without this pattern of setae. Maxilla with apex truncated and entirely covered with a crown of setae (Figures 2a, f), canine poorly developed or vestigial, with a variable number of teeth at the tip (Figures 2d, h), convex inner margin, and laterally serrated on ventral side (Figure 2b); very rarely maxilla falciform without the previous characters (Figures 2i, k). Eggs with chorion sculpturing constituted by geometric macro relief, mesh surface usually smooth and strand surface with hollows and stalk-protuberances, and thread-coiled lateral attachment structures (Figures 7a, c, f); rarely with other net type (Figures 2m, o) and very rarely with folded-thread lateral attachment structures.

Distribution

Oriental, Palearctic and Nearctic.

Species included

T. albai (González del Tánago & García de Jalón, 1983); *T. bauernfeindi* (Thomas, Marie & Dia, 2000); *T. brocha* (Kang & Yang, 1995); *T. changbaishanensis* (Su & You, 1988); *T. chinoi* (Gose, 1980); *T. deficiens* (Morgan, 1911); *T. gracilis* (Tshernova, 1952); *T. hispanica* (Eaton, 1887); *T. jinghongensis* (Xu, You & Hsü, 1984); *T. maculocaudata* (Ikononov, 1961); *T. media* Ulmer, 1939; *T. mesoleuca*

(Brauer, 1857); *T. oriens* (Jacobus & McCafferty, 2006); *T. puigae* n. sp.; *T. punctisetae* (Matsumura, 1931) and *T. subsolana* (Allen, 1973).

Remarks

T. maculocaudata and *T. mesoleuca* are placed in this genus provisionally, until further studies led us to know better their phylogenetic relationships; almost all exceptions in the generic description correspond to these two species. *T. bauernfeindi*, *T. changbaishanensis* and *T. subsolana* are included in this genus following the criteria proposed by Jacobus and McCafferty (2008).

***Teloganopsis media* Ulmer, 1939**

Material examined and stage of conservation

Holotype. ♂ imago in ethanol with apical part of abdomen separated to the rest of body. Left forewing and left legs of pro- and mesothorax also separated from body. Larval ♀ exuvia with mouthparts partially dissected and mounted on a microslide. Larva from Java decapitated (head conserved within the vial) and partially dissected: mouthparts, right legs set, two gills, and part of caudal filaments mounted on microslide by G. Ulmer (n^o. 64). Left legs of meso- and metathorax missing, second and third abdominal segments damage in one side. Larva from Sumatra well preserved.

Descriptions

Male imago

Body length 7.3 mm. General colouration of body yellowish or pale-brown, with abdominal segments transparent (Figure 3a), except genitalia and caudal filaments (Figures 3d–e). Dorsal part of compound eyes whitish and ventral part brownish (Figure 3a). Forewing slender, elliptic, and wing-width in proximal area as wide as in medial area; few intercalary veins and, generally, not attached to the main veins. Hind wing (Figure 3c) small, almost oval, with a well-developed costal projection at 1/3 of wing length; Sc ending near costal projection; only one cross-vein between Sc and RA, very strong, and placed close to costal projection. Forceps straight with first and third segments short and second the longest one (Figure 3e). First segment as wide as base of second one. Base of second segment wider than tip. Third segment small and rounded, but with a pointed inner margin, and slightly displaced towards internal angle of second segment (Figure 3e). Penis length almost half of forceps length. Penis straight until median length and then split in two divergent lobes. Penis lobes projected dorsolaterally (Figure 3d). Shape of penis lobes as in Figure 3e.

Female imago

Unknown.

Larva

Body length 7.6 mm. General colouration of body yellow, with pale maculates in thorax and abdomen (Figures 4a, d, g, j). Compound eyes brownish or dark-orange. Head sutures, antennae, legs and gills pale-yellowish to whitish (Figures 4c, f, i–j).

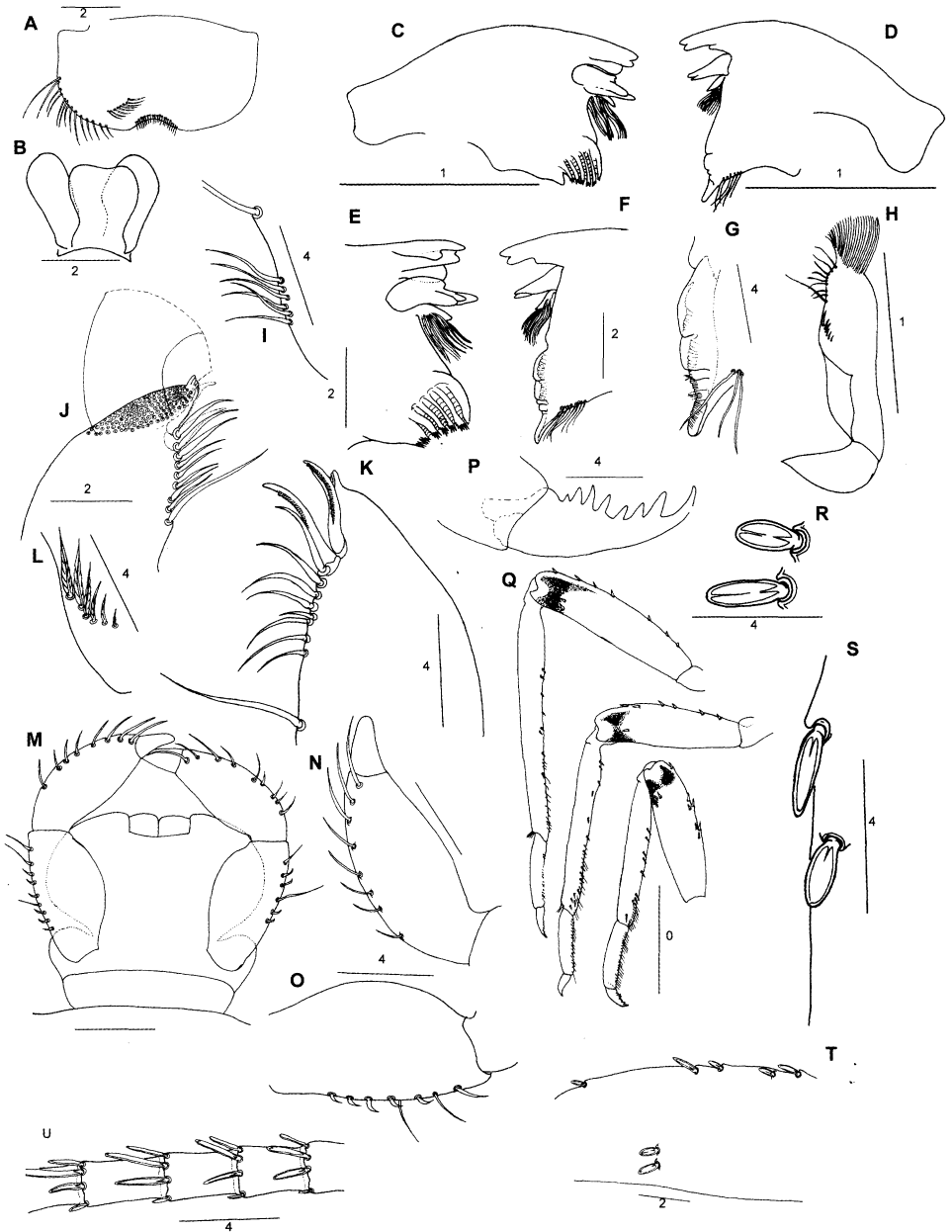


Figure 5. *Teloganopsis media*, (a) labrum; (b) hypopharynx; (c-d) right and left mandibles; (e-f) right and left inner mandibular margins; (g) molar area of left mandible; (h) left maxilla in dorsal view; (i) setae on dorsal surface at base of maxilla; (j-k) right and left maxilla; (l) setae on ventral surface at base of maxilla; (m) labium; (n) segments 2-3 of labial palp; (o) segment 1 of labial palp; (p) claw of foreleg; (q) set of legs; (r-s) setae on dorsal surface and margin of forefemur; (t) forefemur; (u) detail of caudal filament. Scale: 0 = 1 mm, 1 = 0.5 mm, 2 = 0.15 mm, 4 = 0.1 mm.

Head. Head without tubercles or projection, but with vertex-occipital area rough (Figures 4c, f). Antennae as long as head width. Labrum rectangular, about two times wider than long, with distal margin rounded in which appear a wide, relatively

deep, and round central notch; the distal margin is covered by long setae decreasing in length towards the central notch (Figure 5a); feathered setae on dorsal surface and notch edge. Mandibles compact with the outer margin rounded (Figures 5c–d); incisors, kinetodontium and prostheca well-developed, molar area reduced; left mandible with outer incisor constituted by five teeth, one of them internal and close to kinetodontium, which has three teeth and a dorsal ridge (Figure 5e); prostheca constituted by a dorsal lamella and a bunch of fine and relatively long setae; right mandible with a three-teeth outer incisor clearly separated from a bifid kinetodontium; prostheca constituted by a dorsal lamella, smaller than in left mandible, and a bunch of long and fine setae (Figure 5f); molar area as in Figure 5g. Maxillae rectangular (Figure 5h), without maxillary palp, apex truncated obliquely, with a poorly developed canine (Figures 5j–k); apex completely covered with a crown of setae partially serrated (Figure 2b), extending to the ventral surface (Figure 5j); canine ending in several small teeth oriented upwards (Figure 5k), inner margin convex and laterally serrated on ventral surface (Figures 2b, 5j); inner margin of maxilla with two parallel rows of feathered and long setae, two dentisetae also present at the beginning of dorsal row (Figures 2d, 5k); five or six feathered and large setae forming an oblique row at base of maxilla in ventral surface (Figure 5l), many thin and long setae in dorsal surface (Figure 5i). Hypopharynx with concave apex (Figure 5b). Labium with submentum ca. two times wider than paraglossae, glossae as wide as long, and labial palp three-segmented (Figure 5m); inner margin of first segment convex and outer margin with scattered short and hooked setae (Figure 5o); first segment slightly wider than the second; distal margin of second segment as wide as proximal margin of the third segment (Figure 5n).

Thorax. Anterior margin of prothorax as wide as pterothorax width, with antero-lateral angles expanded (Figure 4g). Four large rounded tubercles on the dorsal face of prothorax, a pair in each side of median line (Figures 4d, g). Pterothorax also with large rounded tubercles on dorsal face, but only one tubercle in each side of median line (Figures 4d, g). All legs similar in shape and pigmentation (Figure 5q), but increasing in length from fore to hind leg. Femora slender, ca. 3.5–4 times longer than wide. Dorsal edge of femora with few scattered thick and pointed setae (Figures 5q, s), but in forefemur they do not appear in the proximal third (Figure 5q). Anterior face of forefemur with a transverse row of, at least, two thick, short and acuminate setae close to distal margin (Figures 5r, t). Ventral edge of tibia with sparse and fine setae distally. Claws with subapical denticle practically as long as apical one; third and fourth proximal denticles usually larger (Figure 5p).

Abdomen. Abdominal tergites without tubercles (Figures 4i–j), but tergites II–V with a very small and slight triangular projection in the middle of posterior margin, hardly visible (Figure 4i). Posterior and lateral margins of abdominal tergites with a row of small spatulate setae (Figures 4j–k). Posterolateral projections of abdominal tergites slightly marked (Figure 4k). Gills acuminate on segments III–VII, with ventral lamella bifurcated. Cerci with a whorl of pointed setae, the latter shorter than segment length (Figure 5u).

Eggs

Unknown.

Diagnosis

Male imago of *T. media* is easily distinguished from others *Teloganopsis* species by the morphology of hind wing, and larvae are also easy to identify based mainly on the presence of broad round tubercles on thorax and thick, short and acuminate setae on the anterior face of forefemur.

Teloganopsis puigae n. sp.

Material examined. *Holotype.* 1 larva, Indonesia, East Kalimantan, Malinau Basin, Riv. Seturan, Loc. Seturan (2001-bloc 57), Tamalang, 116°30'46" E, 2°59'22" N, 11.04.2001, Derleth, P. & Feldmeyer, B. leg.; *Paratypes:* 18 larvae, same data as holotype; 7 larvae, same locality, 08.08.2000, Derleth, P. leg.; 9 larvae (one partially on slide), Riv. Seturan, Loc. Seturan (2001-bloc 57), Tamalang, 116°30'29" E, 2°59'50" N, 19.07.2000, Derleth, P. & Béboux, F. leg.; 4 ♂ subimagines, 1 ♀ subimago, same locality, 05.08.2000, Derleth, P. leg.; 3 larvae, Riv. Seturan, Loc. Seturan (2001-bloc 57), Tamalang, 116°30'29" E, 2°59'22" N, 18.07.2000, Derleth, P. & Béboux, F. leg.; 15 larvae, 1 ♂ subimago, same locality, 10.04.2001, Derleth, P. leg.; 1 larva, Riv. Rian, Loc. Langap Sud (1995), Aff. Ngayo, 116°31'11" E, 3°04'41" N, 08.07.2000, Derleth, P. leg.; 1 ♀ subimago, same locality, 14.06.2000, Derleth, P. leg.; 3 larvae (one partially on slide), Riv. Rian, Loc. Langap Sud (1995), Aff. Ngayo, 116°31'15" E, 3°04'41" N, 12.07.2000, Derleth, P. leg.; 2 larvae, Riv. Rian, Loc. Langap Sud (1995), Aff. Ngayo, 116°30'58" E, 3°04'56" N, 08.07.2000, Derleth, P. leg.; 2 ♂ subimagines, 2 ♀ subimagines, same locality, 27.07.2000, Derleth, P. leg.; 3 larvae, Riv. Seturan, Loc. Seturan (2000-bloc 45), Wok (Sungai Guang), 116°33'30" E, 2°59'11" N, 29.06.2000, Derleth, P. leg.; 2 larvae, Riv. Seturan, Loc. Seturan (2000-bloc 44-45), Wok (Sungai Guang), 116°33'11" E, 2°59'12" N, 17.06.2000, Derleth, P. & Gattolliat, J.-L. leg.; 2 larvae (one partially on slide), Loc. Seturan (2000-bloc 43), Aff. Temalat (Sungai Guang), 116°33'29" E, 2°59'29" N, 18.06.2000, Derleth, P. & Gattolliat, J.-L. leg.; 14 larvae (two partially on slide), same locality, 16.08.2000, Derleth, P. & Schlaepfer, R. leg.; 1 larva, same locality, 04.04.2001, Derleth, P. leg.; 4 larvae, Riv. Seturan, Aff. Seturan (unlogged), 116°30'48" E, 3°00'05" N, 28.03.2001, Derleth, P. & Feldmeyer, B. leg.; 4 larvae, 1 ♀ subimago (reared), Riv. Seturan, Aff. Seturan (unlogged), 116°33'29" E, 2°58'54" N, 24.04.2001, Derleth, P., Sartori, M. & Feldmeyer, B. leg.; 2 larvae, Riv. Seturan, Aff. Seturan (unlogged), 116°33'30" E, 2°58'58" N, 26.04.2001, Derleth, P. & Sartori, M. leg.

Other material. 1 larva, Malaysia, Sabah, Crocker Range National park, Headquarters, Station Road, 08.08.2003, M. Whiting's lab leg.

Holotype and most of the paratypes housed in the Museum of Zoology, Lausanne, Switzerland. Some paratypes deposited in Zoologisches Museum Hamburg, Germany, and in LIPI (Museum of Zoology, Bogor, Indonesia).

*Descriptions**Male and female imagines*

Unknown.

Male subimago

Body length 4.8 mm; forewing length 3.7 mm; hind wing length 0.7 mm. General colouration dark-brown; pterothorax whitish with sutures dark-brown; antennae, legs, wings, caudal filaments and genitalia brown-pale to whitish; upper portion of compound eyes whitish and lower portion black (Figure 3b). Forewing as *T. media* (Figure 6a). Hind wing small, elliptic, with a well-developed costal projection close to

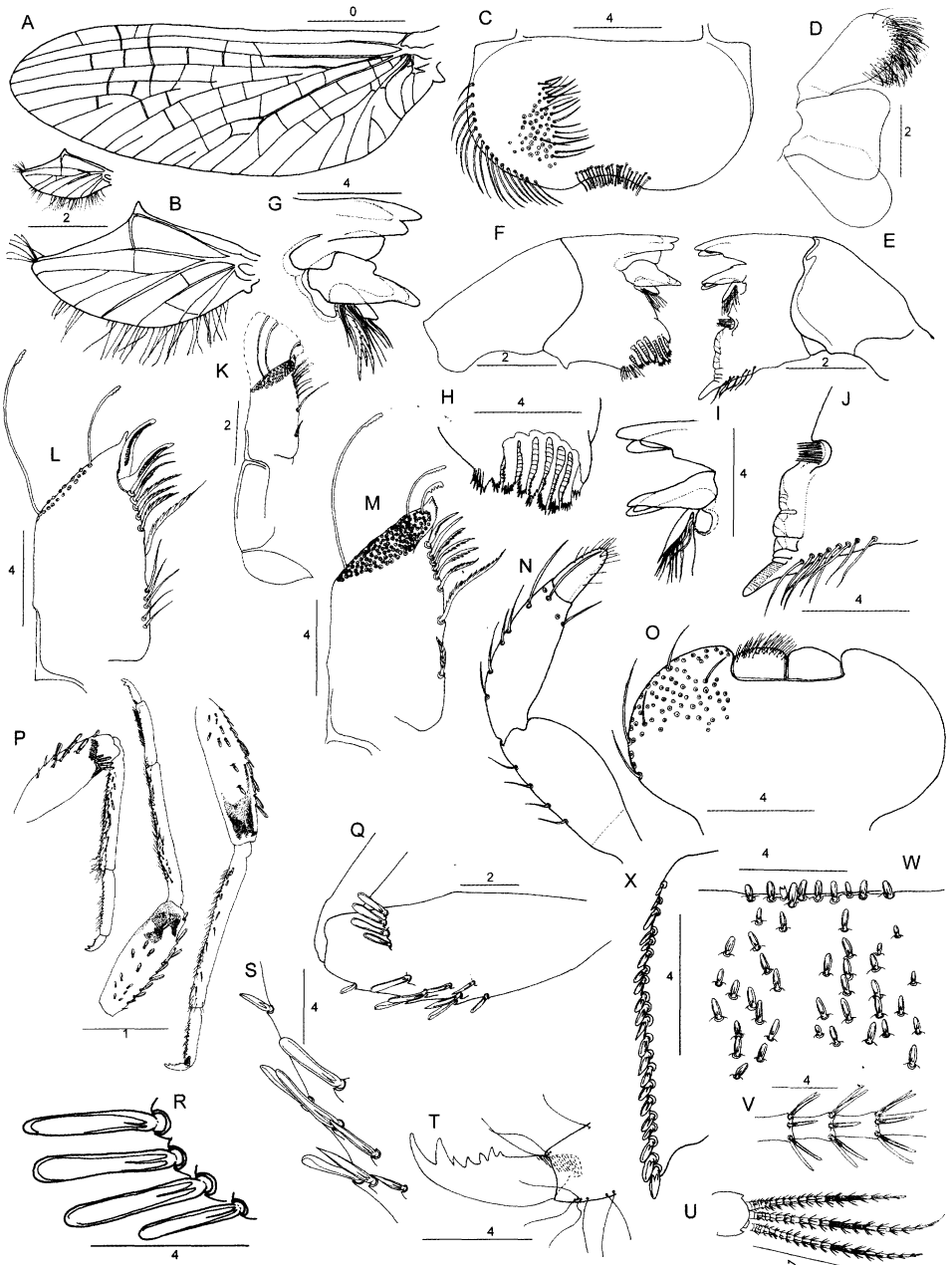


Figure 6. *Teloganopsis puigae* n. sp. (a) wings; (b) hind wing; (c) labrum; (d) hypopharynx; (e–f) left and right mandibles; (g–h) incisor and molar area of right mandible; (i–j) incisor and molar area of left mandible; (k) right maxilla in dorsal view; (l) right maxilla in dorsal view; (m) left maxilla in ventral view; (n) labial palp; (o) labium; (p) set of legs; (q) forefemur; (r–s) setae in dorsal surface and margin of forefemur; (t) claw of foreleg; (u) caudal filaments; (v) detail of caudal filament; (w) detail of abdominal tergite; (x) lateral margin of abdominal tergite. Scale: 0 = 1 mm, 1 = 0.5 mm, 2 = 0.15 mm, 4 = 0.1 mm.

the middle of wing; Sc, RA and crossveins between them as *T. media* (Figures 3f, 6b). Genitalia (Figures 3g–h), with similar characteristics as those *T. media*; third segment of forceps completely rounded.

Female subimago

Body length 5.3 mm; forewing length 4.3 mm; hind wing length 0.8 mm. General colouration similar to the male, but frons, vertex and occiput whitish, compound eyes black, and pterothorax brownish. Other characters as male subimago, except for usual sexual differences.

Larva

Body length 4.2 mm (5.4 mm with caudal filaments). General colouration dark brown with some yellowish maculae on thorax and abdomen (Figures 4b, e, h, l). Head sutures and antennae whitish. Legs light-brown or whitish with dark-brown marks in proximal and distal areas of femur and tibia (Figures 4b, h); tarsal segments brown. Caudal filament light brown with proximal segments dark-brown, although some specimens may also exhibit a dark-brown medial band (Figure 6u).

Head. Head without tubercles or projection (Figures 4e, h). Compound eyes black, in males dorsal portion whitish. Labrum and hypopharynx similar to those *T. media* (Figures 6c–d). Mandibles as those of *T. media*, except as following: mandibles slightly slender with a cuticular thickening that cross in width the dorsal surface (Figures 6e, f); left mandible with incisor constituted by four teeth, some feathered setae also present on prostheca (Figures 6g); right mandible with a three-teeth kinetodontium and a tuft of short setae in a concavity close to the molar area (Figures 6i–j). Maxillae more quadrangular than those of *T. media* (Figures 2a–d, 6k–m), ventral surface with a single large and feathered seta at base of maxilla (Figures 2a, 6m). Labium and submentum as in *T. media* (Figures 6n–o), but setae of outer margin of first segment of labial palp straight, thin and short (Figure 6n).

Thorax. Prothorax narrower than pterothorax, with antero-lateral angles moderately expanded, and without any kind of tubercles or protuberances (Figures 4e, h). All legs similar in shape and pigmentation (Figure 6p). Femora slender, ca. 2.5–3 times longer than wide, with dorsal edges of femora with several thick, long and blunt setae arranged in two rows (in forefemur reduced to the apical two-thirds) (Figures 6q–s). Anterior face of forefemur with a transverse row of 4–5 thick, long and blunt setae distally (Figures 6q–r). Ventral edge of tibia with numerous pointed setae arranged in different rows. Claws with subapical denticle as long as apical one (Figure 6t).

Abdomen. Abdominal tergites without any type of protuberances, spines or cuticle projection (Figure 4l). Small spatulate setae forming a row laterally and in the middle of posterior margins, arranged in two groups at each side of median line on tergites (Figures 6w–x). Posterolateral angles of abdominal segments and gill features as in *T. media* (Figures 4l, 6x). Caudal filaments with a whorl of pointed setae in the posterior edge of each segment, setae as long as segment (Figure 6v).

Egg

Length 151.2 μm ; width 100 μm . Egg ovoid with one polar cap bell-shaped (Figure 7a), constituted of uncountable filaments slightly spiralised, each one apically swelling (Figure 7b). Several lateral attachment structures (LAS) in subpolar areas.

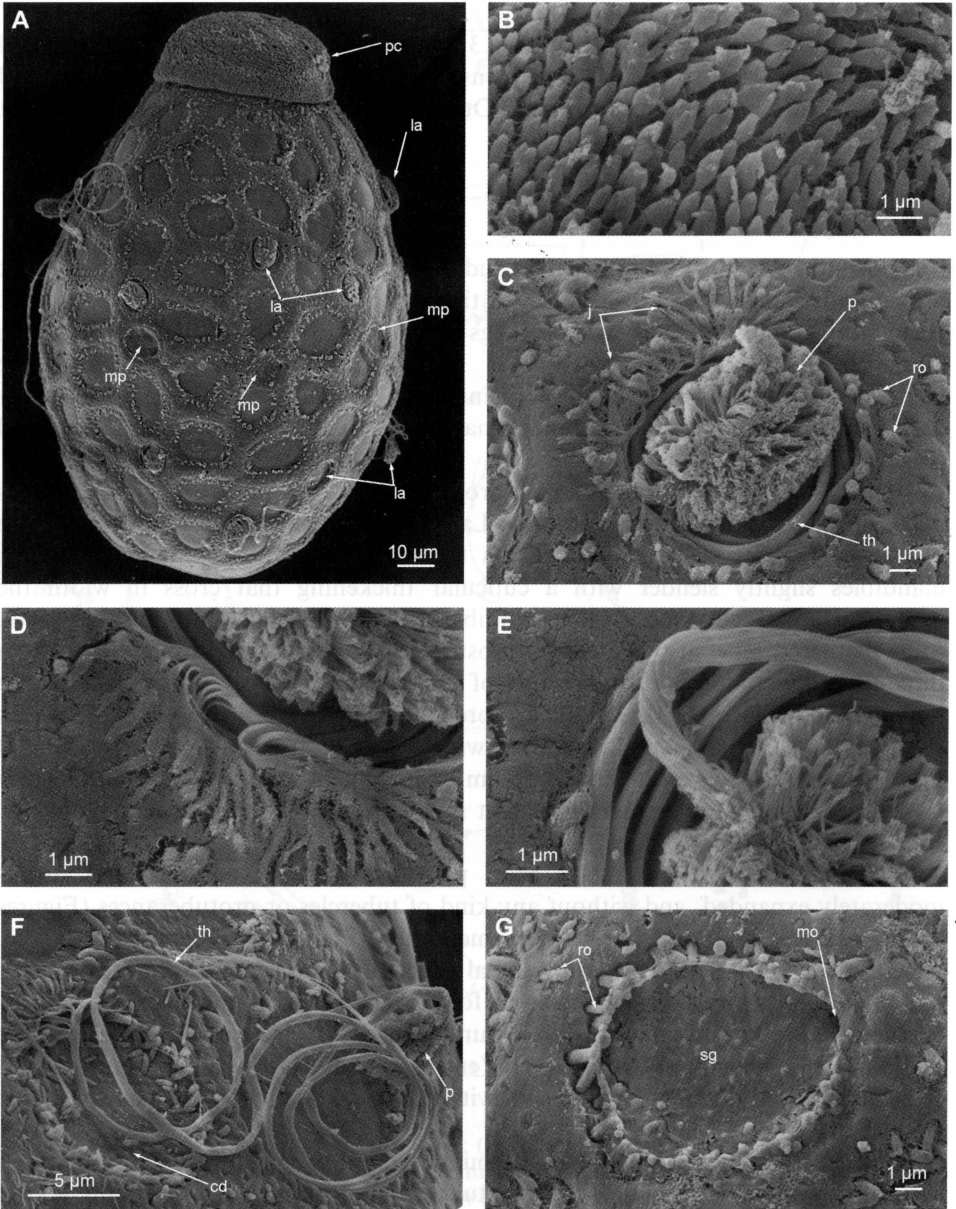


Figure 7. *Teloganopsis puigae* n. sp. Egg morphology: (a) whole egg; (b) detail of polar cap filaments; (c) packing arrangement of lateral attachment structure; (d) detail of thread filaments and chorion joint; (e) detail of thread and pad joint; (f) lateral attachment structure uncoiled; (g) micropyle. Abbreviations: *cd*: chorion depression; *j*: chorion–thread joint; *la*: lateral attachment structure; *mo*: micropylar opening; *mp*: micropyle; *p*: pad of LAS; *pc*: polar cap; *ro*: rod tubercles; *sg*: sperm guide; *th*: thread.

LAS made up of a thread and an oval-pad (Figure 7c); thread constituted by several flattish and weakly twisted filaments (Figures 7d–e), oval-pad formed by numerous microfilaments (Figures 7c, e); thread and pad joint laterally (Figure 7e); LAS coil-arranged on a chorionic circular depression (Figure 7f); thread and chorion joint in the margin of chorion circular depression (Figures 7c–d). Micropyles tagenoform-type in a variable number on equatorial area (Figures 7a, g). Chorionic sculpturing constituted by a geometric macro-relief pattern, with strand raised and mesh depressed (Figure 7a); strand surfaces with uncountable hollows and small rod protuberances (Figures 7f–g).

Distribution

So far known only from the island of Borneo.

Etymology

We named this species in honour of the Spanish hydrobiologist Dr M^a Angeles Puig.

Affinities

Subimago of *T. puigae* is distinguished from other *Teloganopsis* species, except *T. media*, by the characteristics of hind wing. It differs from *T. media* by the pigmentation of body and ventral area of compound eyes. At the larval stage, the shape of the apex of the maxilla, especially the canine, separates *T. puigae* from all other *Teloganopsis* species, except *T. media*, from which it can be told by the absence of broad round tubercles of thorax and the blunt and long setae forming a transverse row in distal margin of dorsal surface of forefemur. Eggs of *T. puigae* are very similar to those of *T. deficiens*, *T. albai*, and *T. brocha*, but differ from those of *T. hispanica* in the chorion pattern, and from *T. maculocaudata* and *T. mesoleuca* in chorion pattern and LAS arrangement.

Key to mature larvae of *Teloganopsis*

- | | |
|--|-------------------------|
| 1A. Broad and round tubercles on thorax (Figures 4d, g)..... | <i>T. media</i> |
| 1B. Thorax without tubercles (Figures 4e, h) | 2 |
| 2A. Unpaired projection at posterior margin of abdominal segments (Tshernova 1952: figure 82)..... | <i>T. gracilis</i> |
| 2B. Posterior margin of abdominal segments without projection (Figure 4l) | 3 |
| 3A. Maxillary palp present (Figure 2i) | 4 |
| 3B. Maxillary palp absent (Figures 2c, g)..... | 5 |
| 4A. Maxillary canine without teeth and lateral margin serrate. Macro relief of chorion with mesh as circular elevation (Figure 2n)..... | <i>T. maculocaudata</i> |
| 4B. Maxillary canine with three teeth and lateral margin smooth. Macro relief of chorion with mesh as circular depression (Figure 2p)..... | <i>T. mesoleuca</i> |
| 5A. Mandible canine elongated (Kang and Yang 1995: figure 5e)..... | 6 |
| 5B. Mandible canine non elongated (Figures 5c–d)..... | 8 |
| 6A. Inner margin of maxilla with a continuous row of setae (Figure 2g)..... | |
| | <i>T. brocha</i> |
| 6B. Inner margin of maxilla with two groups of setae (Figure 2i)..... | 7 |

- 7A. Antero-lateral angle of prothorax expanded (Gose 1980: figure 25) *T. chinoi*
- 7B. Antero-lateral angle of prothorax not expanded (Figure 4h) *T. punctisetae*
- 8A. Body pigmentation with light longitudinal bands (Tong and Dudgeon 2000: figure 1) *T. jinghongensis*
- 8B. Body pigmentation uniform (Figure 4b) 9
- 9A. Whole posterior margin of forefemur with setae (Jacob 1993: figure 2b) ... *T. oriens*
- 9B. Setae at posterior margin of forefemur from middle-length to distal end (Figure 6q)..... 10
- 10A. Setae on dorsal surface of forefemur acuminate (Figure 5r). Glossae longer than broad (González del Tánago and García de Jalón 1983: figure 2e)..... *T. hispanica*
- 10B. Setae on dorsal surface of forefemur spatulate (Figure 6r). Glossae of different ratios 11
- 11A. Teeth of maxillary canine oriented upwards (Figure 2d). Glossae broader than long (Figure 6o)..... *T. puigae* n. sp.
- 11B. Teeth of maxillary canine oriented downwards (Figure 2l). Glossae as long as broad (González del Tánago and García de Jalón 1983: figure 3g)..... 12
- 12A. Denticle-shape of lateral margin of canine blunt. Body pigmentation yellowish or light-brown without any kinds of banding..... *T. albai*
- 12B. Denticle-shape of lateral margin of canine acuminate. Body pigmentation brown, with dark bands on legs and caudal filaments *T. deficiens*

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References

- Allen, R.K. (1965), 'A review of the subfamilies of Ephemerellidae (Ephemeroptera)', *Journal of Kansas Entomological Society*, 38, 105–123.
- Allen, R.K. (1980), 'Geographic distribution and reclassification of the subfamily Ephemerellinae (Ephemeroptera: Ephemerellidae)', in *Advances in Ephemeroptera Biology*, eds. J.F. Flannagan and K.E. Marshall, New York: Plenum Press, pp. 71–91.
- Allen, R.K. (1984), 'A new classification of the subfamily Ephemerellinae and the description of a new genus', *Pan-Pacific Entomologist*, 60, 245–247.
- Belov, V.V. (1979), 'A new mayfly genus (Ephemeroptera, Ephemerellidae) in the USSR fauna', *Doklady Akademii Nauk Ukrainiskoi SSR, Ser. B*, 1979, 577–580.
- Derleth, P. (2003), Benthic macroinvertebrates and logging activities: a case study in a lowland tropical forest in East Kalimantan (Indonesia, Borneo), Ph. D. Thesis, School of Architecture, Civil and Environmental Engineering, Swiss Federal Institute of Technology, Lausanne.
- González del Tánago, M., and García de Jalón, D. (1983), 'New Ephemerellidae from Spain (Ephemeroptera)', *Aquatic Insects*, 5, 147–156.
- Gose, K. (1980), 'The mayflies of Japanese. Key to families, genera and species', *Aquabiology (Nara)*, 2, 366–368.

- Ikonomov, P. (1961), 'Eintagsfliegen (Ephemeroptera) Mazedoniens. Fam. Ephemerellidae', *Acta Musei Macedonici Scientiarum Naturalium*, 8, 53–74.
- Imanishi, K. (1937), 'Mayflies from Japanese torrents VII. Notes on the genus *Ephemerella*', *Annotationes Zoologicae Japonenses*, 16, 321–329.
- Ishiwata, S.-I. (1987), 'Structure and keys of the Family Ephemerellidae (1). Structure and keys to genera from the family Ephemerellidae', *Aquatic Organisms in Kanagawa Prefecture*, 9, 27–34.
- Jacob, U. (1993), 'Zur Systematik und Verbreitung der europäischen Ephemerellidae (Ephemeroptera)', *Verhandlungen Westdeutscher Entomologentag*, 1992, 101–110.
- Jacobus, L.M., and McCafferty, W.P. (2006), 'A new oriental species of *Uracanthella* (Ephemeroptera: Ephemerellidae) from Thailand and Vietnam', *Entomological News*, 117, 276–280.
- Jacobus, L.M., and McCafferty, W.P. (2008), 'Revision of Ephemerellidae Genera (Ephemeroptera)', *Transactions of the American Entomological Society*, 134, 185–274.
- Jacobus, L.M., and Sartori, M. (2004), 'Review of the genus *Hyrtanella* (Ephemeroptera: Ephemerellidae)', *Zootaxa*, 785, 1–12.
- Kang, S.C., and Yang, C.T. (1995), 'Ephemerellidae of Taiwan (Insecta, Ephemeroptera)', *Bulletin of National Museum of Natural Science*, 5, 95–116.
- Kluge, N. Yu. (1997), 'New subgenera of Holarctic mayflies (Ephemeroptera: Heptageniidae, Leptophlebiidae, Ephemerellidae)', *Zoosystematica Rossica*, 5, 233–235.
- Kluge, N. Yu. (2004), *The Phylogenetic System of Ephemeroptera*, Dordrecht: Kluwer Academic Publishers.
- McCafferty, W.P., and Wang, T.-Q. (2000), 'Phylogenetic systematics of the major lineages of pannota mayflies (Ephemeroptera: Pannota)', *Transactions of the American Entomological Society*, 126, 9–101.
- Morgan, A.H. (1911), 'May-flies of Fall Creek', *Annals of the Entomological Society of America*, 4, 93–119.
- Sartori, M., Derleth, P., and Gattolliat, J.-L. (2003), 'New data about the mayflies (Ephemeroptera) from Borneo' in *Research Update on Ephemeroptera & Plecoptera*, ed. E. Gaino, Perugia: Università di Perugia, pp. 403–406.
- Soldán, T. (1982), 'A redescription of *Ephemerella maculocaudata* Ikonov with notes on Balkan species of the genus *Ephemerella* (Ephemeroptera, Ephemerellidae)', *Acta Zoologica Bulgarica*, 20, 44–50.
- Studemann, D., and Landolt, P. (1997), 'Egg of Ephemerellidae (Ephemeroptera)', in *Ephemeroptera & Plecoptera: Biology-Ecology-Systematics*, eds. M. Sartori and P. Landolt, Fribourg: MTL, pp. 362–371.
- Studemann, D., Landolt, P., and Tomka, I. (1989), 'Contribution to the study of European Ephemerellidae (Ephemeroptera). II. Description of the winged stages of *Ephemerella ikonovi* Puthz, 1971, and *Serratella albai* González del Tánago & García de Jalón, 1983', *Bulletin de la Société Entomologique Suisse*, 62, 119–127.
- Studemann, D., Landolt, P., and Tomka, I. (1995), 'Eggs of the European Ephemerellidae (Ephemeroptera)', in *Current Directions in Research on Ephemeroptera*, eds. L. Corkum and J. Ciborowski, Toronto: Canadian Scholar's Publishing, pp. 407–422.
- Studemann, D., and Tomka, I. (1987), 'Contribution to the study of European Ephemerellidae (Ephemeroptera). I. Completion of description of three endemic Iberian species', *Bulletin de la Société Entomologique Suisse*, 60, 361–378.
- Studemann, D., and Tomka, I. (1989), 'Contribution to the study of European Ephemerellidae (Ephemeroptera). III. Synonymy of *Ephemerella maculocaudata* Ikonov, 1961, syn. n. with *Ephemerella mesoleuca* (Brauer, 1857)', *Bulletin de la Société Entomologique Suisse*, 62, 129–130.
- Tong, X., and Dudgeon, D. (2000), 'Ephemerellidae (Insecta: Ephemeroptera) from Hong Kong, China, with descriptions of two new species', *Aquatic Insects*, 22, 197–207.
- Tshernova, O.A. (1952), 'Mayflies of the Amur River Basin and nearby waters and their role in the nutrition of Amur fishes', *Trudi Amurskoi Ikhtiologicheskoi Ekspeditsii 1945–1949* gg, 3, 229–360.
- Tshernova, O.A., Kluge, N. Yu., Sinitshenkova, N.D., and Belov, V.V. (1986), 'Order Ephemeroptera – Mayflies', in *Identification of Insects of Far East USSR*, Vol. 1, ed. P.A. Ler, Leningrad: Leningrad Press, pp. 99–142.

- Ubero-Pascal, N., and Puig, M.A. (2009), 'New type of egg attachment structure in Ephemeroptera and comparative analysis of chorion structure morphology in three species of Ephemerellidae', *Acta Zoologica*, 90, 87–98.
- Ubero-Pascal, N., Puig, M.A., and Fortuño, J.M. (2005), 'New application of air-drying techniques for studying Ephemeroptera and Plecoptera eggs by Scanning Electron Microscopy', *Microscopy Research and Technique*, 68, 264–271.
- Ulmer, G. (1939), 'Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln', *Archiv für Hydrobiologie, Supplement*, 16, 443–692.
- Xu, J.-Z., You, D.-S., and Hsü, Y.-C. (1984), 'A new species of *Ephemerella* (Ephemeroptera: Ephemerellidae)', *Acta Zootaxonomica Sinica*, 9, 413–415.
- Zhou, C.F., Jacobus, L.M., and McCafferty, W.P. (2006), 'New synonyms of *Serratella jinghongensis* (Ephemeroptera: Ephemerellidae) from China', *Entomological News*, 117, 237–238.

Appendix 1. Morphological characters used in the phylogenetic reconstruction

A. Larva

- General pigmentation: uniform (Figures 4a, b) = 0; with light longitudinal bands = 1.
- Occipital tubercles absent (Figures 4e, f) = 0; present (González del Tánago and García de Jalón 1983: figures 3b, f) = 1.
- Labrum: rectangular with round distal margin = 0 (Figure 5a); trapezoidal (Kang and Yang 1995: figure 5g) = 1.
- Canine of mandible: normal (Figures 5c, d) = 0; elongated (Kang and Yang 1995: figure 5e) = 1.
- Outer margin of mandible: rounded = 0 (Figures 5c, d); angular (Kang and Yang 1995: figure 5e) = 1.
- Shape of maxilla: falciform (Figure 2i) = 0; quadrangular (Figures 2a, g) = 1.
- Apex of maxilla: pointed (Figure 2k) = 0; truncated (Figure 2c, g) = 1.
- Teeth in maxillary canine: wide (Figure 2j) = 0; small and thin, visible by light microscopy (Figures 2b, d) = 1; tiny and thin, not visible by light microscopy (Figure 2h) = 2; without teeth = 3.
- Teeth number in maxillary canine: three = 0; two = 1; none = 2.
- Teeth orientation in maxillary canine: downwards (Figure 2i) = 0; upwards (Figure 2d) = 1.
- Crown of setae in maxillary apex: reduced (Figure 2i) = 0; on the whole apex (Figures 2a, f) = 1.
- Crown of setae in maxillary apex extended to the ventral side: yes (Figures 2a, i) = 0; not extended (Figures 2e, f) = 1.
- Crown of setae delimited partially by the lateral margin of maxillary canine on ventral surface: yes (Figures 2a, i) = 0; no (Figures 2e, f) = 1.
- Inner margin of maxillary canine: concave (Figures 2i, j) = 0; convex (Figures 2a, b) = 1.
- Denticles of lateral margin of maxillary canine: serrate = 0; denticulate (Figure 2b) = 1; absent or smooth (Figure 2i) = 2.
- Maxillary dentisetae: present (Figures 2b, l) = 0; absent (Figures 2e, f) = 1.
- Setae at inner margin of maxilla: forming two groups (Figures 2c, k) = 0; forming a continuous row (Figures 2f, g) = 1.
- Number and arrangement of setae at base of maxilla on ventral surface: one (Figure 2a) = 0; in a row (Figures 2i, 5v) = 1; in a group = 2.
- Shape of setae at base of maxilla on ventral surface: thick (Figure 2a) = 0; thin = 1.
- Setae arrangement at base of maxilla in dorsal surface: a row (Figure 2c) = 0; a group (Figure 2k) = 1.
- Maxillary palp: absent (Figures 2a, g) = 0; present (Figure 2i) = 1.
- Hypopharynx apex: convex (Studemann and Tomka 1997: figure 22e) = 0; concave (Figure 5b) = 1.
- First segment of labial palp: wider than second segment (Studemann and Tomka 1997: figure 22a) = 0; as wide as second segment (Figure 5m) = 1.
- Proximal margin of third segment of labial palp: narrowest than distal margin of second segment (González del Tánago and García de Jalón 1983: figure 3g) = 0; as wide as distal margin of second segment (Figure 5n) = 1.

25. Ratio of glossae: longer than broad (González del Tánago and García de Jalón 1983: figures 2e, 3g) = 0; as long as broad (González del Tánago and García de Jalón 1983: figure 1e) = 1; broader than long (Figure 6o) = 2.
26. Antero-lateral angle of prothorax: not expanded (Jacobus and McCafferty 2006: figure 1) = 0; expanded (Figure 4g) = 1.
27. Prothorax as wide as pterothorax (Ishiwata 1987: figure 11a) = 0; narrower than pterothorax (Figure 4h) = 1.
28. Setae at posterior margin of forefemur: on the whole margin (Jacob 1993: figure 2b) = 0; from middle-length to distal margin (Figure 6q) = 1.
29. Setae on dorsal surface of distal margin of forefemur: if present, do not form a perpendicular row to longitudinal axis (Jacob 1993: figures 2a, b) = 0; form a row of 2–5 units perpendicularly to longitudinal axis (Figure 6q) = 1.
30. Shape of setae on dorsal surface of forefemur: spatulate (Figure 6r) = 0; acuminate (Figure 5r) = 1.
31. Subapical denticle of claw: smaller than apical denticle (Studemann and Tomka 1987: figure 4) = 0; as long as apical denticle (Figure 6t) = 1.
32. First denticle of claws: as broad as others (Figure 6t) = 0; broader than the others, but smaller than sub-apical one (Tshernova 1954: figure 86) = 1.
33. Posterior margin of abdominal tergites: with projection and/or longitudinal aristas (Jacob 1993: figure 2a) = 0; without projection (Figure 4l) = 1; with projection and protuberances (Studemann and Tomka 1987: figure 2) = 2.
34. Setae on abdominal tergites: form a wide group to each side of medial area (Figure 6w) = 0; setae sparse in medial area = 1; without this type of setae (Figure 4j) = 2.
35. Setae at distal margin of abdominal tergites: without setae in a medial line (Jacob 1993: figures 2a, b) = 0; a uniform row (Figure 4l) = 1.
36. Setae on head: absent = 0; with microtrichia-like setae = 1; with star-like setae (Studemann and Tomka 1987: figure 3) = 2.
37. Postero-lateral margins of abdominal segments: prolonged and expanded (Studemann and Tomka 1987: figure 19) = 0; expanded but not prolonged (Studemann and Tomka 1987: figure 2) = 1; prolonged but not expanded (Jacob 1993: figure 2b-left) = 2; not prolonged and not expanded (Figures 4j, k) = 3.
38. Setae on caudal filament: form a whorl on each segment and/or a lateral row at full length of caudal filaments (Jacob 1993: figure 2a) = 0; form a whorl at distal margin of each segment and a lateral row from the middle of caudal filament to the tip (Ikononov 1961: figure 1) = 1; form a whorl at the apical margin of each segment, without lateral rows (Figure 6v) = 2.
39. Gill VI: ventral lobe not bifurcate (Kluge 2004: figure 91c) = 0; ventral lobe bifurcate (Kluge 2004: figure 91d) = 1.
40. Shape of gills: not acuminate (Jacob 1993: figure 2a-left) = 0; acuminate (Ikononov 1961: figure 4.1) = 1.

B. Imago/subimago

41. Forewing shape: triangular (Kluge 2004: figure 95a) = 0; elliptic (figure 6a) = 1.
42. Intercalary veins of forewing: not attached to principal veins (Figure 6a) = 0; attached to principal veins (Kluge 2004: figure 95a) = 1.
43. Hind wing costal projection: not developed (Zhou et al. 2006: figure 1) = 0; well-developed (Figures 3c, f) = 1.
44. Hind wing area between Sc and RA: several slight cross-veins (Zhou et al. 2006: figure 1) = 0; a single strong cross-vein connecting (Figures 3c, f) = 1.
45. Hind wing subcosta-vein length: reaches the apex of foremargin (Zhou et al. 2006: figure 1) = 0; terminates close the strong cross-vein (Figures 3c, f) = 1.
46. Penis lobes: separated at base and very divergent at tip (Jacob 1993: figure 1-upper row) = 0; separated at middle-length and divergent at tip (Figure 3e) = 1; not divergent at tip and with a notch of variable size (Studemann and Tomka 1987: figures 26a, 28a) = 2.
47. Second segment of forceps: broad at base and apex (Studemann and Tomka 1987: figure 24) = 0; broad at base but decreasing in width towards apex (Figure 3e) = 1.

48. Third segment of forceps: large (as least twice as long as broad), oval or elliptic (Studemann and Tomka 1987: figures 26a, 28a) = 0; small, spherical or ovoid (Figure 3e) = 1.
49. Tip of penis lobes: not dorsally curved (Studemann and Tomka 1987: figure 28b) = 0; dorsally curved (Studemann and Tomka 1987: figure 26b) = 1.

C. Eggs

50. Arrangement of threads in LAS: folded (Ubero-Pascal and Puig 2009: figures 1–2) = 0; coiled = 1 (Figure 7f).
51. Joint of thread and terminal pad in LAS: in the centre of pad (Ubero-Pascal and Puig 2009: figure 1d) = 0; in one side of pad (Figure 7e) = 1.
52. Arrangement of LAS on chorion depression: yes (Figure 7f) = 0; not (Figure 2m) = 1.
53. Number of micropyles: < 3 units = 0; ≥ 3 units = 1.
54. Rod protuberances on chorion surface: present (Figures 7a, c, f) = 0; absent (Figures 2n, p) = 1.
55. Furrow demarcating the mesh-units: present (Ubero-Pascal and Puig 2009: figure 7b) = 0; absent (Figure 7a) = 1.
56. Type of geometric macro relief: strand as depression and mesh elevated (Figure 2n) = 0; strand as ridge and mesh as depression (Figure 7a) = 1.
57. Mesh shape: polygonal (Figure 7a) = 0; rounded (Figures 2n, p) = 1.
58. Mesh surface: smooth (Figure 7a) = 0; punctuate (Figures 2n, p) = 1.
59. Strand surface: smooth (Figure 2n) = 0; with hollows and protuberances (Figures 7f, g) = 1.