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A revision of Oriental Teloganodidae (Insecta, Ephemeroptera, Ephemerelloidea)

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Abstract

Based on the examination of the type series of *Cloe tristis* Hagen, 1858 (type species of the genus *Teloganodes* Eaton, 1882) and material housed in several institutions, a revision of Oriental Teloganodidae is proposed. A lectotype is designated for *Teloganodes tristis* (Hagen, 1858) and the genus is redefined. The species *T. major* Eaton, 1884, is a subjective junior synonym of *T. tristis* Hagen, 1858 **(syn. nov.)**. The genus *Macafertiella* Wang, 1996 is a subjective junior synonym of *Teloganodes* Eaton, 1882 (**syn. nov**.). A phylogenetic analysis is performed on all available nymphs. *Teloganodes* is restricted to Sri Lanka and the Western Ghats of India and encompasses the type species and *T. dentatus* Navás, 1931, *T. insignis* (Wang & McCafferty, 1996) **(comb. nov.)**, and the following new species: *T. tuberculatus* **sp. nov.** (Sri Lanka), *T. kodai* **sp. nov.** (India), *T. jacobusi* **sp. nov.** (Sri Lanka) and *T. hubbardi* **sp. nov.** (Sri Lanka). The type material of *T. dentata is* redescribed. Species from Southeast Asia are assigned to two new genera. *Dudgeodes* **gen. nov**. includes the type species *D. pescadori* **sp. nov.** (Philippines) and *D. lugens* (Navás, 1933) **comb. nov.** (China), *D. hutanis* **sp. nov.** (Borneo), *D. stephani* **sp. nov.** (Borneo), *D. ulmeri* **sp. nov.** (Java, Sumatra), and *D. celebensis* **sp. nov.** (Sulawesi). The genus *Derlethina* **gen. nov**. is established for *D. eloisae* **sp. nov.** (Borneo). The egg morphology is presented for the first time for the family Teloganodidae. Affinities within the family and between related families are discussed and a key to distinguish all species known at the larval stage is proposed.

Key words: Systematics, new species, new genus, Sri Lanka, India, China, Indonesia, Malaysia, Philippines

Introduction

Currently, the family Teloganodidae (Allen 1965) encompasses a restricted number of ephemerelloid mayflies with a disjunct distribution through the Afrotropical and Oriental realms. In Africa, according to McCafferty & Wang (2000), four genera are known only from the southernmost part of the continent (South Africa, Cape Province): *Ephemerellina* Lestage, 1924 (1 species), *Lithogloea* Barnard, 1932 (1 species), *Lestagella* Demoulin, 1970 (1 species) and *Nadinetella* McCafferty & Wang, 1998 (2 species). One genus, *Manohyphella* Allen, 1973, is found in Madagascar, with tentatively 3 species (McCafferty & Benstead 2002). The Oriental Realm is home to two genera: *Teloganodes* Eaton, 1882 (4 species) widespread from India and Sri Lanka to the Philippines and Borneo and *Macafertiella* Wang, 1996 (1 species) recorded only from Sri Lanka at the moment.

In the nymphal stage, the Teloganodidae can be separated from other families of Ephemerelloidea by the presence of gills on abdominal segment II (contrary to Ephemerellidae), the absence of gills on segment VII (contrary to Austremerellidae, Ephemerellidae and Vietnamellidae), glossae only partially fused with paraglossae (contrary to Tricorythidae), general shape of the body (contrary to Machadorythidae), male eyes divided in two parts (contrary to Ephemerythidae, Teloganellidae and most Leptohyphidae). A unique character shared by all teloganodid nymphs is the presence of stout spatulate setae on margins of coxal projections (Jacobus & McCafferty 2006).The Oriental lineage of Teloganodidae can be separated from the Afrotropical lineage by the absence of gills on abdominal segment I and the reduction of the median caudal filament giving the nymphs a two-tailed appearance.

Historically, the first species of the family was described as *Cloe tristis* by Hagen (1858) on the basis of female subimagos, caught at Rambodde on the island of Ceylon (see Hagen 1859 for a discussion of the type locality name). *Cloe tristis* was used by Eaton (1882) to establish the genus *Teloganodes*. Later Eaton (1884) described another species, *T. major,* from the same locality as *T. tristis* and also from female subimagos. Finally, two other species were described in the 1930's, namely *Teloganodes dentata* Navás, 1931 from Khandala (India), based on numerous adult specimens, and *T. lugens* Navás, 1933 from Chekiang, Chusan (China) based on a single female subimago (Navás 1931; 1933). Except for *T. tristis*, none of these species have been reported since their original description.

The first description of the nymph of *T. tristis* was provided by Ulmer (1939) based on specimens from Java and Sumatra together with imagos of both sexes. Since then, the species has been reported from the Philippines (Hubbard & Pescador 1978), Borneo, Sulawesi, Lombok (Edmunds & Polhemus 1990), and China (Tong & Dudgeon 2000).

Recently, Wang created the genus *Macafertiella* for the species *M. insignis* Wang & McCafferty, 1996 known only in the nymphal stage from Sri Lanka (Wang & McCafferty 1996). According to these authors, this genus is easily distinguished from the *Teloganodes* nymphs described by Ulmer (1939) because it possesses gills on abdominal segments II–VI instead of II–V.

During a survey on benthic macroinvertebrates in a lowland dipterocarp forest in Borneo (Derleth 2003), two species of Teloganodidae were found. One fit the concept of *Teloganodes tristis* sensu Ulmer (1939) whereas the other presented features that challenged its placement in the genus *Teloganodes* (Sartori *et al*. 2003). In order to solve the problem, a comparison with the type material was needed. Thanks to the courtesy of Dr Philip D. Perkins and Stefan Cover, we were able to study the type series of *Cloe tristis* Hagen deposited at the Museum of Comparative Zoology, Harvard University, Cambridge, USA. We were able to do the same with the types of *Teloganodes major* (Dr. David Goodger, Natural History Museum, London, UK) and one existing type specimen of *Teloganodes dentata* (Dr. Jean Legrand, Musée National d'Histoire Naturelle, Paris, France).

In this work, we will first redescribe the type species of the genus *Teloganodes*. Then we will perform a cladistic analysis and make an account of the species found in the Oriental realm, based on the G. Ulmer material housed in the Zoologisches Museum, Hamburg, Germany, on new material deposited in the Museum of Zoology, Lausanne, Switzerland, as well as at the Florida A&M University, including material collected by Hubbard during his stay in Sri Lanka (see Hubbard & Peters 1984 for a review). Eggs for SEM photographs have been treated according to the techniques developed by Ubero-Pascal *et al.* (2005).

Redescription of *Cloe tristis* Hagen, 1858

The type series # 33520 contains 4 pinned specimens that are syntypes of *Cloe tristis*. One specimen is a female imago and the last three are female subimagos. The imago and two subimagos are in poor condition with wings, head or abdomen missing. The last female subimago is in good condition and has been designated as **lectotypus**. It bears the following labels:

i) MCZ Type 33520 3 [red label]
ii) Hagen. [white label typewritten]
iii) 21. [green label typewritten]
iv) Ceylon Nietner [white label handwritten]

This specimen has been treated with trisodic phosphate 0.35% for 24 hours and then removed from the pin and stored in 75% ethanol (Van Cleave & Ross 1947). Original labels are kept dried with the naked pin, whereas the lectotypus bears a copy of the information.

Condition. Left hindleg, right fore- and hindlegs missing.

Size. Body length: 6.5 mm; forewing length: 10.2 mm; hindwing length: 1.5 mm.

Description. General colouration medium brown; thorax dark brown; mesoscutellum without posterior processes. Legs yellowish-brown, claws dissimilar, one obtuse, the other hooked; tarsi without distal hump; tibiae and tarsi covered with setae. Wings uniformly light brown, without any markings. Forewing almost acute at the apex, pterostigmatic area with 4–6 crossveins; numerous crossveins in the radial field; MP_2 well developed but not connected to MP_1; 4 intercalary veins between CuA and CuP (Fig. 1). Hind wing broad:

ratio length/width (measured according to Hubbard 1995), ca. 1.5. Three longitudinal veins visible, the middle forked before the costal process. Two cross veins visible just under the costal process that is asymmetrically rounded (Fig. 3).

Abdominal terga dark brown, tinted with black markings laterally; posterolateral spines visible on segments VII–IX. Gill sockets visible on segments II–VI; subanal plate slightly pointed.

Cerci whitish, with dark rings at each segment; median filament absent.

Eggs pear-shaped; chorionic surface covered by a polygonal mesh; one polar cap, well developed and attached to egg by sharp triangular structures (Fig. 102); opposite pole without accessory structures.

Discussion. The specimen examined here fits the description and illustration given by Eaton (1884, plate XV, fig. 24bis), especially in the shape and venation of the wings; however, the most striking character concerns the abdomen and the gill socket vestiges. It is known, especially in ephemerelloid mayflies, that the subimaginal skin retains traces of the gill insertions present in the nymph. Knowing that position of the nymphal gills is critical in the taxonomy of Ephemerelloidea, [“the characteristic of gill socket vestiges on the adult abdomen is obvious and simple to use” (McCafferty & Wang 2000, p. 42)], and allows, at least at the generic level, the association of nymphal and adult stages.

The current concept of *Teloganodes*, especially *T. tristis*, is derived from Ulmer’s work (1939). In his description, the author mentioned gills present on segments II–V (p. 630). This character was confirmed later by McCafferty & Wang (1997) and Tong & Dudgeon (2000). As the female subimago lectotypus of *T. tristis* bears gill socket vestiges on segments II–VI, we can conclude that the nymph must have gills on segments II–VI. Consequently, the concept of *T. tristis* sensu Ulmer (1939) and subsequent authors is obviously not the same as Hagen’s concept. The nymph described by Ulmer cannot belong to *T. tristis*, nor can the adult stages described by him and others (e.g. Ulmer 1924 and subsequent authors).

The genus *Macafertiella* Wang is known only at the nymphal stage and is easily told from *Teloganodes* sensu Ulmer by the presence of gills on segments II–VI (Wang & McCafferty 1996). These authors predicted that, although unknown, the adults of *Macafertiella* will have “gill socket vestiges on abdominal segment [sic] 2–6” (McCafferty & Wang 1997, p. 406). It becomes then extremely credible that *Macafertiella* represents the immature stage of *Teloganodes* Eaton. Accordingly, the genus *Teloganodes* must be redefined and *“T. tristis”* sensu Ulmer, 1939 must represent another taxon.

Cladistic analysis

Material examined. The material available for this study included mainly nymphs from different parts of the Oriental Realm. Examination revealed that these specimens differed greatly with respect to several morphological characters, although the groundplan was superficially the same. We were able to recognize 10 unique taxa, but their supraspecific assignment was difficult because many of characters were distributed irregularly and no clear-cut generic level was evident.

We then performed a cladistic analysis, assigning an Operational Taxonomic Unit (OTU) to each of the 10 taxa. The names used and localities are as follows:

celebensis: Sulawesi, Indonesia
eloisae: Borneo, Indonesia East Kalimantan; Malaysia, Sabah
hubbardi: Sri Lanka
hutanis: Borneo, Indonesia, East Kalimantan
jacobusi: Sri Lanka
kodai: India, Tamil Nadu State
pescadori: Philippines, Luzon Island

stephani: Borneo, Malaysia, Sabah
ulmeri: Indonesia, Sumatra, Java
tuberculatus: Sri Lanka

These OTUs were analyzed together with another teloganodid, *Manohyphella animosa* McCafferty & Benstead, 2002, from Madagascar. Only nymphal characters were used since too few species are actually known at the imaginal stage.

Character variability

Head

The cephalic capsule presents three characters that are variable among the examined material. The margin of the head can be fringed by a row of long setae from behind the eyes up to above the clypeus, as in *eloisae*, *kodai*, *tuberculatus*, whereas this row stops before the clypeus in the other species. The colouration of the upper face of the compound eyes of the male nymphs is generally blackish, whereas it is clearly orange-yellowish in *hubbardi*, *jacobusi*, *kodai* and *tuberculatus*. Finally, the length of the antennae also vary. Most species have a similar number of segments on the funicle, ranging from 13 to 18 (but 10–11 in *tuberculatus*); the total length may be shorter than head width (e.g. *kodai* or *eloisae*) or greater than head width (e.g. *hutanis* or *stephani*).

Mouthparts

The labrum is consistent in terms of shape, but the setae on the dorsal face are variable. They can be arranged in a single row as in *eloisae*, or in multiple rows as in most of the other taxa. The shape of these setae could also be of phylogenetic importance; all setae may be feathered as in *tuberculatus*, or mostly feathered but with some simple setae as in *jacobusi*, or all simple as in *hutanis* or *pescadori*.

The mandibles offer important characters for the diagnosis. They are nevertheless sometimes difficult to interpret because they are subject to wear. When making slide preparations, one needs to select an appropriate nymph whose mandibles seem as new as possible. All Oriental Teloganodidae have a single robust seta in the middle of the outer margin (two in the case of *tuberculatus*), whereas *M. animosa* has a cluster of >10 setae. The outer incisor of the right mandible may be spoon-shaped (i.e. a unique large tooth concave on its inner face) as in *kodai*, or may consist of a single large tooth as in *celebensis*, or the incisor can be indented as in *stephani*. A row of setae is always present below the mola of the right mandible, but this row may be well developed as in *kodai* or reduced as in *eloisae*. The inner incisor of the left mandible always has two teeth, but they may be similar in size as in *kodai*, or one may be larger than the other as in *hubbardi*. There is no row of setae below the mola of the left mandible in the Oriental lineage, compared to those from the Afrotropics, as in *M. animosa*.

The maxillae are very uniform; the maxillary palp is always reduced to a thin seta, and the crown of the galea-lacinia is composed of two dentisetae, serrated on their inner margin, as well as 3–4 stout setae. There is one seta present on the dorsal face of the inner margin of the maxilla at the articulation of the galea-lacinia, whereas the ventral face may bear four feathered setae, as in *tuberculatus* or *jacobusi*, or a single one as in *hutanis* or *pescadori*.

Other mouthparts are less informative. The labium is homogenous, with almost no differences in the shape of the submentum, glossae or paraglossae; the third segment of the labial palp may be more or less developed, and the articulation between first and second segments more or less well marked. The lingua of the hypopharynx may be wide or narrow, and the superlinguae oval or somewhat quadrate.

Thorax

The legs of the Oriental Teloganodidae present important characters, especially in relation to the forelegs. The forefemora of some species are extremely dilated, as in *hubbardi* or *celebensis*. The dorsal surface can bear a transverse row of stout setae as in *eloisae*, or this row may be absent, such as in *tuberculatus*. The posterior margin of the foretibiae generally has a well marked row of thin setae (always thinner than on the anterior margin), but this row may be replaced by scattered thin setae as in *pescadori*. The middle and hind legs generally bear similar ornamentation. The tarsal claws present interesting differences. The ground plan is 3–5 teeth in the middle of the claw followed apically by two large teeth, one on the ventral side and one on the dorsal side, such as in *hutanis* or *jacobusi*. But the ventral tooth may be absent as in *stephani*, or both apical teeth may be absent as in *celebensis*.

Abdomen

Gills may be present on abdominal segments II–VI; gills on segment I are always absent in the Oriental lineage, but present in *M. animosa*. Gills differ in number and shape, but accurate observation requires delicate slide preparation because gill VI is much reduced and difficult to see. The gills on segment II are large, operculate or semioperculate, with an oval dorsal lamella, with margin entire, and with a cluster of fibrillae ventrally. The gills on segment III always consist of a dorsal lamella incised apically and fibrillae ventrally. Gills on segment IV are of the same structure as on segment III, except in *eloisae* where the dorsal lamella is entire and the ventral fibrillae are lacking. The dorsal lamella of gills on segment V can be either entire without ventral fibrillae, as in *hubbardi*, or incised apically without ventral fibrillae, as in *pescadori*, or even incised apically with ventral fibrillae, as in *kodai*. Segment VI generally lacks gills except in *tuberculatus* and *kodai*, where the gills are composed of an entire dorsal lamella without fibrillae. In summary, gills may be present on segments II–IV, II–V or II–VI. The common character is that the last pair of gills always lacks the ventral fibrillae.

Abdominal terga generally bear median tubercles which are more or less developed within and among taxa. They may be well developed on each segment, such as in *tuberculatus*, or absent on the first segments and weakly developed on the last ones, as in *eloisae*, with all possible arrangements in between. The same happens with the posterolateral projections of the abdomen, which are always lacking or weakly developed on segments II–III, but may be well developed on segments VI–IX, as in *hubbardi*, or weakly developed on the same segments, as in *hutanis*, with all possible arrangements in between. Finally, the lateral margins of terga generally bear long, thin setae, but these can be short and thin *(tuberculata)* or short and stout *(kodai)*.
The terminal filament is always reduced in the Oriental lineage, compared to the Afrotropical species, such as *M. animosa*. The ratio between body length and cercal length presents a cline, some taxa having cerci longer than the body, such as in *hubbardi* (ratio ca. 0.8), whereas *tuberculatus* exhibits the shortest cerci compared to body length (ratio ca. 1.6). The whorls of spines on the cerci may be shorter than the corresponding segment, as in *kodai*, or longer as in *stephani*.

Reconstruction. We performed a cladistic analysis using PAUP 4.0b10 (Swofford 2002). Table 1 contains characters and their states for the 10 Oriental taxa and *M. animosa* as outgroup. An explanation of the characters and character states is presented in Table 2. A heuristic search was performed using parsimony as the optimality criterion. Starting tree(s) were obtained via stepwise addition and tree-bisection-reconnection (TBR) was used as the branch-swapping algorithm. Topological constraints were not enforced and trees were unrooted. All characters were considered as unordered and unpolarized.

The heuristic search retained a single most parsimonious tree of 40 steps. The phylogram obtained is presented in Fig. 7. The bootstrap method was applied with 1000 replicates and 50% majority-rule was used as a cut-off (Fig. 8).

The Oriental lineage is clearly separated from the Madagascar species *(Manohyphella animosa)* and char-

acterised by at least three unique characters: terminal filament reduced; setae on the margin of the mandibles reduced to a single seta or, in one case, two setae; and left mandible without setae below the mola. Within this lineage, one can recognize three groups in both the most parsimonious and the consensus trees:

- *eloisae*
- *tuberculatus* + *kodai* + *hubbardi* + *jacobusi*
- *hutanis* + *stephani* + *pescadori* + *celebensis* + *ulmeri*

TABLE 1. Matrix of the nymphal character states used for the phylogenetic reconstruction of the Oriental lineage.

Taxa/Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
tuberculatus	1	1	1	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	2
kodai	0	1	1	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	1	0	1	1	2
hutanis	0	0	0	1	0	0	1	2	1	1	1	2	0	0	1	0	0	1	1	1	0	1	1
stephani	0	0	2	1	0	0	1	2	1	1	1	2	0	0	1	0	1	1	1	1	0	1	1
jacobusi	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	0	1	1	2
hubbardi	0	0	1	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	1	0	1	1	2
pescadori	0	0	0	1	0	0	1	1	1	1	1	2	0	0	0	0	2	1	1	1	1	1	1
celebensis	0	0	0	1	0	0	1	1	0	1	1	2	0	0	1	0	2	1	1	1	1	1	2
eloisae	0	1	0	0	1	0	1	1	1	1	1	1	0	0	1	1	0	2	1	0	0	1	2
ulmeri	0	0	2	1	0	0	1	2	1	1	1	0	1	0	1	0	0	1	1	1	1	1	0
animosa	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

The first group is restricted to the most apotypic *eloisae* which possesses two autapomorphies (hind femora with dorsal margin concave and gills present on segments II–IV only) and is recovered as the sister group to all others in the most parsimonious tree (Fig. 7). This reconstruction is nevertheless not well supported and the bootstrap value (Fig. 8) indicates that *eloisae* is in fact probably the sister group of (*hutanis* + *stephani* + *pescadori* + *celebensis* + *ulmeri*), bringing support for a monophyletic Southeast Asia lineage.

The second group (*tuberculatus* + *kodai* + *hubbardi* + *jacobusi)* encompasses all taxa found in Sri Lanka and India and is characterized by the following apomorphies: male eyes are reddish-brown and setae on the dorsal face of the labrum are feathered. The taxa *tuberculatus* and *kodai* form a well supported group, having gills on segments II–VI, and no row of setae on the dorsal face of forefemora. The other two taxa, *hubbardi* and *jacobusi*, have gills on segments II–V, but relationships between them are weakly supported.

The third group (*hutanis* + *stephani* + *pescadori* + *celebensis* + *ulmeri)* gathers together taxa from Southeast Asia and is defined by two characters: the last gill is always incised medially and the antennae are longer than head width. Also of importance is the shape of the outer incisor of the right mandible, which is never spoon-shaped (plesiomorphic condition found also in *M. animosa*), but this character is also found in *eloisae*.

This reconstruction suggests some intriguing results. The most important is that the reduction in number of gills seems to have happened independently at least three times in the Oriental lineage suggesting that for *Teloganodes* the number of gill pairs may have no generic value.

Each of these taxa represents true biological species, but the supraspecific assignment is still problematic. We can consider the whole Oriental lineage as belonging to a single, variable genus (namely *Teloganodes*), but we think this choice will hide the evolutionary history of the lineage. The other possibility is to consider taxa from Sri Lanka and India as belonging to one genus *(Teloganodes)* and those from Southeast Asia to another one. Finally we choose to follow the consensus tree reconstruction and propose three genera, one (*tuberculatus* + *kodai* + *hubbardi* + *jacobusi*) for the Indian lineage, one (*hutanis* + *stephani* + *pescadori* + *celebensis* + *ulmeri*) for Southeast Asia and one for *eloisae*.

The major problem with this reconstruction, as already mentioned, is the clade formed by (*tuberculatus* + *kodai* + *hubbardi* + *jacobusi*). One group (*tuberculatus* + *kodai*) is well defined, having gills on segment VI and no row of setae on the forefemora, whereas the others (*hubbardi* and *jacobusi*) possess a row of setae on the forefemora and lacks gills on segment VI. Moreover, these two OTU do not seem to be sister species. For now, we treat the India-Sri Lanka lineage as belonging to a single genus. Further studies, based on more material and different stages, may prove this genus to be paraphyletic, and *hubbardi* and *jacobusi* will have to be assigned to one or more genera.

TABLE 2. Nymphal characters and states for 10 Oriental Teloganodidae taxa. Number used in Table 1.

	Character	Character State
1	ratio body length/cerci length	0 = < 1.3, 1 = >1.3
2	fringe of setae on the cephalic capsule	0 = only on the lateral margins up to the clypeus, 1 = all around the head
3	colour of male eyes:	0 = black, 1 = reddish brown, 2= yellowish
4	ratio head width/antenna length	0 = > 1.0, 1 = <1.0
5	setation of the labrum	0 = multiple rows or scattered, 1 = a single row
6	shape of the setae on the labrum	0 = simple, 1 = feathered
7	setae on the margin of mandibles	0 = in a bunch, 1 = simple (or double)
8	right mandible, outer incisor	0 = spoon-shaped, 1 = large entire tooth, 2 = indented tooth
9	right mandible, row of setae below the mola	0 = well developed (ca 8 setae), 1= reduced (ca 4 setae)
10	left mandible, teeth of the inner incisor	0 = same size, 1 = one larger than the other
11	left mandible, row of setae below the mola	0 = present, 1 = absent
12	maxilla, ventral setae on the inner margin	0 = multiple feathered setae, 1 = two short feathered setae, 2 = a single long seta
13	fore femora, ratio length/width	0 = > 1.6, 1 = < 1.6
14	fore femora, row of setae on the dorsal face	0 = present, 1 = absent
15	fore tibia, setae on the outer margin	0 = scattered, 1 = in a row
16	hind tibia, shape of the outer margin	0 = convex or straight, 1 = markedly concave
17	subapical teeth of the claw	0 = both present, 1 = one reduced, 2 = both reduced
18	last gill presence	0 = on segment 6, 1 = on segment 5, 2 = on segment 4
19	gill on segment 1	0 = present, 1 = absent
20	last gill	0 = margin entire, 1 = margin incised medially
21	whorl of spines on cerci	0 = longer than the corresponding segment, 1 = shorter than the corresponding segment
22	terminal filament	0 = well developed, 1 = completely reduced
23	base of the dorsal margin of fore femora	0 = with a bunch of setae, 1 = with some setae, 2 = without setae

Material deposition. The studied material, including holotypes and paratypes of new species, is deposited in the following institutions:

AMG	Albany Museum, Grahamstown, South Africa
BMNH	Natural History, British Museum, London, UK
CUAC	Clemson University Arthropod Collection, Clemson, USA
FAMU	Arthropod collection of Florida A&M University, Tallahassee, USA
LIPI	Museum of Zoology, Bogor, Indonesia

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
MNHN	Musée National d'Histoire Naturelle, Paris, France
MZL	Museum of Zoology, Lausanne, Switzerland
USNM	National Museum of Natural History, Smithsonian Institute, Washington D.C., USA
ZMH	Zoologisches Institut und Museum, Hamburg, Germany

Teloganodes Eaton, 1882

Type species: *Cloe tristis* Hagen, 1858 by original designation
nec *Teloganodes* sensu Ulmer, 1939 and subsequent authors
=*Macafertiella* Wang (in Wang & McCafferty), 1996 **syn. nov.**
(((*tuberculatus* + *kodai*) + *hubbardi*) + *jacobusi*)

Description. Adult: Forewing (Figs. 1–2) long and slender; pterostigmatic area with numerous crossveins reaching subcostal vein; vein MP_2 long, free or connected to MP_1 and CuA by crossveins; cubital field with one long intercalary vein and 1–3 smaller ones, all free. Hindwing (Figs. 3–4) broad with costal process rounded; 3 longitudinal veins. Mesoscutellum without posterior processes. Claws of all legs dissimilar, one obtuse, the other hooked. In male foreleg, length of tibia ca. 1.3 length of tarsus. Male gonopods 3-segmented (Figs. 5–6); second segment shorter than first, and third much reduced. Penis lobes fused except at apex (Fig. 6), elongated but shorter than gonopods. Styliger plate distinctly convex (Figs. 5–6). Subanal plate of female slightly pointed. Gill socket vestiges visible on abdominal segments II–VI or II–V. Terminal filament absent.

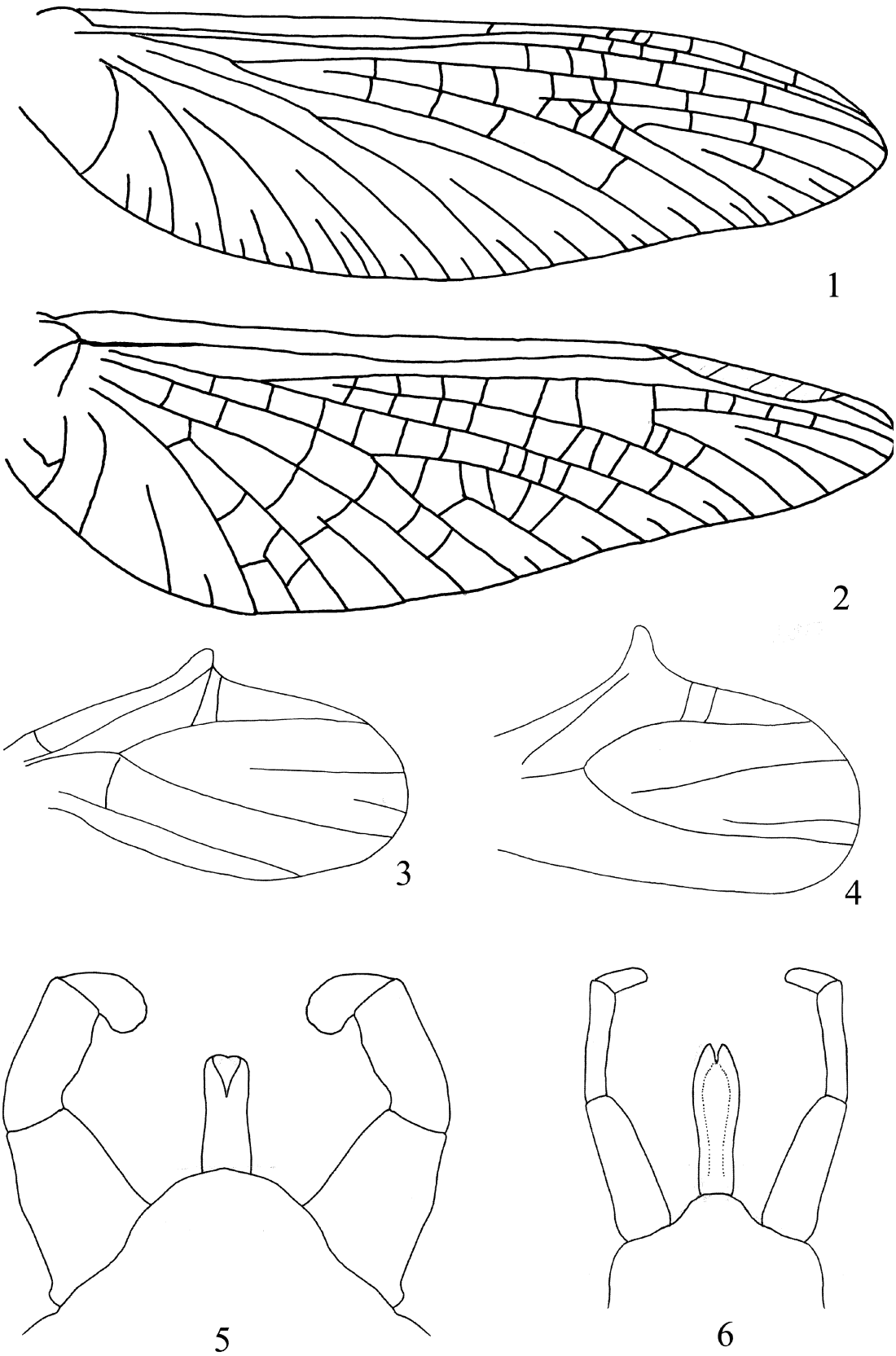
Nymph (Figs. 120, 123, 126,129): Body somewhat flattened. Eyes in dorsal position and always brownish orange in late instar male nymphs. Head capsule with long forked setae on lateral margins. Antenna shorter than or as long as head width. Labrum covered with numerous long and feathered setae (Figs. 16–21). Femora normal or dilated (Figs. 59–64). Gills on abdominal segments II–V or II–VI; gill II with dorsal lamella entire, gills III–IV with dorsal lamella posteriorly incised; gill II through penultimate gill with ventral fibrillae, final gill with dorsal lamella only and with entire margin (Figs. 82–90). Median tubercles on abdominal terga well developed. Posterolateral expansions poorly or well developed. Terminal filament absent.

Egg pear-shaped, chorion lacking attachment structures, one polar cap with epithema; a row of triangular chorionic structures close to the epithema (Figs. 98–102).

Species included:
Teloganodes tristis (Hagen, 1858) (Sri Lanka)
Teloganodes dentatus Navás, 1931 (India)
Teloganodes insignis (Wang & McCafferty, 1996) **comb. nov.** (Sri Lanka)
Teloganodes tuberculatus Sartori sp. nov. (Sri Lanka)
Teloganodes kodai Sartori sp. nov. (India)
Teloganodes jacobusi Sartori sp. nov (Sri Lanka)
Teloganodes hubbardi Sartori sp. nov.. (Sri Lanka)
Distribution. Sri Lanka, India (restricted to the Western Ghats)

Teloganodes tristis (Hagen, 1858)
(Figs. 1–3, 102)

Cloë tristis Hagen, 1858:476.
Leptophlebia tristis; Eaton, 1873:394.
Teloganodes tristis; Eaton, 1882:208; 1884:135.
Teloganodes major Eaton, 1884:136 **syn. nov**.
nec *Teloganodes tristis* sensu Ulmer 1924:44; 1939:512; 627 and subsequent authors



FIGURES 1–6. *Teloganodes* spp. Fig. 1: Forewing of the female subimago lectotype of *Teloganodes tristis* (Hagen) [MCZ]; Fig. 2: Forewing of a male subimago syntype of *Teloganodes major* Eaton [MCZ]. Fig. 3: Hindwing of the female lectotype of *Teloganodes tristis* (Hagen) [MCZ]; Fig. 4: Hindwing of the male holotype of *Teloganodes dentatus* Navás [MNHN]; Fig. 5: Genitalia of a male subimago syntype of *Teloganodes major* Eaton [MCZ]; Fig. 6: Genitalia in ventral view of the male holotype of *T. dentatus* Navás [MNHN].

Material examined. Besides the type specimens mentioned above (MCZ), very few specimens identified as *T. tristis* are known. In the collections of BMNH are housed 3 specimens identified as *T. tristis*, presumably belonging to R. McLachlan's collection. We have no evidence that these specimens have been seen or studied by Eaton, and none of them (1 male imago, 1 female imago and 1 female subimago) fit Hagen's specimens diagnosis. In the BMNH collection is housed the lectotypus of *Teloganodes major* Eaton, a female subimago (Kimmins 1960). Two syntypes are also held in the collection of the Museum of Comparative Zoology in Cambridge and these specimens were also available for study. One of them is completely embedded in fungi. The other one is a male subimago in good condition. This specimen has also been relaxed, removed from the pin, and stored in ethanol.

Male subimago. Body length: 7.5 mm; forewing length: 11.0 mm; hindwing length: 1.5 mm.
The upper portion of the eye is reddish brown. All characters of wings (Fig. 2) and abdomen are similar to those of the *T. tristis* lectotypus, except that vein MP2 is attached, not free and crossveins are more numerous (see also Figs 9 and 11). The gonopods are three-segmented, the third segment is much shorter than the preceding segment. The styliger plate is definitively convex. Penis lobes are fused for their entire length, except at the apex where a ventral ridge is visible (Fig. 5).
This species has been described from material from the same locality as *T. tristis*. Consequently, we establish that *T. major* Eaton, 1884 is a junior subjective synonym of *T. tristis* (Hagen, 1858).

Note on the type locality. In the original description, Hagen (1858) mentioned "Rainbodde" as the type locality. In a subsequent publication (Hagen, 1859), this name was corrected to Rambodde, due probably to confusion resulting from interpretation of the handwritten label of the collector, Mr. Nietner, a German entomologist who spent some years in Ceylon (Tennent 1860, p. 247). Rambodde is presently called Ramboda and is a village situated on the road from Kandy to Nuwara Eliya. The exact location of Hagen's "Rambodde" is not known with certainty, but in the 19th century, there was no village, only tea plantations. The altitude ranges between 1200 m (village Ramboda) and 2000 m (Ramboda Pass)

Known stages. *Teloganodes tristis* is known only from females and male subimago. The male imago and the nymphal stage remain to be described (but see below).

***Teloganodes dentatus* Navás, 1931**
(Figs. 4, 6)

Teloganodes dentata Navás, 1931:19.

Material examined. In the collections of the MNHN is housed the holotype of *Teloganodes dentatus* described by Navás in 1931. According to the ICZN, the ending *–odes* is masculine; therefore the adjective used by Navás to name his species should be spelled *dentatus* and not *dentata*. The species is described in detail and illustrated. Although Navás is supposed to have seen several specimens ("varios ejemplares") collected in Khandala (India) 20–22 May 1928 and 14 October 1927, a single specimen is housed in Paris. It is a pinned male imago in perfect condition; no piece broken except the tip of the cerci. It bears the following labels:

i) Khandala (India) 14.X. [19]27 [white label handwritten]
ii) Teloganodes dentata Nav. [handwritten] P. Navás S.J. det [typewritten]
iii) Typus [red label handwritten]
iv) Museum Paris Longin Navas legit 19 [white label typewritten]

Description. This specimen shares most of the characters found in *T. tristis*, particularly: upper part of compound eyes reddish brown, vein MP_2 of forewing long, 3 intercalary veins in cubital area of forewing,

hindwing broad (Fig. 4), no posterior processes on mesoscutellum, gill socket vestiges on segments II–VI, terminal filament absent, cerci whitish with purple rings. The forelegs have the following proportion: tibia ca.1.8 times femur length and 1.3 times tarsi length. It mainly differs from *T. tristis* by the darker colour of the abdomen, and shape of the costal process of the hind wing. Genitalia (Fig. 6) resemble the subimaginal genitalia of *T. tristis* (as in Fig. 5), i.e. gonopods 3-segmented, the first segment slightly longer than the second, the third one about two times as long as wide. Penis lobes fused for entire length except the apex "U" shaped. Ventrally a groove is visible that ends at the middle of the penes. The styliger plate is markedly convex.

***Teloganodes insignis* (Wang & McCafferty, 1996) comb. nov.**

= *Macafertiella insignis* Wang & McCafferty, 1996:16.

Material examined. None

Description. The description of the nymph is available in Wang & McCafferty (1996). The illustrated specimen is obviously characterised by its used and worn mouthparts, especially the mandibles and maxillae. Gills are present on segments II–VI.

Thanks to the courtesy of Dr. J. M. Webb (Purdue University) who examined the type material, we can amend the original description. The most important character concerns the presence of a row of setae below the mola of the left mandible. All species examined here lack these setae, but such a row was illustrated by Wang & McCafferty (1996, fig. 3). In fact these setae are also absent in *T. insignis.* The outer margin of the fore femora bears about 12–15 short, thick and pointed setae together with long and thin setae; a row of submarginal blunt and short setae is also present; the middle and hind femora have similar patterns. The median tubercle on tergum X is slightly longer or subequal in length to that on tergum III.

Adult stages unknown.

***Teloganodes tuberculatus* Sartori sp. nov.**
(Figs. 16, 17, 26, 33, 40, 51, 59, 82–86, 120–122)

Material examined. Holotype: 1 nymph (not mature), Sri Lanka, Kandy District, Haloya, Khone Palama, 17.III.1978, M. Hubbard [USNM].

Paratypes: 3 nymphs, same data as holotype [2 in FAMU, 1 partially mounted on slide preparation in MZL].

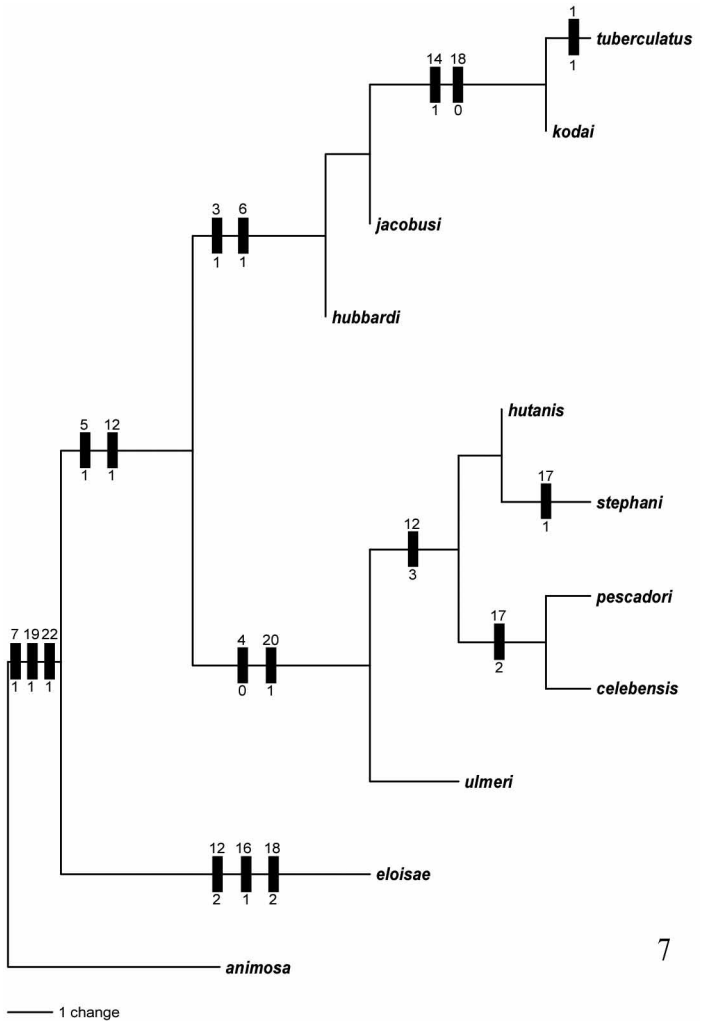
Description. Nymph

Body length at least 4.5 mm without cerci. Cerci length ca. 1.6 times body length.

General colouration of head, thorax and abdomen medium brown dorsally; sterna and legs uniformly yellowish (Figs. 120–121).

Outer margin of head fringed with a row of setae from behind eyes to labrum insertion (Fig. 120). Antennae short, 0.7 times head width, flagellum with 10–11 segments. Labrum compact, ca. 2 times wider than long, with smooth anterior emargination (Fig. 16); dorsal face covered medially by 2–4 rows of long feathered setae (Fig. 17); anterior margin with a row of small thin setae. Mandibles (Figs. 26, 33) slender with 2 thin setae in middle of outer margin; right mandible (Fig. 26) with outer incisor with inner tooth; inner incisor with 2 teeth; prostheca reduced to a cluster of thin setae; a row of long, thin setae below mola; left mandible (Fig. 33) with long outer incisor rounded; inner tooth close to inner incisor; inner incisor with 3 teeth, prostheca well developed with cluster of small setae. Maxillae (Fig. 40) slender, with a well developed canine and 2 dentisetae; 3 long inner setae apically and a cluster of long, simple setae at crown; inner margin at base of lacinia with one long feathered seta dorsally and row of 3–4 short feathered setae ventrally; maxillary palp reduced to a simple

seta. Submentum moderately developed laterally; glossae and paraglossae partially fused; glossae rhomboid and paraglossae slightly falciform (similar to Fig. 50); labial palp three-segmented, segment 1 subequal in length to segments 2 and 3 combined (Fig. 51).



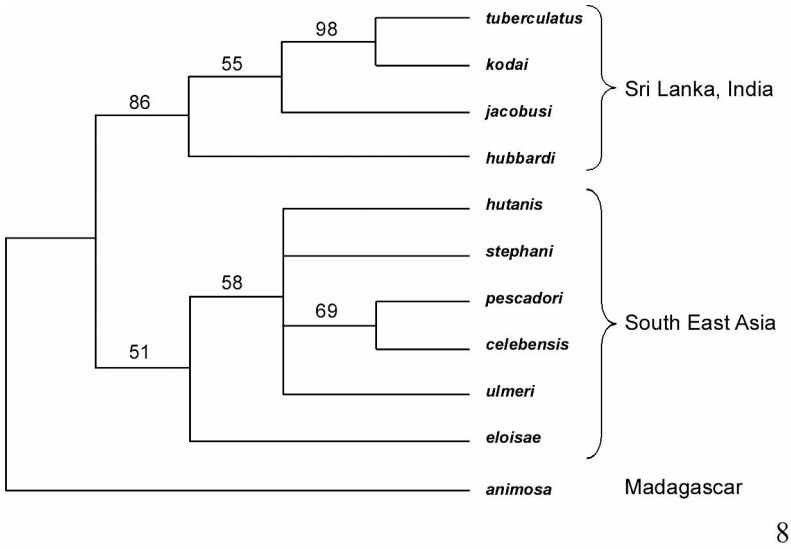


FIGURE 7, 8. Fig. 7: Phylogram of the single most parsimonious tree reconstructed: synapomorphies are represented by black boxes, number above the box: character as in table 1, number below the box: character state. Fig. 8: Bootstrap 50% majority-rule consensus tree: bootstrap support values indicated before each node.

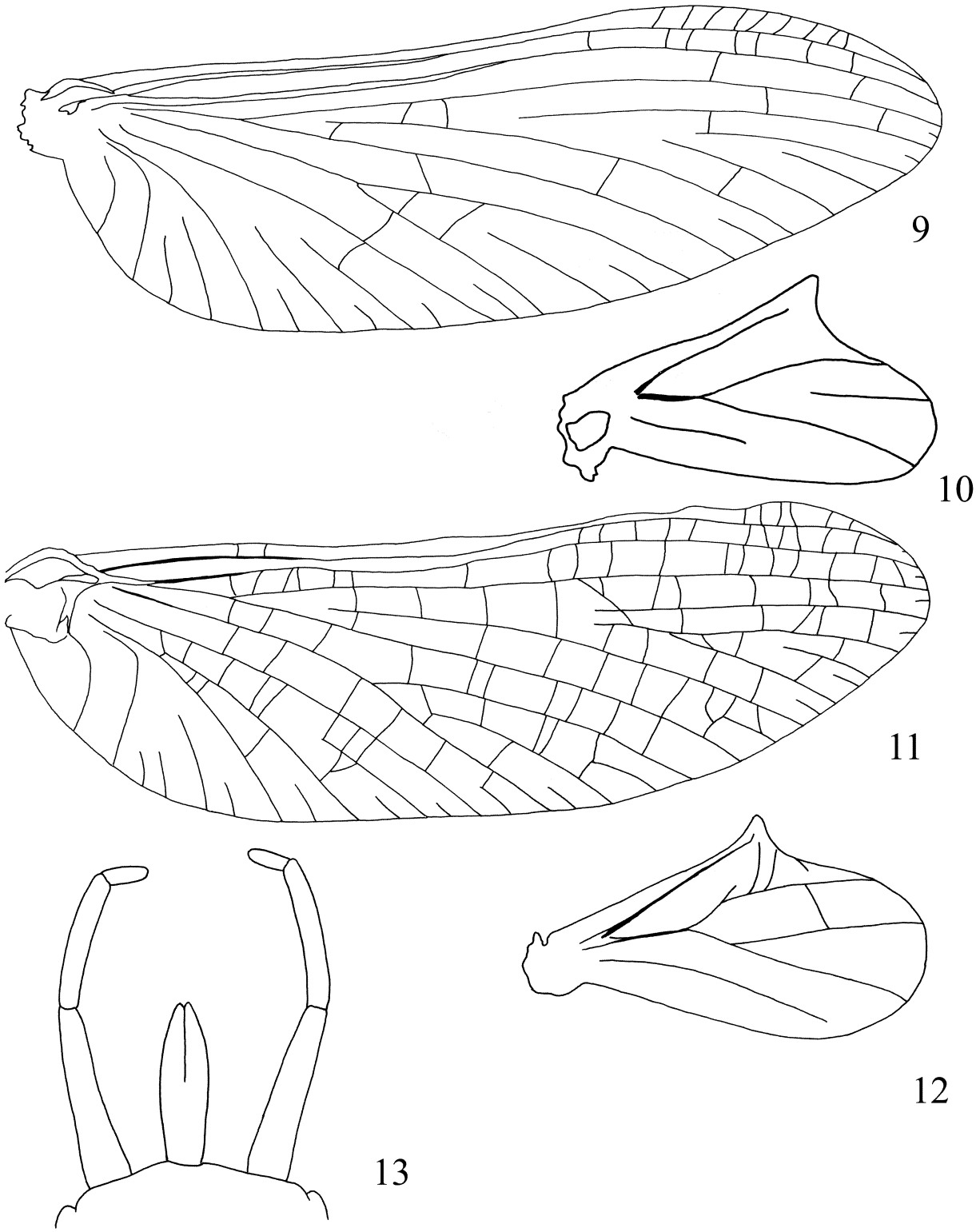
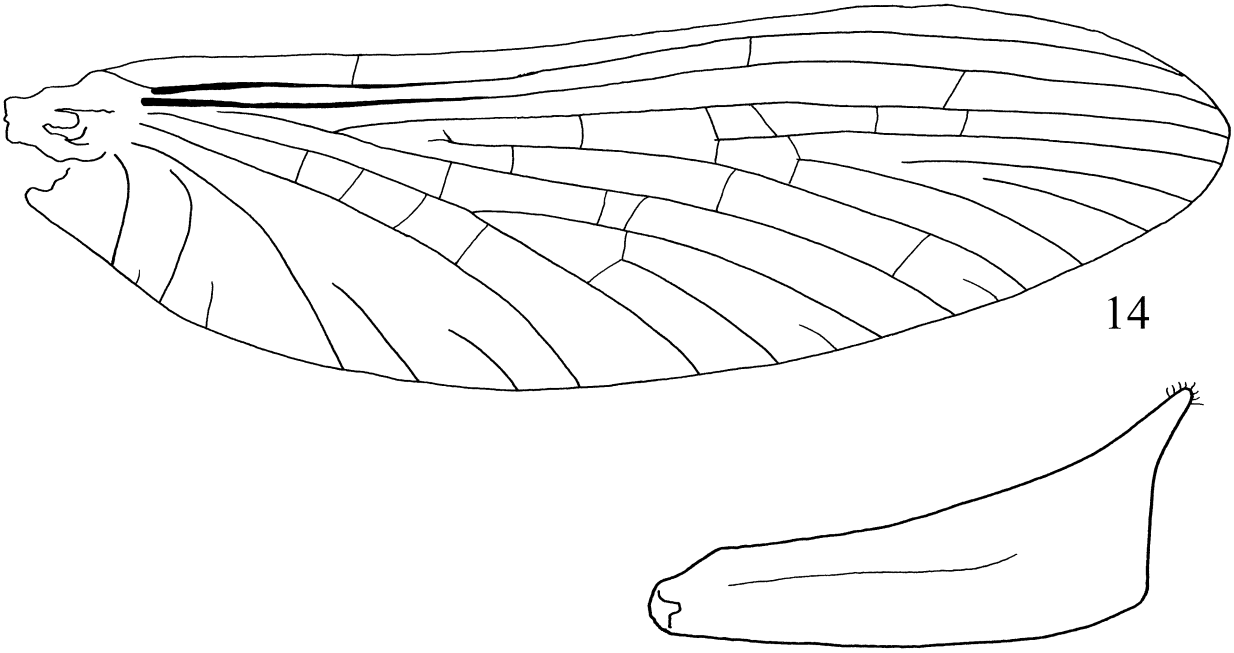


FIGURE 9–13. *Dudgeodes* spp. Fig. 9: Female subimago forewing of *Dudgeodes hutanis*; Fig. 10: Hindwing of *D. hutanis*; Fig. 11: Male imago forewing of *Dudgeodes pescadori*; Fig. 12: Hindwing of *D. pescadori*; Fig. 13: Genitalia in ventral view of *D. pescadori*.

Prothorax with 6 rounded tubercles on dorsal face; mesothorax with 5. All legs similar in shape and ornamentation. Femur (Fig. 59) moderately slender, ca. 2.2 times longer than wide; outer margin covered by thin and long setae together with 6–7 sharp, thick and pointed setae; submarginal row of short and blunt setae almost absent in foreleg, but distinct on middle and hind femora; inner margin with a row of long and thin

setae, the row continuing on dorsal face, close to articulation with trochanter. Tibia with a row of long and thin setae, starting on proximal part close to outer margin and ending in distal part close to inner margin. Tarsal claw hooked, bearing 3 blunt teeth medially, and 2 pointed teeth subapically; apex of claw with two rows of small setae laterally.



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FIGURES 14–15. *Derlethina eloisae*. Fig. 14: Forewing; Fig. 15: Hindwing.

All abdominal terga with well developed median tubercle, slightly increasing in size posteriorly (Fig. 122). No posterolateral projections on segments II–VII, slightly marked on segments VIII and IX (Fig. 121). Lateral margins of terga with short and thin setae. Gills (Figs. 82–86) on abdominal segments II–VI. Gill II with dorsal lamella operculate and covering others, oval with margin entire; gills III–V with dorsal lamella incised medially; gill VI with dorsal lamella reduced and entire; ventral lobe flabellate, well developed and purple on gills II–V. Cerci with a whorl of spines every 2–3 segments; spines shorter than length of corresponding segment.

Winged stages unknown

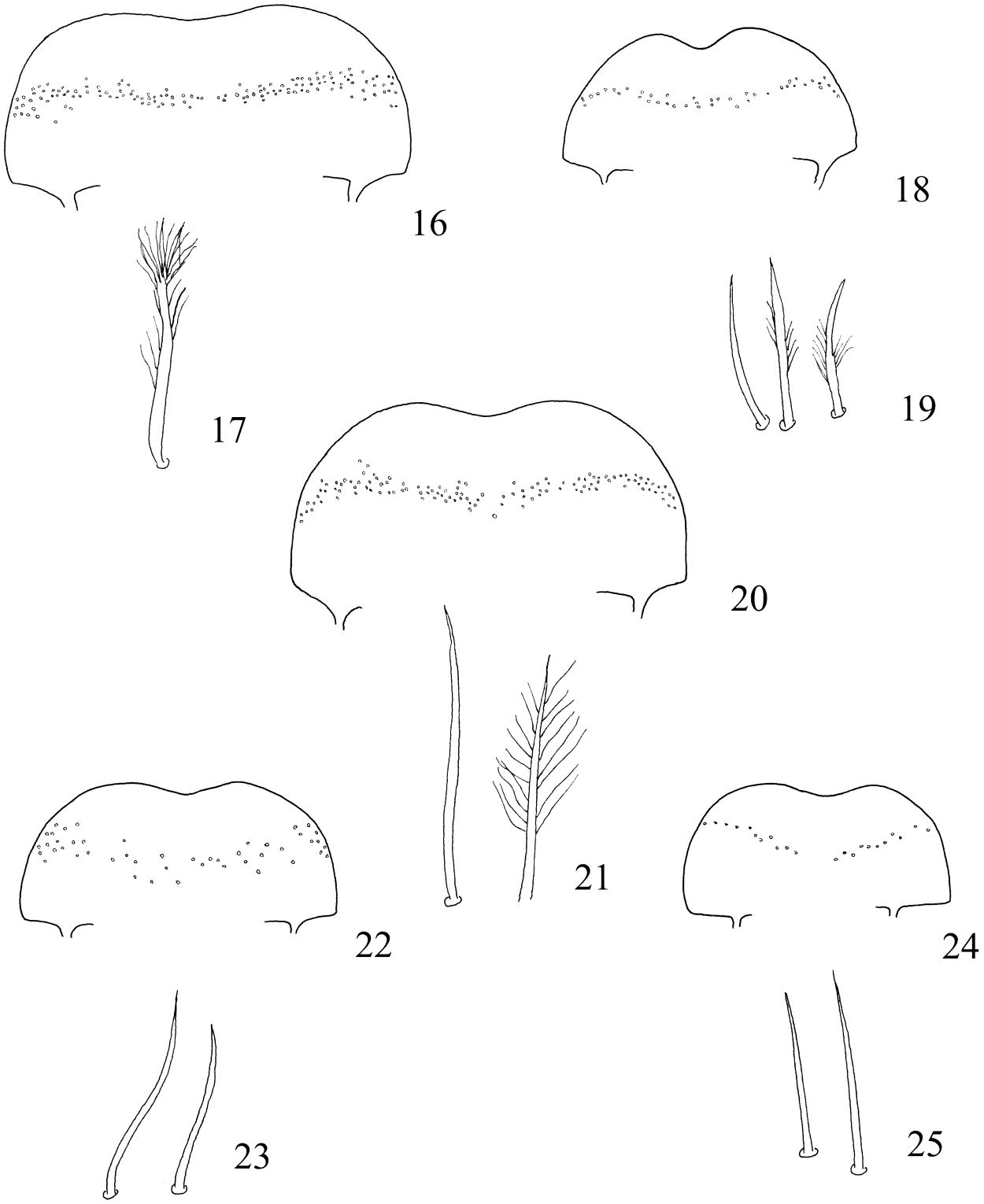
Diagnosis. The nymph of *T. tuberculatus* can be easily distinguished from that of *T. insignis* by the shape of the labrum, the number of setae on the dorsal margin of the mandibles and the shape and ornamentation of the femora.

Etymology. The epithet "tuberculatus" refers to the well developed tubercles found on the thorax and abdomen of this species.

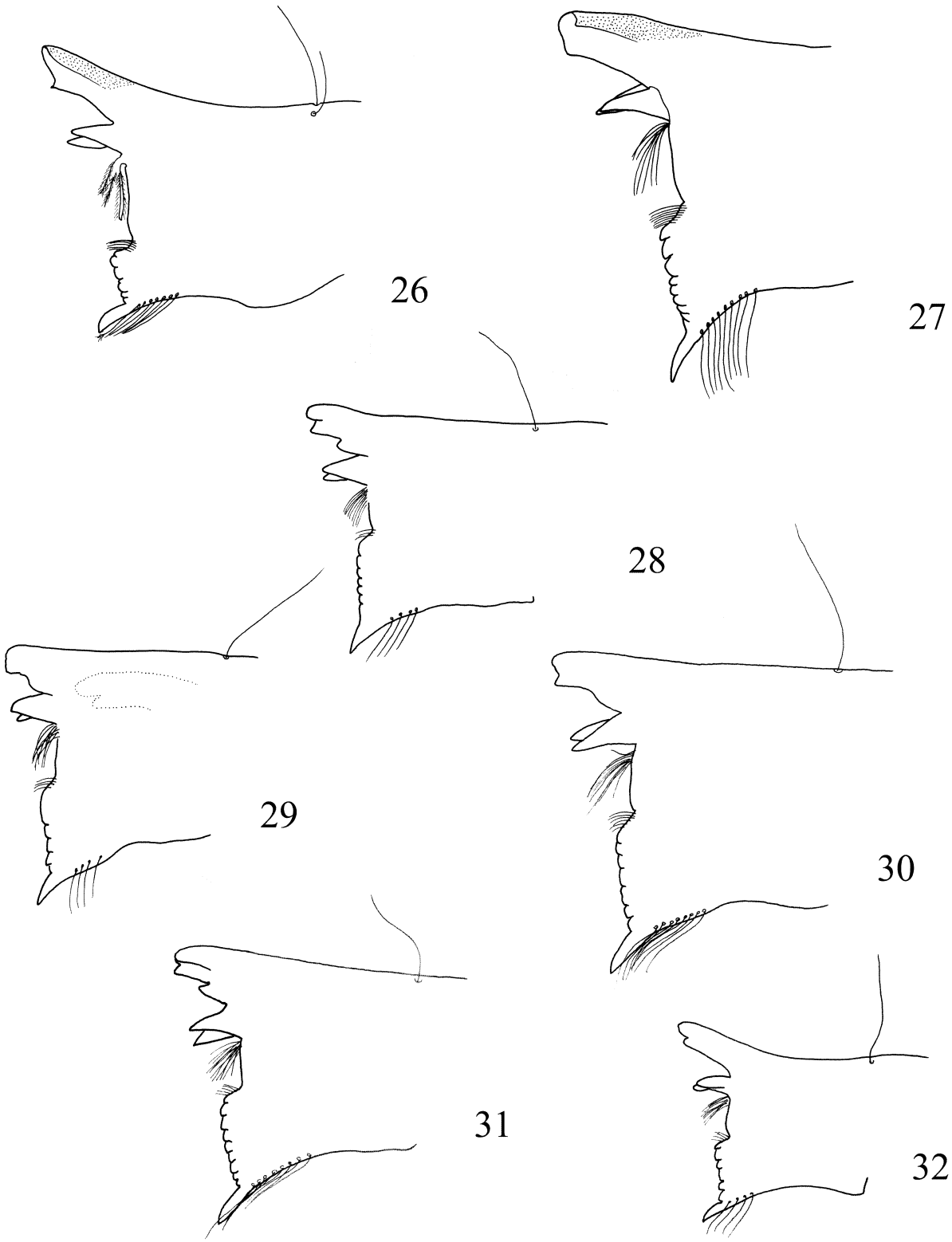
***Teloganodes kodai* Sartori sp. nov.**
(Figs. 43, 60, 123–125)

Material examined. Holotype: 1 nymph (not mature), India, Tamil Nadu State, 6 km below Kodaikanal, 1800 m., 19.III.1978, K. Wood [MZL].

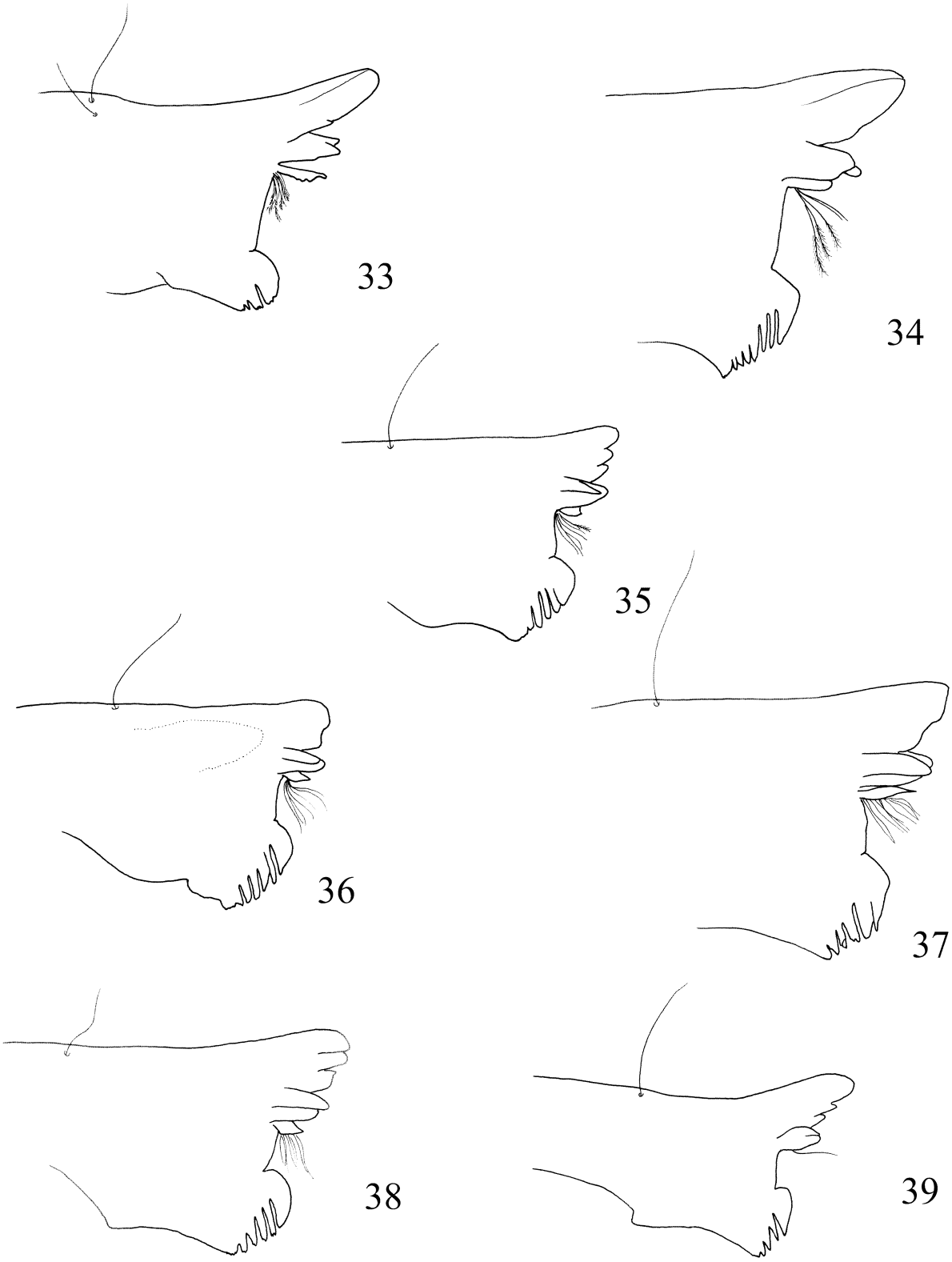
Paratypes: 26 nymphs, same data as holotype [15 in FAMU, 11 in MZL, of which 1 partially mounted on slide preparation].



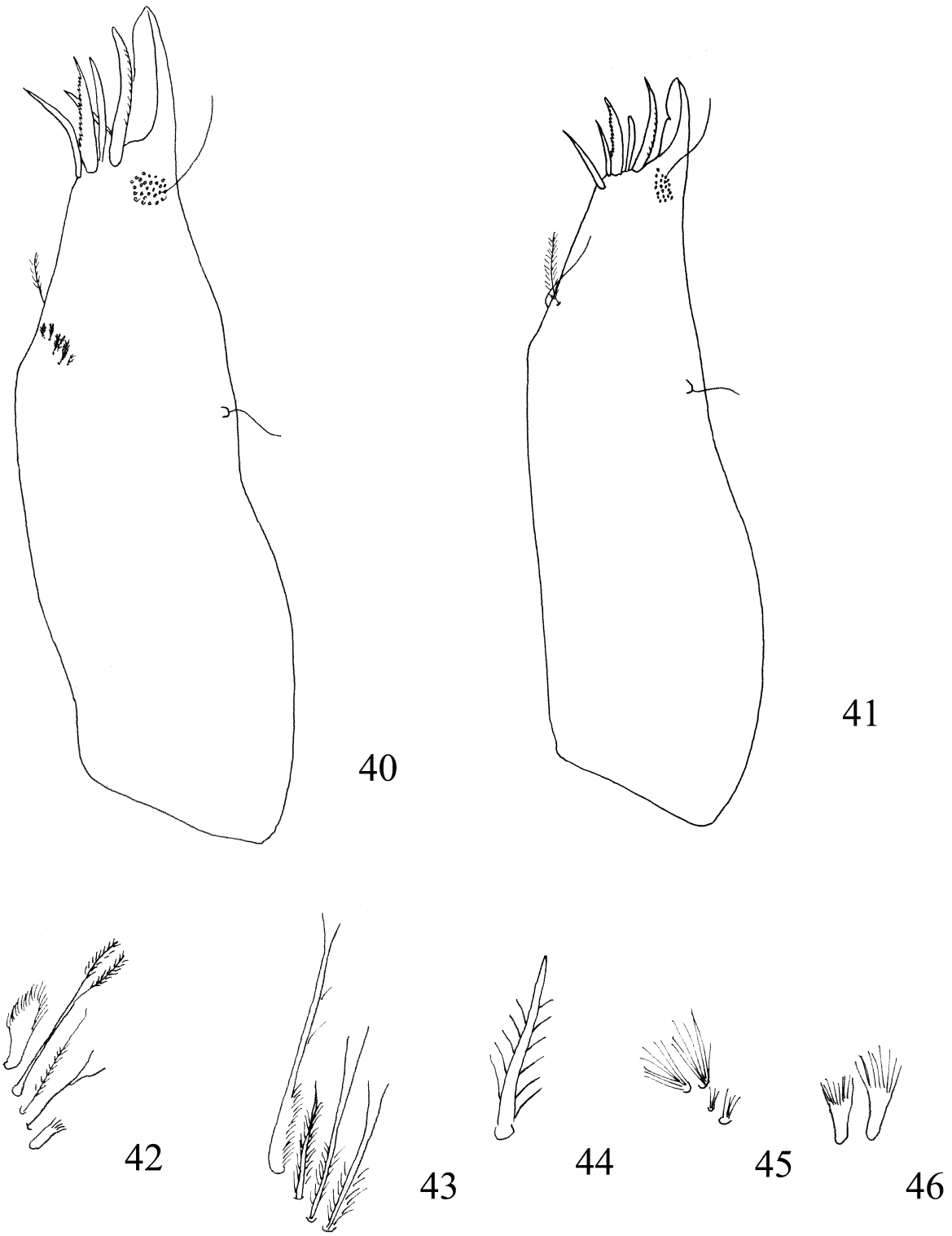
FIGURES 16–25. Labrum (16, 18, 20, 22, 24), with details of the dorsal setae (17, 19, 21, 23, 25), of Oriental Teloganodidae. Insertion of the setae indicated by dots on the labrum. Figs. 16–17: *Teloganodes tuberculatus*; Figs. 18–19: *T. hubbardi*; Figs. 20–21: *T. jacobusi*; Figs. 22–23: *Dudgeodes hutanis*; Figs. 24–25: *Derlethina eloisae*. All labra at same scale and all setae at same scale, two times enlarged compared to the labra.



FIGURES 26–32. Right mandible of Oriental Teloganodidae. Fig. 26: *Teloganodes tuberculatus*; Fig. 27: *T. jacobusi*; Fig. 28: *Dudgeodes hutanis*; Fig. 29: *D. pescadori* (shape of the new mandible in dotted line); Fig. 30: *D. celebensis*; Fig. 31: *D. ulmeri*; Fig. 32: *Derlethina eloisae*. All same scale.



FIGURES 33–39. Left mandible of Oriental Teloganodidae. Fig. 33: *Teloganodes tuberculatus*; Fig. 34: *T. jacobusi*; Fig. 35: *Dudgeodes hutanis*; Fig. 36: *D. pescadori* (shape of the new mandible in dotted line); Fig. 37: *D. celebensis*; Fig. 38: *D. ulmeri*; Fig. 39: *Derlethina eloisae*. All same scale.



FIGURES 40–46. Maxillae (40, 41) and detail of the setae on the apico-ventral part (42–46) of Oriental Teloganodidae. Fig. 40: *Teloganodes tuberculatus*; Fig. 41: *Dudgeodes hutanis*; Fig. 42: *T. jacobusi*; Fig. 43: *T. kodai*; Fig. 44: *D. pescadori*; Fig. 45: *D. ulmeri*; Fig. 46: *Derlethina eloisae*.

Description. Nymph

Body length at least 6 mm and 7 mm, without cerci, in male and female nymphs respectively. Cerci slightly longer than body length.

General colouration of head, thorax and abdomen dark brown dorsally; light brown ventrally, sterna VII and VIII washed with grey; legs brownish orange (Figs. 123–124).

Outer margin of head fringed with a row of setae from behind eyes to labrum insertion. Antennae short, 0.85 times head width, flagellum with 13–14 articles. Mouthparts very similar to those of *T. tuberculatus*, except as following: mandibles with one long thin seta in middle of outer margin; maxillae with one long feathered seta dorsally and row of 4–5 long feathered setae ventrally on inner margin, at base of lacinia (Fig. 43); labial palp with segment 1 shorter than length of segments 2 and 3 combined, segments 1 and 2 subequal.

Prothorax with 2 rounded tubercles dorsally; mesothorax with 3. All legs similar in shape and ornamentation. Femur (Fig. 60) moderately broad, ca. 1.8 times longer than wide; outer margin covered by thin long setae only; submarginal row of numerous short blunt setae, the same scattered setae also present on dorsal surface; inner margin with a row of long thin setae, row continuing on dorsal surface to near articulation with trochanter. Tibia and tarsal claw as in *T. tuberculatus*, except claw bears 4 blunt teeth medially.

Abdominal terga with moderately developed median tubercle on segments I and X, strongly developed on segments II–IX (Fig. 125). No posterolateral projections on segments II–III, slightly marked on segments IV–VI, well developed on segments VII–IX (Fig. 124). Lateral margins of terga with short and stout setae. Gills and cerci as in *T. tuberculatus*.

Winged stages unknown

Diagnosis. The nymph of *T. kodai* can be easily distinguished from that of *T. insignis* by the shape of the labrum, the proportions of the femora, as well as the relative sizes of the median tubercle on abdominal terga III and X ($T_3 < T_{10}$ in *T. insignis*, whereas $T_3 > T_{10}$ in *T. kodai*). *T. kodai* is also easily separated from *T. tuberculatus* mainly by the length of the antennae, the ornamentation of the femora and the posterolateral projections of the abdomen.

Etymology. The noun in apposition "kodai" is in reference to the region where specimens were collected.

***Teloganodes jacobusi* Sartori sp. nov.**
(Figs.20, 21, 27, 34, 42, 47, 61, 62, 87–90, 126–128)

Material examined. Holotype: 1 male nymph, Sri Lanka, Nuwara Eliya district, Nuwara Eliya, stream below Lover's Leap, 2.IV.1978, M. Hubbard [USNM].

Paratypes: 19 nymphs, same data as holotype [MZL, of which 1 partially mounted on slide preparation]; 21 nymphs, same data as holotype, but 19.III.1978 [FAMU], 85 nymphs, Nuwara Eliya, small Lover's Leap stream, 1.IV.1978, M. Hubbard [66 in FAMU, 2 in AMG, 17 in MZL of which 1 partially mounted on slide preparation]; 25 nymphs, Nuwara Eliya district, Hakgala – Kande Ella, 3.IV.1978, M. Hubbard [FAMU], 41 nymphs, Kandy district, Haloya, Khone Palama, 17.III.1978, M. Hubbard [MZL of which 1 partially mounted on slide preparation], 2 nymphs, Ratnapura District, Belihuloya, Belihul Oya, 9.IV.1978, M. Hubbard [FAMU], 1 nymph, Maskeliya Region, Maskeliya Riv. at base of Adam's Peak, about 1 km above Maskeliya impoundment, 1800 m, 1.XII.1970, F. Starmuehlner [FAMU].

Description. Nymph

Body length up to 6.0 mm and 5.0 mm, without cerci, in female and male nymphs respectively; cerci length subequal to body length.

General colouration variable dorsally, ranging from middle to dark brown; young specimens generally paler; legs light brown; with medium brown maculae on dorsal face, uniformly cream-coloured ventrally (Figs. 126–127).

Antennae 0.65–0.80 times head width, flagellum with 13–15 segments. Dorsal part of male eyes orange. Labrum (Fig. 20) compact, ca. 2 times wider than long, with smooth anterior emargination; dorsal surface covered medially by numerous, mainly long feathered setae, together with some long simple setae. Mandibles slender with one, sometimes 2, thin setae in middle of outer margin; right mandible (Fig. 27) with outer incisor compact, spoon shape; inner incisor with 2 teeth; prostheca reduced, comprised of a cluster of thin setae; a row of long, thin setae below mola and a cluster of short setae above mola; left mandible (Fig. 34) with outer incisor compact and rounded; inner incisor with 2 teeth inserted transversely, one smaller and pointed, the other large and rounded, prostheca small with a cluster of small setae; no setae below mola. Maxillae slender, with a well developed canine, 2 indented dentisetae and 3 long inner setae apically and a bunch of long simple setae at crown; inner margin at base of lacinia with one long feathered seta dorsally and a row of 4–5 thin feathered setae ventrally (Fig. 42); maxillary palp reduced to a single simple seta. Hypopharynx (Fig. 47) with superlinguae angular laterally, a row of long feathered setae at apex. Submentum moderately developed laterally; glossae and paraglossae partially fused; paraglossae larger than glossae; labial palp 3-segmented, segments 1 and 2 subequal in length, segment 2 slightly wider distally, segment 3 small and rounded, ca. 1.5 times as long as wide at base (Fig. 50).

Prothorax with 6 rounded tubercles on dorsal surface; mesothorax embossed, without distinct tubercles. Forefemur (Fig. 61) moderately dilated, ca. 2 times longer than wide; outer margin covered by stout and long setae, meeting a transverse row of stout, relatively short setae (Fig. 62) across dorsal face; a submarginal row of stout and short setae, the same scattered over dorsal face; inner margin with a long row of long and thin setae almost reaching articulation with tibia. Middle and hind femora similar, slightly more slender, ca. 2.2–2.3 times longer than wide; dorsal and inner margins with a row of long and stout setae, without transverse row. Tibia with a row of long and stout setae on inner margin, and a row of long and thin setae on outer margin. Tarsal claw hooked, bearing 4–6 blunt teeth medially and 2 pointed teeth subapically; apex of claw with two rows of small setae laterally.

Abdominal terga with a well developed median tubercle on segments I–VIII, more developed on segment IX and absent on segment X (Fig. 128). Posterolateral projections weakly developed on segments II–V, well marked on segments VI–IX (Fig. 127). Lateral margins of terga with both thin and stout short setae. Gills (Figs. 87–90) on abdominal segments II–V. Gill II with dorsal lamella operculate, oval and with entire margin; gills III–IV with dorsal lamella incised medially; gill V entire; ventral lobe flabellate, well developed and purple on gills II–IV.

Cerci with stout setae shorter than length of corresponding segment.

Winged stages unknown

Diagnosis. *T. jacobusi* is easily separated from *T. insignis, T. tuberculatus* and *T. kodai* by the absence of abdominal gills on segment VI, by the dissimilar teeth of the inner incisor of the left mandible and by the forefemora dilated and with a transverse row of setae.

Etymology. This species is named after Dr Luke M. Jacobus (Columbus, Indiana, USA) to acknowledge his major contributions on Oriental Ephemerelloidea and for his constant support during this research.

***Teloganodes hubbardi* Sartori sp. nov.**
(Figs. 18,19, 48, 52, 63, 64, 77, 98–101, 129–131)

Material examined. Holotype: 1 male nymph, Sri Lanka, Kandy district, Haloya, Khone Palama, 17.III.1978, M. Hubbard [USNM].

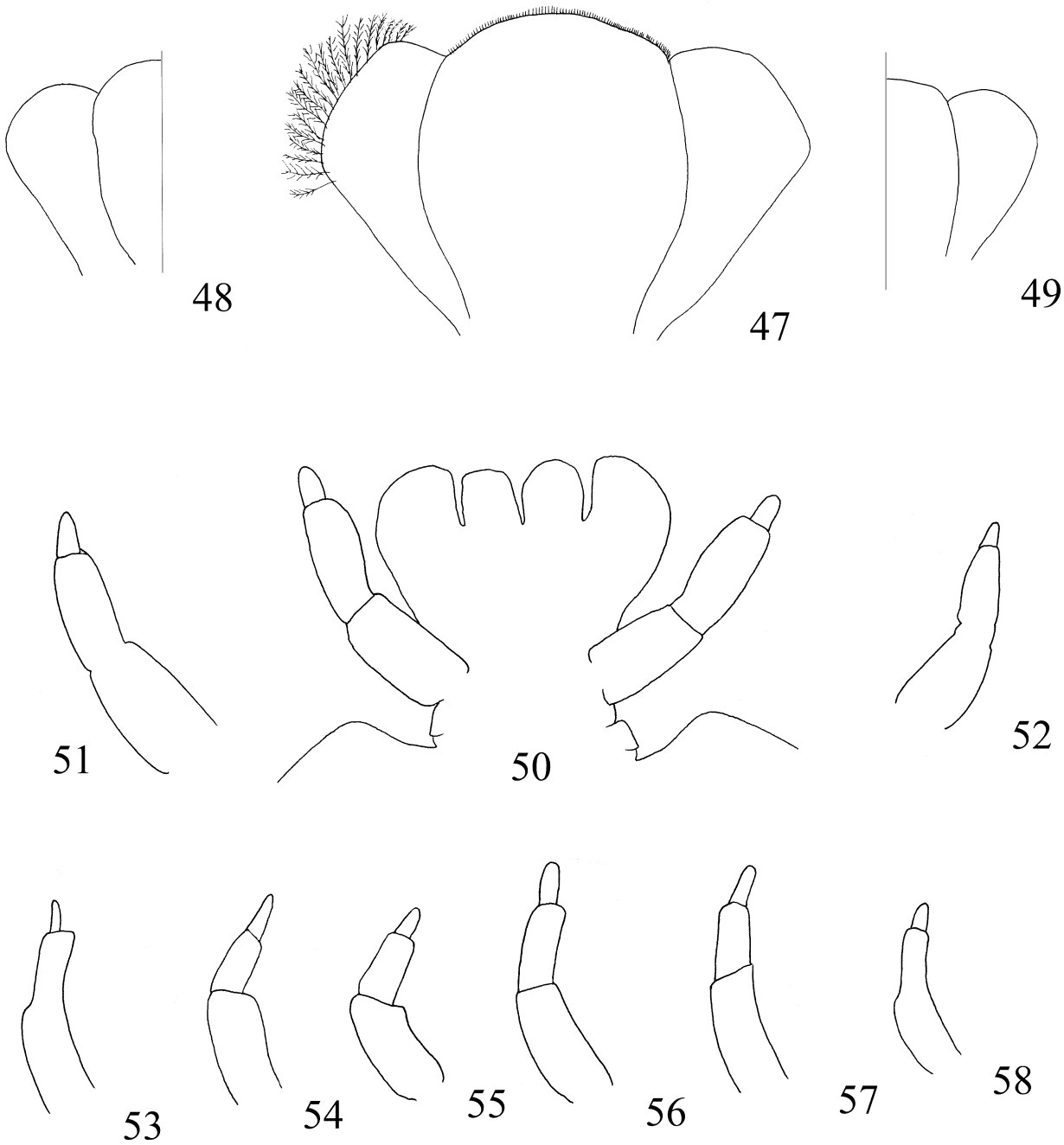
Paratypes: 25 nymphs, same data as holotype [21 in FAMU, 4 in MZL of which 1 partially mounted on slide preparation]; 8 nymphs, Kandy district, Haloya, Hasalaka, Gorulupatha Ella, 15.III.1978, M. Hubbard [5 in FAMU, 3 in MZL of which 1 partially mounted on slide preparation]; 4 nymphs, Galle District, stream

crossing road above Kanneliya, 7.III.1978; 4 nymphs, Galle District., Kanneliya, stream above hydrological station, 8.III.1978, 4 nymphs, Kalutara District, Wayangale, 4.III.1978; 1 nymph, Kegalle District, Kitulgala Rest House, 20.II.1978, all M. Hubard [FAMU].

Description. Nymph

Body length up to 4.5 mm and 4.0 mm, without cerci, in female and male nymphs respectively; cerci length up to 4.0 mm and 3.0 mm in female and male nymphs respectively.

General colouration dark brown dorsally, except head and abdominal segment X yellowish to whitish, legs whitish with 4 dark brown maculae on dorsal face, maculae sometimes merging; ventrally, uniformly creamy (Figs. 129–130).



FIGURES 47–58. Hypopharynx (47–49), labium (50) and labial palp (51–58) of Oriental Teloganodidae. Fig. 47: *Teloganodes jacobusi* (setae on the left superlingua not drawn); Fig. 48: *T. hubbardi* (half right); Fig. 49: *Dudgeodes hutanis* (half left); Fig. 50: *T. jacobusi*; Fig. 51: *T. tuberculatus*; Fig. 52: *T. hubbardi*; Fig. 53: *D. hutanis*; Fig. 54: *D. stephani*; Fig. 55: *D. celebensis*; Fig. 56: *D. ulmeri*; Fig. 57: *D. pescadori*; Fig. 58; *Derlethina eloisae*. Hypopharynx at same scale; labium and labial palps at same scale.

Antennae 0.9–1.1 times head width, flagellum with 12–14 articles, first segment more than 2 times length of second. Dorsal part of male eyes orange.

Labrum with same ornamentation as in *T. jacobusi*, but anteromedian emargination more pronounced (Fig. 18), scattered setae on dorsal face less numerous and less feathered (Fig. 19). Mandibles and maxillae similar to those of *T. jacobusi*. Hypopharynx (Fig. 48) with superlinguae rounded laterally, a row of feathered and long setae at apex; lingua relatively narrow. Labium similar to that of *T. jacobusi*, except segment 2 of palp not enlarged distally (Fig. 52).

Pro- and mesothorax as in *T. jacobusi*. Forefemur (Fig. 63) greatly dilated, ca. 1.3–1.4 times longer than wide; outer margin covered by stout and long setae, a transverse row of stout and long setae across dorsal face (Fig. 64); no other setae on dorsal face; inner margin with a long row of long and thin setae almost reaching articulation with tibia. Middle femur more slender, ca. 1.6–1.8 times longer than wide; dorsal and inner margins with a row of long and stout setae. Hind femur even more slender, ca. 2 times longer than wide, with the same ornamentation as middle femur. Tibia with a row of long and stout setae on inner margin, and a row of long and thin setae on outer margin. Tarsal claw hooked, bearing 4 acute medial teeth, and 2 pointed and extremely developed teeth subapically; apex of claw with two rows of thin and long setae laterally (Fig. 77).

Abdominal terga with a well developed median tubercle on segments I–V, more developed on segments VI–IX and absent on segment X (Fig. 131). Posterolateral projections weakly developed on segments II–III, more marked on segments IV–V, and extremely developed on segments VI–IX (Fig. 130). Lateral margins of terga with long and thin setae. Gills on abdominal segments II–V, the same than those of *T. jacobusi*.

Cerci with stout setae shorter than length of corresponding segment.

Winged stages unknown.

Egg. Pear-shaped, ca. 185 µm / 100 µm (Fig. 98). Chorion lacking attachment structures, and constituted by polygonal plates separated by a ridge of ca. 2–3 µm . One micropyle visible situated near polar cap and directed toward opposite pole (Fig. 100). Triangular chorionic structures arising from chorion to “set” the polar cap (Figs. 99–100). Polar cap constituted by two kind of epithema; a multitude of short, non-coiled threads and larger non-coiled threads compacted into a droplet structure (Fig. 101), those arranged regularly around polar cap (Fig. 99).

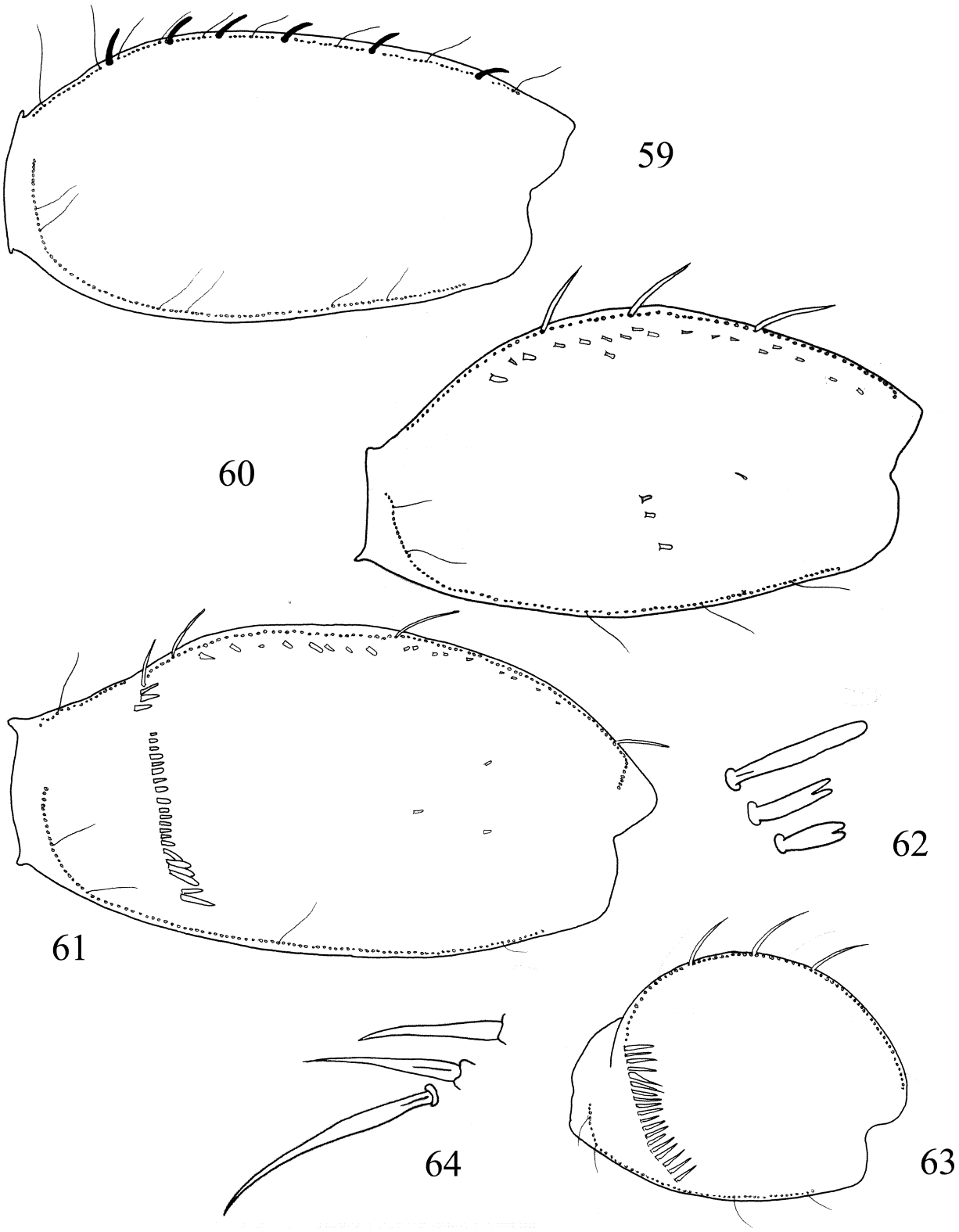
Diagnosis. *T. hubbardi* is most similar to *T. jacobusi* from which it can be easily told by the shape of the posterolateral projections which are much more developed on abdominal segments VI–IX, the anteromedian emargination of the labrum more incised, superlinguae of the hypopharynx more rounded, and forefemora more dilated without submarginal stout setae.

Etymology. This species is named after our colleague and friend Prof. Michael D. Hubbard (Florida A & M University, USA) who collected most of the Ceylon material used in this study.

General remark on *Teloganodes* species and stages

Two species with gills on abdominal segments II–VI are known from Sri Lanka in the larval stage only (*T. tuberculatus* and *T. insignis*) whereas another one *(T. tristis)* is only known in the winged stages. It is therefore possible that either *T. tuberculatus* or *T. insignis* correspond in fact to the larval stage of *T. tristis*. Unfortunately, we have neither morphological nor geographical evidence allowing us to solve this problem.

As already mentioned in the cladistic analysis, winged stages of *T. jacobusi* and *T. hubbardi* are unknown, and it is possible that they present some distinct features compared to those of *T. tristis* or *T. dentatus*, besides the fact that they may have only vestigial gill sockets on segments II–V.



FIGURES 59–64. Forefemur (59, 60, 61, 63) and setae on the transverse row (62, 64) of *Teloganodes* spp. Insertion of the setae on the margins indicated by dots; only some setae drawn. Fig. 59: *T. tuberculatus*; Fig. 60: *T. kodai*; Figs. 61–62: *T. jacobusi*; Figs. 63–64: *T. hubbardi*. Femora at same scale; setae at same scale.

Teloganodes kodai is known from India in the larval stage whereas *T. dentatus* is only known from the winged stages. It is plausible, but unlikely, that *T. kodai* constitutes in fact the larval stage of *T. dentatus*. Type localities are more than 1000 kilometres distant, *T. dentatus* being caught below 800 m in Maharashtra State whereas *T. kodai* lives in streams at more than 1500 m a.s.l. Both places belong to the Western Ghats, an area of unique biodiversity and endemism in the Indian subcontinent (Myers *et al.* 2000).

Dudgeodes **Sartori gen. nov**

Type species: *Dudgeodes pescadori* Sartori sp. nov. by present designation
= *Teloganodes* sensu Ulmer and subsequent authors, nec Eaton, 1882
(hutanis + stephani + pescadori + celebensis + ulmeri)

Description. Adult: forewing long and slender, posterior margin regularly convex (Figs. 9, 11). Pterostigmatic area with 7–10 crossveins reaching subcostal vein; vein MP_2 short and free or long and attached to CuA and MP_1, cubital field with 1–4 intercalary veins. Hind wing small with costal process acute; 3 longitudinal veins well developed (Figs. 10, 12). Claws of all legs dissimilar, one obtuse, the other hooked. In male foreleg, length of tibia ca. 1.8 length of tarsus. Styliger plate slightly concave medially. Male gonopods (Fig. 13) three-segmented; first segment subequal in length to second and third combined; third much reduced. Penis lobes completely fused, except at apex, elongated but shorter than gonopods (Fig. 13). Subanal plate of female slightly rounded. Gill socket vestiges visible on segments II–V. Terminal filament absent.

Nymph (Figs. 132, 135, 138, 141, 144): Body flattened, eyes in dorsal position blackish or yellowish in male nymphs; head capsule with hair like setae on lateral margins ending in front of eyes. Labrum covered with numerous long and simple setae (Fig. 22). Forefemora broad and dilated with a transverse row of setae on dorsal face (Figs. 65, 67, 69 71 73). Gills on abdominal segments II–V (Figs. 91–94); gills II–IV with ventral lobes, gill V without; gills III–V incised. Abdominal carina (median tubercles on terga) well or poorly developed. Posterolateral expansions poorly or well developed. Lateral margins of terga with long and thin setae. Terminal filament absent.

Egg: ovoid, chorion lacking attachment structures, one polar cap with epithema; a row of polygonal chorionic structures close to the epithema (Figs. 103–114).

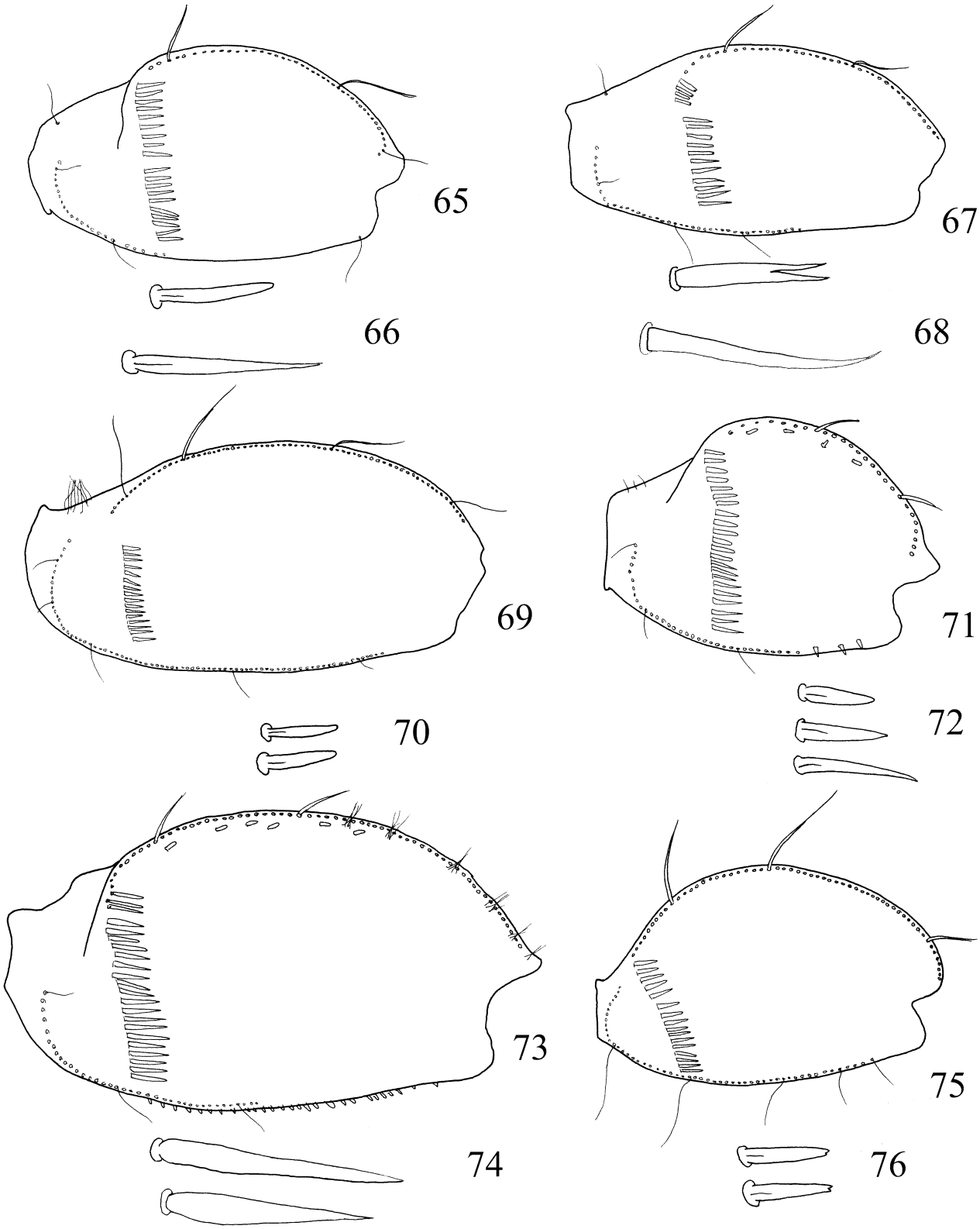
Etymology. The new genus is an arbitrary combination of letters to honour Prof. David Dudgeon (Hong Kong University) for his outstanding contributions to the ecology of Oriental aquatic macroinvertebrates, especially mayflies; followed by the suffix *–odes* to remember its relationship with *Teloganodes*. The gender is masculine.

Diagnosis. The genus *Dudgeodes* is easily distinguished from *Teloganodes* by the following characters: in the adult stage, outer margin of forewing regularly convex, hindwing smaller with acute costal process, tarsi of male foreleg shorter than in the previous genus, styliger plate not strongly convex; in the larval stage, by the absence of gill VI and last gill always incised (entire in *Teloganodes*), by the shape of the incisor of the right mandible and by the single seta on the ventral face of the galea-lacinia (except multiple in *D. ulmeri*).

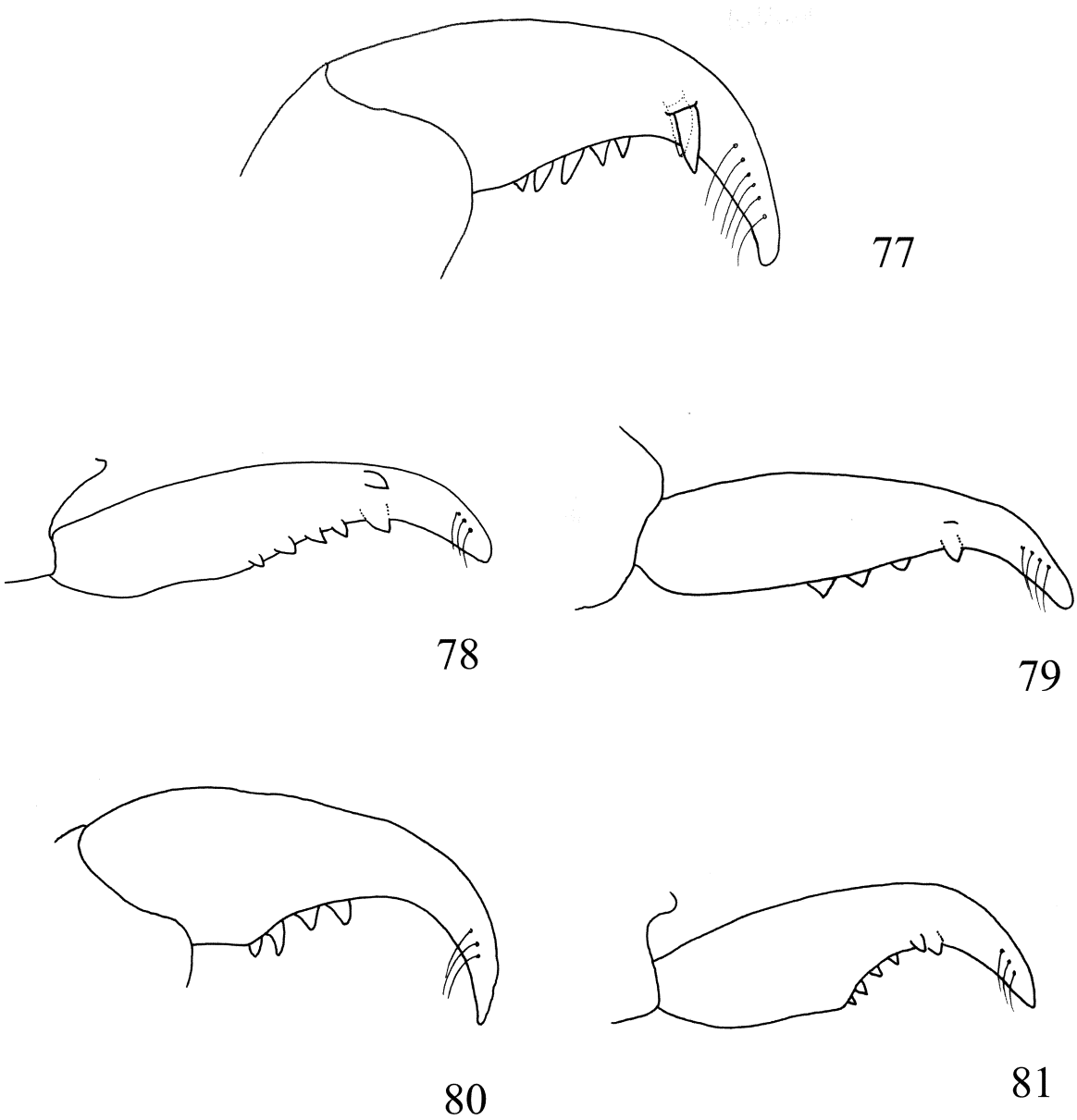
Species included:

Dudgeodes hutanis Sartori sp. nov. (Borneo)
Dudgeodes lugens (Navás, 1933) **comb. nov.** (China)
Dudgeodes stephani Sartori sp. nov. (Borneo)
Dudgeodes ulmeri Sartori sp. nov. (Java, Sumatra)
Dudgeodes pescadori Sartori sp. nov. (Philippines)
Dudgeodes celebensis Sartori sp. nov. (Sulawesi)

Distribution. From South China, throughout Southeast Asia up to Sulawesi (Australasian Realm)



FIGURES 65–76. Forefemur (65, 67, 69, 71, 73, 75) and setae on the transverse row (66, 68, 70, 72, 74, 76) of *Dudgeodes* spp. and *Derlethina eloisae*. Insertion of the setae on the margins indicated by dots; only some setae drawn. Figs. 65–66: *D. hutanis*; Figs. 67–68: *D. stephani*; Figs. 69–70: *D. ulmeri*; Figs. 71–72: *D. pescadori;* Figs. 73–74: *D. celebensis;* Figs. 75–76: *D. eloisae*. Femora at same scale; setae at same scale.



FIGURES 77–81. Tarsal claw of Oriental Teloganodidae. Fig. 77: *Teloganodes hubbardi*; Fig. 78: *Dudgeodes hutanis*; Fig. 79: *D. stephani*; Fig. 80: *D. celebensis*; Fig. 81: *Derlethina eloisae*. All claws same scale.

***Dudgeodes hutanis* Sartori sp. nov.**
(Figs. 9, 10, 22, 23, 28, 35, 41, 49, 53, 65, 66, 78, 91–94, 103–108, 132–134)

Material examined. Holotype: 1 male nymph, Indonesia, East Kalimantan, Malinau Basin, Seturan (2000-petak 43), Temalat (Sungai Guang), trib. Seturan, 2°59´29"N, 116°33´29"E, 16.IV.2001 (B0813), P. Derleth [MZL]

Paratypes: 115 nymphs, same data as holotype [6 of each in FAMU, ZMH, LIPI, AMG, the remaining in MZL, of which 4 partially mounted on slide preparations]; 1 nymph, Langap Sud (1995), Ngayo, trib. Rian, 3°4´56"N, 116°30´58"E, 13.VII.2000 (B0431) P. Derleth; 15 nymphs, same locality, 14.IV.2001 (B0433), P. Derleth & M. Sartori; 13 nymphs, Seturan (2001-petak 57), Tamalang, trib. Seturan, 2°59´22"N, 116°30´29"E, 10.IV.2001 (B0513), P. Derleth; 24 nymphs, Seturan (2001-petak 57), Tamalang, trib. Seturan, 2°59´22"N, 116°30´46"E, 8.VIII.2000 (B0531), P. Derleth; 11 nymphs 2 female subimagos, with corresponding exuviae, Seturan (2000-petak 43), Temalat (Sungai Guang), trib. Seturan, 2°59´29"N, 116°33´29"E,

18.VI.2000 (B0811), P. Derleth & J.-L. Gattolliat; 8 nymphs, same locality, 16.VIII.2000 (B0812), P. Derleth & R. Schaepfer [all MZL]

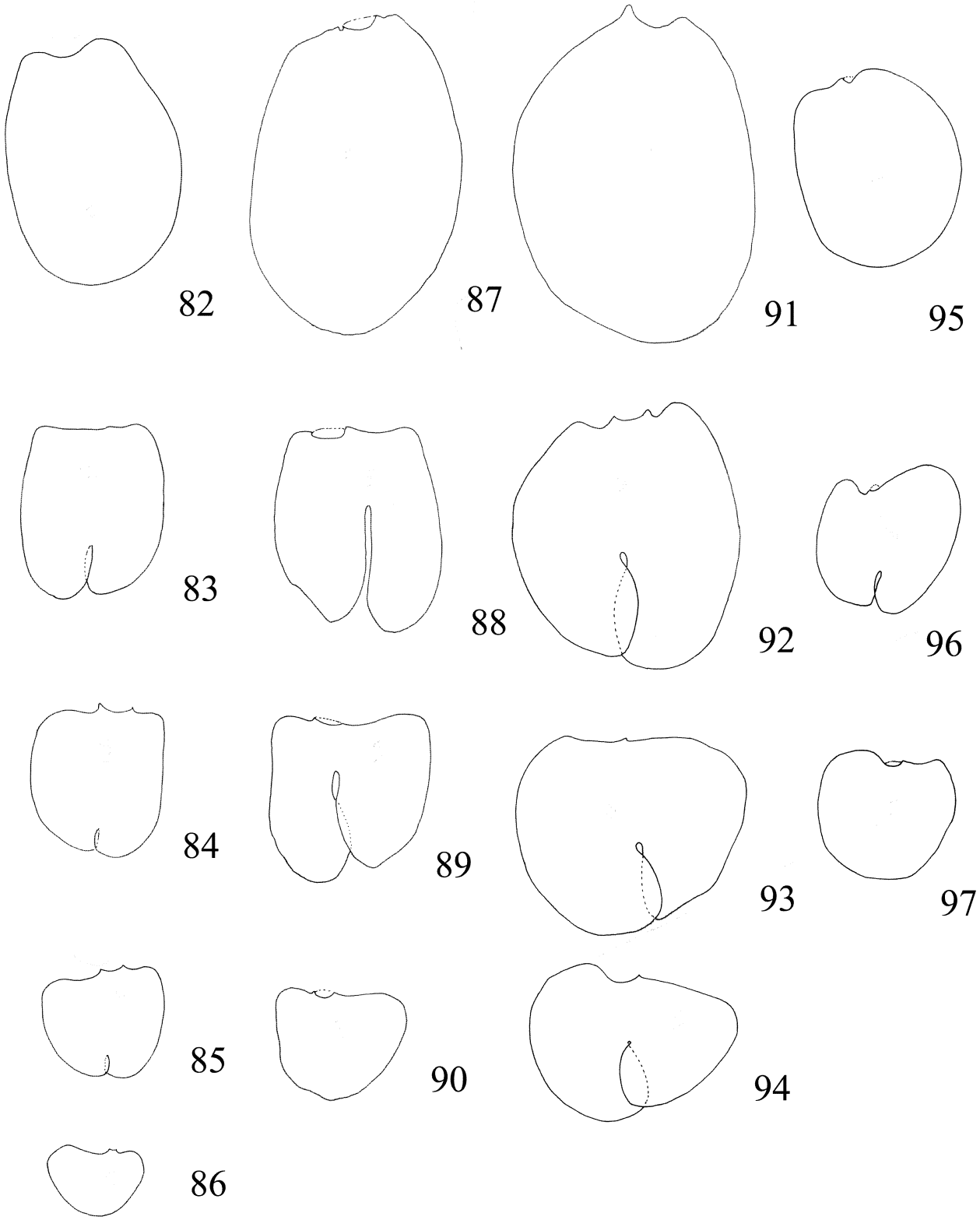
Other material: 6 nymphs, Langap Sud (1997-petak 6), Belakau, trib. Rian, 3°4´4"N, 116°30´26"E, 13.VI.2000 (B0111), P. Derleth; 11 nymphs, same locality, 20.IV.2001 (B0113), P. Derleth & M. Sartori; 2 nymphs, Langap Sud (1997-petak 6), Belakau, trib. Rian, 3°4´4"N, 116°30´26"E, 7.VII.2000 (B0121), P. Derleth; 1 nymph, same locality, 18.IV.2001 (B0123), P. Derleth & M. Sartori; 3 nymphs, Seturan (1999-petak 39-40), Temalat (Sungai Guang), trib. Seturan 3°0´10"N, 116°32´24"E, 27.III.2001 (B0213), P. Derleth; 1 nymph, Langap Sud (1995), Ngayo, trib. Rian, 3°4´41"N, 116°31´11"E, 14.VI.2000 (B0410), P. Derleth; 6 nymphs, Seturan (2001-petak 57), Tamalang, trib. Seturan, 2°59´22"N, 116°30´46"E, 11.IV.2001 (B0533), P. Derleth & B. Feldemeyer; 7 nymphs, Seturan (2001-petak 57), Tamalang, trib. Seturan, 2°59´22"N, 116°30´46"E, 19.VIII.2000 (B0541), P. Derleth & R. Schaepfer; 6 nymphs, Seturan (2000-petak 44-45), Wok (Sungai Guang), trib. Seturan, 2°59´12"N, 116°33´11"E, 5.IV.2001 (B0713), P. Derleth & B. Feldemeyer; 1 nymph, Seturan (2000-petak 43), Temalat (Sungai Guang), trib. Seturan, 2°59´29"N, 116°33´29"E, 4.IV.2001 (B0823), P. Derleth; 5, nymphs, same locality, 16.IV.2001 (B0833), P. Derleth & M. Sartori; 14 nymphs, Seturan (1998-petak 32-33), Rian, 3°0´57"N, 116°32´16"E, 30.III.2001 (B1013),P. Derleth; 12 nymphs, Langap Sud (1999-petak 24), Rian, 3°1´40"N, 116°31´5"E, 11.VII.2000 (B1211), P. Derleth; 3 nymphs, Seturan (unlogged forest), Seturan, 3°0´5"N, 116°30´48"E, 28.III.2001 (B1313), P. Derleth & B. Feldemeyer; 2 nymphs, Seturan (unlogged forest), Seturan, 2°58´58"N, 116°33´30"E, 26.IV.2001 (B1423), P. Derleth & M. Sartori [all MZL]

Description. Nymph

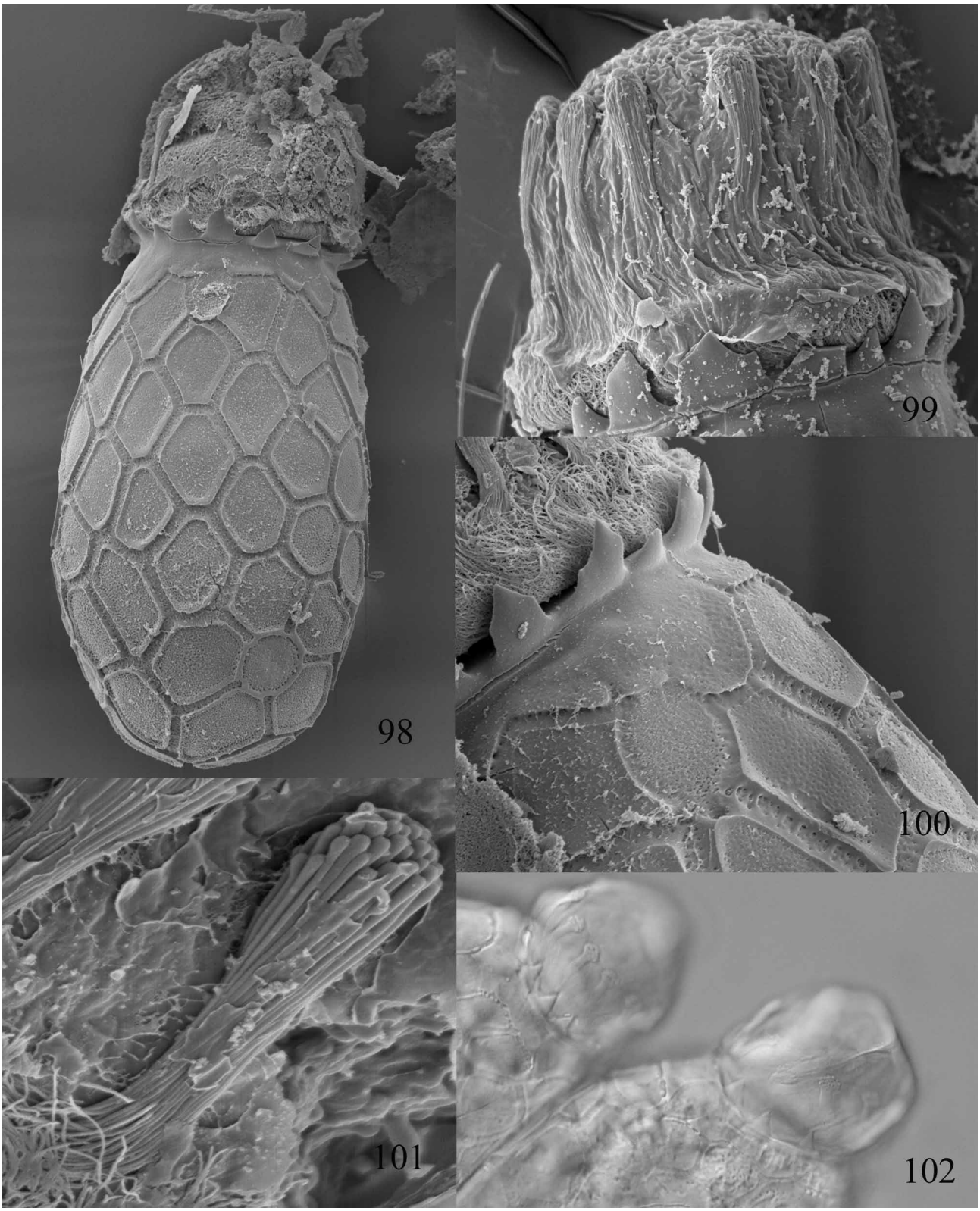
Body length up to 4.5 mm and 4.0 mm, without cerci, in female and male nymphs respectively; cerci length subequal to body length.

General colouration very variable, ranging from middle to dark brown; young specimens generally paler; legs light to middle brown, with femora bearing 4 characteristic maculae (Fig. 132). Outer margin of head fringed with a row of short, basally forked setae from in front of eyes to labrum insertion. Antennae 1.2 times head width, flagellum with 15–17 segments. Dorsal part of male eyes blackish. Labrum (Fig. 22) compact, ca. 2 times wider than long, with smooth anterior emargination; dorsal face covered medially by scattered simple and long setae (Fig. 23); anterior margin with a row of small thin setae. Mandibles slender with one thin seta in middle of outer margin; right mandible (Fig. 28) with outer incisor composed of 3 teeth; inner incisor with 2 teeth; prostheca reduced, comprised of a cluster of thin setae; a small row of 4 long and thin setae below mola and some short setae above mola; left mandible (Fig. 35) with outer incisor with 3 teeth; inner incisor with 2 teeth inserted transversely, one smaller and pointed, other large and rounded, prostheca small with a group of small setae; no setae below mola. Maxillae (Fig. 41) slender, with a well developed carina, 2 indented dentisetae and 3 long setae on inner apical part and a bunch of long, simple setae at crown; inner margin at base of lacinia, with 2 feathered and long setae, one dorsally and one ventrally; maxillary palp reduced to a single simple seta. Hypopharynx (Fig. 49) with superlinguae oval with a row of long, simple setae at apex. Submentum moderately developed laterally; glossae and paraglossae partially fused; paraglossae larger than glossae; labial palp three-segmented, articulation between segments 1 and 2 barely visible and indicated by a constriction; segment 3 ca. 2.5 times as long as wide (Fig. 53).

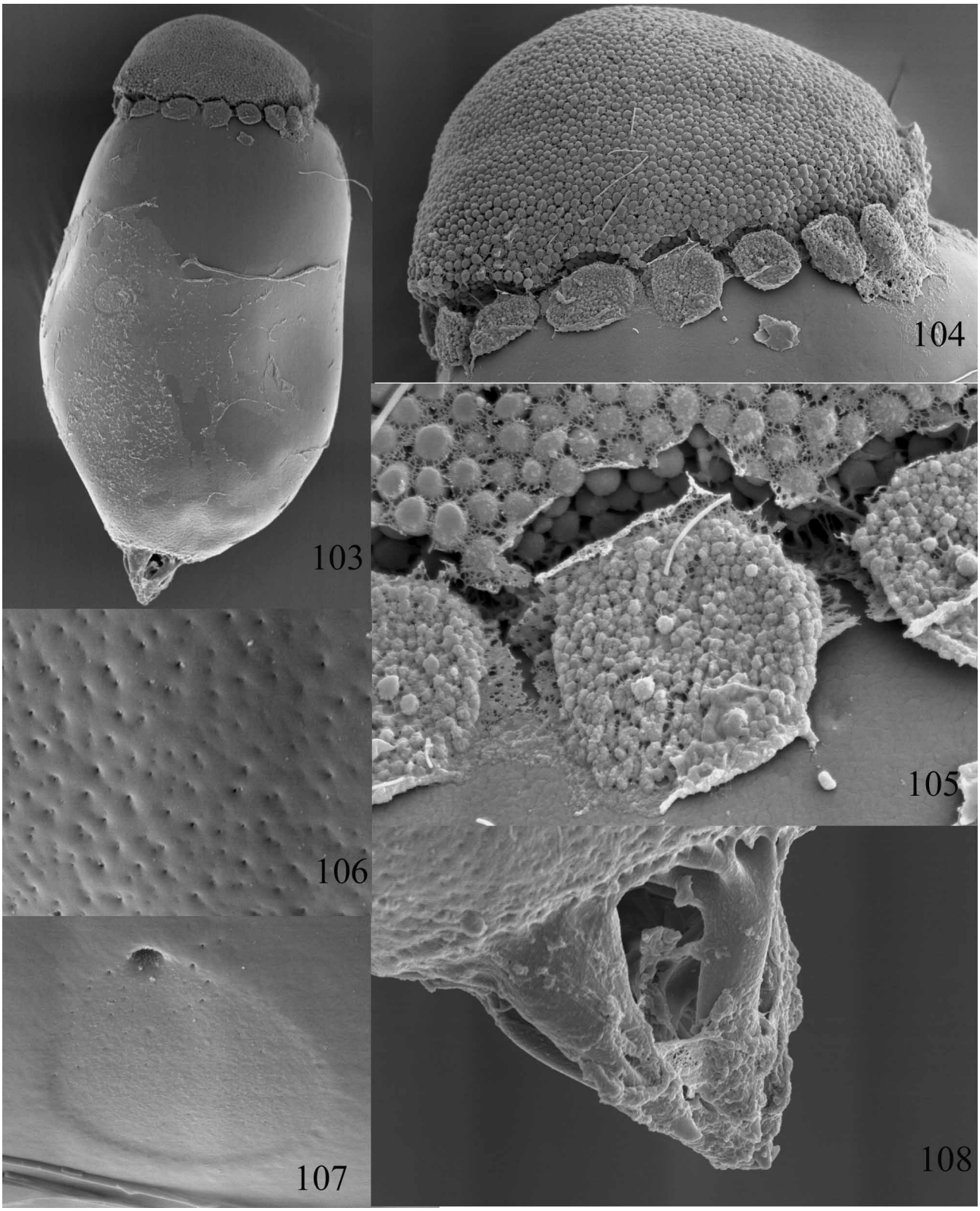
Prothorax with 4 rounded tubercles on dorsal face; mesothorax with none. Forefemur (Fig. 65) dilated, ca. 1.5 times longer than wide; outer margin covered by stout and long setae, meeting a transverse row of long and pointed setae across dorsal face (Fig. 66); inner margin with a short row of long and thin setae proximally reaching distally to transverse row. Middle and hind femora similar, more slender, ca. 2 times longer than wide; dorsal and inner margins with a row of long and stout setae. Tibia with a row of long and stout setae on inner margin, and a row of long and thin setae on outer margin. Tarsal claw hooked, bearing 3–4 blunt teeth medially, and 2 pointed teeth subapically; outer tooth well developed, inner one smaller; apex of claw with two rows of 3–4 thin setae laterally (Fig. 78).



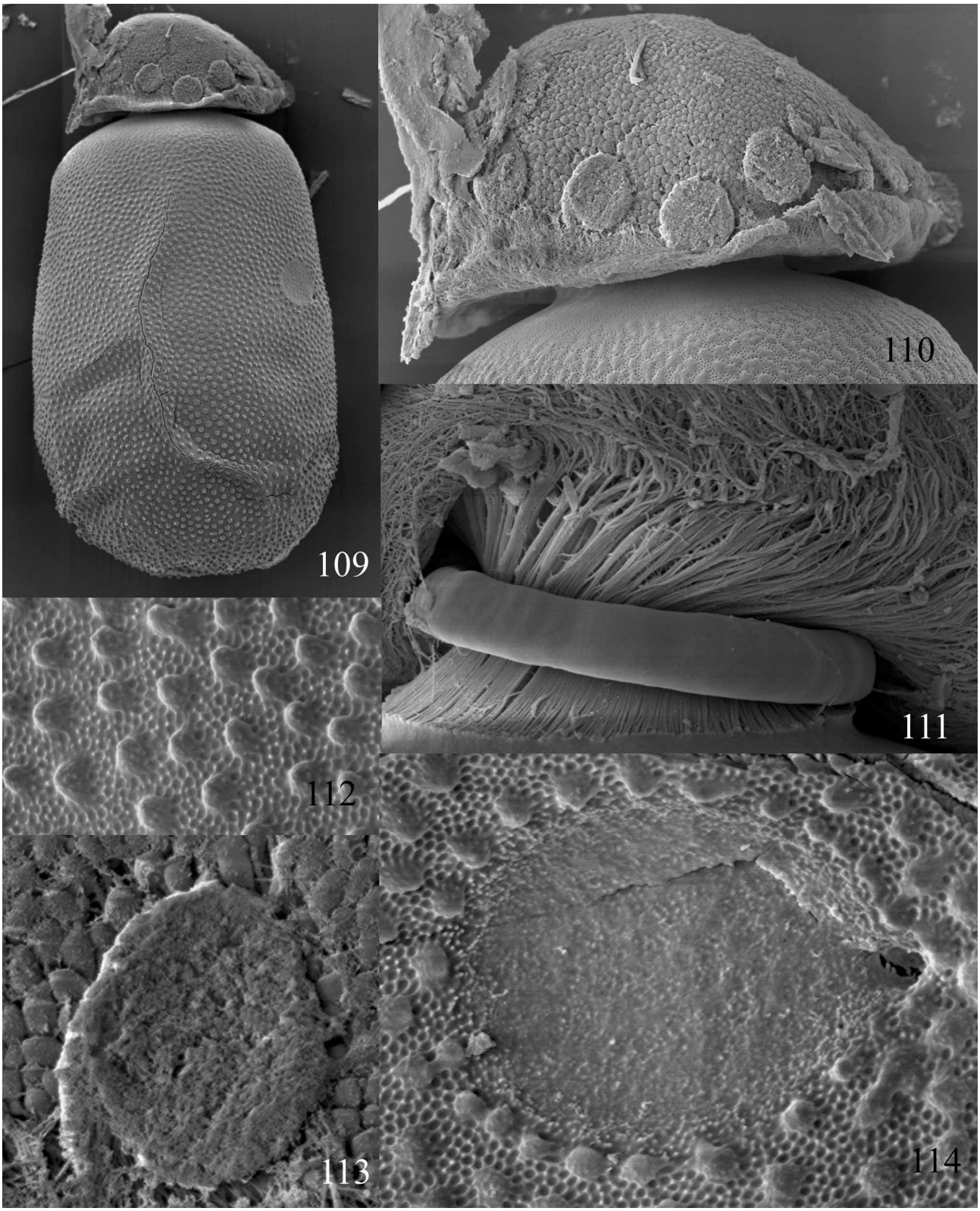
FIGURES 82–97. Gill II (82, 87, 91, 95), gill III (83, 88, 92, 96), gill IV (84, 89, 93, 97), gill V (85, 90, 94) and gill VI (86) of Oriental Teloganodidae; only upper lamellae drawn. Figs. 82–86: *Teloganodes tuberculatus*; Figs. 87–90: *T. jacobusi*; Figs. 91–94: *Dudgeodes hutanis*; Figs. 95–97: *Derlethina eloisae*. All gills same scale.



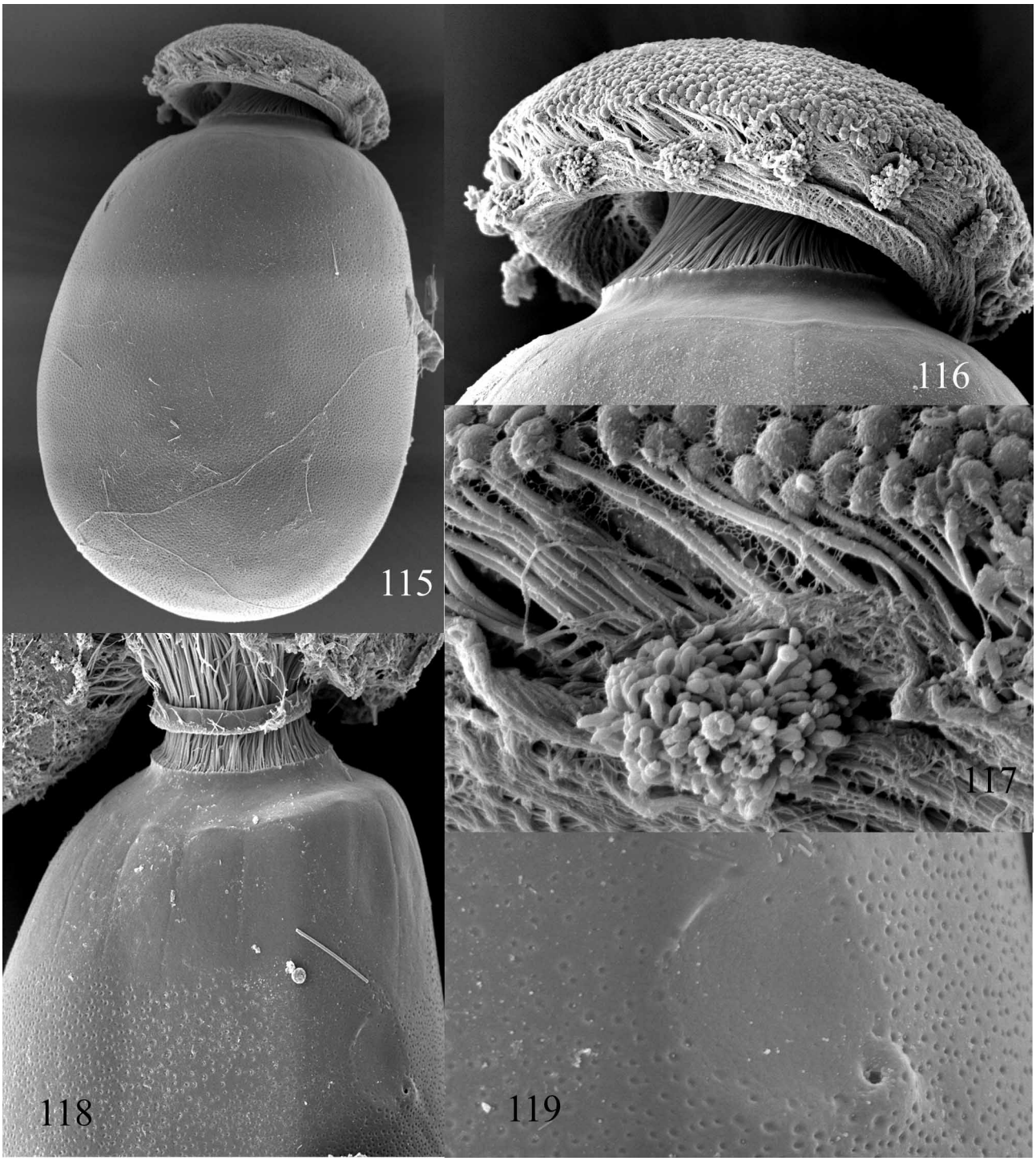
FIGURES 98–102. Egg structure of *Teloganodes hubbardi* (98–101, SEM pictures) and *T. tristis* (102, light microscope). Fig. 98: Shape of the egg; Fig. 99: Detail of the polar cap; Fig. 100: Micropyle area and crown of sets; Fig. 101: Detail of the uncoiled tread of the epithema; Fig. 102: Partial view of polar caps where crown and uncoiled threads are visible.



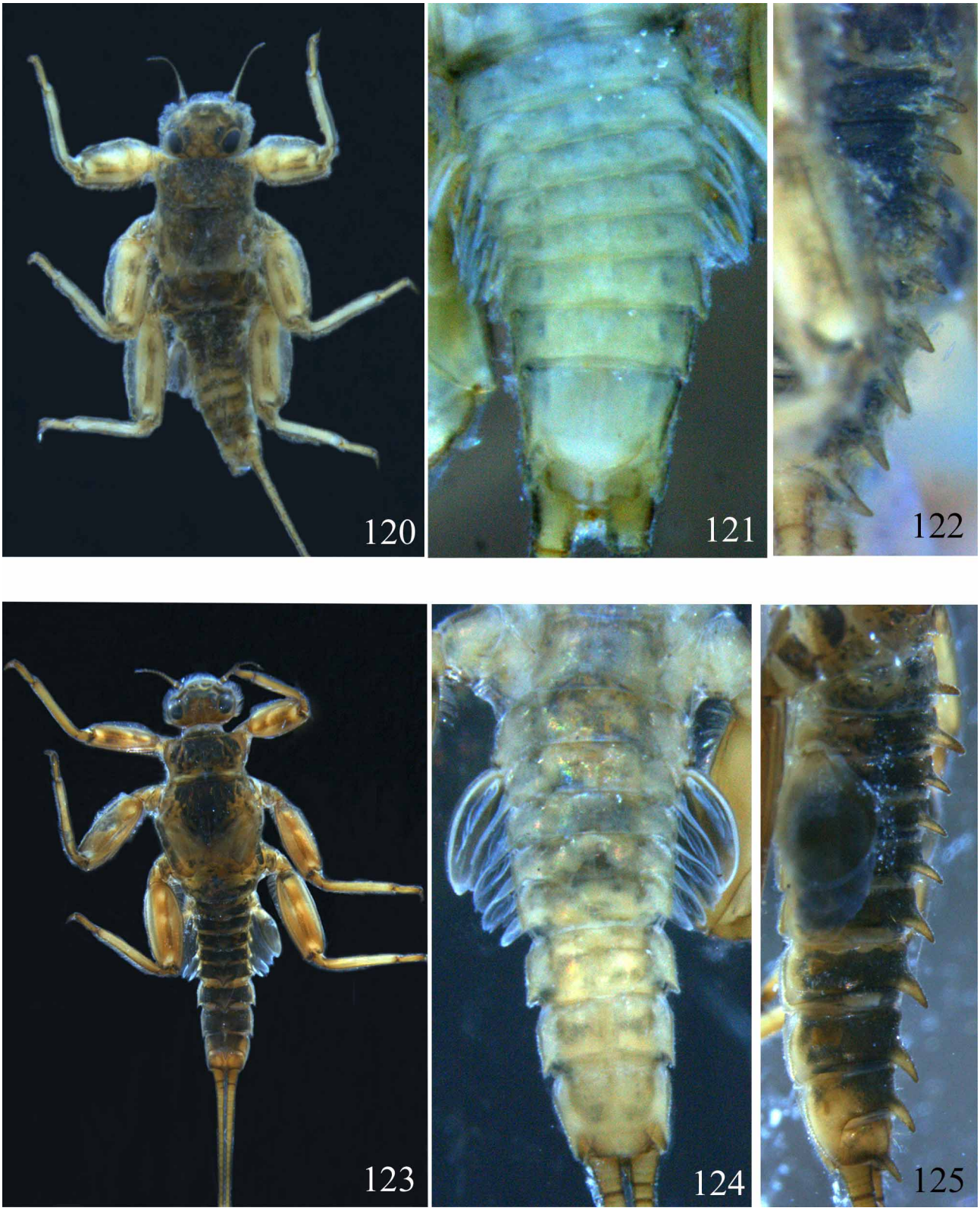
FIGURES 103–108. Egg structure of *Dudgeodes hutanis* (SEM pictures). Fig. 103: Shape of the egg; Fig. 104: Detail of the polar cap; Fig. 105: Detail of the lateral attachments with coiled threads; Fig. 106: Detail of the chorion; Fig. 107: Micropyle area; Fig. 108: Detail of the structure located opposite to the polar cap.



FIGURES 109–114. Egg structure of *Dudgeodes pescadori* (SEM pictures). Fig. 109: Shape of the egg; Fig. 110: Detail of the polar cap; Fig. 111: Detail of the collar with threads of the epithema; Fig. 112: Detail of the chorion; Fig. 113: Detail of the lateral attachments; Fig. 114: Micropyle area.



FIGURES 115–119. Egg structure of *Derlethina eloisae* (SEM pictures). Fig. 115: Shape of the egg; Fig. 116: Detail of the polar cap; Fig. 117: Detail of the coiled threads of the epithema; Fig. 118: Detail of the different chorionic structures; Fig. 119: Micropyle area.



FIGURES 120–125. Holotypes of *Teloganodes* spp. in dorsal view (120, 123), abdomen in ventral view (121, 124) and in lateral view (122, 125). Figs. 120–122: *T. tuberculatus*; Figs. 123–125: *T. kodai*.

Abdominal terga with a moderately developed median tubercle on segments I–V, more developed on segments VI–X (Fig. 131). No posterolateral projections on segments II–IV, slightly marked on segments VI–IX (Fig. 130). Gills as in Figs. 91–94; gill II with dorsal lamella operculate, oval and with entire margin; gills III–V with dorsal lamella incised medially; ventral lobe flabellate, well developed and purple on gills II–IV.

Cerci with stout setae every 2–3 segments; setae longer than length of corresponding segment.

Female subimago. Body length: 4.5 mm. Forewing length: 5.2 mm. Hindwing length: 0.7 mm.

General colouration of body blackish, without markings. Wings greyish with small paler spots scattered over surface. Forewing (Fig. 9) with hind margin regularly convex. Pterostigmatic area with 7–9 crossveins reaching subcostal vein. Vein MP_2 short. Cubital field with a single long intercalary vein. Hind wing (Fig. 10) small, with costal process acute. 3 longitudinal veins distinct. Gill sockets visible on segments II–V. Subanal plate rounded.

Egg. Ovoid, 160 µm by 110 µm; chorion without attachment structures, with two kinds of surfaces: a completely smooth surface on the half of egg close to polar cap (Figs.103–104), and a fine punctuated surface on opposite pole (Fig. 106), with a gradient in-between (in light microscopy, the area close to the polar cap appears light brown, whereas the one close to the opposite pole appears dark brown). One micropyle in equatorial area (Fig. 107), directed transversely to egg axis. Polar cap with two kinds of epithema: numerous non-coiled threads (Fig. 104) and coiled threads located close to margin with chorion (Fig. 105). On pole opposite polar cap, a characteristic cluster of 4–5 needle-like spines (Fig. 108).

Etymology. The epithet “hutanis” comes from the Indonesian word “hutan” meaning “forest” and refers to the beautiful Bulungan forest where the material comes from.

Dudgeodes lugens (Navás, 1933) comb. nov.

Teloganodes lugens Navás, 1933: 17

Material examined. None

Description. This species was described from a single female subimago from Southeast China, “Chekiang, Chusan”, captured 11.VI.1931 by O. Piel. This location is nowadays known as Zhou Shan Island, in Zhejiang province. The type material could not be located, and this specimen is neither housed in the Museum national d’Histoire Naturelle de Paris (Berthelemy 1965, J. Legrand, comm. pers.) nor in the Museum of Zoology of Barcelona (Alba-Tercedor & Peters 1985). Based on the drawing of the hindwing, we think it plausible that this species belongs to the genus *Dudgeodes*; the shape of the costal process and the length/width ratio (ca. 1.8) is similar to that of *D. hutanis*. *Dudgeodes lugens* would differ from *D. hutanis* by having more numerous intercalary veins in the cubital field. The only other mention of Teloganodidae from continental China was made by Tong & Dudgeon (2000) who mentioned two nymphs of *“Teloganodes tristis”* from Tai Pau Forest, Hong Kong. The drawings clearly indicate that this species belongs to the genus *Dudgeodes* and is closely related to *D. hutanis*. The status of Chinese *Dudgeodes*, whether the nymphs from Hong Kong are the immature stage of *D. lugens* or are in fact conspecific with those of another species described here or even a new species may be solved when more material becomes available.

Dudgeodes stephani Sartori sp. nov.
(Figs. 54, 67, 68, 79, 141–143)

Material examined. Holotype: 1 male nymph, Malaysia, Sabah, Liwagu River, at bridge, Ranau, 335 m., 11–16.VIII.1972, W.L. & J.G. Peters [FAMU].

Paratypes: 36 nymphs, same data as holotype [18 in FAMU, 18 in MZL of which 2 partially mounted on slide preparation];

FIGURES 126–131. Holotypes of *Teloganodes* spp. in dorsal view (126, 129), abdomen in ventral view (127, 130) and in lateral view (128, 131). Figs. 126–128: *T. jacobusi*; Figs. 129–131: *T. hubbardi*.

Description. Nymph

Body length up to 4.0 mm, without cerci, in female and male nymphs; cerci length slightly longer than body length.

General colouration medium brown dorsally and light brown ventrally; thoracic ganglia tinted with purple; general colouration paler in younger nymphs; legs yellowish, with same 4-stripe pattern as in *D. hutanis* (Fig. 141).

Antennae 1.2–1.4 times head width, flagellum with 15–18 segments. Dorsal part of male eyes yellowish. Labrum, mandibles and maxillae similar to those of *D. hutanis*. Hypopharynx with superlinguae broad and rhomboid, a row of long, simple setae at apex. Labium as in *D. hutanis*; labial palp three-segmented, articulation between segments 1 and 2 clearly visible, constricted on inner margin; segment 3 more than 3 times as long as wide at base (Fig. 54).

Prothorax with 4 rounded tubercles on dorsal face; mesothorax with none. All legs similar to those of *D. hutanis*, but forefemora less dilated (Fig. 67) and setae of transverse row sometimes bifid (Fig. 68). Tarsal claw hooked, bearing 3–4 blunt teeth medially and 1 outer pointed subapical tooth, the inner tooth being regressed and almost invisible; apex of claw with two rows of 3–4 thin setae laterally (Fig. 79).

Abdominal terga with a moderately developed median tubercle on segments I–II, more developed on segments III–X (Fig. 143). No posterolateral projections on segments II–III, slightly marked on segments IV–VI and well developed on segments VII–IX (Fig. 142). Gills similar to those of *D. hutanis*. Cerci with stout setae every 2–3 segments; setae longer than length of corresponding segment.

Winged stages unknown.

Diagnosis. *D. stephani* can be separated from *D. hutanis* by the colouration of the eyes in the male nymphs, the shape of the labial palps and the hypopharynx, the tarsal claw with ventral subapical tooth absent, abdominal tubercles and strongly produced posterolateral projections.

Etymology. This species is dedicated in memoriam of Stephane Jaquenoud (1960–2007), friend of the first author and outstanding museographer.

***Dudgeodes ulmeri* Sartori sp. nov.**
(Figs. 31, 38, 45, 56, 69, 70, 138–140)

Teloganodes tristis sensu Ulmer, 1939: 627

Material examined. Holotype: 1 male nymph, Indonesia, Sumatra, stream south of Balige, 5.IV.1929, Prof. Feuerborn [code FT6 in Ulmer, 1939] [ZMH] According to Ulmer (1939), this material was collected by Feuerborn, but on the slide preparations made by Ulmer appears the name of Thienemann!

Paratypes: 5 nymphs, partially mounted on 4 slide preparations by Ulmer, same data as holotype [ZMH, MZL], 1 male subimago, same locality, but 16.IV.1929, Prof. Feuerborn [code FT16], 1 nymph Indonesia, Java, Lamongan area, Ranu Bedali, waterfall, in bryophytes, 21.XI.1928, Prof. Feuerborn [code FM26a] [ZMH]; 1 nymph, Java, dikes of fishponds at Punten, near Malang [first author translation of "Teichwirtschaft Punten, near Malang, Gräben"], 18.X.1929, Prof. Thienemann [code P1a] [MZL]

Description. Nymph

Body length up to 7.0 and 6.0 mm, without cerci, in female and male nymphs respectively; cerci length slightly longer than body length.

General colouration uniformly light brown, without any pattern, probably due to inadequate preservative medium added to ethanol (after the collection was deposited in ZMH in 1963 ? formalin ?) (Fig. 138). This is confirmed by the slide preparations made by Ulmer where the typical patterns of the femora are well visible and similar to those of *D. hutanis* (see also Ulmer, 1939, Figs. 296–298).

FIGURES 132–137. Holotypes of *Dudgeodes* spp. in dorsal view (132, 135), abdomen in ventral view (133, 136) and in lateral view (134, 137). Figs. 132–134: *D. hutanis*; Figs. 135–137: *D. pescadori*

Antennae ca. 1.2 times head width, flagellum with 15–16 articles. Dorsal part of male eyes yellowish brown, according to Ulmer (1939, p. 627: "isabellfarben"). Labrum, mandibles and hypophayrynx similar to those of *D. hutanis*. Maxilla similar in shape, but inner margin at base of lacinia with one feathered and long seta dorsally, and 4 short and feathered setae ventrally (Fig. 45). Labium as in *D. hutanis*; labial palp three-segmented, articulation between segments 1 and 2 clearly visible, without constriction on inner margin, segment 3 less than 3 times as long as wide at base (Fig. 56).

Prothorax with 4 small and flattened tubercles on dorsal face; mesothorax with none. Forefemur (Fig. 69) moderately dilated, ca. 1.8 times longer than wide; outer margin covered by stout and long setae; transverse row across dorsal face short, not reaching both margins and constituted by relatively short and stout setae (Fig. 70); inner margin with a long row of long and thin setae; proximal area of outer margin with a bunch of thin setae. Middle and hind femora similar, more slender, ca. 2.2 times longer than wide; dorsal and inner margins with a row of long and stout setae. Tibiae and tarsi as those of *D. hutanis*.

Abdominal terga with a weakly developed median tubercle on segment I, moderately developed on segments II–VI (V), and well developed on segments VII (VI)–X (Fig. 140). No posterolateral projections on segments II–IV, moderately marked on segments V–IX (Fig. 139). Gills similar to those of *D. hutanis*. Cerci with stout setae every 2–3 segments; setae shorter than the length of corresponding segment.

Male subimago. A single specimen in poor condition, colourless, and with wings torn.

Wing venation, as far as it can be seen, similar to that of *D. hutanis.*

Diagnosis. *D. ulmeri* can be separated from *D. hutanis* and *D. stephani* by the ornamentation of the forefemora, especially the transverse row of setae, the length of the row of setae on the inner margin, the bunch of setae on the proximal part of the outer margin (reduced to a single seta in all other species of the genus). The setae on the inner margin of the lacinia are also unique among the genus (plesiomorphic condition).

Etymology. This species is named in honour of Dr Georg Ulmer (1877–1963), who first described this species, and outstanding specialist of Ephemeroptera of Southeast Asia as well as worldwide.

***Dudgeodes pescadori* Sartori sp. nov.**
(Figs. 12, 13, 29, 36, 44, 57, 71, 72, 109–114, 135–137)

Teloganodes tristis sensu Ulmer, 1924: 44

Material examined. Holotype: 1 male nymph, Philippines, Luzon, Laguna Prov., Mud springs, Los Banos, 28.IX.1969, Reisen & Basio [FAMU]

Paratypes: 9 nymphs; same data as holotype [MZL, of which 1 partially mounted on slide preparation]; 1 female subimago, same locality, but 29.IX.1969 [FAMU]; 21 nymphs, same locality, but 20-XII-1969 [FAMU]; 58 nymphs, Philippines, Luzon, Laguna Prov., College, Molawin Creek, 28.VII.1977, C.R. Realon [27 in FAMU, 31 in MZL of which 1 partially mounted on slide preparation]; 3 nymphs, same data, 20-IX-1969; 11 nymphs, picnic area, Los Banos, 29.IX.1969, Reisen & Basio [FAMU]; 1 nymph, Molawin Creek, Los Banos, 2.VI.1967. M.L. Pescador [FAMU]; 3 male imagos, same locality, 7.VI.1967, M. Pescador [MZL]; 1 male imago, same locality, 13.VI-1967 [FAMU]; 2 male imagos, Laguna Prov., Balanc Riv., Pagsajam, 3.XI.1967, M.L. Pescador & D. Z. Llamas Jr. [FAMU]; 1 nymph, Mountain Prov., Talugin Stream, Talubin Boni, 2.X.1967, M.L. Pescador [FAMU].

Other material: 3 male subimagos, 1 female imago, Philippines, Mindanao, Dansalam, 5.II.1915, Boettger [ZMH]

Description. Nymph

Body length up to 7.0 mm and 6.0 mm, without cerci, in female and male nymphs respectively; cerci length slightly shorter than body length.

FIGURES 138–143. Holotypes of *Dudgeodes* spp. in dorsal view (138, 141), abdomen in ventral view (139, 142) and in lateral view (140, 143). Figs. 138–140: *D. ulmeri*; Figs. 141–143: *D. stephani*

FIGURES 144–149. Holotypes of *Dudgeodes* and *Derlethina* in dorsal view (144, 147), abdomen in ventral view (145, 148) and in lateral view (146, 149). Figs. 144–146: *Dudgeodes celebensis*; Figs. 147–149: *Derlethina eloisae*

General colouration medium brown dorsally and light brown ventrally; thoracic ganglia tinted with purple; general colouration paler in younger nymphs; legs yellowish, with 4-stripe pattern, the outer ones sometimes fused into a single stripe (Fig. 129).

Antennae 1.1 times head width, flagellum with 16–18 articles. Dorsal part of male eyes blackish. Labrum and maxillae similar to those of *D. hutanis*. Mandibles slender with one thin seta in middle of outer margin; right mandible (Fig. 29) with outer incisor composed of one large and one small tooth, the latter barely visible when mandible is worn; inner incisor with 2 teeth; prostheca reduced, constituted by a bunch of thin setae; a row of 3–4 long and thin setae below mola and some short setae above mola; left mandible (Fig. 36) with outer incisor made of one tooth rounded when new but tabular when worn; inner incisor with 2 teeth inserted transversally, one small and pointed, other large and rounded, prostheca small with a bunch of small setae; no setae below mola. Ventral seta on the maxilla moderately developed (Fig. 44). Hypopharynx with superlinguae moderately broad and ovoid, a row of simple and long setae at apex. Labial palp three-segmented, articulation between segments 1 and 2 clearly visible, constricted on outer margin; segment 3 ca. 2.5 times as long as wide at base (Fig. 57).

Prothorax with 2 rounded tubercles on dorsal face; mesothorax with none. Forefemur (Fig. 71) greatly dilated, ca. 1.3–1.4 times longer than wide; outer margin serrated and covered by stout and long setae, meeting with transverse row across dorsal face (Fig. 72); 4–5 submarginal short and blunt setae along outer margin; inner margin with an expanded row of long and thin setae ending distally with 2–3 short and blunt setae. Foretibia with clearly visible row of long and thin setae on inner margin, but with scattered very thin setae along outer margin. Middle and hind femora similar, more slender, ca. 1.7–1.8 times longer than wide; dorsal and inner margins with a row of long and stout setae. Tibia with a row of long and stout setae on inner margin, and a row of long and thin setae on outer margin. Tarsal claw hooked, bearing 4–5 blunt teeth medially and no pointed teeth subapically; apex of claw with two rows of 2–3 thin setae laterally.

Abdominal terga with a moderately developed median tubercle on segments I–III, more developed on segments IV–V and well developed on segments VI–X (Fig. 137). Posterolateral projections weakly developed on segments II–III, and well developed on segments IV–IX (Fig. 136). Gills as in *D. hutanis*. Cerci with stout setae every 2–3 segments; setae shorter than length of corresponding segment.

Female subimago. Body length: 6.8 mm; forewing length: 6.5 mm, cerci broken.
General colouration middle to dark brown; head and pronotum greyish brown, mesothorax and wings medium brown; legs yellowish brown, femora with 4 darker longitudinal maculae, as in nymph, coxae of all legs with one blackish dot on dorso-distal part, and one on ventro-distal part. Abdominal terga medium brown, washed with dark brown maculae; sterna uniformly yellowish brown; cerci yellowish at base.

Male imago. Body length: 6.0–6.5 mm; forewing length: 5.8–6.2 mm

General colouration dark brown. Upper part of eyes well developed and grey. Wings completely translucent, with a brownish marking at base; pterostigmatic area milky. Legs yellowish, femora with characteristic 4 longitudinal maculae; coxae as in female subimago; apex of tibiae with a blackish ring. Foreleg with following proportions: tibia ca. 1.5 times femur length and ca. 1.8 times tarsus length.

Abdomen dark brown, sterna lighter than terga; gonopods, styliger plate and penis yellowish. Cerci whitish with purple banding at junction of each segment.

Forewing (Fig. 11) with pterostigmatic area with 6–8 crossveins. Numerous crossveins throughout wing. Cubital field with 4 intercalary veins; CuP very characteristic, forming almost a right angle near base. Hindwing (Fig. 12) moderately broad, with an acute costal process.

Styliger plate straight to slightly concave (Fig. 13); gonopods 3-segmented, segment 1 ca. same length as segments 2 and 3 combined; segment 1 subcylindrical; segment 2 slightly enlarged at apex; segment 3 elongated, ca. 2.5–3 times as long as broad at base. Penis lobes fused, outer margin convex, i.e. the maximum width about mid length of lobes; a longitudinal groove clearly visible between lobes (Fig. 13).

Egg. Ovoid, ca. 155 µm by 110 µm; chorion without attachment structures (Fig. 109), and uniformly granular (Fig. 112), except for micropyle area, smooth. One micropyle in equatorial area, directed transversally to egg axis (Fig. 114). Polar cap with two kinds of epithema, similar to those of *D. hutanis* (Figs. 110, 111, 113). No spines present on pole opposite epithema.

Diagnosis. *D. pescadori* can be separated from the previously described species by the tarsal claw without subapical teeth, the shape of the mandibles, the absence of a well defined row of setae on the outer margin of the foretibiae, and by the whorls of spines on the cerci shorter than the corresponding segment.

Etymology. This species is named in honour of Prof. Manuel (Manny) Pescador (Florida A&M University) good friend and colleague, who collected the beautiful male imagos.

Remark. The winged specimens deposited in ZMH, and identified by Ulmer as *Teloganodes tristis* Hagen, are preserved in ethanol but are in bad condition, having been dried probably and not well rehydrated. They are referred to here as *D. pescadori*, mainly on the base of the marking on the coxae and wing venation, similar to those of the type material, especially vein CuP (see also Fig. 19 in Ulmer, 1924).

***Dudgeodes celebensis* Sartori sp. nov.**
(Figs. 30, 37, 55, 73, 74, 80, 144–146)

Material examined. Holotype: 1 male nymph, Indonesia, North Sulawesi, vicinity of Manado, Kali Village, site 1, Kali stream at Kali village, above bridge, 01,41412°N; 124,84214°E, 206 m., 8.XII.2004, C. Geraci, M. Dien, F. Mirah, D. Lapasi [FAMU]

Paratypes: 31 nymphs, same data as holotype [18 in FAMU, 6 in CUAC, 7 in MZL, of which 2 partially mounted on slide preparation]; 1 nymph, Indonesia, North Sulawesi, Minahasa Selantan District, Tenga River at Tenga Village, bridge; 01.16394°N, 124.44313°E, 75 m, 11.XII.2004, C. Geraci, M. Dien, C. Rante [FAMU].

Description. Nymph (not full grown)

Body length at least 5 mm, cerci subequal to body length.

General colouration medium to dark brown dorsally and greyish brown ventrally; thoracic ganglia tinted with purple; general colouration sometimes more contrasted in some specimens; legs yellowish to light brown, upper face of femora with variable patterns around the "classic" 4 maculae: in some specimens, these maculae are reduced to tiny lines whereas in others, they are large and well contrasted (Fig. 144).

Antennae 1.0–1.1 times head width, flagellum with 17–18 articles. Dorsal part of male eyes blackish. Labrum and maxillae similar to those of *D. pescadori*. Mandibles slender with one thin seta in middle of outer margin; right mandible (Fig. 30) with outer incisor composed of one large tooth, slightly indented medially; inner incisor with 2 teeth; prostheca reduced, constituted by a cluster of thin setae; a row of 7–9 long, thin setae below mola and some short setae above mola; left mandible (Fig. 37) with outer incisor consisting of one slightly concave tooth, inner incisor with 2 teeth inserted transversely, one small and pointed, the other large and rounded, prostheca small with a cluster of small setae; no setae below mola. Hypopharynx with superlinguae ovoid and regularly rounded, a row of simple and long setae at apex. Labial palp three-segmented, articulation between segments 1 and 2 clearly visible, constricted on inner margin; segment 3 ca. 2.0 times as long as wide at base (Fig. 55).

Prothorax with 6 flat tubercles on dorsal face; mesothorax with none. Forefemur greatly dilated (Fig. 73), ca. 1.4–1.5 times longer than wide; outer margin covered by stout and long setae, with a transverse row across dorsal face (Fig. 74); 6–7 submarginal short and blunt setae along outer margin; inner margin with a row of long and thin setae reaching ca. 2/3 of femur length; on distal half of inner margin, a row of stout and blunt or pointed spines. Foretibia with one distinct row of long and thin setae on inner margin, and another on outer margin. Middle and hind femora similar, more slender, ca. 1.8–2.0 times longer than wide; dorsal and inner

margins with a row of long and stout setae. Tibia with a row of long and stout setae on inner margin, and a row of long and thin setae on outer margin. Tarsal claw hooked, with 4 medial blunt teeth, and no pointed teeth subapically; apex of claw with two rows of 3–4 thin setae laterally (Fig. 80).

Abdominal terga with a moderately developed median tubercle on segments I–II, well developed on segments III–IX and less developed on segment X (Fig. 146). Posterolateral projections weakly developed on segment II, moderately developed on segments III–IV, and well developed on segments V–IX (Fig. 145). Gills similar to those of *D. pescadori*. Cerci with stout setae shorter than length of corresponding segment.

Winged stages unknown

Diagnosis. *D. celebensis* is similar to *D. pescadori* from which it can be separated by the presence of well defined row of setae on the outer margin of the foretibiae, the shape of the incisors of the mandibles and mainly by the ornamentation of the forefemora.

Etymology. The epithet comes from the Celebes, the former name of Sulawesi Island.

Remark. *D. celebensis* is the only teloganodid mayfly known from the Australasian Realm. The genus was already mentioned from Sulawesi by Edmunds & Polhemus (1990) under the name *"Teloganodes"* and without specific identification.

Derlethina **Sartori gen. nov.**

Type species: *Derlethina eloisae* Sartori sp. nov. by present designation
Teloganodes sp. sensu McCafferty & Wang (1997)
Teloganodes sp. T3 sensu Kluge (2004)
eloisae

Description. Adult: Forewing (Fig. 14) long and slender, posterior margin regularly convex. Pterostigmatic area without crossveins; vein MP_2 very short, and free; cubital field with 2 intercalary veins. Hind wing (Fig. 15) minute with costal process acute and located almost at apex of wing; a single simple longitudinal vein. Claws of all legs dissimilar. Dorsal margin of hind femora concave. Subanal plate of female almost straight. Gill socket vestiges visible on segments II–IV. Terminal filament absent.

Nymph (Fig. 147): Body flattened, eyes in dorsal position blackish in male nymphs; outer margin of head fringed with a row of forked setae from behind eyes to labrum insertion. Labrum with a single row of simple setae (Fig. 24). Galea-lacinia with 2 setae on ventral side (Fig. 46). Forefemora broad and dilated with a transverse row of setae on dorsal face (Fig. 75). Hind femora with a distinct concave outer margin (Fig. 147). Gills on abdominal segments II–IV (Figs. 95–97); gills II–III with ventral lobes, gill IV without ventral lobe and entire (not incised), gill III incised. Abdominal carina (median tubercles on terga), poorly developed. Posterolateral expansions very well developed on segments VI–IX. Lateral margins of terga with very long and thin setae. Terminal filament absent.

Egg: rounded, chorion without attachment structures, one polar cap, no triangular or polygonal structures at the base of the cap (Figs. 115–119).

Diagnosis. *Derlethina* winged stages can easily be told from *Teloganodes* and *Dudgeodes* by the shape of the hindwing, the absence of crossvein in the pterostigmatic area of the forewing, and the shape of the hind femur; the nymphal stage is distinguished by the absence of gill V and the shape of the posterior femora.

Etymology. This new genus is named after Dr Pascale Derleth (Lausanne), wife of the first author, who collected most of the material during her work in East Kalimantan, and was the first to recognize it as a separate genus. The gender is feminine.

Distribution. Known only from Borneo (East Malaysia – Sabah - and Indonesia – East Kalimantan)

Derlethina eloisae **Sartori sp. nov.**
(Figs. 14, 15, 24, 25, 32, 39, 58, 75, 76, 81, 95–97, 115–119, 147–149)

Material examined. Holotype: 1 male nymph, Indonesia, East Kalimantan, Malinau Basin, Seturan (old growth forest) – Seturan, 3°00'05"N, 116°30'48"E, 28.III.2001, P. Derleth & B. Feldmeyer (B1313) [MZL]
Paratypes: 12 nymphs, same data as holotype [5 in FAMU, remaining in MZL]; 92 nymphs, Seturan (2000-petak 43) - Temalat (Sungai Guang), trib. Seturan, 2°59'29"N, 116°33'29"E, 16.IV.2001, P. Derleth (B0813) [5 in each LIPI, ZMH, AMG, remaining in MZL]; 32 nymphs, same locality but 18.VI.2000, P. Derleth & J.L. Gattolliat (B0811) [of which 2 partially mounted on microscopic slide]; 11 nymphs, same locality but 14.VIII.2000, P. Derleth & R. Schlaepfer (B0812) [of which 2 partially mounted on microscopic slide]; 2 nymphs, Langap Sud (1995) - Ngayo, trib. Rian, 3°04'56"N, 116°30'58"E, 13.VII.2000, P. Derleth (B0431) [of which 1 partially mounted on microscopic slide]; 3 nymphs, same locality but 14.IV.2001, P. Derleth & M. Sartori (B0433); 5 nymphs, Seturan (2001-petak 57) - Tamalang, trib. Seturan, 2°59'22"N, 116°30'29"E, 18.VII.2000, P. Derleth & F. Béboux (B0511); 9 nymphs, same locality but 10.IV.2001, P. Derleth (B0513); 6 nymphs, Seturan (2001-petak 57) - Tamalang, trib. Seturan, 2°59'22"N, 116°30'46"E, 08.VIII.2000, P. Derleth (B0531) ; 9 nymphs, same locality but 11.IV.2001, P. Derleth & B. Feldmeyer (B0533); 1 female imago, Seturan (2000-petak 44-45) - Wok (Sungai Guang), trib. Seturan, 2°59'12"N, 116°33'11"E, 05.IV.2001, P. Derleth & B. Feldmeyer (B0713) ; 23 nymphs, Seturan (2000-petak 43) - Temalat (Sungai Guang), trib. Seturan, 2°59'29"N, 116°33'29"E, 16.IV.2001, P. Derleth & M. Sartori (B0833); 1 nymph, Seturan (unlogged forest) – Seturan, 2°58'54"N, 116°33'29"E, 24.IV.2001, P. Derleth & M. Sartori (B1413); 6 nymphs, Seturan (unlogged forest) – Seturan, 2°58'58"N, 116°33'30"E, 26.IV.2001, P. Derleth (B1423) [MZL].

Other material: 1 nymph, Indonesia - East Kalimantan - Malinau - Langap Sud (1997-petak 6) - Belakau, trib. Rian, 3°04'04"N, 116°30'26"E, 20.IV.2001, P. Derleth & M. Sartori (B0113); 3 nymphs, same locality but 05.VII.2000, P. Derleth (B0111); 1 nymph, same locality but 13.VI.2000, P. Derleth (B0110); 2 nymphs, Langap Sud (1997-petak 6) - Belakau, trib. Rian, 3°04'04"N, 116°30'26"E, 18.IV.2001, P. Derleth & M. Sartori (B0123); 3 nymphs, same locality but 07.VII.2000, P. Derleth (B0121); 2 nymphs, Seturan (1999-petak 39-40) - Temalat (Sungai Guang), trib. Seturan, 3°00'10"N, 116°32'24"E, 27.III.2001, P. Derleth (B0213) ; 3 nymphs, Langap Sud (1995) - Ngayo, trib. Rian, 3°04'41"N, 116°31'11"E, 14.VI.2000, P. Derleth (B0410); 4 nymphs, same locality but 08.VII.2000, P. Derleth (B0411); 1 nymph, Seturan (2001-petak 57) - Tamalang, trib. Seturan, 2°59'22"N, 116°30'29"E, 10.IV.2001, P. Derleth (B0513) ; 5 nymphs, Seturan (2001-petak 57) - Tamalang, trib. Seturan, 2°59'50"N, 116°30'29"E, 19.VII.2000, P. Derleth & F. Béboux (B0521) ; 8 nymphs, Seturan (2001-petak 57) - Tamalang, trib. Seturan, 2°59'22"N, 116°30'46"E, 18.VIII.2000, P. Derleth & R. Schlaepfer (B0541) ; 3 nymphs, Seturan (2000-petak 45) - Wok (Sungai Guang), trib. Seturan, 2°59'11"N, 116°33'30"E, 29.VI.2000, P. Derleth (B0631) ; 8 nymphs, Seturan (2000-petak 44-45) - Wok (Sungai Guang), trib. Seturan, 2°59'12"N, 116°33'11"E, 05.IV.2001, P. Derleth & B. Feldmeyer (B0713); 8 nymphs, Seturan (2000-petak 43) - Temalat (Sungai Guang), trib. Seturan, 2°59'29"N, 116°33'29"E, 04.IV.2001, P. Derleth (B0823); 1 nymph, same locality but 21.VI.2000, P. Derleth & J.L. Gattolliat (B0821); 1 nymph, Seturan (1998-petak 32-33) – Rian, 3°00'57"N, 116°32'16"E, 30.III.2001, P. Derleth (B1013); 1 nymph, Langap Sud (1999-petak 24) – Rian, 3°01'40"N, 116°31'05"E, 11.VII.2000, P. Derleth (B1211); 1 nymph, Seturan (unlogged forest) – Seturan, 2°59'49"N, 116°31'22"E, 27.IV.2001, P. Derleth & M. Sartori (B1513)[all MZL]. 1 female imago, Indonesia, East Kalimantan, Kelian River, tributary of Mahakan River, 250 km West of Samarinda, 13.IX.1992, C. Yule; 12 nymphs; same locality but 7.IX.1990; 1 nymph, Malaysia, Sabah, Liwagu river, north of Kundassan, 915 m., 16–17.VIII.1972, W.L. & J.G. Peters; 1 nymph ibid, but W.M. Beck; 2 nymphs, Malaysia, Sabah, Silau stream, north of Kinabalu National Park headquarters, 1585 m., 11–16.VIII.1972, W.M. Beck; 1 nymph Malaysia, Sabah, Mantukungam River, Poring Hot Springs, 365 m, 12.VIII.72, W.L. & J.G. Peters [all FAMU].

Description. Nymph

Body length up to 3.5–4.0 mm and 4.5–5.0 mm in male and female respectively, cerci slightly longer than body length.

General colouration greyish black dorsally; scape and flagellum of the antennae whitish, pedicel blackish; legs yellowish, femora darker, with 4 dark brown maculae on dorsal face, maculae sometimes merging; apex of tibiae brownish (Fig. 147).

Outer margin of head fringed with a row of setae from behind eyes to labrum insertion. Antennae 0.9–1.0 times head width, flagellum with 15–16 articles. Dorsal part of male eyes blackish (Fig. 147). Labrum (Fig. 24) with a wide anteromedian emargination; anterior margin covered by thin setae; dorsal face with a row of long and simple setae (Fig. 25). Mandibles slender with one thin seta in middle of outer margin; right mandible (Fig. 32) with outer incisor composed of one tooth, slightly indented medially; inner incisor with 2 teeth; prostheca reduced, constituted by a group of thin setae; a row of 3–4 long, thin setae below mola and some short setae above mola; outer incisor of left mandible (Fig. 39) composed of one tooth indented basally, inner incisor with 2 teeth inserted transversally, one small and pointed, the other large and rounded, prostheca reduced with one well developed seta; no setae below mola. Maxillae moderately slender, with a well developed canine, 2 dentisetae and 3 long setae on inner apical part and a bunch of long, simple setae at crown; inner margin at base of lacinia with one feathered and long seta dorsally and 2 short feathered setae ventrally (Fig. 46); maxillary palp reduced to a simple seta. Hypopharynx with lingua broad, superlinguae quadrangular, outer margin almost straight, a row of simple and long setae at apex. Labial palp three-segmented, articulation between segments 1 and 2 not visible; segment 3 ca. 2.0 times as long as wide at base (Fig. 58).

Prothorax and mesothorax without tubercles on dorsal face. Forefemur (Fig. 75) dilated, ca. 1.5–1.6 times longer than wide; outer margin covered by stout and long setae, and dorsal face with a transverse row of stout and blunt setae (Fig. 76) almost reaching inner margin; inner margin with a row of long and thin setae almost reaching apex of femur. Foretibia with one visible row of long and thin setae on inner margin, and another on outer margin. Middle femur more slender, ca. 1.9–2.0 times longer than wide; dorsal and inner margins with a row of long and stout setae. Tibia with a row of long and stout setae on inner margin, and a row of long, thin setae on outer margin. Hind leg similar, except femur even more slender, ca. 2.5 longer than wide, outer margin very characteristic and concave. Tarsal claw hooked, with medial 3–4 pointed teeth, and 2 pointed teeth subapically, the inner tooth reduced; apex of claw with two rows of 3–4 thin setae laterally (Fig. 81).

Abdominal terga without median tubercle on segments I–IV, poorly developed on segments V–IX, and none on segment X (Fig. 149). No posterolateral projections on segments II–IV, well developed on segments V–IX (Fig. 148). Gills (Figs. 95–97) on abdominal segments II–IV, gills II with dorsal lamella operculate, oval and with entire margin; gills III with dorsal lamella incised medially; gills IV with dorsal lamella little reduced and entire; ventral lobe flabellate, well developed and purple on gills II–III.

Cerci with stout setae longer than length of corresponding segment.

Female imago. Body length (without cerci): 3.5 mm; Forewing length: 4.0 mm; hindwing length: 0.27 mm

General colouration as in the nymph, especially pedicel blackish, and with the same patterns on femur and tibia. Cerci yellowish, without banding.

Outer margin of hind femora concave. Wings completely hyaline; forewing (Fig. 14) with Sc and R_1 veins dark brown, other longitudinal veins light brown. In addition to character states given in the generic diagnosis, crossveins hardly visible, CuP vein with a short stem. Hindwing almost invisible (less than 0.3 mm length), with a very characteristic shape (Fig. 15).

Egg. Rounded (Fig. 115), ca. 125 µm by 105 µm; chorion without attachment structures and finely pitted which grades to a smooth surface near the polar cap (Fig. 119). Micropyle close to polar cap, and directed transversely to egg axis (Figs. 118–119). Polar cap constituted by two kinds of epithema: a cluster of coiled threads, and small coiled threads arranged in circle around polar cap (Figs. 116–117).

Etymology. This species is dedicated to the youngest daughter of the first author, Miss Eloise Sartori.

Notes on Teloganodidae egg structure

Prior to this study, eggs of Teloganodidae were virtually unknown, having not been treated by Koss (1968) and Koss & Edmunds (1974) in their study of Ephemeroptera eggs, nor by McCafferty & Wang (1997; 2000) in their revision of Teloganodidae.

Although only 5 among 13 Oriental species are now known in that stage, some general patterns may be drawn. All examined eggs lack chorionic attachment structures, compared, for instance, to those of most Ephemerellidae (Studemann *et al.* 1995; Studemann & Landolt 1997). They all possess a single polar cap, but the epithema is not uniform and is always comprised of two kinds of structures.

Teloganodes eggs are pear-shaped and seem characterized by the presence of triangular, tooth-like structures arising from the chorion and delimiting the polar cap; the micropyle is located close to the polar cap and directed to the opposite pole. The threads of the epithema are non-coiled.

Dudgeodes eggs are ovoid; the micropyle is located in the equatorial area and directed transversely to the egg axis. The threads of the epithema are non-coiled for part of them and coiled for those forming the lateral attachments. *Dudgeodes hutanis* possess a very peculiar structure on the pole opposite to the polar cap, whose function is unknown at the moment (secondary attachment structure? remains of a second polar cap?).

Derlethina eggs are almost round, the micropyle is located near the polar cap and directed transversely to the egg axis. The threads of the epithema are all coiled.

Based on the terminology of Koss and Edmunds (1974), the polar cap of *Teloganodes* and *Dudgeodes* would be intermediate between type I (non-coiled, single unit cap) and II (non-coiled, multi-unit cap), whereas *Derlethina* eggs are close to type III (multi-threaded coiled cap). Obviously, more detailed investigations are needed on the ultrastructure of Teloganodidae eggs.

Key to known nymphs of Oriental Teloganodidae

In this key, *T. insignis* is tentatively placed, although we have not seen any material.

1. Abdominal gills present on segments II–IV (Figs. 95–97), last gill entire; outer margin of hind femora clearly concave (Fig. 147); posterolateral projections on abdomen well developed on segments VI–IX (Fig. 148) ..... *Derlethina eloisae*
- Abdominal gills present on segments II–VI (Figs. 82–86) or II–V (Figs. 91–94); outer margin of the hind femora never concave; posterolateral projection on abdomen variable 2
2. Gills present on abdominal segments II–VI; forefemora without a row of transverse setae on dorsal face (Figs. 59–60); teeth of inner incisor of left mandible similar in size (Fig. 33) 3
- Gills present on abdominal segments II–V; forefemora with a row of transverse setae on dorsal face (e.g. Fig. 65); teeth of inner incisor of left mandible dissimilar (e.g. Fig. 35) 5
3. Outer margin of forefemora with a dense row of thin setae only (Fig. 60) ..... *Teloganodes kodai*
- Outer margin of forefemora with a dense row of thin setae and some scattered thick and pointed setae (Fig. 59) 4
4. Labrum ca. 2 times wider than long (Fig. 16); outer margin of mandibles with 2 stout setae (Figs. 26, 33); outer margin of forefemora with 5–7 thick and pointed setae (Fig. 59) ..... *Teloganodes tuberculatus*
- Labrum ca. 3 times wider than long; outer margin of mandibles with one stout seta; outer margin of forefemora with 12–15 thick and pointed setae ..... *Teloganodes insignis*
5. Gill V entire (Fig. 90); outer incisor of the right mandible spoon-shape (Fig. 27); eyes of male nymphs

orange brown; tergum X without tubercle 6

- Gill V incised apically (Fig. 94); outer incisor of the right mandible normally built (e.g. Fig. 28); eyes of male nymphs black or yellowish; tergum X with a tubercle 7

6. Forefemora ca. 2 times longer than wide; outer margin of forefemora with a submarginal row of stout setae (Fig. 61); hypopharynx with superlinguae quadrate (Fig. 47)..... *Teloganodes jacobusi*

- Forefemora ca. 1.3–1.4 times longer than wide; outer margin of forefemora without a submarginal row of stout setae (Fig. 63); hypopharynx with superlinguae oval (Fig. 48)..... *Teloganodes hubbardi*

7. Tarsal claw with at least one subapical tooth (Fig. 78).....8

- Tarsal claw without subapical tooth (Fig. 80).....10

8. Tarsal claw with 2 well developed subapical teeth (Fig. 78); third segment of labial palp ca. 2.5 longer than wide at base (Figs. 53, 56) 9

- Tarsal claw with inner subapical tooth reduced (Fig. 79); eyes of the male nymph orange-yellowish; third segment of the labial palp more than 3 times longer than wide at base (Fig. 54) ..... *Dudgeodes stephani*

9. Transverse row on forefemora with both long and stout setae (Fig. 66), apex of outer margin with a single thin seta and inner margin with row of setae ending ca. middle of the margin; a single ventral long seta on inner margin of galea lacinia (Fig. 41); eyes of male nymph black ..... *Dudgeodes hutanis*

- Transverse row on forefemora with short, stout setae only (Fig. 70), apex of outer margin with a cluster of thin setae and inner margin with row of setae for most of its length; 2–3 ventral short setae on inner margin of galea lacinia (Fig. 45); eyes of male nymph yellowish brown..... *Dudgeodes ulmeri*

10. Outer margin of foretibiae with scattered setae; row of 4 setae below mola of right mandible (Fig. 29); inner margin of forefemora with a few stout setae distally (Fig. 71) ..... *Dudgeodes pescadori*

- Outer margin of foretibiae with a row of setae; row of 7–8 setae below mola of right mandible (Fig. 30); inner margin of forefemora with numerous stout setae in distal half (Fig. 73) ..... *Dudgeodes celebensis*

Conclusions

As already mentioned by several workers, e.g. Edmunds (1972; 1975; 1979), McCafferty & Wang (1997), McCafferty (1999), Teloganodidae is an ancient group of Gondwanian origin. Our cladistic analysis based on new material from the Oriental Realm establishes the existence of three lineages supported by both morphological and biogeographical features.

Jacobus & McCafferty (2006) state that the Oriental lineage (*Teloganodes* and *Macafertiella* at that time) and the Madagascar genus *Manohyphella* are sister groups. Our study cannot confirm or refute it since no other African species have been studied. But we can suppose that their ancestor was isolated during the Gondwana break-up and evolved for a while on the Madagascar + Indian subcontinent. The separation of Madagascar from the Deccan plate and its subsequent drift towards Asia led to the *Manohyphella* lineage in Madagascar and the *Teloganodes* lineage in Asia. This last lineage evolved in two directions: a first lineage that remained around its original distribution (genus *Teloganodes*), and a second one which dispersed throughout tropical Southeast Asia, evolving into what is now *Dudgeodes*, a branch giving rise to the most apotypic *Derlethina* in Borneo.

We may suspect that the distribution of the early lineage on Madagascar + Indian subcontinent has been restricted for the following reason. The distribution of *Manohyphella* in Madagascar is restricted to the East coast covered by tropical rain forest (Elouard *et al.* 2003). The distribution of *Teloganodes* is restricted to Sri Lanka and the Western Ghats. These areas were closely connected on the proto-island (Wells 2003).

Our revision of Oriental Teloganodidae brings significant new information on mayfly taxonomy and biodiversity in the investigated area. The concept of *Teloganodes tristis*, supposed to be widespread from Sri Lanka to Philippines, encompasses in fact two genera and six species. We suspect the diversity of *Dudgeodes*

to be much higher than reported here. For instance, this study focused mainly on the Sunda Islands, but almost nothing on continental Southeast Asia. Teloganodidae have also been reported (under the name *Teloganodes*, but most probably belonging to the new genus *Dudgeodes*) from Vietnam (Soldán 1991), from Thailand (Sites *et al.* 2001), from Cambodia (Anonymous 2006) and also from the Lesser Sunda Islands (Lombok to Timor) (Edmunds & Polhemus 1990). It is likely that some of these populations represent new species.

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