Phylogenetic Systematics of the Family Teloganodidae (Ephemeroptera: Pannota)

by

W. P. MCCAFFERTY and **T. Q. WANG**
(Department of Entomology, Purdue University,
West Lafayette, IN 47907 USA)

ABSTRACT

Teloganodidae **stat. nov.** is recognized at the family rank and shown to be a sister group to Ephemerellidae. Cladistic analysis of monophyletic species groups was performed, and the most parsimonious cladogram is presented and discussed in terms of evolutionary trends and instances of homoplasy. There are two major clades; these are recognized as the subfamilies Austremerellinae **subfam. nov.** and Teloganodinae. Genera are defined cladistically by autapomorphies, and sequencing conventions within the context of a strictly phylogenetic classification allow their recognition at this rank. Two genera are recognized in Austremerellinae: *Austremerella* from Australia and *Vietnamella* from southeastern Asia. Six genera are recognized in the Teloganodinae: *Ephemerellina*, *Nadinella* **gen. nov.**, *Lithogloea*, and *Lestagella* from southern Africa, and *Macafertiella* and *Teloganodes* from southern Asia. Previous interpretations of *Austremerella* and *Lithogloea* as subgenera of *Ephemerellina* were based on symplesiomorphies and are untenable. Each genus is distinctive in both larval and adult stages, and a stage-correlated key is provided. Descriptive and geographic accounts for each higher taxon are given, and known species listed. The new genus *Nadinella* contains two nominal species: *N. crassi* (Allen and Edmunds) **comb. nov.** and *N. brincki* (Demoulin) **comb. nov.** Australian and South African genera are shown to be archaic phylogenetic relicts with origins in Gondwanaland prior to the initial breakup of that landmass. It is hypothesized that the presence of Oriental lineages has resulted from Australasian interchange in the case of Austremerellinae, and Africa to Asia transport via the Indian subcontinent in the case of Teloganodinae.

INTRODUCTION

The family Teloganodidae **stat. nov.** is a group of pannote mayflies (McCafferty and Edmunds 1979) known from South Africa, the Orient, and Australia. These mayflies have not been generally well known in the past, and incomplete and sometimes erroneous information has resulted in a history of divergent interpretations. There are only 15 species currently described in the Teloganodidae. This may in part be attributed to the relict nature of the older Gondwanan element of the family; however, we anticipate that several more will be described from the more recent Oriental fauna within the family. For example, we know of at least five undescribed species from southeast Asia at this time.

The ecology of Teloganodidae is poorly known. Available collecting data, however, indicate that larvae of all genera are restricted to mountain streams and rivers where they occur on stones or vegetation in mostly swift currents. Our collecting records from South Africa, Sri Lanka, and Borneo indicate that teloganodid larvae are commonly found on the vertical substrates of waterfalls. Thus, an appropriate vernacular name for the family would be "the waterfall mayflies." Harrison and Agnew (1962) found that certain of the South African teloganodids were restricted to acid waters and gave some additional ecological data. The only gut sample study (Tshernova 1972) indicates that the larvae of the Oriental *Vietnamella* Tshernova are periphyton feeders. Differences we have found in development of filtering setae on mouthparts of different genera, however, suggest that teloganodid larvae may also be fine detritus collectors to various degrees. McShaffrey and McCafferty (1990a, 1990b) found a considerable range of feeding behavior in certain members of the related family Ephemerellidae. The fact that Barnard (1932) has also reported teloganodid larvae from under stones suggests detritus deposit feeding. According to Barnard (1932), some teloganodid larvae crawl out of the water prior to emerging to the subimago, although it is not known if this is facultative or obligatory behavior, or if it is widespread among species. Edmunds and McCafferty (1988) noted that such behavior is predominant in primitive extant mayflies.

We will show that the Teloganodidae is a monophyletic lineage, and is a sister group to the larger, generally more well known, and more apotypic Holarctic and Oriental family Ephemerellidae, within which it was previously considered a subfamily (Allen 1965). Our conclusions are based on the phylogenetic data we present herein. Furthermore, our linear higher classification of Teloganodidae into subfamilies and genera is completely congruent with our cladistics data, in that it is strictly phylogenetic and permits reproduction of the deduced cladogram of the taxa, as was advocated by McCafferty (1991a).

The original concept of the family Ephemerellidae dates to Eaton (1883-88) with his Section 6 of *Ephemerella*, which included the Holarctic and Oriental genus *Ephemerella* Walsh and Oriental genus *Teloganodes* Eaton, as they were known at that time. Klapálek (1909) first used the family rank designation, but included only *Ephemerella*. Ulmer (1920) added the South American genus *Melanemerella* Ulmer to the family, and Lestage (1924) added the South African genus *Ephemerellina* Lestage. Various other genera were described in the family up to the time that Edmunds and Traver (1954), in their outline of higher reclassification, included the following world genera in the Ephemerellidae: *Ephemerella*, *Ephemerellina*, *Lithogloea* Barnard (South Africa), *Melanemerella*, *Teloganella* Ulmer (Oriental), *Teloganodes*, and *Teloganopsis* Ulmer (Oriental).

Demoulin (1955) removed *Melanemerella* from the family Ephemerellidae and placed it in a new subfamily Melanemerellinae of Tricorythidae, and Edmunds et al. (1963) recognized this subfamily but returned it to Ephemerellidae. Wang and McCafferty (1996a) recently removed *Melanemerella* from Ephemerellidae by demonstrating that it is not a member of the Pannota but probably an aberrant member of Leptophlebiidae.

Allen (1965) erected the subfamily Teloganodinae within the Ephemerellidae and included in it the genera *Teloganodes* and *Ephemerellina*. He considered *Austremerella* Riek, from Australia, to be synonymous with *Ephemerellina*; he did not mention *Lithogloea*. Demoulin (1970) described the South African genus *Lestagella* Demoulin in the Ephemerellidae, but did not place it any subfamily. He also placed *Lithogloea* as a subgenus of *Ephemerellina*. Tshernova (1972) described the Oriental genus *Vietnamella* in the family Ephemerellidae, and although Allen (1980, 1984) placed this genus in the Ephemerellinae, Edmunds and Murvosh (1995) correctly recognized that it belonged to the Teloganodinae. Furthermore, Wang and McCafferty (1995) showed that those Oriental species placed in *Ephemerellina* (Allen and Edmunds 1963a, Tshernova 1972) are in actuality species of *Vietnamella*. Allen (1973) described the genus *Manohyphella* Allen from Madagascar and added it to the Teloganodinae along with *Teloganella*. Although never stated by Allen, *Lestagella* was also, by default, considered in the subfamily Teloganodinae, because he did not include it in Ephemerellinae (Allen 1980, 1984).

In 1990, Hubbard listed the following genera in Teloganodinae: *Ephemerellina*, *Lestagella*, *Manohyphella*, *Teloganella*, and *Teloganodes*. Since then, Wang et al. (1995) have removed *Teloganella* from the Teloganodinae and Ephemerellidae, showing that it is instead a member of the family Tricorythidae. Its classification previously had been argued by Edmunds and Polhemus (1990) and Peters and Peters (1993), but neither paper offered any supporting data. McCafferty and Wang (1995) have also removed *Manohyphella* from Ephemerellidae and Teloganodinae, showing that it also is a member of the Tricorythidae. McCafferty and de Moor (1995) re-established the genus *Lithogloea*, thus adding it to the Teloganodinae. As mentioned above, *Vietnamella* was shown to be a member of Teloganodinae (Edmunds and Murvosh 1995). Finally, the Sri Lankan genus *Macafertiella* Wang was recently described in Teloganodinae by Wang and McCafferty (1996b).

Taking into account the complex history of the group, and the results of our cladistic analysis, we recognize herein the following genera in the family Teloganodidae: *Austremerella*, *Ephemerellina*, *Lestagella*, *Macafertiella*, *Nadinella* **gen. nov.** from South Africa, *Teloganodes*, and *Vietnamella*. The entire higher classification is shown in Table 1. We will show that the previous synonymies of *Austremerella* with *Ephemerellina*, and *Lithogloea* with *Ephemerellina* were essentially based on symplesiomorphies.

TABLE 1. Higher classification and general distribution of the Teloganodidae

Family Teloganodidae
- Subfamily Austremerellinae **subfam. nov.**
  - Genus *Austremerella* (Australian)
  - Genus *Vietnamella* (Oriental)
- Subfamily Teloganodinae
  - Genus *Ephemerellina* (Southern Afrotropical)
  - Genus *Nadinella* **gen. nov.** (Southern Afrotropical)
  - Genus *Lithogloea* (Southern Afrotropical)
  - Genus *Lestagella* (Southern Afrotropical)
  - Genus *Macafertiella* (Oriental)
  - Genus *Teloganodes* (Oriental)

The extensive material that we have been able to bring together for comparative analysis has been of vital importance in unravelling the systematics of this group. In particular, this has included Oriental material donated from the George F. Edmunds, Jr. collection (including a recent gift from T. Soldán from Vietnam), previously held at the University of Utah and now held in the Purdue Entomological Research Collection (PERC herein), West Lafayette, Indiana; Australian material loaned and donated by the Australian CSIRO (Australian National Collection, or ANC herein); South African material loaned by the Albany Museum (AM herein); and the extensive material collected in South Africa by the first author and Nadine McCafferty in 1990. The latter and donated material resides in PERC.

Resolving the generic classification and assignment of species and stages in southern Africa (where we recognize four endemic genera) was especially challenging. This was due to numerous factors. Many species were originally incompletely described or characteristics were not described accurately. Some species were subsequently misidentified in the literature, and larval and adult stages were not always associated correctly. Some geographic records attributed to African teloganodines proved to be misidentifications of tricorythid mayflies. We were able to recognize erroneous stage correlations by employing a method discovered and used by McCafferty and Wang (1994) wherein it was shown that the position and relative development of larval structures, such as tubercles, other cuticular processes, and gills, can be represented in the adult stage by recognizable vestiges or associated vestiges (e.g., gill socket vestiges). As an example, we demonstrate that adults assigned to *Ephemerellina barnardi* Lestage by Barnard (1940) were misidentified and do not match adults correctly assigned by him to this species earlier (Barnard 1932). Moreover, the misidentified adults can be associated with larvae originally described as *Ephemerellina crassi* Allen and Edmunds (1963a), which is the type of our new genus *Nadinella*. True larvae of *E. barnardi* were part of the original series of larvae that had been incorrectly associated by Barnard (1932) with *Lithogloea harrisoni* Barnard.

Although our higher classification of the Teloganodidae (Table 1) is based on results of our phylogenetic research, which is essentially represented by a cladogram of species groups, we present the cladistic methods, analysis, and discussion following presentation of the taxonomic keys and systematic accounts of the taxa. The Key to Genera we present is a stage-associated key, meaning that larvae and adults of each genus ideally are keyed together at the same place and in the same sequence in the key. For each genus in the Accounts of Taxa, we give a generic synonymy and type species, descriptions of larval and adult stages, diagnostic information, species included with specific synonymies, distribution, material examined, and remarks regarding systematics and ecology. In addition, 90 morphological figures, including a dorsal whole larval habitus of each genus, are included.

ACCOUNTS OF TAXA

Family Teloganodidae stat. nov.

Description of Mature Larvae

Eyes dorsal or dorsolateral (Figs 2-10), those of males (Figs 4, 10) divided into two distinct parts. Mouthparts more or less prognathous, with branched, hairlike setae present, with variously sized setules (e.g., Figs 47-64); labium relatively small. Forewingpads (Figs 2-10) fused with mesonotum for most of their length, not juxtaposed posteriorly; posterior margin of mesonotum between apices of wingpads with well-developed submedial lobes and medial V-shaped emargination. Hindwingpads present. Simple, filamentous gills absent or present laterally on abdominal segment 1; lamellate gills (Figs 2-10) dorsal and present on abdominal segments 2-5, 2-6, or 2-7; gills on abdominal segment 2 operculate (Figs 7-10), semi-operculate (Figs 4-6), or not operculate (Figs 2, 3); when gills on abdominal segment 2 operculate or semi-operculate, then such gills more or less elongate-rounded and always well separated from each other. Median caudal filament developed (three tailed) (Figs 2-7) or reduced and rudimentary (two tailed) (Figs 8-10).

Description of adult

Eyes of male each divided into two distinct parts. Forewings (Figs 80-87) usually with many short, detached, marginal intercalaries (Figs 80, 83-87) or sometimes with most short intercalaries attached (often to crossveins) (Figs 81, 82); one to four main CuA intercalaries present. Hindwings present. Abdominal segment 2 with gill socket vestiges (Fig. 89). Male genitalia (Figs 90, 91) with three segmented forceps; forceps segment 1 relatively long, more than twice as long as wide. Median caudal filament developed (three tailed) or reduced (two tailed).

Diagnosis of the family

The Teloganodidae is distinct from other families of pannote mayflies. Larvae are distinguished from the Ephemerellidae by the presence of gills on abdominal segment 2. They differ from other families of Pannota with gills on abdominal segment 2 (e.g., Leptohyphidae, Tricorythidae, Caenidae) by the posterior aspect of the mesonotum that has submedian lobes and a V-shaped median notch, and by the subdivided eyes of the mature (pharate) males. Adults of Teloganodidae share generalized, ancestral wing venation and derived divided male eyes with the Ephemerellidae, but differ from them with respect to their distinctly more elongate basal segment of the male genital forceps. All adults of Teloganodidae can be told from all adults of Ephemerellidae by possession of gill socket vestiges on abdominal segment 2. The adults can be told from other pannote mayflies by their general cubital venation, and, with the exception of Ephemerythus (Tricorythidae), by the presence of short marginal intercalaries along the outer margin of the forewings.

Key to Genera

(Couplets 2-4 pertain to genera known from Australia and the Orient; couplets 5-7 pertain to genera known form southern Africa)

1. Larva: Gills present on abdominal segment 7; gills on abdominal segment 2 not operculate or semi-operculate (Figs 2, 3).
Adult: Forewings (Figs 80-82) with stigmatic costal interspace divided by secondary longitudinal vein into upper and lower series of many cellules.
....Subfamily Austremerellinae, 2

— Larva: Gills absent on abdominal segment 7; gills on abdominal segment 2 operculate or semi-operculate (Figs 4-10).
Adult: Forewings (Figs 83-87) with stigmatic costal interspace not divided into upper and lower series of many cellules.
....Subfamily Teloganodinae, 3

2. Larva: Head (Fig. 3) with pair of prominent, elongate, anteriorly directed cephalic horns originating anterior to eyes; forefemora (Fig. 3) very broad and denticulate anteriorly.
Adult: Mesothorax without pair of long membranous processes posteriorly; head with cephalic horn vestiges; forewings (Figs 81, 82) with most marginal intercalaries basally attached.
....Genus ***Vietnamella***

— Larva: Head (Fig. 2) without pair of cephalic horns; forefemora (Fig. 2) not as above.
Adult: Mesothorax (Fig. 88) ending posteriorly with pair of narrow-elongate, membranous processes; head without cephalic horn vestiges; forewings (Fig. 80) with most marginal intercalaries not attached basally.
....Genus ***Austremerella***

3. Larva: Two tailed, with median caudal filament reduced (Figs 8-10).
Adult: Two tailed, with median caudal filament reduced.
....4

— Larva: Three tailed, with well-developed median caudal filament (Figs 4-7).
Adult: Three tailed, with well-developed median caudal filament.
....5

4. Larva: Gills present on abdominal segment 6; median row of dorsal abdominal tubercles well developed (Fig. 8), with tubercle on tergum 10 longer than that of tergum 3.
Adult: Unknown; distribution may be limited to Sri Lanka.
....Genus ***Macafertiella***

— Larva: Gills absent on abdominal segment 6; median row of tubercles absent (Fig. 10) or only poorly developed (Fig. 9), with tubercle on tergum 10, when present, shorter (Figs 9, 10) or longer than that of tergum 3.
Adult: Not comparable because adult of *Macafertiella* unknown; generally distributed in Southeast Asia from India to Philippines.
....Genus ***Teloganodes***

5. Larva: Lamellate gills present on abdominal segments 2-5; claws (Fig. 71) with two rows of denticles; abdomen with pairs of dorsal tubercles (Figs 5, 74, 76) or broad, straight-margined or slightly bifurcated posteromedial protuberances (Figs 75, 76) on at least some terga.
Adult: Abdominal terga 2-5 with gill socket vestiges; terga 3-5 each with small, broad thickening medially, usually with two minute tubercles, or without apparent tubercle vestiges; if tubercle vestiges absent, then IMP of forewings longer than MP_2 and both directly attached to each other (Fig. 84).
....Genus ***Nadinella* gen. nov.**

— Larva: Lamellate gills on abdominal segments 2-4 or 2-6; claws (Figs 70, 72, 73) with one row of denticles; abdomen (Figs 4, 6, 7) without paired or broad, straight-margined or bi-lobular, posteromedial dorsal tubercles or protuberances.
Adult: Abdominal terga 2-4 or 2-6 with gill socket vestiges; terga 3-5 (or more) with no dorsal tubercle vestiges or with only single median tubercle vestige; if tubercle vestiges absent, then IMP of forewings shorter than MP_2 and basally detached from MP_2 (Fig. 86).
....6

6. Larva: Head (Fig. 7) margined with long setae anteriorly; gills on abdominal segment 2 (Fig. 7) operculate.
Adult: Abdominal segment 5 without gill socket vestiges; IMP of forewings shorter than MP_2 (Fig. 86).
....Genus ***Lestagella***

— Larva: Head (Figs 4, 6) not margined with long setae; gills on abdominal segment 2 (Figs 4, 6) semi-operculate, with part of following gill pair exposed.
Adult: Abdominal segment 5 with gill socket vestiges; IMP of forewings shorter (Fig. 85) or longer (Fig. 83) than MP_2.
....7

7. Larva: Abdomen (Fig. 4) with median dorsal row of sharp tubercles; Gills absent on abdominal segment 1.
Adult: Abdominal terga 3-6 (Fig. 89) each with small, median tubercle vestige; IMP of forewings longer than MP_2, and MP_2 attached directly to IMP (Fig. 83).
....Genus ***Ephemerellina***

— Larva: Abdomen (Fig. 6) with single median row of dorsal tubercles represented by broad-based and attenuated extensions of the posterior tergal margins; Gills present on abdominal segment 1.
Adult: Abdominal terga 3-6 without tubercles; IMP of forewings shorter than MP_2 and detached from it (Fig. 85).
....Genus ***Lithogloea***

Subfamily Austremerellinae subfam. nov.

Diagnosis

Larvae of the Austremerellinae may be told from those of the Teloganodinae by the presence of gills on abdominal segment 7 (Figs 2, 3). Gills on abdominal segment 2 are not operculate or semi-operculate in Austremerellinae (Figs 2, 3). The inner margins of the cerci have elongate, relatively dense, and sometimes forked, hairlike setae along the medial margin (Figs 77, 78). Larvae of Austremerellinae also possess a double row of small, sharp tubercles on abdominal terga (Figs 2, 3), whereas only in the South African genus *Nadinella* **gen. nov.** can a double row of tubercles be found in the Teloganodinae, and these tend to be blunt. Adults of Austremerellinae possess forewings with a complex stigmatic area, being longitudinally subdivided by a secondary vein into extensive upper and lower rows of cellules between the Costa and Subcosta (Figs 80-82). Forewings of Austremerellinae also have more elongate intercalary veins in that area between IMP and CuA, and have three or more CuA intercalary attachments to CuA. Adults also possess gill socket vestiges on abdominal segment 7, although they may be difficult to discern.

Genus *Austremerella* Riek

(Figs 2, 11, 20, 29, 38, 47, 56, 77, 80, 88)

Austremerella Riek, 1963:50. (Larva and adult) Type: *Austremerella picta* Riek, by original designation.
Ephemerellina (subgenus *Austremerella*), Allen, 1965:264.

Description of mature larva

Head (Fig. 2) without cephalic horns. Labrum (Fig. 11) subquadrate, approximately twice as broad as long, with short, scattered setae over entire dorsal surface. Mandibles (Figs 20, 29) robust; incisors oriented distally; medioapical setal patch of setae developed on left mandible (Fig. 29). Maxillae (Fig. 38) with palpi absent. Superlinguae of hypopharynx (Fig. 47) moderately developed, slightly concave laterally and not extending beyond lingua distally; apical margin of lingua convex. Labium (Fig. 56) with well-divided and apically narrowed glossae and paraglossae; palpal segment 3 longer than width of segment 2. Pronotum (Fig. 2) short, more than twice as broad as long, not produced anterolaterally. Forefemora (Fig. 2) moderately broad. Tarsal claws with one row of denticles. Simple filamentous gills absent on abdominal segment 1; lamellate gills present on abdominal segments 2-7; gills on abdominal segment 2 (Fig. 2) not operculate or semi-operculate. Paired dorsal abdominal tubercles present (Fig. 2). Caudal filaments not banded; median caudal filament well developed (three tailed).

Description of adult

Head without pair of cephalic horn vestiges. Mesothorax ending posteriorly with pair of elongate membranous processes (Fig. 88). Forewings (Fig. 80) with IMP longer than MP_2; MP_2 attached directly to IMP; most marginal intercalaries free, not attached. Abdominal segments 2-7 with gill socket vestiges. Median caudal filament well developed (three tailed).

Diagnosis

The larvae of Austremerella can be distinguished from those of Vietnamella by their lack of cephalic horns, maxillary palpi, and gills on abdominal segment 1. Furthermore, segment 3 of the labial palpi are much longer; the mandibles are not modified apically as in *Vietnamella* (Figs 21, 30); and the labrum of *Austremerella* has short setae scattered over the entire dorsal surface, whereas in *Vietnamella,* the setae are confined to the distal half of the dorsal surface of the labrum. The adults of *Austremerella* have a unique pair of membranous filaments as described above, and most marginal intercalary veins in the forewings are typical of the family and also Ephemerellidae, in that they are unattached. Most short marginal intercalaries of the forewings of *Vietnamella* are attached to other veins.

SPECIES INCLUDED

Austremerella picta Riek
Austremerella picta Riek, 1963:50.
Ephemerellina picta (Riek), Allen, 1965:264.

DISTRIBUTION

Australia: Queensland.

MATERIAL EXAMINED

Austremerella picta: AUSTRALIA: Larvae, Queensland, Flaggy Cr., Mistake Mtns. via Laidley, S. E. Old, II-11-1973, S. R. Monteith, ANC, PERC. Female adult paratype, Queensland, Lamington Natl. Park, VIII-11-1942, E. F. Riek, PERC.

REMARKS

This monotypic genus is defined by the following autapomorphies (see also Phylogenetics, below): the elongation of labial palpal segment 3, and the presence of unusual mesothoracic processes in the adults. Within the subfamily Austremerellinae, they are further defined by loss of the gills on abdominal segment 1 and the loss of maxillary palpi. Otherwise, the genus appears to be the most plesiotypic genus within the family (with the possible exception of *Ephemerellina* of the subfamily Teloganodinae), retaining a preponderance of plesiomorphic character states. Riek (1963) did not notice the pair of gills on abdominal segment 7 of the larvae, and this led to some historical confusion about the integrity of the genus. Allen (1965) incorrectly considered it a subgenus of *Ephemerellina*. The male adults of *A. picta* remain unknown. Above, we provide new collecting data associated with the larvae. Unfortunately, the only ecology known of *Austremerella* is that larvae have been found in mountain streams.

Genus *Vietnamella* Tshernova

(Figs 3, 12, 21, 30, 39, 48, 57, 69, 78, 81, 82)

Vietnamella Tshernova, 1972:366. (Larva) Type: *Vietnamella thani* Tshernova, by original designation.
Vietnamella, You and Su, 1987:176. (Adult).
Vietnamella, Wang and McCafferty, 1995:193. (Revision).

DESCRIPTION OF MATURE LARVA

Head (Fig. 3) with prominent, anteriorly directed cephalic horns anterior to eyes. Labrum (Fig. 12) with lateral margins convergent distally, approximately twice as broad as long, with scattered moderately long setae in distal half dorsally. Mandibles (Figs 21, 30) narrow basally, broad apically; incisors fused and oriented more or less laterally; medioapical patch of setae developed on left mandible. Maxillae (Fig. 39) with three-segmented palpi. Superlinguae of hypopharynx (Fig. 48) moderately developed, rounded laterally, and slightly shorter than lingua; apical margin of lingua straight. Labium (Fig. 57) with short and broad, apically truncate glossae and paraglossae; palpal segment 3 very short, with length less than width of segment 2. Pronotum (Fig. 3) about 1.5 times as broad as long, anterolateral corners produced into processes. Tarsal claws (Fig. 69) with one denticle. Simple, filamentous gills present on abdominal segment 1; lamellate gills present on abdominal segments 2-7; gills on abdominal segment 2 (Fig. 3) not operculate or semi-operculate. Paired dorsal abdominal tubercles present (Fig. 3). Caudal filaments not banded; median caudal filament well developed (three tailed).

Description of adult

Head with pair of cephalic horn vestiges. Mesothorax without pair of elongate membranous processes. Forewings (Figs 81, 82) with IMP nearly as long as MP_2; MP_2 attached to IMP near base; most short marginal intercalaries are attached to crossveins or longitudinal veins. Abdominal segments 2-7 with gill socket vestiges. Median caudal filament well developed (three tailed).

Diagnosis

The larvae of *Vietnamella* can be distinguished from those of *Austremerella* by the presence of cephalic horns, restricted setae on the labrum, fused and laterally oriented incisors on the mandibles, maxillary palpi, the shorter terminal labial palpal segments, the truncate glossae and paraglossae, the longer prothorax, the single denticle of the tarsal claws, and gills on abdominal segment 1. The adults of *Vietnamella* have vestiges of the larval cephalic horns on the head, and they do not have the specialized mesothoracic filaments present in *Austremerella*.

Species included

Vietnamella dabieshanensis You and Su
    Vietnamella dabieshanensis You and Su, 1987:176.
Vietnamella guadunensis Zhou and Su, 1995:48.
Vietnamella ornata (Tshernova)
    Ephemerellina ornata Tshernova, 1972:368.
    Vietnamella ornata (Tshernova), Wang and McCafferty, 1995.
Vietnamella qingyuanensis Zhou and Su, 1995:47.
Vietnamella sinensis (Hsu)
    Ephemerella sinensis Hsu, 1936:325.
    Ephemerellina sinensis (Hsu), Allen and Edmunds, 1963a:15.
    Vietnamella sinensis (Hsu), Wang and McCafferty, 1995:193.
Vietnamella thani Tshernova
    Vietnamella thani Tshernova, 1972:367.

Distribution

The genus is known from Vietnam and southern and southeastern China (Yunnan, Anhui, Fujian, Jiang Xi, and Zhejiang Provinces).

Material examined

Vietnamella thani: VIETNAM: Larvae, Vinh Phu Prov., R. Dan, Tran Dao, X-17-1984, T. Soldán, PERC.

Remarks

This genus is defined by the following autapomorphies (see also Phylogenetics, below): the presence of cephalic horns in the larvae (including their vestiges in the adults), the laterally oriented, fused mandibular incisors, the apically truncate paraglossae, the single claw denticle, and the fact that most short marginal intercalaries in the forewings are attached either to crossveins or longitudinal veins. The relatively large number of autapomorphies of *Vietnamella* shows that it is a relatively apotypic genus within an old subfamily. It is phenetically so different from other teloganodids that we consider it aberrant. It is not surprising that all workers previous to Edmunds and Murvosh (1995) considered it in Ephemerellidae (Ephemerellinae). Wang and McCafferty (1995) showed that all Oriental species that were previously known as adults and that were called *Ephemerellina* were in fact *Vietnamella*. The taxonomy of species is somewhat dubious at the present because species have not been adequately compared with each other. For example, the known alate forms of *V. ornata* (unknown as larvae) may prove to be associated with the larvae of *V. thani* (unknown in alate stages). In addition, *V. sinensis* and *V. dabieshanensis* have been taken from the same general area in the Dabie Mountains of southeastern China, and they might prove to be synonymous, and Zhou (pers. comm.) has indicated that he believes that *V. guadunensis* and *V. qingyuanensis* are actually immature *V. dabieshanensis*.

Little is known of the habitat or habits of this genus, although Tshernova (1972) indicated that the larvae of *V. thani* were periphyton feeders. Adaptive convergences in mouthpart structure found in *Vietnamella* and the genera *Lestagella* and *Teloganodes* of the subfamily Teloganodinae (reduced mandibles, and well-developed filtering setae marginally on the labrum, on short superlinguae, and on paraglossae and somewhat fused glossae) suggest that there are close feeding similarities, including filtering ability in the three genera.

Subfamily Teloganodinae

Diagnosis

Larvae of the Teloganodinae may be distinguished from those of the Austremerellinae by the absence of gills on abdominal segment 7, by the presence of either operculate (Figs 7-10) or semi-operculate (Figs 4-6) gills on abdominal segment 2, and their shorter and more sparsely setaceous cerci (Fig. 79). All larvae lack maxillary palpi (Figs 40-46) and tubercles or horns on the head (Figs 4-10). Also, larvae either possess a double row of blunt tubercles (Figs 5, 74-76), a single row of sharp or blunt tubercles (Figs 4, 6, 8, 9), or no dorsal tubercles (Figs 7, 10) on the abdominal terga. Adults of Teloganodinae do not have a forewing stigmatic area that is divided by a secondary longitudinal vein into two rows of several cellules, and there are fewer intercalary veins between IMP and CuP (Figs 83-87). They also lack gill socket vestiges on abdominal segment 7 (Fig. 89).

Genus *Ephemerellina* Lestage

(Figs 4, 13, 22, 31, 40, 49, 58, 65, 70, 79, 83, 89)

Ephemerellina Lestage, 1924:346. (Adult). Type: *Ephemerellina barnardi* Lestage, by original designation.
Ephemerellina, Barnard, 1932:251. (Larva).
Ephemerellina, Allen, 1965:293. (Incl. *Austremerella*).
Ephemerellina, Demoulin, 1970:123. (Incl. *Lithogloea*).
Ephemerellina, McCafferty and de Moor, 1995:472. (Excl. *Lithogloea*).
Ephemerellina, Wang and McCafferty, 1995:193. (Revision).

Description of Mature Larva

Head (Fig. 4) without well-developed marginal fringe of setae. Labrum (Fig. 13) broadly subquadrate, apical width approximately three times length, with scattered short setae over entire dorsal surface; apical margin broadly and gradually emarginate. Mandibles (Figs 22, 31) broadly robust; inner and outer incisors divergent; long mediolateral seta absent; outer incisor with at least one sharp denticle and apicomedial patch of setae developed on left mandible (Fig. 31). Maxillae as in Fig. 40. Superlinguae of hypopharynx extended distally beyond apices of lingua [Fig. 49, Fig. 12g of Demoulin (1970)], lateral margins nearly straight; lingua convex apically. Labium (Fig. 58) with well-demarcated glossae and paraglossae; paraglossae somewhat bluntly pointed medioapically. Prosternum (Fig. 65) with bi-lobular, spinous process medially. Forefemora (Fig. 4) relatively narrow. Tarsal claws (Fig. 70) with single row of denticles. Simple, filamentous gills absent on abdominal segment 1; lamellate gills present on abdominal segments 2-6; gills on abdominal segment 2 (Fig. 4) semi-operculate. Abdomen (Fig. 4) with single row of relatively narrow-elongate and sharp tubercles dorsally; posterolateral processes only poorly developed and approximate to base of following segment. Caudal filaments banded; median caudal filament well developed (three tailed).

Description of adult

Forewings (Fig. 83) with IMP longer than MP_2 and both veins directly attached to each other in basal half of wing. Abdominal segments 2-6 (Fig. 89) with gill socket vestiges; abdominal terga 3-5 (sometimes others also) each with small, conical, medial tubercle vestige (Fig. 89). Median caudal filament well developed (three tailed).

Diagnosis

The larvae of *Ephemerellina* are distinguished from those of other genera of Teloganodinae by their possession of a unique, spinous and bi-lobular, prosternal process, and by their possession of a labrum (Fig. 13) that is subquadrate, relatively broad, covered by short setae over nearly its entire dorsal surface, and somewhat emarginate along the apical margin. Larvae may be further distinguished from other African genera of Teloganodinae by their single row of relatively narrow-elongate dorsal abdominal tubercles. A combination of characteristics must be used to diagnose the adults of *Ephemerellina* from those of other Teloganodinae (see Key to Genera, above). They differ from other African genera of Teloganodinae by the presence of a single median row of conical tubercle vestiges on the abdominal terga.

Species Included

Ephemerellina barnardi Lestage, 1924:348.
Ephemerellina sp. Allen and Edmunds, 1963a:15.

Distribution

South Africa: Western Cape Province.

Material examined

Ephemerellina barnardi: SOUTH AFRICA: Male and female adults, Gt. Winterhoek Mts., 4500 ft., XI-1916, AM. Larva, Gt. Winterhoek Mts., IX, XI-1932, K. H. Barnard, AM. Larva, Cedarbergen, I-1930, K. H. Barnard, AM. Larvae, West Cape, Jonkershoek Mts., waterfall of 2nd trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larva, Great Berg R., Lower forest reserve, Driefontein Bridge, VII-19-1950, AM. Larva, Viljoen's Pass, Elgin, S side, X-29-1931, K. H. Barnard, AM.

Remarks

This monotypic genus is defined by the autapomorphic spinous, bi-lobular, prosternal process in the larvae (see also Phylogenetics, below). It can be viewed as the most plesiotypic genus of the Teloganodinae, in that it retains the greatest number of plesiomorphic character states. It also rivals *Austremerella* of the Austremerellinae as the most plesiotypic genus of the entire family. There have been various attempts to place representatives of other lineages in this genus. Allen (1965) considered *Austremerella* a subgenus of *Ephemerellina.* Demoulin (1970) considered *Lithogloea* a subgenus of *Ephemerellina,* and also placed species, either as subgenus *Ephemerellina* or subgenus unknown in *Ephemerellina* that actually belong to *Nadinella* **gen. nov.** From our cladistic analysis, it is now clear that symplesiomorphy was the basis of all of the above interpretations. Allen and Edmunds (1963a) and Tshernova (1972) placed certain species, now known to belong to *Vietnamella*, in the genus *Ephemerellina*. This latter situation was resolved by Wang and McCafferty (1995), and the historically confused taxonomy of African Teloganodidae is resolved herein. In Lestage's (1924) original description of the adults, he incorrectly reported two terminal segments of the male genital forceps. This was corrected by Barnard (1932), who at the same time, provided description of the larval stage.

Ephemerellina is known from temperate mountain streams in the extreme southwest of the African continent. We consider it a temperate Gondwanaland relict (see Biogeography discussion under Phylogenetics, below). The first author and N. McCafferty collected larvae in abundance from moss on vertical rock faces of waterfalls of small mountain tributaries of the Eerste River near Stellenbosch. Based on data from small tributaries and waterfalls, it appears that the habitat is similar to that of *Nadinella* **gen. nov.** (see below). King (1981) reported some spatial and temporal data for *E. barnardi* in the Eerste River. She found larvae throughout the year and most commonly from stones in the upper reaches of the river. Barber-James and de Moor (pers. comm.) indicated that larvae have been found on the straplike leaves (ca. 1 mm width) of *Isolepis* (Cyperaceae), where this plant occurs in mats in swift current of acidic streams of the Western Cape.

Genus *Nadinella* gen. nov.

(Figs 5, 14, 23, 32, 41, 50, 59, 66, 71, 74-76, 84, 90)

Type species

Ephemerellina crassi Allen and Edmunds.

Description of mature larva

Head (Fig. 5) without well-developed marginal fringe of setae. Labrum (Fig. 14) subquadrate and relatively narrow, with apical width only approximately 1.5 times length; setae in transverse medial third of dorsum; apical margin deeply notched medially. Mandibles (Figs 23, 32) somewhat narrow in basal half and gradually broadening apically; incisors separated but not divergent; left mandible with outer incisor with three semi-blunt poorly demarcated denticles and without medioapical setal patch (Fig. 32). Maxillae as in Fig. 41. Superlinguae of hypopharynx (Fig. 50) moderately developed, rounded laterally, and subequal in length to lingua; lingua with apical margin nearly straight. Labium (Fig. 59) with well-divided glossae and paraglossae; glossae rounded apically; paraglossae bluntly pointed apically. Prosternum (Fig. 66) without medial spinous process. Forefemora (Fig. 5) relatively narrow. Tarsal claws (Fig. 71) with two rows of denticles. Simple, filamentous gills present or absent on abdominal segment 1; lamellate gills present on 2-5; gills on abdominal segment 2 (Fig. 5) semi-operculate. Abdomen (Fig. 5) with two rows of blunt dorsal tubercles, sometimes coalescing on some segments into short and broad, apically straight-margined or rounded processes (Figs 74-76); posterolateral processes poorly developed and approximate to base of following segment. Caudal filaments banded; median caudal filament well developed (three tailed).

Description of adult

Forewings (Fig. 84) with IMP longer than MP_2, and both veins directly attached to each other in basal half of wing. Abdominal segment 2-5 with gill socket vestiges; abdominal terga 3-5 (sometimes others also) with small transverse thickening medially, each bearing two small, conical tubercle vestiges [see Figs 8c, 8d of Barnard (1940)]; tubercle vestiges may not be evident in some specimens. Male genitalia as shown in Fig. 89. Median caudal filament well developed (three tailed).

Diagnosis

The larvae of *Nadinella* can be distinguished from larvae of all other genera of Teloganodinae by the presence of two rows of denticles on the claws, the relatively narrow and deeply notched labrum, and the double row of dorsal abdominal tubercles. Among the African genera of Teloganodidae, it can further be differentiated by the presence of lamellate gills on abdominal segments 2-5. *Ephemerellina* and *Lithogloea* larvae have lamellate gills on abdominal segments 2-6, and *Lestagella* larvae have lamellate gills on abdominal segments 2-4. Some *Nadinella* larvae have the double tubercles coalesced into a single, broad, posteromedian protuberance. *Lithogloea* larvae have single, somewhat broad, medial tubercles that may be blunt or sharp apically. In those *Nadinella* larvae in which the paired tubercles have become coalesced into a broad protuberance, some bifurcation will usually still be evident on at least some of the segments. If no bifurcation is evident, then often some, if not most, of the protuberances will be very broad and straight along their apical margin [Figs 75, 76, Fig. 13l in Demoulin (1970)]. In any case, it would be prudent not to rely solely on the presence of the double row of tubercles for identifying *Nadinella.*

The adults of most Nadinella are distinct among the Teloganodinae, in that they have short, broad medial processes, with small paired tubercle vestiges evident on at least abdominal terga 3-5. They may be differentiated among the African genera of Teloganodidae by the presence of gill socket vestiges on abdominal segments 2-5. The former characteristic may not be evident on adults associated with those few larvae that have coalesced tubercles (see discussion, above), and the latter character can be difficult to see in some specimens. Because *Nadinella* has a relatively elongate IMP that is directly attached with MP_2, it cannot be confused with *Lithogloea* or *Lestagella,* even though the dorsal abdominal tubercle vestiges may not be evident in any of these genera. The male genitalia of *N. crassi* and *L. harrisoni* are also distinctive, particularly with regard to the shape of the penes (Figs 90, 91).

Etymology

Nadinella is named for Nadine McCafferty, who was instrumental in carrying out the field work in South Africa that facilitated the study of Teloganodidae.

Species included

Nadinella brincki (Demoulin) **comb. nov.**
    Ephemerellina brincki Demoulin, 1970:125.
Nadinella crassi (Allen and Edmunds) **comb. nov.**
    Ephemerellina crassi Allen and Edmunds, 1963a:12.

Distribution

South Africa: Western Cape Province.

Material examined

Nadinella crassi: SOUTH AFRICA: Holotype larva, paratype larvae and male subimago, Great Berg R., French Hoek Reserve, XI-20, 21-1950, A. D. Harrison, PERC. Larva, Gt. Winterhoek, IX,XI-1932, K. H. Barnard, PERC. Larvae, West Cape, Jonkershoek Mts., waterfall of 2nd trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek Mts., waterfall of 1st trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek St. Forest, rivulet trib. Eerste R. IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek Mt. Reserve, Eerste R. near bridge at end of dirt road, IX-28-1990, W. P. and N. McCafferty, PERC. Subimago with larval exuviae, Great Berg R., railway bridge above Groot Drakenstein, XI-11-1953, AM.

Nadinella brincki: SOUTH AFRICA: Larva, Eerste Stellenbosch, X-25-1930, AM (incorrectly labeled by K. H. Barnard as *Lithogloea harrisoni*).

Nadinella sp.: SOUTH AFRICA: Kruig R., III-8-1960, AM.

REMARKS

This genus is defined by the autapomorphic double row of denticles on the tarsal claws (see also Phylogenetics, below). The deeply notched condition of the labrum also appears to be autapomorphic within the Teloganodidae, but we do not know how consistent it will prove to be on a generic level. Demoulin (1970) originally considered *N. crassi* as "*Ephemerellina* (subg.?)." He also described at that time what he termed as the "simplex" form of *N. brincki* and placed it in *Ephemerellina* (subgenus *Ephemerellina*). This latter species, however, clearly belongs to *Nadinella*, having the double row of claw denticles, lamellate gills on abdominal segments 2-5, etc. It is atypical of most of the individuals we have seen of *Nadinella*, in that the usual double row of dorsal abdominal tubercles has coalesced into a single broad and straight-margined tubercle, or protuberance. We do not know if this represents a variation of *N. brincki* or perhaps another species. Presumably, it lacks the simple gills on abdominal segment 1, although this is not clear from Demoulin's account. We have seen variations of *N. crassi* (a species with simple gills on abdominal segment 1) with similar, and even more extreme, tubercle variation (Figs 74-76). Barnard (1940) included an adult of *Nadinella* as part of a series of *Ephemerellina barnardi* Lestage. The presence of a double row of tubercle vestiges on the terga of that specimen [Figs 8c, 8d of Barnard (1940)] clearly excludes it from *Ephemerellina*.

Nadinella is restricted to temperate mountain streams in the extreme southwest of the African continent. We consider it a temperate Gondwanaland relict (see Biogeography discussion under Phylogenetics, below). The first author collected larvae in abundance from moss growing on the rock faces of waterfalls of tributaries of the Eerste River near Stellenbosch, as well as from habitats with less gradient. We have also seen collecting labels for *Nadinella* larvae that specifically noted that they had been taken in *Wardia* moss on rocks.

Genus *Lithogloea* Barnard

(Figs 6, 15, 24, 33, 42, 51, 60, 67, 72, 85, 91)

Lithogloea Barnard, 1932:252. (Larva and adult). Type: *Lithogloea harrisoni* Barnard, by monotypy.
Ephemerellina (subgenus *Lithogloea*), Demoulin, 1970:128.
Lithogloea, McCafferty and de Moor, 1995:472.

DESCRIPTION OF MATURE LARVA

Head (Fig. 6) without well-developed marginal fringe of setae. Labrum (Fig. 15) with apical margin nearly straight and lateral margins slightly convergent apically; dorsal surface with irregular transverse rows of setae at midlength and apical fourth; basal width approximately twice length. Mandibles (Figs 24, 33) narrowed, slightly broader apically; inner and outer incisors divergent; long mediolateral seta absent; left mandible with outer incisor with at least one sharp denticle and without apicomedial patch of setae (Fig. 33). Maxillae as in Fig. 42. Superlinguae of hypopharynx (Fig. 51) with apical margins approximately subequal with that of lingua, lateral margins rounded; lingua convex apically. Labium (Fig. 60) with well-divided glossae and paraglossae; paraglossae somewhat bluntly pointed medioapically. Prosternum (Fig. 67) without bi-lobular, spinous process. Forefemora (Fig. 6) relatively narrow. Tarsal claws with single row of denticles. Simple filamentous gills present on abdominal segment 1; lamellate gills on abdominal segments 2-6; gills on abdominal segment 2

(Fig. 6) semi-operculate. Abdomen (Fig. 6) with single row of poorly developed, short, usually broad-based tubercles dorsally; posterolateral processes well developed, elongate-subtriangular, sharply attenuated, and well separated from base of following segment; middle segments with short lateral setae (Fig. 6). Caudal filaments banded; median caudal filament well developed (three tailed).

Description of adult

Forewings (Fig. 85) with IMP shorter than MP_2 and detached from it. Abdominal segments 2-6 with gill socket vestiges; abdominal terga without tubercle vestiges. Male genitalia as shown in Fig. 91. Median caudal filament well developed (three tailed).

Diagnosis

The larvae of *Lithogloea* are distinguished from those of other genera of the Teloganodinae by their well-developed, elongate, and remote abdominal posterolateral processes, which are widely separated from the base of the following segment. At least one species of the Oriental genus *Teloganodes* also has posterolateral processes nearly as developed as those of the *Lithogloea,* and *Lestagella* has moderately developed posterolateral processes. In the latter genera, however, gills are absent on abdominal segment 6, there is a well-developed setal fringe on the head, and lateral abdominal setae are much longer. With respect to dorsal abdominal tubercles, there are some aberrant forms of *Nadinella* that could be confused with *Lithogloea.* This situation is discussed in the Diagnosis of *Nadinella*, above. Adults of *Lithogloea* are distinguished from those of other genera of Teloganodinae by the combination of an IMP in the forewings that is much shorter than MP_2 and detached from it, and the presence of gill socket vestiges on abdominal segments 2-6. The nearly apically truncate penes (Fig. 91) of *Lithogloea* should also be of some aid in differentiating the adult in Africa.

Species included

Lithogloea harrisoni Barnard, 1932:253.
Ephemerellina harrisoni (Barnard), Demoulin, 1970:129.
Lithogloea harrisoni Barnard, McCafferty and de Moor, 1995:472.

Distribution

South Africa: Western Cape. There are unconfirmed records of *Lithogloea* from the Eastern Cape Prov. and Kwazulu-Natal Prov., South Africa (Crass 1947), Swaziland (Stander 1963), and the Northern Transvaal Prov., South Africa and Malawi (Harrison and Agnew 1962). We have seen material labeled *Lithogloea* spp. in the Albany Museum from the Crocodile River (Eastern Transvaal), Schageni, Karino, the Itawa River (Zambia), Usutu River (Swaziland), and Malawi all collected in the 1950's and 60's. These all represent misidentified material of *Ephemerythus* Gillies (Tricorythidae). *Ephemerythus* was not described until 1960 (Gillies 1960), and up to that time had been known as "ephemerellid genus ?" (e.g., Kimmins 1955). It remains poorly known by non-specialists. A record of *Lithogloea* from Zaire by Marlier (1954) is most likely attributable to the baetid genus *Acanthiops* Waltz and McCafferty (see Barber-James and McCafferty 1997). Whereas it is possible that *Lithogloea* eventually may be confirmed from temperate and mountainous areas of the Eastern Cape and Kwazulu-Natal provinces of South Africa, we have been unable to substantiate such a distribution at this time, and a more northern range in Africa can neither be substantiated nor is it predicted by the general biogeography of Teloganodidae (see Biogeography under Phylogenetics, below). In fact, the only materials of actual teloganodines that we have examined from outside the Western Cape are *Lestagella* from the Eastern Cape, misidentified and mislabeled as *Lithogloea*, and all of what Crass referred to as *Lithogloea* may be attributable to *Lestagella*. This is understandable because *Lestagella* was not known until 1970 (Demoulin 1970) and was not generally recognized after that. From all of the above we must assume that *Lithogloea* is restricted to the Western Cape of South Africa.

MATERIAL EXAMINED

Lithogloea harrisoni: SOUTH AFRICA: Male and female adults, Gt. Winterhoek, XI-1932, K. H. Barnard, AM. Subimagos, Gt. Drakenstein. Larva, West Cape, Jonkershoek Mts., Eerste R. nr bridge at end of dirt rd, IX-28-1990, W. P. and N. McCafferty, PERC.

REMARKS

This genus is defined by the autapomorphic well-developed, elongate abdominal posterolateral processes (see also Phylogenetics, below). The bluntly fused and pointed maxillae that lack denticles also appear to be unique within the family; the maxillae of *Lestagella* are also reduced, but differently. Barnard (1932) originally described *Lithogloea* based on *L. harrisoni*. Later he (Barnard 1940) recognized part of the material he had considered as *L. harrisoni* as another species *L. penicillata*, which was later recognized as another genus, *Lestagella*, by Demoulin (1970).

Little is known of the ecology of this species. It was not taken from waterfalls in the Jonkershoek Mountains by the first author as was *Nadinella* and *Ephemerellina*, but was found cohabiting with them in other habitats with less gradient. King (1981) and King et al. (1988) provided some spatial and temporal data with respect to *L. harrisoni* in the Jonkershoek mountain reaches of the Eerste and Long rivers. Larvae have recently been taken on the 1 mm wide leaves of *Isolepis* (Cyperaceae), where this plant occurs in mats in swift currents of certain streams in the Western Cape (Barber-James and de Moor, pers. comm.). The range of *Lithogloea* is somewhat dubious at this time (see Distribution, above), and records other than those from the Western Cape need to be authenticated with further study of material. Such records are likely attributable to *Lestagella*, because that genus was not recognized as a separate genus until after the questionable records appeared. Since workers were presumably using Barnard (1940) for identification, they would have easily confused *Lithogloea* and *Lestagella*.

Genus *Lestagella* Demoulin

(Figs 7, 16, 25, 34, 43, 52, 61, 68, 72, 86)

Lestagella Demoulin, 1970:130. (Larva and adult). Type: *Lithogloea penicillata* Barnard, by original designation.

DESCRIPTION OF MATURE LARVA

Head (Fig. 7) with well-developed marginal fringe of setae, long anteriorly, shorter laterally. Labrum (Fig. 16) with rounded lateral margins and slightly emarginate apical margin; dorsum with medial transverse row of setae; basal width nearly three times length. Mandibles (Figs 25, 34) narrow throughout and atrophied apically; mediolateral elongate seta present, not bristlelike, sometimes broken or missing; left mandible without apicomedial setal patch (Fig. 34). Maxillae as in Fig. 43. Superlinguae of hypopharynx (Fig. 52) shorter than lingua, with straight lateral margins; apical margin of lingua with small notch medially. Labium (Fig. 61) with poorly divided glossae and paraglossae; paraglossae rounded apically. Prosternum (Fig. 68) without bi-lobular, spinous process medially. Forefemora (Fig. 7) broad. Tarsal claws (Fig. 73) with single row of denticles. Simple filamentous gills present on abdominal segment 1; lamellate gills present on abdominal segments 2-4; gill on abdominal segment 2 (Fig. 7) fully operculate. Abdomen (Fig. 7) without dorsal abdominal tubercles; posterolateral processes subtriangular and moderately developed, not elongate and sharply attenuated, and moderately separated from base of following segment; middle segments with long lateral setae (Fig. 7). Caudal filaments banded; median caudal filament well developed (three tailed).

Description of adult

Forewings (Fig. 86) with IMP shorter than MP_2 and detached from it. Abdominal segments 2-4 with gill socket vestiges; abdominal terga without dorsal abdominal tubercle vestiges. Median caudal filament well developed (three tailed).

Diagnosis

Lestagella larvae can be told from larvae of other Teloganodinae by the reduced and atrophied mandibles, the modified apices of the maxillae, and the medial notch of the lingua of the hypopharynx. Other than these mouthpart characteristics, which will require slide mounting to examine efficiently and may possibly prove to be species specific, the combination of the three tails and the well-developed marginal fringe of setae on the head will distinguish the larvae of *Lestagella* from all others. The adults of *Lestagella* can be told from those of all other teloganodines by the combination of three tails, the relatively short and detached IMP in the forewings, and the presence of gill socket vestiges only on abdominal segments 2-4.

Species included

Lestagella penicillata (Barnard).
    Lithogloea penicillata Barnard, 1940:637.

Distribution

South Africa: Western Cape and Eastern Cape. Unusual specimens from the Amatola Mountains of the Eastern Cape were tentatively identified as *Lithogloea harrisoni* by Crass (1947). Although we could not find that material, we maintain that the record is attributable to either *Lestagella* or *Ephemerythus* (family Tricorythidae). Other materials we have seen labeled as *Lithogloea* are actually *Lestagella*. The latter two genera have been commonly misidentified as *Lithogloea* (see Distribution, under *Lestagella*).

Material examined

Lestagella penicillata: SOUTH AFRICA: Larvae, South Cape, Wit R., IX-18-1989, AM. Larvae, West Cape, Jonkershoek Mts., waterfall of 2nd trib. Eerste R., IX-28-1990. W. P. and N. McCafferty, PERC. Larva, West Cape, Jonkershoek Mts., waterfall of 1st trib. Eerste R., IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Jonkershoek Mts. Reserve, Eerste R., nr bridge at end of dirt rd, IX-28-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, upper Kirstenbosch Nat'l. Bot. Gard., Skeleton Gorge Stream, X-1-1990, W. P. and N. McCafferty, PERC. Larvae, West Cape, Kirstenbosch Nat'l. Bot. Gard., Window Stream at rd, IX-29-1990, W. P. and N. McCafferty, PERC. Larva, Eastern Cape, Madonna and Child, X-7-1989, AM. Subimago and larvae, Tweck's Pont, IX-1933, K. H. Barnard, AM. Larvae, Gt. Winterhoek Mts., IX-11-1932, K. H. Barnard, AM.

Remarks

This genus is defined by the autapomorphic atrophy of the apical mandibular armature (see also Phylogenetics, below). The notched lingua of the hypopharynx also appears unique among the Teloganodidae. *Lestagella* belongs to a clade that also includes the Oriental genera *Macafertiella* and *Teloganodes*. As such, it represents a transition between the archaic African fauna and the Oriental teloganodines (see Biogeography under Phylogenetics, below). Barnard (1940) originally considered this genus as part of *Lithogloea*; however, Demoulin (1970) recognized its distinctiveness and established the genus.

Although *Lestagella* is known from a number of mountain streams in the Western and Eastern Cape, little is known of its ecology.

Genus *Macafertiella* Wang

(Figs 8, 17, 26, 35, 44, 53, 62)

Macafertiella Wang (in Wang and McCafferty), 1996:15. (Larva). Type: *Macafertiella insignis* Wang and McCafferty, by original designation.

Description of mature larva

Head (Fig. 8) with well-developed marginal fringe of setae, setae longest posterior to antennae. Labrum (Fig. 17) with distally convergent lateral margins and slightly emarginate apical margin; dense transverse row of long filtering setae located at approximately 3/4 distance from base and curved laterally, following marginal shape of labrum; basal width approximately three times length. Mandibles (Figs 26, 35) narrow throughout, slightly broader apically; long mediolateral seta present, bristlelike; left mandible with outer incisors blunt and not divergent, and with sparse medioapical patch of setae (Fig. 35). Maxillae as Fig. 44. Superlinguae of hypopharynx (Fig. 53) extending beyond lingua, with straight lateral margins; apical margin of lingua straight with slightly produced area medially. Labium (Fig. 62) with poorly divided glossae and paraglossae; glossae nearly completely fused medially; paraglossae rounded apically. Prosternum without bi-lobular, spinous process medially. Forefemora (Fig. 8) relatively narrow. Tarsal claws with single row of denticles. Simple filamentous gills absent on abdominal segment 1; lamellate gills present on abdominal segments 2-6; gill on abdominal segment 2 (Fig. 8) fully operculate. Abdomen (Fig. 8) with single row of sharp medial tubercles dorsally; posterolateral processes poorly developed and approximate to base of following segment. Cerci not banded. Median caudal filament vestigial (two tailed).

ADULT UNKNOWN

DIAGNOSIS

Larvae of *Macafertiella* are distinguished from those of other Teloganodinae by the unique labrum, but also by the combination of being two tailed and having gills on abdominal segment 6. Although initially Wang and McCafferty (1996b) indicated there were size differences between the abdominal tubercles of *Macafertiella* and *Teloganodes*, the range in size of *Teloganodes* tubercles has since been found to include the size of those of *Macafertiella*. The adults are unknown, but assuredly will have a reduced median caudal filament as well as larva-associated vestiges of the median row of dorsal abdominal tubercles and gill socket vestiges on abdominal segment 2-6. Together, these should allow recognition of the unknown adult and prevent confusion with the genus *Teloganodes*, which may be taken sympatrically and is similarly two tailed, but which has no gill socket vestiges on abdominal segment 6.

SPECIES INCLUDED

Macafertiella insignis Wang and McCafferty, 1996:16.

DISTRIBUTION

Sri Lanka.

MATERIAL EXAMINED

Macafertiella insignis: SRI LANKA: Larval holotype and paratype, Belihuloya Region, Veli-Oya, trib. of Walawe-Ganga, 700 m, XII-8-1970, F. Starmühlner, PERC. Larva paratype, Kitilgala Region, Rambukpoth-Oya, nr Pitawela, trib. Kelani-Ganga, 650 m, XII-27-1970, F. Starmühlner, PERC.

REMARKS

This genus is defined by the apomorphic labrum and labral setation (see also Phylogenetics, below). Although *Macafertiella* is clearly a sister group of *Teloganodes* and a member of a rather distinctive clade consisting also of *Lestagella*, it is somewhat aberrant, particularly with respect to mouthparts and legs. It has been found cohabiting with undescribed species of *Teloganodes* as well as *T. tristis* in Sri Lanka. There remains the possibility that the larvae of *M. insignis* is associated with an adult from Sri Lanka that was named *Teloganodes major* by Eaton (1884). If this proves to be true, then *T. major* would become the type of *Macafertiella*. Virtually nothing is known of the ecology of *Macafertiella*.

Genus *Teloganodes* Eaton

(Figs 9, 10, 18, 19, 27, 28, 36, 37, 45, 46, 54, 55, 63, 64, 87)

Teloganodes Eaton, 1882:208. (Adult). Type: *Cloe tristis* Hagen, by original designation.
Teloganodes, Ulmer, 1939:627. (Larva).

Description of mature larva

Head (Figs 9, 10) with well-developed marginal fringe of setae, longer setae posterior to antennae (Fig. 9) or over entire margin (Fig. 10). Labrum (Figs 18, 19) with tapering lateral margins, and slightly emarginate apical margin; dorsum with transverse area of setae at midlength area or slightly beyond midlength; basal width approximately 2.5 times length. Mandibles (Figs 27, 28, 36, 37) narrow; long mediolateral seta present and bristlelike; left mandible with incisors separate and juxtaposed with denticles of outer incisor blunt (Fig. 36), or with denticles of outer incisor fused and blunt (Fig. 37). Maxillae (Figs 45, 46) often with small lateral nodules. Superlinguae of hypopharynx (Figs 54, 55) shorter than lingua, with lateral margins slightly concave; apical margin of lingua convex. Labium (Figs 63, 64) with glossae and paraglossae very poorly divided, glossae nearly completely fused medially; paraglossae rounded apically. Prosternum without bi-lobular, spinous process medially. Forefemora (Figs 9, 10) relatively broad. Tarsal claws with single row of denticles. Simple, filamentous gills on abdominal segment 1 absent; lamellate gills present on abdominal segments 2-4 or 2-5; gills on abdominal segment 2 (Figs 9, 10) fully operculate. Abdomen with single row of poorly to well-developed dorsal tubercles (Fig. 9) or without dorsal tubercles (Fig. 10); posterolateral processes poorly (Fig. 9) to moderately developed (Fig. 10), if moderately developed, then posterolateral processes slightly upturned and middle segments with long lateral setae (Fig. 10). Cerci not banded. Median caudal filament reduced (two tailed).

Description of adult

Forewings (Fig. 87) with IMP shorter than MP_2 and detached from it. Abdominal segments 2-4 or 2-5 with gill socket vestiges; abdominal terga with or without median row of tubercle vestiges. Median caudal filament reduced.

Diagnosis

The larvae of *Teloganodes* are distinguished from those of other Teloganodinae by the combination of being two tailed and having no gills on abdominal segment 6. The adults of Teloganodinae can be told from those of other Teloganodinae by the combination of the two-tailed condition and the absence of gill socket vestiges on abdominal segment 6.

Species included

Teloganodes dentata Navás, 1931:19.
Teloganodes lugens Navás, 1933:17.
Teloganodes major Eaton, 1884:136.
Teloganodes tristis (Hagen).
  Cloe tristis Hagen, 1858:476.
  Teloganodes tristis (Hagen), Eaton, 1884:135.

Distribution

Southern Asia: China: Zhejiang Province (Navás 1933); Hong Kong (Dudgeon 1990); India: Maharashtra Province (Navás 1931); Indonesia: Borneo, Celebes, Java (Ulmer 1939), Lombok, Sumatra (Ulmer 1939); Malaysia: Sabah, West Malaysia; Philippines; Sri Lanka.

MATERIAL EXAMINED

(All material deposited in PERC; all material larvae, except where noted).

Teloganodes tristis: MALAYSIA (EAST): Sabah, Sungai Moyog, 3 mi E of Penampung, IX-27-29-1978, G. F and C. Edmunds. Sabah, Sungai Moyog at trib. 8 mi E Penampung, X-1-1978, G. F. and C. Edmunds. MALAYSIA (WEST): Larvae and male subimagos, Selangor, large trib. Sungai Selangor, 6 mi NE Kota Kuba Baharu (Mile 44), XI-1-1987, G. F. and C. Edmunds. SRI LANKA: Male adults and larva, Ceylon, Newara Eliya Dist., Bakers Falls nr Farr's Inn, Horton Plains, 7000′, VIII-28-1968.

Teloganodes spp: INDONESIA (BORNEO): Kalimantan Timur Prov., Waterfall and stream, 11 km NE of Samarinda, VIII-27-1985, J. T. and D. A. Polhemus. INDONESIA (CELEBES): Sulawesi Selatan Prov., Pattunuang R., 7 km SW of Bantimurung, X-13-1985, 0-100 m, J. T. and D. A. Polhemus. Sulawesi Tengah Prov., stream 10 km SE Kamarora, Lore Lindu Nat. Park, 830 m, X-8-1985, J. T. and D. A. Polhemus. Sulawesi Utara Prov., Toraut R., Dumoga-Bone Nat. Park 0°34′N, 123°53-54′E, IX-3-5-1985, D. A. Polhemus. Sulawesi Utara Prov., upper Metelanga R., 10 km S. of Doloduo, IX-4-7-1985, J. T. and D. A. Polhemus. Sulawesi Utara Prov., forest stream S. of Lake Mala, 1200 m, IX-11-1985, D. A. Polhemus. INDONESIA (LOMBOK): Nusa Tenggara Barat Prov., Aik Jut R., 1 km N of Sesaot, 30 km NE Mataram, X-23-1985, 350 m, J. T. and D. A. Polhemus. MALAYSIA (EAST): Sabah, Sungai Moyog at tributary 8 mi E of Penampung, X-1-1987, G. F. and C. Edmunds. Sabah, Sungai Moyog, 3 mi E of Penampung, IX-27-29-1987, G. F. and C. Edmunds. Sabah, Sungai Tuaran, Tamparuli, X-3-1987, G. F. and C. Edmunds. Sabah, Liwagu, Moyog, N of Kundassan, 915 m, VIII-16-17-1972, G. F. and C. Edmunds. Sabah, Liwagu R. at bridge, Ranau, 335 m, VIII-11-16-1972, G. F. and C. Edmunds. Pahang, Fraser Hill, Jeriau Falls (20°C), VIII-30-1978, G. F. and C. Edmunds. MALAYSIA (WEST): Perak, Sungai Jor: Cameron Highlands Road, 19 Prov., IX-22-23-1978, G. F. and C. H. Edmunds. Larvae, male and female subimagos, Selangor, large trib. Sungai Selangor, 5 - 10 mi. NE Kota Kuba Baharu (Mile 42, 43, 44, 48), 31-VIII-78, IX-1-13-1978, G. F. and C. Edmunds (24°C). Selangor, Sungai Tua, 2 - 6 mi. N. Batu Caves, IX-14-15-1978, G. F. and C. Edmunds. Selangor, trib. of Sungai Gombak, 16 mi., 27-VIII-78, G. F. and C. Edmunds. Selangor, Sungai Kanching, Templer Park, VIII-28-1978, G. F. and C. Edmunds. Trengganu, Kampong Sungai Tong, IX-9-1978, G. F. and C. Edmunds. PHILIPPINES: Leyte, Leyte Prov., Lusig R. at Hilusig, VII-15-1985, J. T. and D. A. Polhemus. Leyte, Leyte Prov., Pangusungan R., N. of Baybay, CL 1988, VII-17-1985, J. T. and D. A. Polhemus. Luzon, Benguet Prov., 7 km, Asia Hot Springs Rd., VII-7-1985, J. T. and D. A. Polhemus. Luzon, Benguet Prov., stream below Camp John, Hay hydro. nr. Tuba mines, VII-8-1985, 900 m, J. T. and D. A. Polhemus. Luzon, Pangasinan Prov., Bayaling R., 100 m, 15 km E. of Bauang, VII-6-1985, J. T. and D. A. Polhemus. Luzon, Quezon Prov. Nat. Botanic Gardens, Llavac, VII-11-1985, J. T. and D. A. Polhemus. Mindanao, South Cotabato Prov., Lahit R., nr. Lake Sebu, VII-19-1985, J. T. and D. A. Polhemus. Mindanao, Zamboanga del Sur Prov., Bituti R., 7 km NW of Zamboanga City, 100 m, VII-22-1985, J. T. and D. A. Polhemus. Larva, female adult, Mindoro, Mindoro Oriental Prov., Apararai Cr., 22 km SW of Calapan, VII-13-1985, J. T. and D. A. Polhemus. SRI LANKA: Deniyaya Region, Medadola trib. of Gin-Ganga R., Sinharaja Range 1000 m, XI-9-1971, F. Starmühlner. Deniyaya Region, Nagahaketa-Dola trib. of Nilwala-Ganga R. 500 m, XI-13-1970, F. Starmühlner. Deniyaya Region, Campden Hill Dola trib. of Gin-Gana R., 700 m, XI-9-1970, F. Starmühlner. Deniyaya Region, Nagahaketa-Dola trib. of Nilwala-Ganga R., 500 m, XI-13-1970, F. Starmühlner. Deniyaya Region, Campden Hill Dola trib. of Gin-gana R., 700 m, XI-11-1970, F. Starmühlner. Kitulgala Region, Ambukpoth-Oya, near Pitawela, trib. of Kelani-Ganga, 650 m, XII-26-27-1970, F. Starmühlner. Kitulgala Region, Kelani Ganga near resthouse by Kitulgala, XII-28-1970, F. Starmühlner. Kitulgala Region, Hal-Oya near Ginigathhena, trib. of Kelani-Ganga 700 m, XII-27-1970, F. Starmühlner. Maskeliya Region, Gartmore Dola 2000 m, at waterfall XI-29-1970, F. Starmühlner. Maskeliya Region, backwaters of Gartmore Dola waterfall, 1800 m, XI-30-1970, F. Starmühlner. Maskeliya Region, Mocha R., trib. of Maskeliya R., dam by Adam's Peak estate, 1800 m, XI-28-1970, F. Starmühlner, PERC. Maskeliya Region, Maskeliya R. at base of Adam's Peak, about 1 km above Maskeliya impoundment 1800 m, XII-7-1970, F. Starmühlner. Maskeliya Region, Hakgala-Dola brook above Hakgala, near Nuwara Eliya 2000 m, XII-2-1970, F. Starmühlner. Ratnapura Region, Ira-Handha-Pana-Ela, right bank fork trib. of Kalu-Ganga R., 100 m, XI-23-1970, F. Starmühlner.

Remarks

This genus is defined by the loss of gills on abdominal segment 6 within the *Macafertiella* + *Teloganodes* lineage (see also Phylogenetics, below). It is a relatively diverse and highly apotypic genus, showing some variability in characters that are stable in other genera of Teloganodidae. Eaton (1882) named the genus for Sri Lankan adults that had previously been described under the genus *Cloe* by Hagen (1858). Eaton (1884) added an additional species from Sri Lanka, *T. major*, also known only from the adult, and figured a forewing of an unnamed species from West Malaysia. We can assume that Eaton's generic placement of these additional species was correct, since he was aware of the fact that *Teloganodes* lacks a middle tail. Nonetheless, his *T. major* could eventually prove to be the adult of *Macafertiella*, which is also known from Sri Lanka. Ulmer (1924) provided the first male adult description. Navás (1931) described a species from India, *T. dentata*, and one from China, *T. lugens*, both based only on adults. Ulmer (1940) described the larval stage of *Teloganodes* for the first time as *T. tristis*, from Sumatra and Java. We have examined larvae from Sri Lanka that are almost identical to those described by Ulmer, and therefore consider his species identification correct. Hubbard and Pescador (1978) reported *T. tristis* from the Philippines.

Very little is known of the ecology of the genus *Teloganodes*. Hubbard and Peters (1984), however, indicated that, in Sri Lanka, larvae were taken from 90-2100 m, always on stones in swift currents in small to large streams (sometimes at waterfalls), with water temperatures ranging from 14°C to about 26°C. Our records also show that *Teloganodes* is common in waterfalls, also having been taken from waterfalls in Borneo by J. T. and D. A. Polhemus and from waterfalls in Sri Lanka by F. Starmühlner (see Material examined, above). These data are in general agreement with data available on the African Teloganodinae, resulting from collections by the first author and N. McCafferty of *Ephemerellina* and *Nadinella* in abundance at waterfalls.

PHYLOGENETICS

Cladistics

Cladistic methodology for deducing phylogeny is after Ross (1937, 1974) and Hennig (1950, 1966). Operational taxonomic units (OTUs) analyzed consisted of eight distinctive species groups (Fig. 1) that each appeared monophyletic, based on their possession of unique or specialized characteristics (cladistic analysis substantiated monophyly for each OTU). The outgroup for determining character state polarity consisted of all other pannote mayflies.

Thirty comparative characters with different character states distributed among the OTUs were used in the analysis, and these are presented in terms of their apomorphic and plesiomorphic states in Table 2. Among the cladistic characters, 20 have only one apomorphy expressed in the

Teloganodinae; three are phenoclinal within the Teloganodidae in that there are two stepwise apomorphies, the first of which is transitional to the next (see apomorphies 12 and 24; 21 and 26; 22 and 27); and two are bi-directional, in that the two apomorphies cited are different and independent (see apomorphies 6 and 23; 8 and 17).

Results of the cladistic analysis are given in the form of a most parsimonious cladogram (Fig. 1) deduced from our data. Numbers in Figure 1 refer to all synapomorphies that define the particular clade or lineage where they appear and correspond to those listed in Table 2. Some of these character states are given in abbreviated form in the table, but details can be found in the text and figures.

Character Evolution

The deduced cladogram (Fig. 1) represents the most parsimonious arrangement that could be generated from our data; it is not, however, the only alternative. Thus, in accepting the parsimonious cladogram, convergences with respect to some character states must also be accepted. Below, we present an interpretation of character state evolution, particularly in regard to homoplasy, that must be accounted for in light of the deduced phylogeny of the Teloganodidae.

Multistate phenoclinal characters are often highly indicative of phylogenetic relationships (Ross 1974). We interpret that this is also the case in the Teloganodidae. One phenocline involves the relative operculate nature of the gills on abdominal segment 2 [see apomorphies 12 and 24 (Fig. 1, Table 2)], in which the semi-operculate condition (12) is intermediate to the full operculate condition (24). A parallel transition is seen in the phylogeny of the *Timpanoga* complex (Ephemerellidae) (McCafferty and Wang 1994). The second phenocline involves the development of the long mediolateral seta on the mandibles [see apomorphies 21 and 26 (Fig. 1, Table 2)], in which the appearance of a long hairlike seta (21) is intermediate to that seta becoming bristlelike (26). Such a bristlelike seta has been independently derived in the Prosopistomatidae. The third phenocline involves the degree of fusion of the glossae [see apomorphies 22 and 27 (Fig. 1, Table 2)], in which the poorly divided condition (22) is intermediate to the nearly completely fused condition (27). Numerous other synapomorphies express the same branching sequence as demonstrated by these phenoclines.

Lestagella, *Nadinella*, *Ephemerellina*, and *Lithogloea* all possess distinctive black bands on the larval caudal filaments, and this characteristic might very likely represent an apomorphy. Nonetheless, the most apotypic members (*Macafertiella* and *Teloganodes*) of the clade that also includes these four (Fig. 1) do not have the black banding. Because of the distinctive synapomorphies that define the entire large clade [apomorphies 11-12 (Fig. 1, Table 2), we hypothesize that the black banding was secondarily lost in the ancestor of *Macafertiella* and *Teloganodes*, both of which also lost the developed middle tail. The appearance of the black banding in various members of the family Ephemerellidae and Neoephemeridae, for example, indicates that this is probably an adaptive characteristic.

From the parsimonious cladogram (Fig. 1), it appears that the loss of certain gill pairs occurs independently, and therefore must either not be used, or used with caution, for deducing phylogeny. In the case of the Teloganodidae larvae, the loss of the already reduced gills on abdominal segment 1 is one example of not being usable. The loss of this gill pair evidently has occurred independently in three different lineages: *Austremerella*, *Ephemerellina*, one species of *Nadinella*, and in the *Macafertiella* + *Teloganodes* lineage. Although the absence of these simple filamentous gills may help distinguish individual lineages, the character must be discounted for phylogenetic deduction,

TABLE 2. Character states used to hypothesize phylogenetic relationships of the higher taxa of Teloganodidae [numbered apomorphies are cited on the cladogram (Fig. 1)]

Apomorphy	Plesiomorphy
1. Male forceps segment 1 elongate (Figs 90, 91).	1´. Forceps segment 1 short.
2. Forewing stigmatic area subdivided into rows of cellules (Figs 80-82).	2´. Stigmatic area not modified as such (Figs 83-87).
3. Cerci medially with long and dense setae (Figs 77, 78).	3´. Cerci without such long and dense setae (Fig. 79).
4. Cephalic horns present (Fig. 3).	4´. Cephalic horns absent.
5. Mandibular incisors laterally oriented (Figs 21, 30).	5´. Incisors distally oriented (e.g., Figs 20, 29).
6. Paraglossae apically truncate (Fig. 57).† [see 23]	6´. Paraglossae somewhat pointed (e.g., Figs 56, 58).
7. Forewings with most short intercalaries attached basally (Figs 81, 82).	7´. Most marginal intercalaries free (e.g., Figs 80, 83).
8. Larval claws with single basal denticle. (Fig. 69).† [see 17]	8´. Claws with single row of denticles (Figs 70, 72, 73).
9. Labial palpal segment 3 elongated (Fig. 56).	9´. Segment short (e.g., Figs 77, 78).
10. Adult mesothorax with posterior processes (Fig. 88).	10´. Mesothorax not modified.
11. Gills on abdominal segment 7 absent.	11´. Gills 7 present.
12. Gills on abdominal segment 2 covering large portion of following gills (Figs 4-10).* [see 24]	12´. Gills 2 not covering more than half of following gill (Figs 2, 3)
13. Larval prosternum with spinous bi-lobular process (Fig. 65).	13´. Prosternum without process (Figs 66-68).
14. Labrum with dorsal setae in medial rows (Figs 14-19)	14´. Labrum with scattered setae dorsally (Figs 11, 13).
15. Mandibles narrowed (Figs 23-28).	15´. Mandibles robust (Figs 20, 22).
16. Left mandibles with medioapical setal patch reduced (Figs 32-36).	16´. Left medioapical setal patch developed (Figs 29-31).
17. Larval claws with two rows of denticles (Fig. 71).† [see 8]	17´. Claws with one row of denticles (Figs 70, 72-73).
18. Forewings with IMP shorter than, and detached from, MP_2 (Figs 85-87).	18´. IMP long and directly attached with MP_2 (Figs 80-84).
19. Larval abdominal posterolateral processes elongate-triangular and widely separated from base of following segment (Fig. 6)	19´. Posterolateral processes moderately developed and approximate (Figs 2, 3, 4, 5, 8, 9).
20. Larval cephalic setal fringe well developed, at least anterior to eyes (Figs 7-10).	20´. Setal fringe not developed (Figs 2, 4-6).
21. Mandibles with elongate mediolateral seta (Figs 34-37).* [see 26]	21´. Mandibles without such such seta (Figs 29-33).
22. Glossae and paraglossae poorly divided (Figs 61-64).* [see 27]	22´. Glossae and paraglossae deep divided (Figs 56-60).
23. Paraglossae rounded apically (Figs 61-64).† [see 6]	23´. Paraglossae somewhat pointed (Figs 56, 58-60).
24. Gills on abdominal segment 2 fully operculate (Figs 7-10).* [see 12]	24´. Gills 2 semi-operculate (Figs 4-6).
25. Incisors and molae of mandibles atrophied (Figs 25, 34).	25´. Incisors and molae not reduced.
26. Mandible with long mediolateral seta well developed and bristlelike (Figs 35-37).* [see 21]	26´. Seta not bristlelike (Fig. 34).
27. Glossae nearly fused (Figs 62-64).* [see 22]	27´. Glossae poorly divided (Fig. 61).
28. Median caudal filament reduced in both adults and larvae (Figs 8-10).	28´. Three tailed (Figs 2-7).
29. Labrum with dense, curved row of long filtering setae dorsally (Fig. 17).	29´. Setae not as developed (Figs 14-16, 18, 19).
30. Gills 6 absent.	30´. Gills 6 present.

* One of two phenoclinal apomorphies of the character.

† One of two bi-directional apomorphies of the character.

because only in the case of the common ancestry of *Macafertiella* and *Teloganodes* would it have served as a supplementary defining synapomorphy. The loss of gills on abdominal segment 6 is an example of an apomorphy that must be used with caution. It cannot be used to deduce common ancestry of lineages, because, based on parsimony, it evidently occurred convergently in *Nadinella*, *Lestagella* and *Teloganodes*. It does serve, however, as a defining autapomorphy for the *Teloganodes* lineage, and as such is critical to defining *Teloganodes* as a monophyletic genus distinct from its sister *Macafertiella* lineage.

There are certainly instances when the loss of gills on particular abdominal segments is of importance for deducing common ancestry. The loss of gills on abdominal segment 2, for example, is a synapomorphy that defines the entire family Ephemerellidae, and the loss of gills on abdominal segment 7 in Teloganodidae is a synapomorphy that helps define one of two major, most basal clades within the family [see apomorphy 11 (Fig. 1, Table 2)] that we consider a separate subfamily (see below).

It might be argued that the reduction of the median caudal filament is so widespread in disparate lineages in Ephemeroptera, and thus so highly subject to homoplasy, that it is of little or no use in deducing phylogeny. It is, moreover, highly probable that in certain lineages the median caudal filament becomes secondarily re-developed and lengthened from the reduced condition (see McCafferty 1979). Nonetheless, loss of the middle tail in certain individual monophyletic groups of mayflies recognized at the family level, such as among Teloganodidae or Heptageniidae larvae, is an obvious independent evolutionary event that provides cladistic information. The common ancestry of *Macafertiella* and *Teloganodes* was deduced in part by using the only instance of this loss in the Teloganodidae. Furthermore, this common ancestry is supported by two other synapomorphies [see apomorphies 26-28 (Fig.1 and Table 2)]. On the other hand, if one were developing a cladogram of the entire family Baetidae, the innumerable instances of reduction of the middle tail would obviously constitute misleading information for deducing major lineages.

Dorsal abdominal tubercles are developed on the larval abdomens of many mayflies, but are probably most common among the Ephemerellidae and Teloganodidae. Such tubercles have certainly developed as independent apomorphies in such groups as the genus *Acanthiops* of the family Baetidae (see Waltz and McCafferty 1987, Barber-James and McCafferty 1997), and the genus *Anepeorus* of the family Heptageniidae (as *Spinadis* in Edmunds and Jensen 1974, Edmunds et al. 1976). As first suggested by Demoulin (1967), the general habitus of the larvae of certain *Acanthiops* are amazingly similar to some Teloganodidae, but this is especially true for the recently discovered *Macafertiella* because of its single row of tubercles and two-tailed condition. Such tubercles are even found independently developed in other aquatic insect orders, such as certain stoneflies (see e.g., Illies 1961, Hynes 1970).

With respect to the current study, we hypothesize that dorsal abdominal tubercles were present in the immediate common ancestor of the Teloganodidae and Ephemerellidae because of their relative pervasiveness in these groups. We also infer that ancestrally they occurred in two rows on the abdominal terga. This inference derives from the fact that the double row condition is found throughout the Ephemerellidae and in three lineages of Teloganodidae. Based on other data, the teloganodids lineages with double rows represent one of the two basally derived clades within the Teloganodidae (*Austremerella* + *Vietnamella*), and the somewhat plesiotypic *Nadinella* of the latter's sister group. In other Teloganodidae, the double tubercle rows have either become a single median row, or tubercles are secondarily lost. A glimpse of how this evolution has perhaps easily occurred is seen in the variation of tubercles found in individual larvae of *Nadinella* (Figs 5, 74-76), where on various terga, the tubercles of a pair can be broadened and juxtaposed medially, coalesced into a single broad protuberance, and sometimes appear as a single median tubercle. In other teloganodids, there is either a single row of dorsal abdominal tubercles (*Ephemerellina*, *Lithogloea*, *Macafertiella*, and plesiotypic species of *Teloganodes*) or such tubercles have entirely disappeared (*Lestagella* and apotypic species of *Teloganodes*). Considering the cladogram, the single row condition appears to have preceded the loss of tubercles which has occurred independently in *Lestagella* and within *Teloganodes*.

A distinctive setal fringe is developed on the entire cephalic margin of the *Lestagella* + *Macafertiella* + *Teloganodes* clade. It is independently developed, but only laterally in *Vietnamella*. Other cases of homoplasy are found in other families of mayflies, e.g., *Haplohyphes* in the Leptohyphidae (see Lugo-Ortiz and McCafferty 1995), *Dicercomyzon* in the Tricorythidae [present but not figured by Demoulin (1954a)], and *Epeorus* in the family Heptageniidae (see e.g., Edmunds et al. 1963).

Abdominal posterolateral processes are well developed in many different lineages of Ephemerellidae [to the extreme in *Timpanoga* (see McCafferty and Wang 1994)] and some other families of mayflies. They are also well developed independently in *Lithogloea*, somewhat in *Lestagella*, and in at least one species of *Teloganodes* within the Teloganodidae. In *Lithogloea*, the processes are sharply attenuated; in *Lestagella* and *Teloganodes*, they are not as attenuated.

Although it is somewhat difficult to determine the exact plesiomorphic state of the mandibular incisors among teloganodids by using outgroup methodology, a generalized form of the armature of the more variable left mandible appears to be represented by the mandibles of *Nadinella* (Fig. 32) and most species of *Teloganodes* (Fig. 36), for which almost exact matches can be found among the Ephemerellidae (see e.g., Fig. 40 of Allen and Edmunds (1963b)]. In these mandibles, the incisors are separate, only slightly divergent from each other, oriented distally, and the outer incisor has three blunt denticles. Only slight modifications of this plan are found in *Ephemerellina*, *Lithogloea*, and *Macafertiella*. However, in *Lestagella* (Figs 25, 34), the incisors are completely reduced; in *Vietnamella* (Figs 21, 30), the incisors are fused and laterally oriented; and in at least one species of *Teloganodes* (Figs 28, 37), the outer incisor is blunt and without denticles and the inner incisor is highly reduced. Differences in the incisors were of no use cladistically, possibly owing to the adaptive nature of such structures. Caution must always be used in assessing the condition of the incisors of mayfly mandibles, even for diagnostic use, because they can become worn in long-lived instars. There is also evidently some change in characteristics from young to older instar larvae, for example, see comparative mouthpart figures of *Lestagella* provided by Demoulin (1970, Fig. 15).

Other characteristics of the mandibles did provide valuable cladistic information, including the phenoclinal development of the long mediolateral seta as discussed above. In addition, there has been a strong tendency for the body of the mandible to become narrowed in teloganodids [see apomorphy 15 (Fig. 1) (Table 2)]. This may be phenoclinal, but we cannot be sure. In the clade having the narrowed mandible, *Nadinella* is most apotypic and also has a mandible that does not appear as narrowed as others in the clade. Outside of this clade, *Vietnamella* also shows some narrowing of the mandibles, and while this may be viewed as generally convergent, it is different from that seen in the others because the mandibles are abruptly narrowed in the basal two-thirds, with the apices remaining broad. A small patch of setae occurs on the medial margin near the apices of the mandibles of Ephemerellidae and Teloganodidae; however, it is lost in the left mandible of the clade made up of *Nadinella*, *Lithogloea*, *Lestagella*, *Macafertiella*, and *Teloganodes*. The only incongruent character state distribution is that it occurs weakly developed in *Macafertiella*. Since so many other synapomorphies (Fig. 1) corroborate the phylogenetic placement of *Macafertiella*, we can only assume that the setal patch was re-developed subsequently in *Macafertiella*.

Other characters of the mouthparts were of some value, but quite predictably were always subject to some degree of homoplasy. Dorsal setal patterns on the labrum evolved from generally scattered dorsal setae, similar to that found in *Austremerella* and *Ephemerellina*, which happen to be the most plesiotypic lineages in both of the major clades. Setae become restricted to irregular, transverse rows in the midregion of the labrum [see apomorphy 14 (Fig. 1, Table 2)]. The most ordered setal row is found in *Macafertiella* amongst those with this condition. In *Vietnamella*, the generally scattered setae have independently become absent from the basal half of the labrum, but remain relatively scattered throughout the distal half.

As mentioned above the phenoclinal development of fusion in the glossae of the labium is instructive, but in addition to this, the apical shape of the paraglossae is important. The plesiomorphic condition is one in which the paraglossae are bluntly pointed apically, and sometimes this point is oriented medioapically. In the clade of *Lestagella* + *Macafertiella* + *Teloganodes*, the apices of the paraglossae have become narrowly rounded. A different apomorphy of this bi-directional character is seen in *Vietnamella*, in which the apices of the paraglossae have become flat and truncate [see apomorphies 6 and 23 (Fig. 1, Table 2)].

Maxillary palpi are absent in all but *Vietnamella* among the Teloganodidae, perhaps indicating that the palpi were lost independently in *Austremerella* and the common ancestor of the other major clade (Fig. 1). An alternative explanation for this would be that the palpi were absent in the common ancestor of the family Teloganodidae, but re-appeared in the aberrant *Vietnamella* lineage. Generally, structures are not expected to reappear (Ross 1974) but there are exceptions. Small nodule-like rudiments of the maxillary palpi are present on the maxillae of many *Teloganodes*.

Finally, with respect to wing venation in the Teloganodidae, the appearance of a free, additional longitudinal vein in the stigmatic area of the forewing, with numerous small cells, or cellules, on either side of it (Figs 80-82) is an important synapomorphy for the *Austremerella* + *Vietnamella* lineage [see apomorphy 2 (Fig. 1, Table 2)]. Somewhat similar modifications of the forewing have evolved independently in some other mayflies. For example, in certain Heptageniidae genera, the stigmatic area contains a secondary longitudinal vein, but cellules are not as developed, and in certain genera of a number of families, stigmatic crossveins may be more or less anastomosed, sometimes giving the impression of cellules (see Edmunds et al. 1976). Within the Teloganodidae, in fact, the forewings of African genera of Teloganodinae show some slight reticulation or tendency for such in the stigmatic area (Figs 83-86). Although this cannot be confused with the *Austremerella* + *Vietnamella* synapomorphy, it does indicate that the common ancestor of the Teloganodidae probably had some slight reticulation in the stigmatic area. The shortening of IMP compared to MP_2, and its detachment from MP_2 in the forewings is a stable and important apomorphy for establishing *Lithogloea* in the *Lithogloea* + *Lestagella* + *Macafertiella* + *Teloganodes* clade [see apomorphy 18 (Fig. 1, Table 2)].

Phylogenetic Classification

Although cladistic methods have recently been employed to hypothesize phylogeny in Ephemeroptera (e.g., McCafferty 1979, McCafferty and Edmunds 1979, Peters 1980, Savage and Peters 1983, Domínguez 1995), it is only more recently that phylogenetic classifications have been strictly derived from cladistic data, or cladograms (Bae and McCafferty 1991; McCafferty 1991a, 1991b; McCafferty and Wang 1994; Lugo-Ortiz and McCafferty 1996; Barber-James and McCafferty 1997). Based on our cladistic analysis of the Teloganodidae, we also present a strictly phylogenetic classification as elaborated and endorsed in general by Wiley (1981) and in particular with respect to Ephemeroptera by McCafferty (1991a). We also incorporate sequencing conventions (Nelson 1972, 1973), which were thoroughly discussed by McCafferty and Wang (1994) with respect to their application to the *Timpanoga* complex (Ephemerellidae).

The strictly phylogenetic hierarchical classification of the Teloganodidae is given in Table I. As such, the cladogram (Fig. 1) is entirely reproducible from the linear classification. The most basal bifurcate branching in the cladogram (Fig. 1) is reflected in the classification as the subfamilial delineation.

Within the subfamily Teloganodinae (Fig. 1), sequential branches of species group OTUs are recognized as separate genera by sequencing. All such genera are further defined by autapomorphies. This is both a phylogenetic and practical classification because all the genera as such are easily distinguishable in both the larval and adult stages (see the Key to Genera, above). It would be tempting to recognize some highly specialized species in *Teloganodes* as a separate taxon, either genus or subgenus; however, the remainder of *Teloganodes* would be left without an autapomorphy to define them, and thus would essentially become a non-allowable paraphyletic group.

Biogeography

The Teloganodidae can be viewed as a group of Old World Gondwanan origin based on its restricted distribution in the Orient, Australia and southern Africa. Its sister family Ephemerellidae is essentially Holarctic and Laurasian. Edmunds (1972, 1975, 1981, 1982), Bae and McCafferty (1991), and McCafferty et al. (1992) have argued that mayflies are ideal candidates for studying historical biogeography because of the order's antiquity, restriction to freshwater as larvae, short-lived and fragile nature of alate stages, and conservative vagility. Such qualities may be expected to be particularly amenable to reflecting ancient patterns affected primarily by vicariance (Croizat et al. 1974), as could be expected by Southern Hemisphere lineages old enough to have participated in continental drift. By superimposing the distributions of the genera of Teloganodidae (Table 1) on the cladogram of the genera (Fig. 1), it is possible to hypothesize certain aspects of the historical biogeography of the various lineages (Ross 1974, Rosen 1975).

We hypothesize a Gondwanan origin for the Teloganodidae prior to the initial breakup of Gondwanaland. The family's restriction to the Old World Southern Hemisphere and tropical Asia would suggest this. We hypothesize that the subfamily Austremerellinae originated prior to the breakup of Gondwanaland, subsequently becoming isolated in Australia and more recently dispersing through Wallacea to the tropical Orient [most probably circa 25 to 17 mya (million years ago) (Raven and Axelrod 1974, Hamilton 1979)], where it is now represented by the relatively aberrant genus *Vietnamella*. The subfamily is represented in Australia by the phylogenetic relict *Austremerella*, with an ancestry that possibly dates to the Triassic. While dispersal from Australia to the Orient has been relatively uncommon and relatively recent (Raven and Axelrod 1972, Hamilton 1979), models of earth history [with Australia and the Orient at somewhat opposite ends of Pangaea (see e.g., Pielou 1979)], preclude other explanations at this time.

We hypothesize that the subfamily Teloganodinae arose in Gondwanaland and subsequently became isolated in temperate South Africa. A considerable biota in temperate South Africa is regarded as Gondwanan in origin and has been referred to as the palaeogenic [not to be confused with the Paleogene period of Tertiary (see e.g., Stanley 1989)], or old, element in the Afrotropics (e.g., Brinck 1955a, 1955b; Stuckenberg 1962; Harrison 1965). *Ephemerellina*, *Nadinella*, and *Lithogloea* are restricted to the mountainous southern temperate area of the Western Cape Province of South Africa. *Lestagella* apparently has a somewhat more extensive range that includes mountainous areas of extreme southeastern Africa as well. We have been able to substantiate Eastern Cape records of *Lestagella*. Reports of *Lithogloea* outside of the Western Cape, however, are apparently erroneous (see especially Distribution under *Lithogloea* and *Lestagella* in the Account of Taxa, above). In any case, all African genera qualify as temperate Gondwanaland, phylogenetic relicts, the origin of which can be traced to 135 to 200 mya (see, e.g., Pielou 1979) and possibly much earlier.

Harrison (1965) considered the leptophlebiid mayfly genera *Aprionyx* Barnard and *Castanophlebia* Barnard as South African representatives of an "old-element, palaeo-endemic" fauna because they were thought to have affinities with South American and Australasian Leptophlebiidae. Peters and Edmunds (1964) suggested that the South African leptophlebiid genera *Aprionyx* and *Adenophlebia* Eaton had Paleoantarctic affinities. Harrison (1965) included *Ephemerellina* and *Lithogloea* (the only South African genera of Teloganodidae recognized at that time) as only candidates for inclusion in his "old-element" category because their broader biogeographic affinities were not known outside of South Africa. Our phylogenetic data on the Teloganodidae substantiate the inclusion of African teloganodids in his biogeographic grouping.

The African genus *Lestagella* and two, more apotypic, Oriental genera *Macafertiella* and *Teloganodes* make up the most derived clade in the subfamily Teloganodinae. We hypothesize that the origin of this clade was temperate South Africa, and that it originated relatively early. Whereas all other genera of African Teloganodidae are evidently restricted to the Western Cape, we have examined specimens of *Lestagella* from the Eastern Cape and also believe that other specimens from the Amatola Mountains, Eastern Cape, tentatively identified as *Lithogloea harrisoni* by Crass (1947) are either *Lestagella* or *Ephemerythus* (Tricorythidae). Harrison and Agnew (1962) noted that teloganodids had been seen from the Transvaal and as far north as Malawi, but those reports are attributable to *Ephemerythus* based on our examination of material (see Distribution under *Lithogloea* and *Lestagella*, in the Accounts of Taxa, above). *Lestagella*, therefore, appears to be both part of the temperate Gondwanaland element but also may be typical of many such groups in Africa in having become distributed eastward and sometimes northward along mountain chains (Harrison 1965). The geography of *Lestagella* would appear to be compatible with the transitional nature of this lineage depicted by its phylogenetic position (Fig. 1) and its hypothesized more recent participation as a faunistic link between the African and Oriental members of the subfamily Teloganodinae [the trans-Indian Ocean track (Craw 1988) as seen in the Teloganodidae].

The *Macafertiella* + *Teloganodes* lineage became isolated and radiated in tropical Asia. Given our hypothesis of a temperate southern Africa origin for the Teloganodinae, the trans-Indian Ocean track of this group could be explained by movement of the Indian subcontinent northward from southern Africa-Madagascar landmass [beginning circa 150 mya and culminating circa 45 mya (e.g., see Kummel 1970)]. Dispersal during pluvial periods through Asia Minor [perhaps circa 17 mya (Raven and Axelrod 1974)], as for example has been hypothesized for certain mayfly genera such as *Afromera* (McCafferty and Gillies 1979) and *Povilla* (Hubbard 1984), does not appear to be a viable possiblity. This is because teloganodids are entirely absent from Asia Minor and east Africa, where they would be expected if there had been such a dispersal. There are examples of a strong Afro-Oriental affinity in many other lineages of mayflies, sometimes with genera distributed exclusively in southern Africa and the Orient (e.g., see Gillies 1957, Peters et al. 1964, McCafferty and Edmunds 1973, Edmunds 1979, Waltz and McCafferty 1994, Provonsha and McCafferty 1995). The Afro-Oriental relationship may be special among the teloganodids and some Leptophlebiidae because of their general restriction to mountain streams. Today, the Oriental teloganodid fauna apparently consists of two independently derived lineages of Teloganodidae, represented by the subfamilies Austremerellinae and Teloganodinae.

Based on all of the above, one might expect Teloganodidae (esp. Teloganodinae) to be a reasonable candidate for distribution in Madagascar. However, as pointed out by Edmunds (pers. comm.), one should not always expect a uniform biota in all the divided parts of a former landmass, as for example is the case with *Tricorythus* Eaton (Tricorythidae), because few genera and species are widespread on the present landmasses. In the case of the Teloganodidae, Madagascar is evidently not represented in the trans-Indian Ocean track. On the other hand, in the case of the *Teloganella* complex of genera (*Manohyphella*, *Provonshaka* McCafferty and Wang, and *Teloganella*), which are currently regarded in the Tricorythidae (McCafferty and Wang 1995, Wang et al. 1995), it is Africa that is excluded from representation in their trans-Indian Ocean track.

Consideration of the relict genera of Teloganodidae in South Africa and Australia indicates that they are typical of other known phylogenetic, or evolutionary, relicts among the Ephemeroptera in several respects. Interesting comparisons can be made with the Amphinotic families such as Ameletopsidae, Oniscigastridae, Nesameletidae-Rallidentidae, and Coloburiscidae that consist only of genera that are phylogenetic relicts of Transantarctica and are now found only in Australia, New Zealand, and southern temperate South America (see Edmunds 1975, McCafferty 1991a). The genera are small, with only one or very few species each, and they are highly distinctive but at the same time demonstrate some degree of convergence among relatives. These common characteristics of such taxa are predictable by their age and the decimation of related species (after Gould 1989). Such phylogenetic relicts should probably be referred to as "survivors" rather than relicts, as has been aptly pointed out by Udvardy (1969). Such archaic forms figuratively have outlived all other members of once possibly thriving taxa, and on a grand scale, they fit the final stage of the taxon cycle elaborated by Ricklefs and Cox (1972), in that descendant species have dwindled, leaving only a few perhaps fortuitous survivors.

None of the Transantarctic, Amphinotic families of mayflies mentioned above are found in Africa (or Madagascar or the Indian subcontinent). On the other hand, no Teloganodidae show the Transantarctic pattern. In generally accepted models of the breakup of Gondwanaland (e.g., Wegener 1929, Kummel 1970, Colbert 1973), Africa separated from Transantarctica prior to the breakup of Transantarctica, respectively into West and East Gondwana. From this, one can conclude that the teloganodid lineages represented in South Africa and Australia can be traced to southern Pangaea, at least to 200 mya. This makes them as old or older than the strictly Amphinotic groups, which may have originated subsequently in West Gondwana, showing the classical patterns that are apparent in some more well known organisms, for example the flightless birds (see Cracraft 1973). This being the case, some adjustment may be required among ephemeropterists with respect to any "conventional wisdom" that extant pisciform mayflies are the oldest living mayflies.

Unfortunately, scant Ephemeroptera fossil data are available from the Southern Hemisphere to shed additional light on these theories (see McCafferty 1990). Triassic mayfly fossils known from South Africa are not clearly related to any extant mayflies (Riek 1976, Hubbard and Riek 1977), and fossils from Australia are no older than the Lower Cretaceous (Jell and Duncan 1986). McCafferty (1997), however, has recently found an African fossil from Lower Cretaceous Lebanese amber that belongs to a clade of Atalophlebiine Leptophlebiidae containing both Amphinotic and Afrotropical extant genera. That paleonological data undoubtedly substantiates the primitive position of the clade hypothesized from phylogeny by Peters and Edmunds (1970). The only ancient fossil that has been assigned to anything possibly remotely related to the Teloganodidae was a partial larva of *Turfanerella tingi* (Ping), from the Jurassic in China, which was placed in the Ephemerellidae by Demoulin (1954b). Edmunds (1972), however, noted that this fossil was probably a pisciform mayfly. Despite the dearth of paleontological information available, cladistics of the phylogenetic relicts of Ephemeroptera have provided rather compelling data for inferring historical biogeography of the Teloganodidae.

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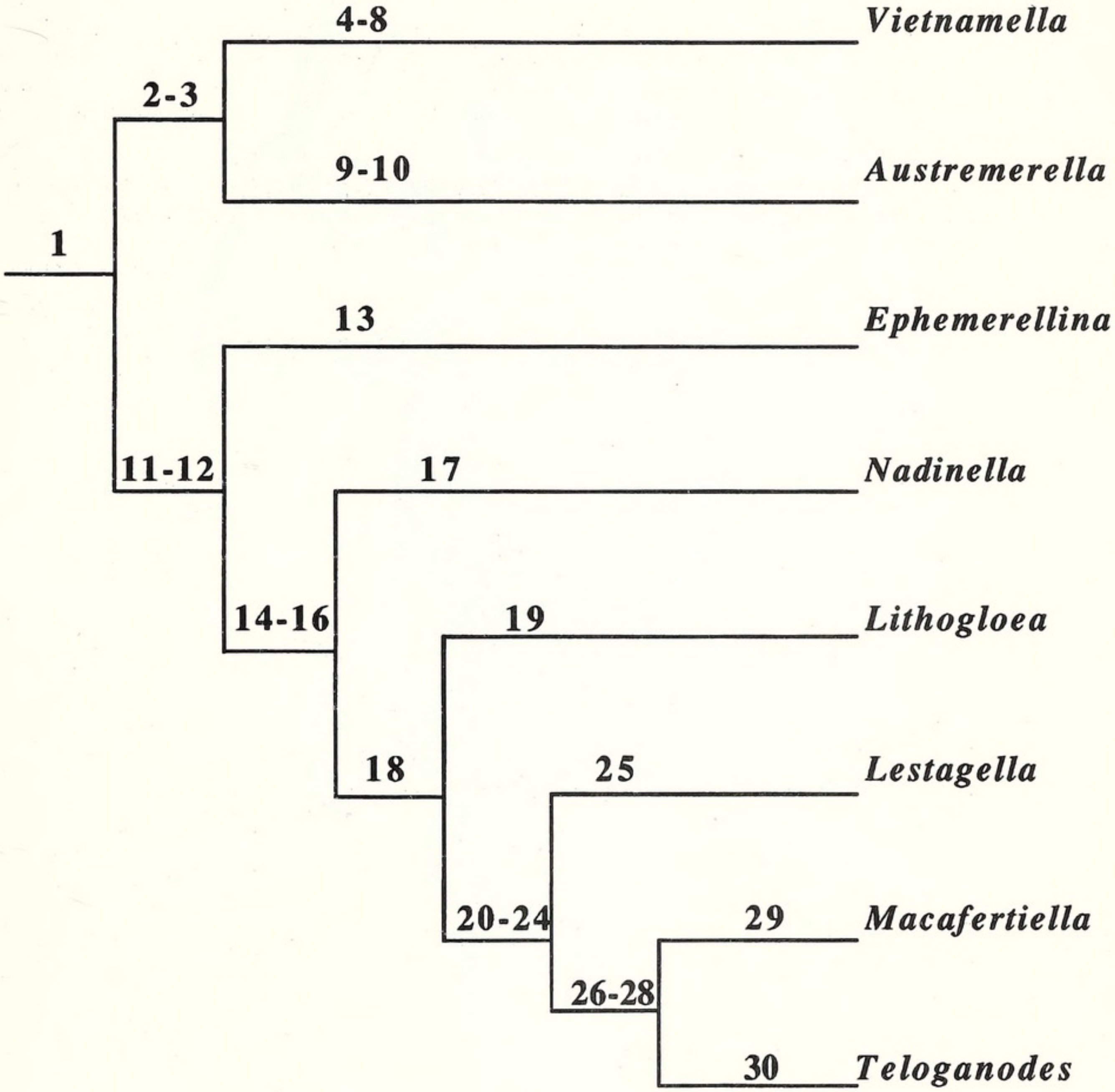


Fig. 1. Cladogram of monophyletic species groups of Teloganodidae.

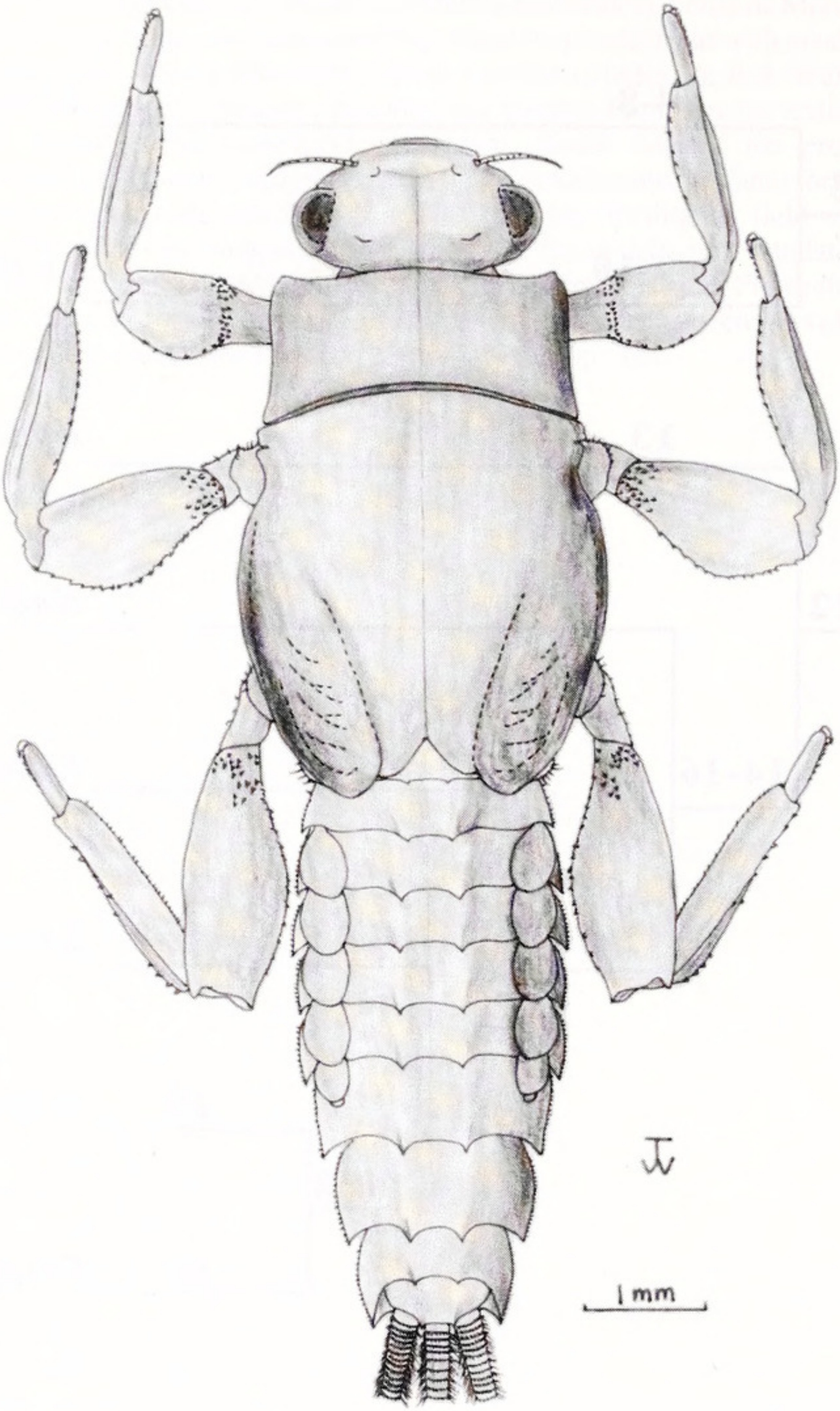


Fig. 2. *Austremerella picta*, larval habitus.

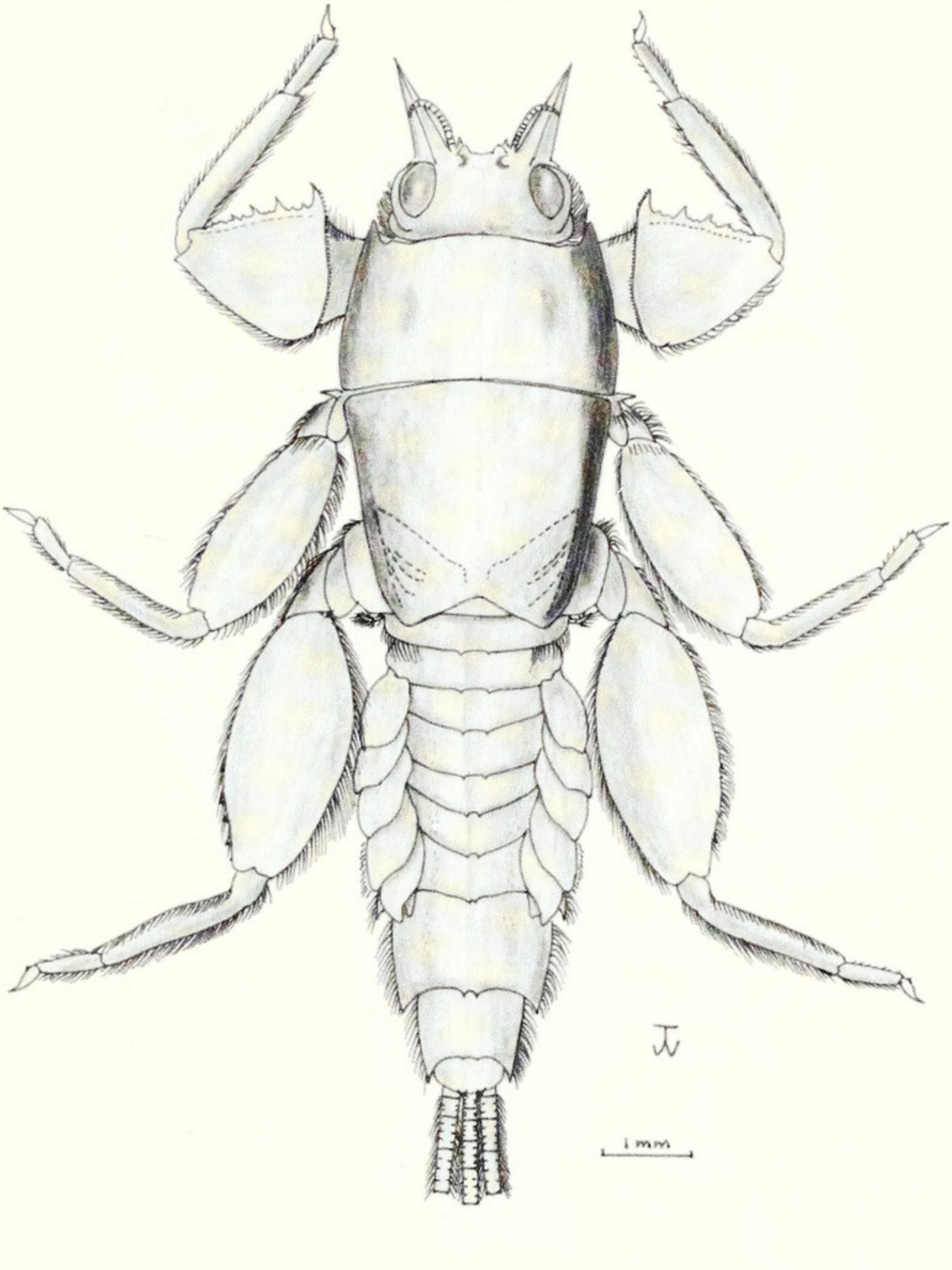


Fig. 3. *Vietnamella thani*, larval habitus.

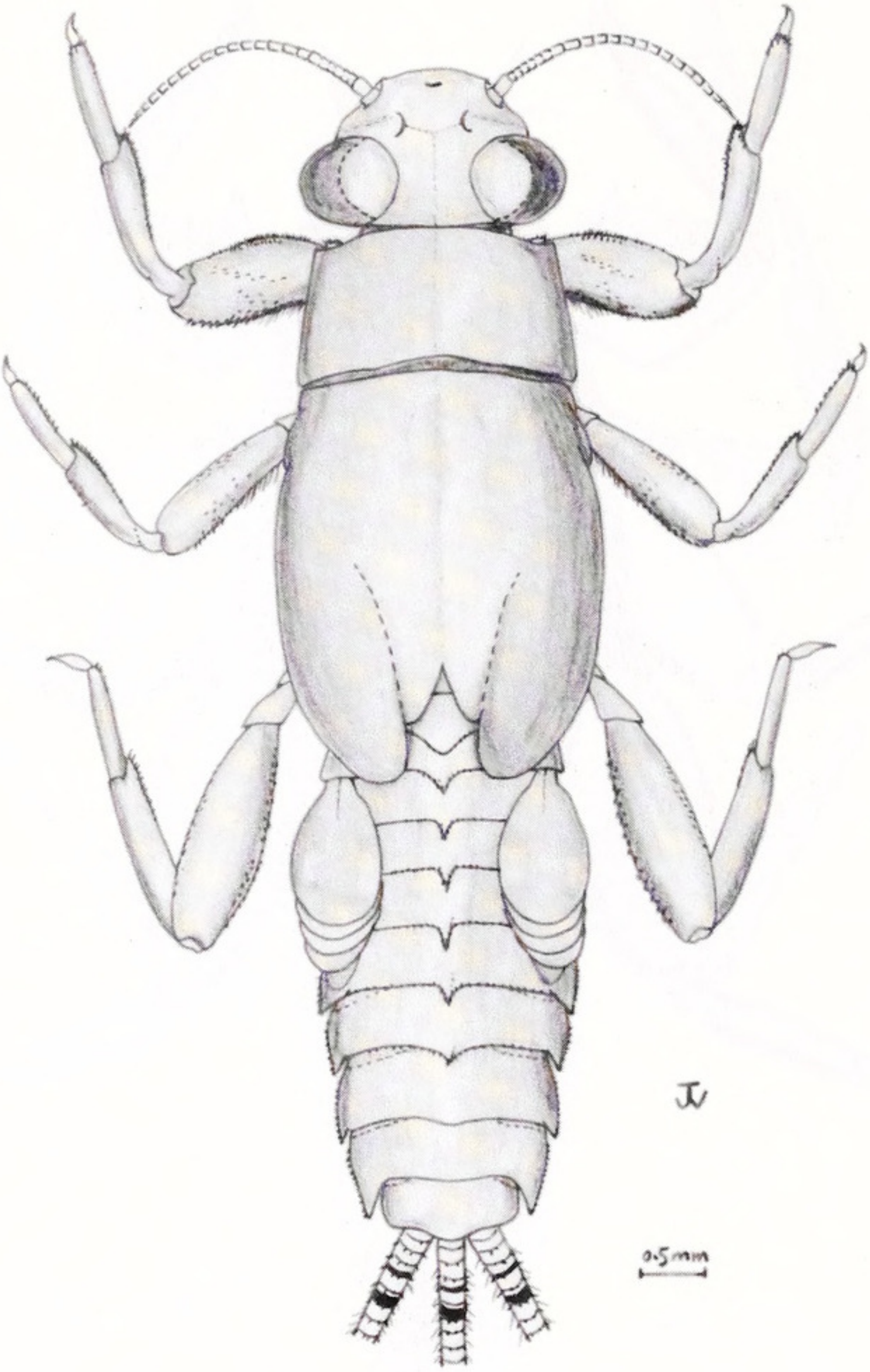


Fig. 4. *Ephemerellina barnardi*, larval habitus.

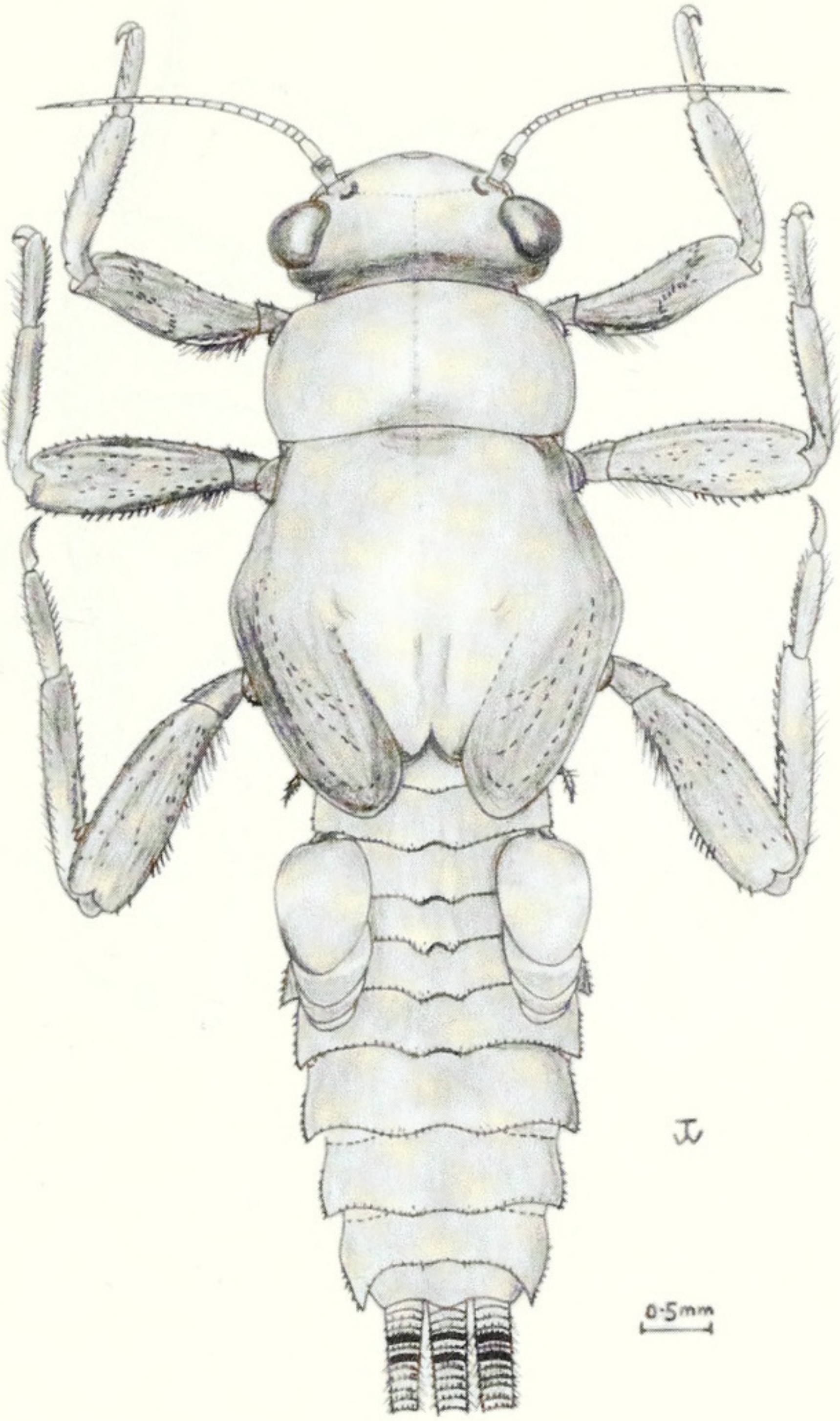


Fig. 5. *Nadinella crassi*, larval habitus.

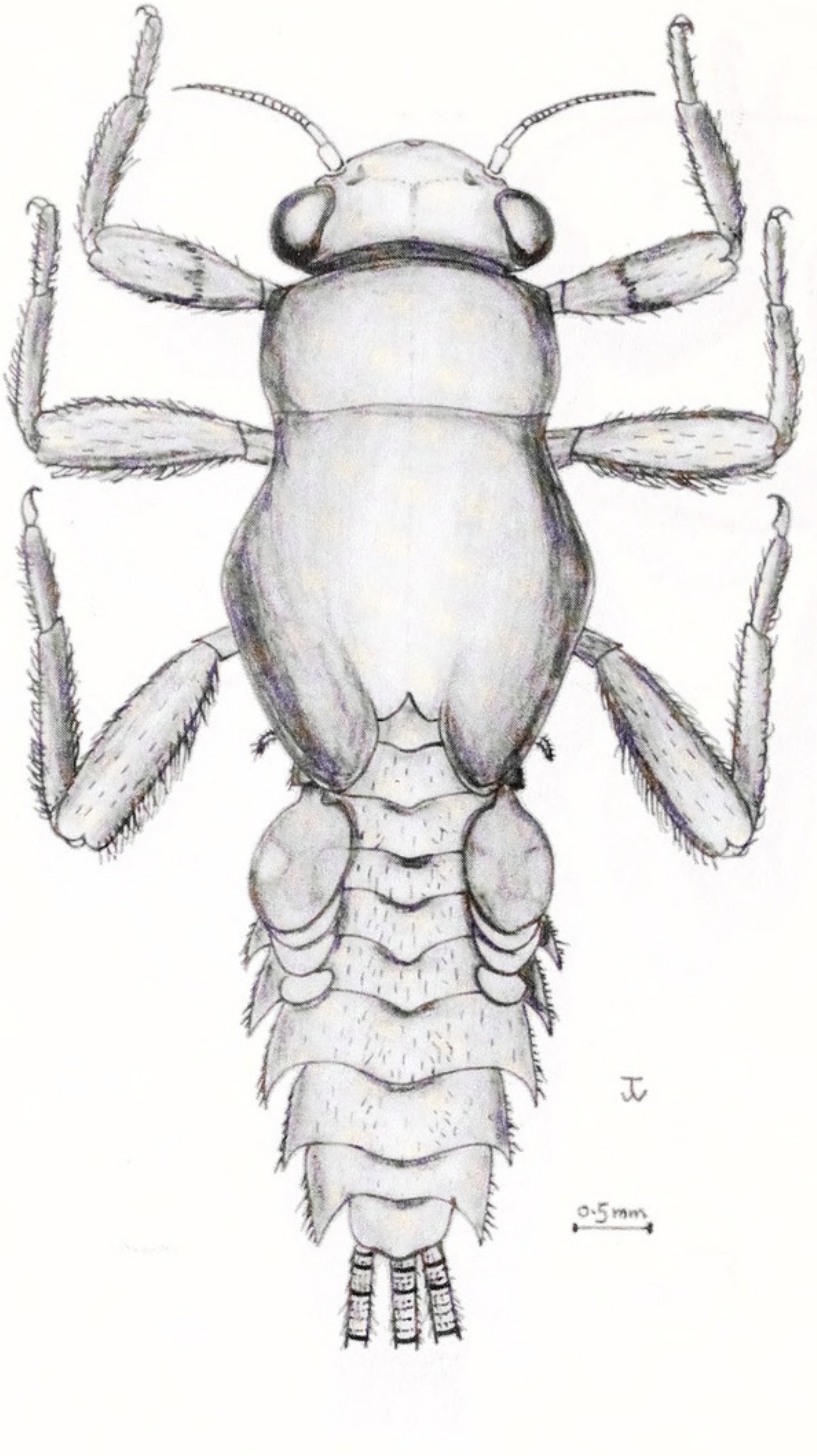


Fig. 6. *Lithogloea harrisoni*, larval habitus.

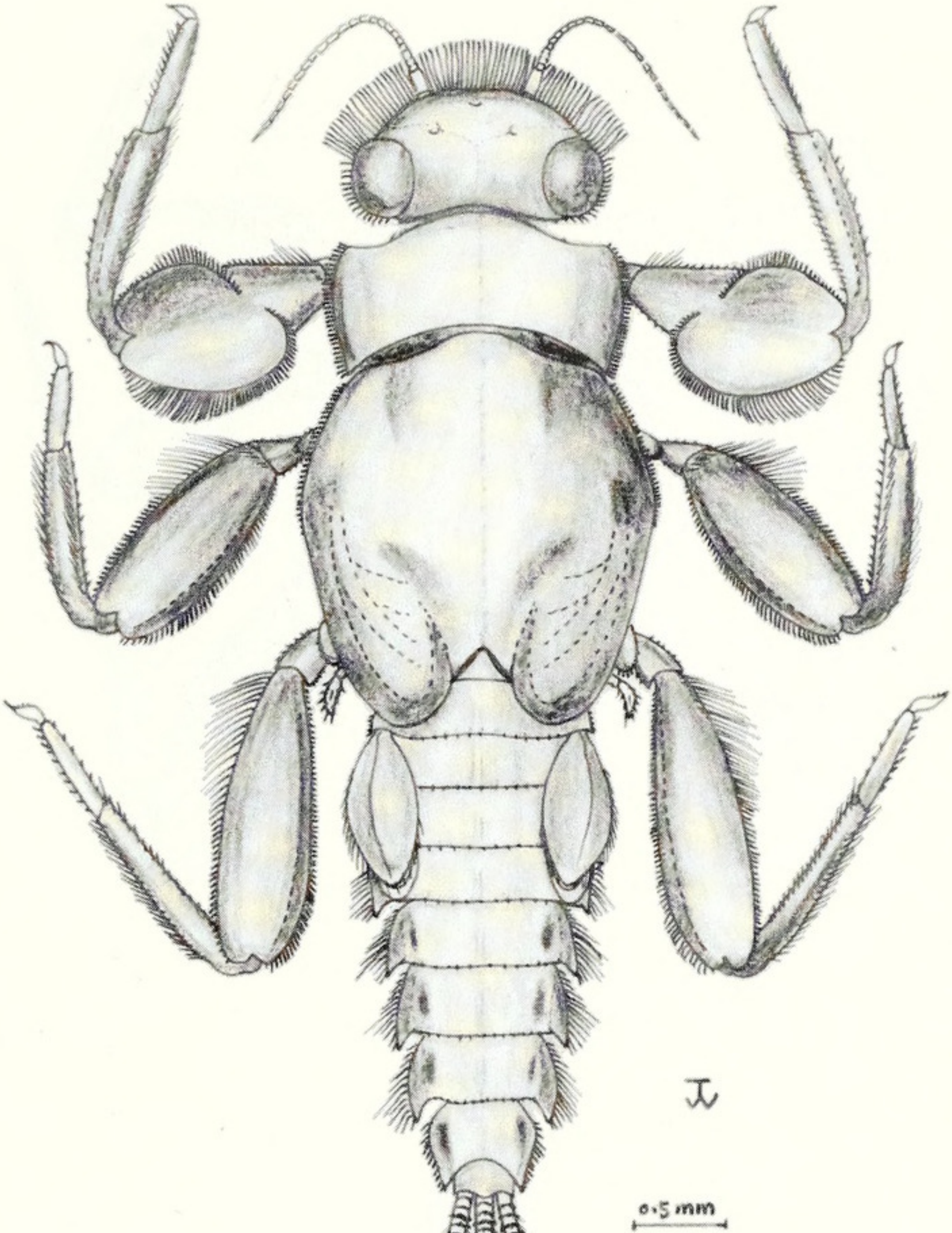


Fig. 7. *Lestagella penicillata*, larval habitus.

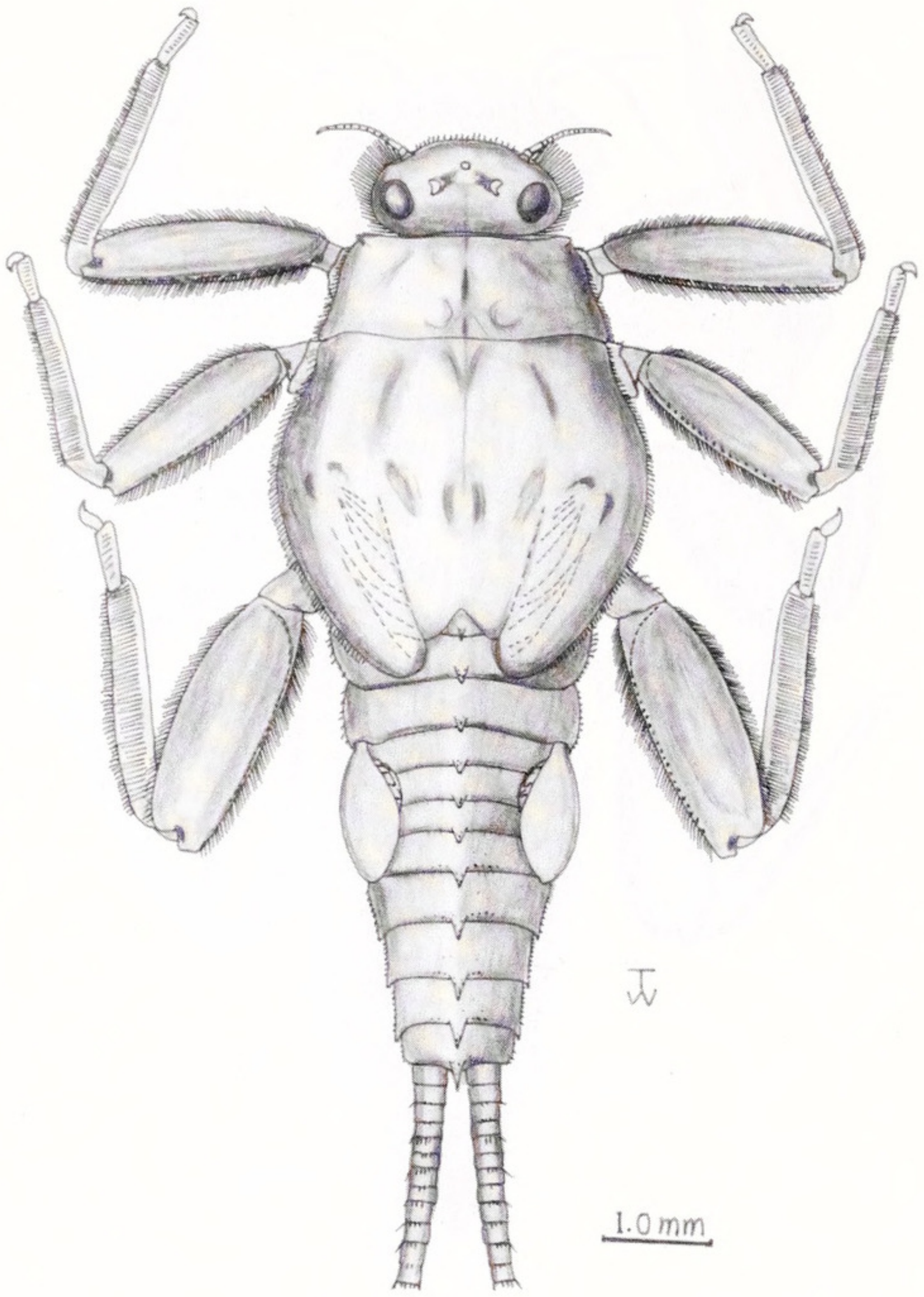


Fig.8. *Macafertiella insignis*, larval habitus.

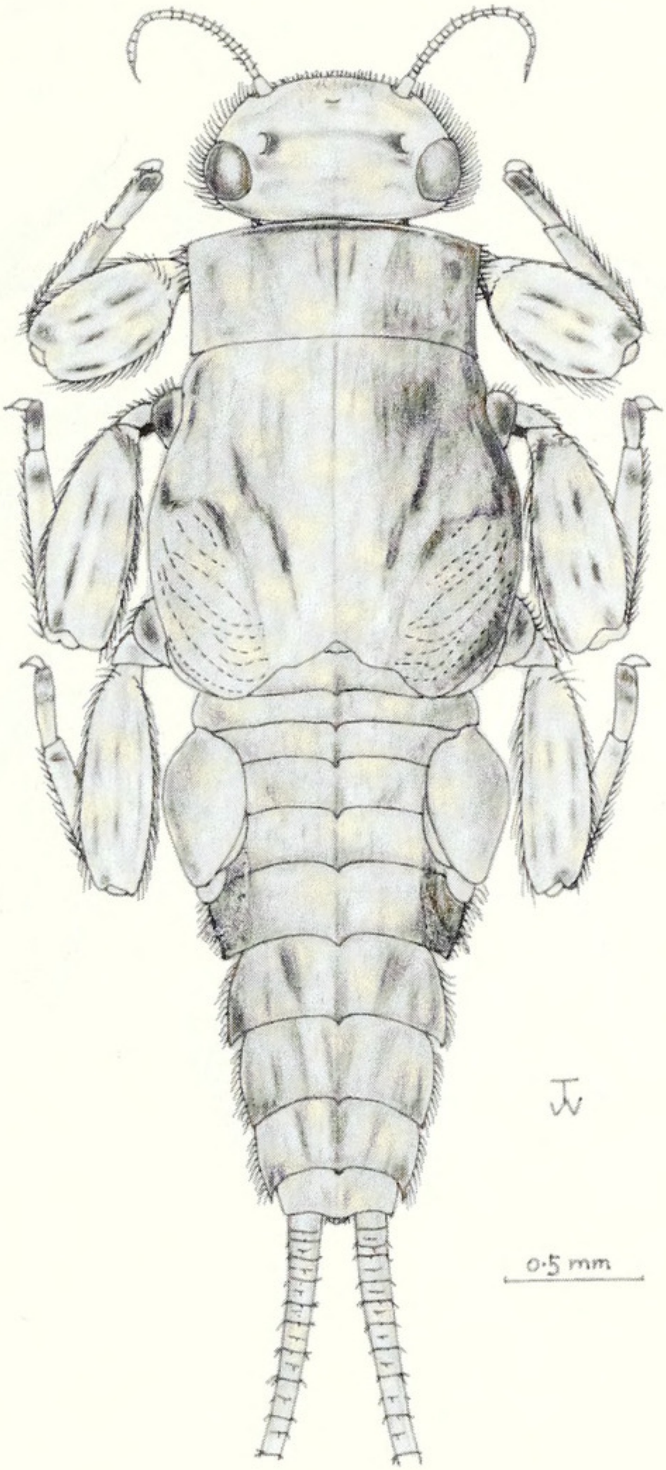


Fig. 9. *Teloganodes tristis*, larval habitus.

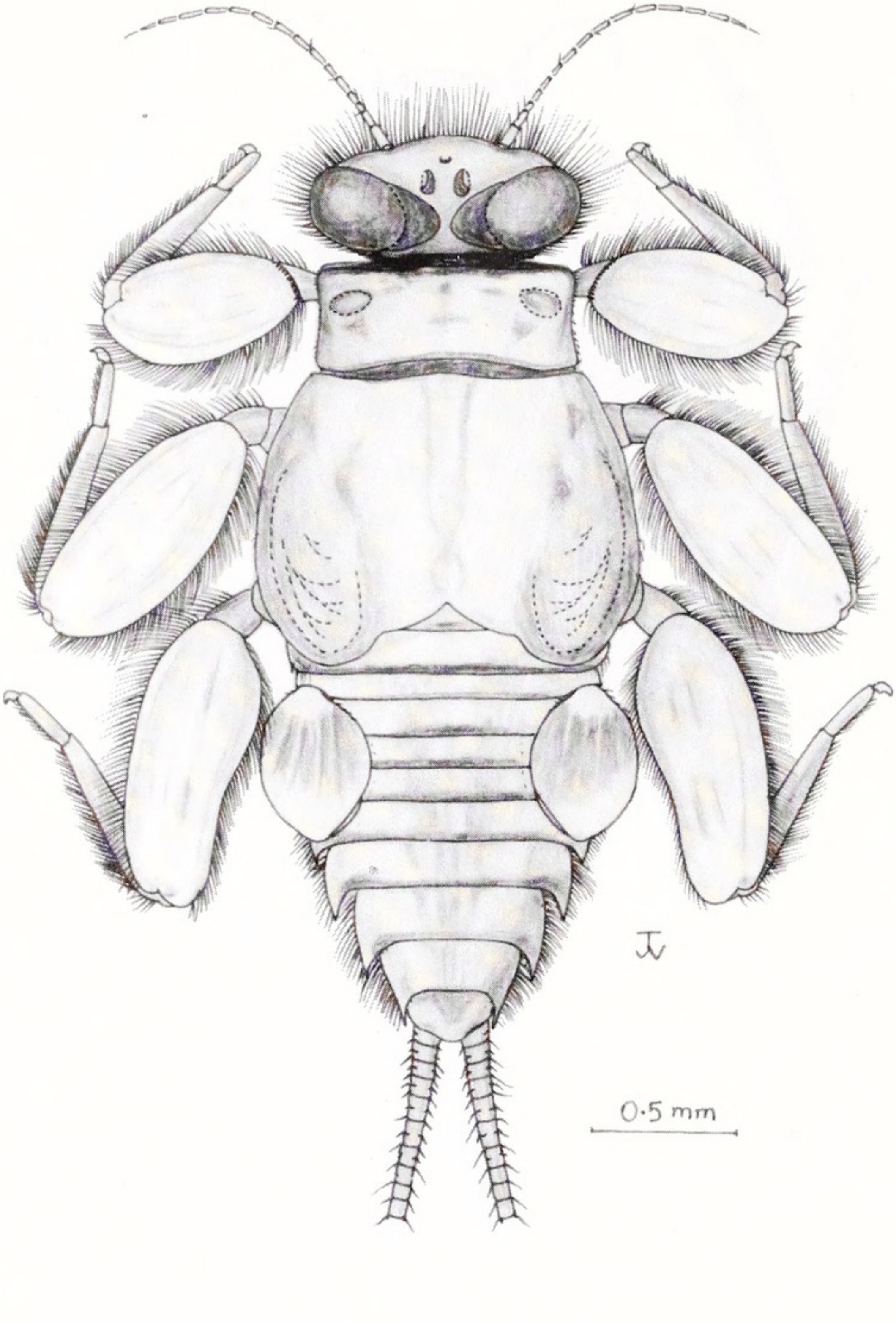
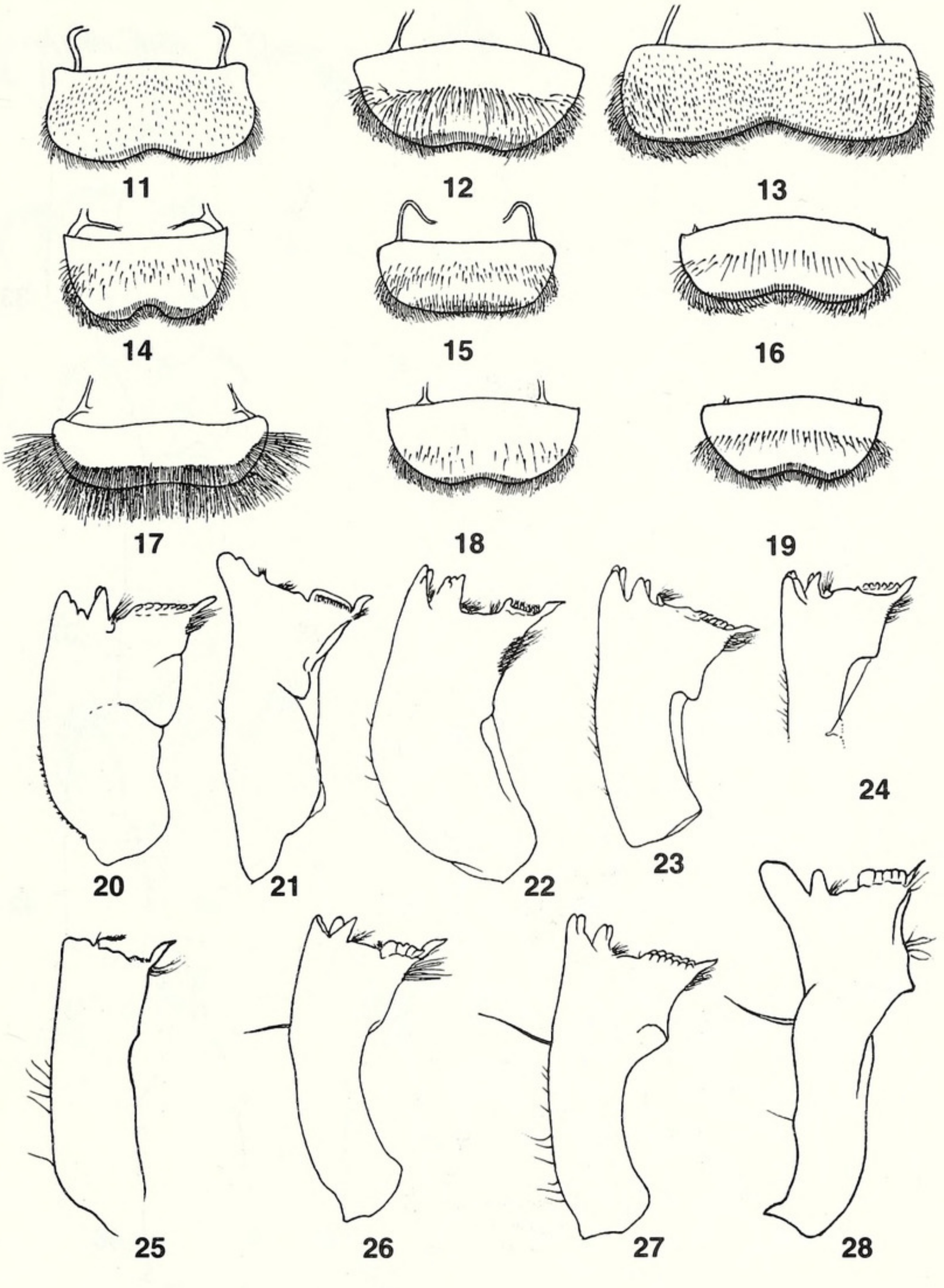
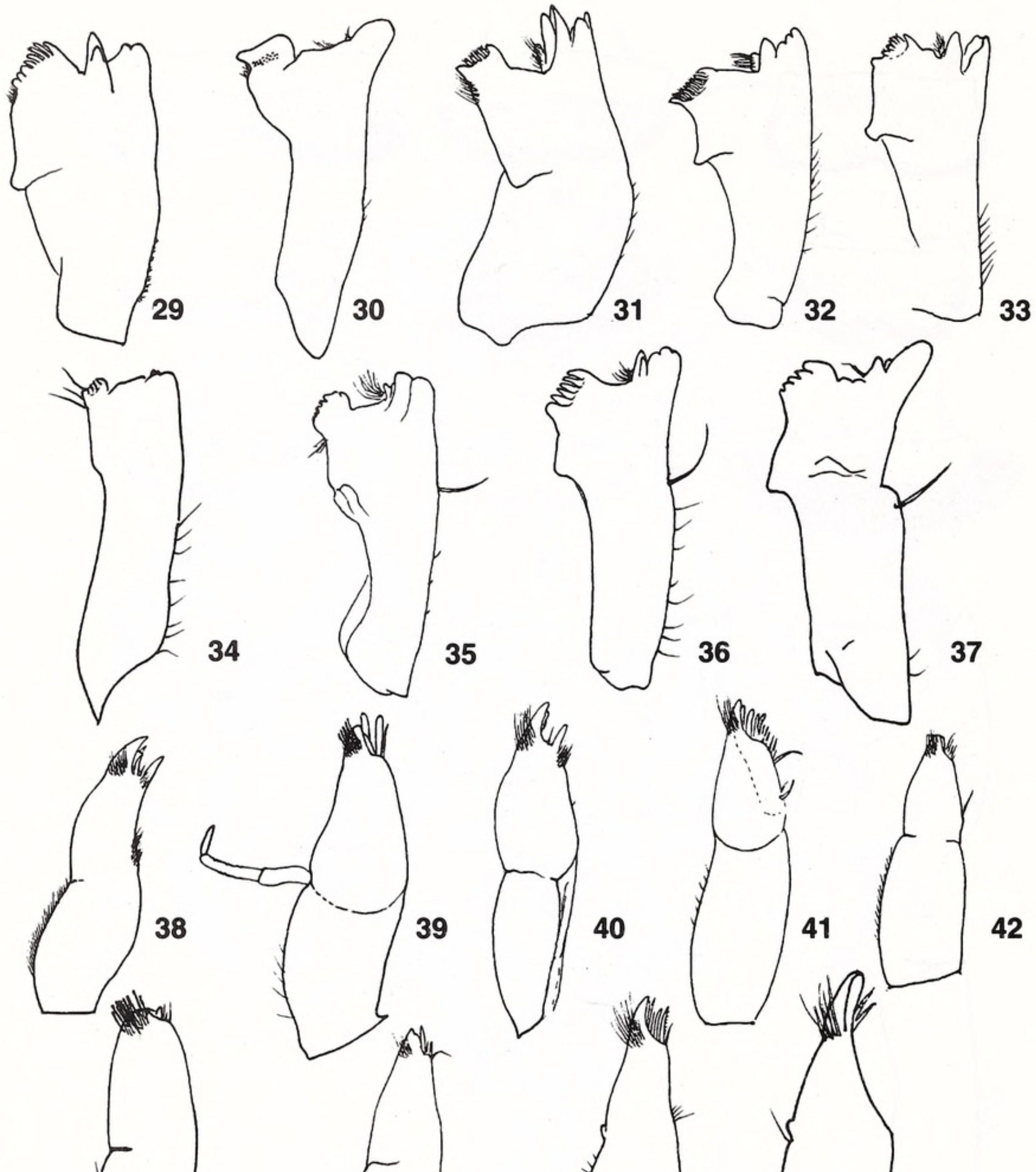


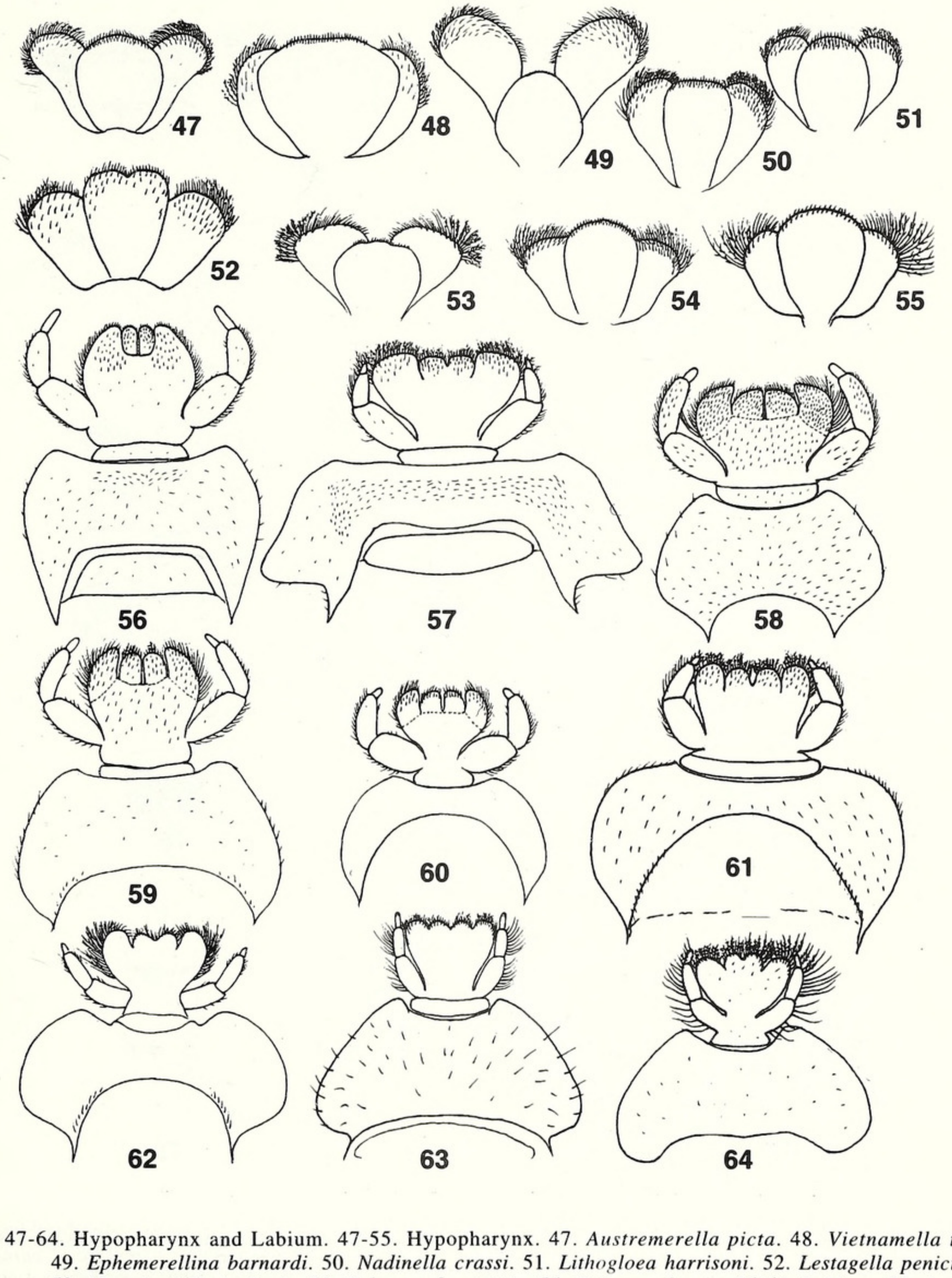
Fig. 10. *Teloganodes* sp., larval habitus.



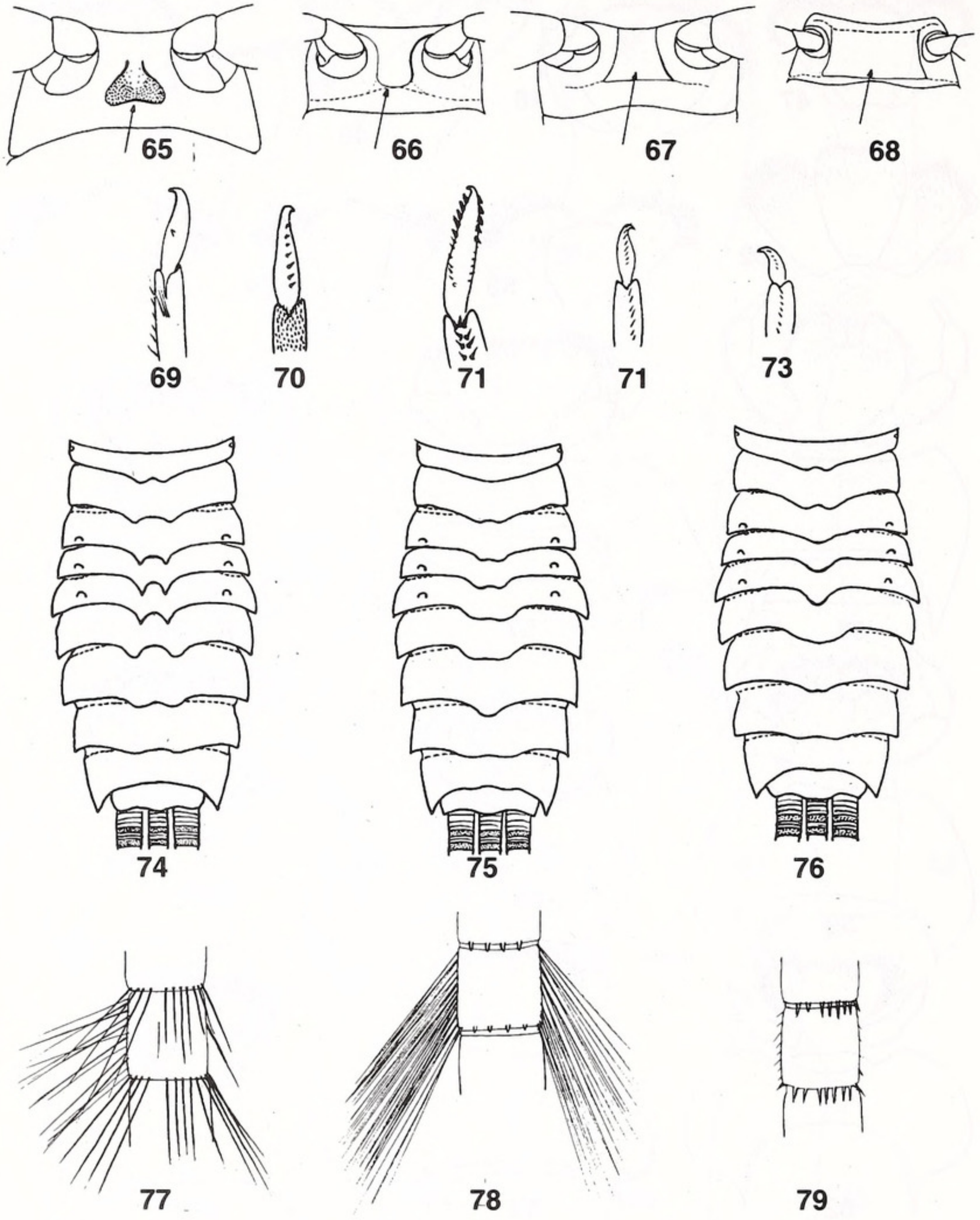
Figs 11-28. Labrum and right mandible. 11-19. Labrum, dorsal. 11. *Austremerella picta*. 12. *Vietnamella thani*. 13. *Ephemerellina barnardi*. 14. *Nadinella crassi*. 15. *Lithogloea harrisoni*. 16. *Lestagella penicillata*. 17. *Macafertiella insignis*. 18. *Teloganodes tristis*. 19. *Teloganodes* sp. 20-28. Right mandible. 20. *A. picta*. 21. *V. thani*. 22. *E. barnardi*. 23. *N. crassi*. 24. *L. harrisoni*. 25. *L. penicillata*. 26. *M. insignis*. 27. *T. tristis*. 28. *T*. sp.



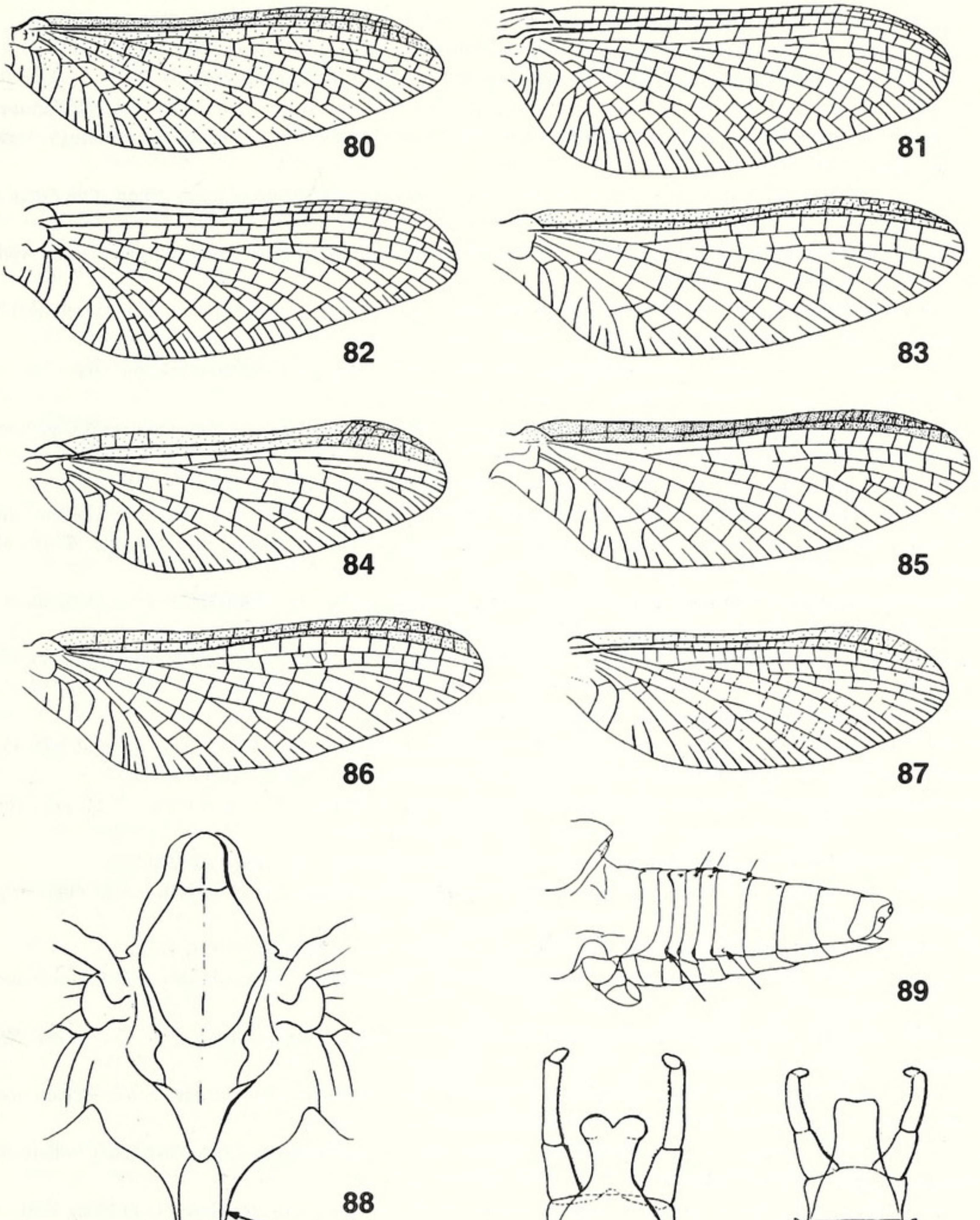
Figs 29-46. Left mandible and right maxilla. 29-37. Left mandible. 29. *Austremerella picta*. 30. *Vietnamella thani*. 31. *Ephemerellina barnardi*. 32. *Nadinella crassi*. 33. *Lithogloea harrisoni*. 34. *Lestagella penicillata*. 35. *Macafertiella insignis*. 36. *Teloganodes tristis*. 37. *Teloganodes* sp. 38-46. Right maxilla. 38. *A. picta*. 39. *V. thani*. 40. *E. barnardi*. 41. *N. crassi*. 42. *L. harrisoni*. 43. *L. penicillata*. 44. *M. insignis*. 45. *T. tristis*. 46. *T.* sp.



Figs 47-64. Hypopharynx and Labium. 47-55. Hypopharynx. 47. *Austremerella picta*. 48. *Vietnamella thani*. 49. *Ephemerellina barnardi*. 50. *Nadinella crassi*. 51. *Lithogloea harrisoni*. 52. *Lestagella penicillata*. 53. *Macafertiella insignis*. 54. *Teloganodes tristis*. 55. *Teloganodes* sp. 56-64. Labium. 56. *A. picta*. 57. *V. thani*. 58. *E. barnardi*. 59. *L. harrisoni*. 60. *L. penicillata*. 61. *M. insignis*. 62. *T. tristis*. 63. *T.* sp.



Figs 65-79. Larval structure. 65-68. Prosternum. 65. *Ephemerellina barnardi*. 66. *Nadinella crassi*. 67. *Lithogloea harrisoni*.68. *Lestagella penicillata*. 69-73. Claw. 69. *Vietnamella thani*. 70. *E. barnardi*. 71. *N. crassi*. 72. *L. harrisoni*. 73. *L. penicillata*. 74-76. *N. crassi*, dorsal abdominal tubercle variations. 77-79. cercus, middle segments (left: medial margin; right: outer margin). 77. *Austremerella picta*. 78. *V. thani*. 79. *E. barnardi*.



Figs 80-91. Adult structures. 80-87. Forewing. 80. *Austremerella picta*. 81. *Vietnamella ornata* [redrawn from Tshernova (1972)]. 82. *V. dabieshanensis* [modified from You and Su (1987)]. 83. *Ephemerellina barnardi*. 84. *Nadinella crassi*. 85. *Lithogloea harrisoni*. 86. *Lestagella penicillata*. 87. *Teloganodes tristis*. 88. *Thoracic nota, A. picta* (arrow: process). 89. Abdomen, lateral, *E. barnardi* (top arrows: tubercle vestiges; bottom arrows: gill socket vestiges). 90-91. Male genitalia. 90. *N. crassi*. 91. *L. harrisoni*.

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