

Cladistic resolution and ecology of the Madagascar genus *Manohyphella* Allen (Ephemeroptera : Teloganodidae)

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Keywords : *Manohyphella*, mayfly, Madagascar, cladistics, ecology.

The discovery of male larvae from Madagascar [only a female larva was known so far] confirm their identification to the family Teloganodidae and genus *Manohyphella* Allen, due to their dioptic compound eyes. Generic level characterization and intergeneric comparisons are given for the first time. In addition, two new species are described from larvae : *Manohyphella sphyxia*, n. sp. and *M. animosa*, n. sp. Cladistic analysis shows *Manohyphella* to represent a basal branch of a clade that includes all Teloganodidae except *Ephemerellina* Lestage and that it is closest in grade to the southern African genus *Nadinetella* McCafferty & Wang. Historical biogeographic relationships with regard to Gondwana and the trans-Indian Ocean track are discussed. Larvae were abundant on stones in current in a protected forest stream in Ranomafana National Park in eastern Madagascar but were at significantly lower densities in five other area streams, including three in the park's agriculture peripheral zone. The relatively undisturbed condition of the stream where they were found in abundance may in part account for such distribution ; however, gradient characteristics of the stream that produce waterfalls were also typical of habitats documented for other Teloganodidae. The diet of *Manohyphella* consists mainly of fine detritus. Feeding data from other ephemeroptera are compared, and maxillary morphology appears well adapted for brushing and scraping.

Résolution cladistique et écologie du genre malgache *Manohyphella* Allen (Ephemeroptera : Teloganodidae)

Mots-clés : *Manohyphella*, éphémère, Madagascar, cladistique, écologie.

La découverte de larves mâles provenant de Madagascar [seule une larve femelle était connue jusqu'ici] confirme leur appartenance à la famille des Teloganodidae et au genre *Manohyphella* Allen, en raison de leurs yeux composés dioptiques. La caractérisation au niveau générique et des comparaisons intergénériques sont données pour la première fois. En outre, deux espèces nouvelles sont décrites à partir de ces larves : *Manohyphella sphyxia*, n. sp. et *M. animosa*, n. sp. Une analyse cladistique montre que *Manohyphella* représente une branche basale d'un clade qui inclue tous les Teloganodidae excepté *Ephemerellina* Lestage, et que ce genre est le plus proche hiérarchiquement du genre Sud-africain *Nadinetella* McCafferty & Wang. Les relations biogéographiques historiques en ce qui concerne le Gondwana et la voie trans-Océan Indien sont discutées. Les larves étaient abondantes sur les pierres en courant dans un cours d'eau en forêt protégé dans le Parc National Ranomafana, partie orientale de Madagascar, mais se trouvaient à des densités significativement plus faibles dans cinq autres cours d'eau de la région, dont trois dans la zone agricole périphérique du parc. Les conditions relativement peu perturbées du cours d'eau où elles ont été trouvées en abondance peuvent en partie expliquer une telle répartition ; cependant, les caractéristiques de pente de ce cours d'eau entrecoupé de chutes d'eau, sont aussi typiques d'habitats connus pour d'autres Teloganodidae. Le régime alimentaire de *Manohyphella* consiste essentiellement en fins débris particuliers. Une comparaison est faite avec les données trophiques sur d'autres éphéméroptères, et la morphologie des maxilles apparaît bien adaptée pour broser et râcler.

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1. Introduction

The genus *Manohyphella* was described by Allen (1973) based only on female adults that were taken in Madagascar. Allen (1973) placed the genus in the family Ephemerellidae, which would have been logical given the very broad concept of that family and state of comparative knowledge of Southern Hemisphere mayflies at that time. McCafferty & Wang (1995), after studying one of the paratypes of *M. keiseri* Allen, determined that wing venation was similar to that of *Teloganella* Ulmer and thus removed *Manohyphella* from consideration under the broad concept of Ephemerellidae and considered it instead under the broad concept of the family Tricorythidae. McCafferty & Wang (1995) also reported what was apparently the larval stage of *Manohyphella* based on a single, poorly preserved, female specimen taken in Madagascar by George Edmunds in 1971. McCafferty & Wang (1995) made anecdotal reference to only a few of the morphological characteristics associated with that larval specimen.

Later, McCafferty & Wang (1997) showed that Gondwanan (Afrotropical, Neotropical, southern Oriental, and Australian) genera of pannota mayflies that had historically been assigned to Ephemerellidae were distinct from the strictly Northern Hemisphere lineages, and erected the family Teloganodidae for them. Further refinement of the higher classification of such mayflies was possible only after an intensive phylogenetic study of all pannota mayflies throughout the world (McCafferty & Wang 2000). This latter work restricted the Teloganodidae even more (excluding Austremereidae) in order to avoid a paraphyletic classification. Based on a comprehensive analysis of wing venation, McCafferty & Wang (2000) were able to place the Madagascar genus *Manohyphella* in the family Teloganodidae *sensu stricto*.

The assignment of *Manohyphella* to Teloganodidae was based on wing venation traits associated with the female adult holotype of *M. keiseri* only (see McCafferty & Wang 2000). The female paratype of *M. keiseri* that McCafferty & Wang (1995) had studied and based their earlier conclusion that *Manohyphella* belonged to another lineage (the historical broad concept of Tricorythidae), was not *M. keiseri*, but represented an undescribed species of Teloganellidae (previously a part of that broad concept of Tricorythidae). Because some critical phylogenetic data were based on male adult characteristics and because larval characteristics of Teloganellidae were based only on the single genus *Teloganella*, McCafferty & Wang (2000) could not be sure whether the single female larva from Madagascar that they had earlier thought to be *Manohyphella* be-

longed to the Teloganodidae or the Teloganellidae. Although those authors hypothesized that the larva belonged to Teloganodidae based on comparisons with the South African genera of Teloganodidae, they pointed out that it would be critical to study male larvae to determine if the compound eyes were dioptic, as found in the Teloganodidae and the more plesiotypic families of the Ephemerelloidea (the historical broad concept of Ephemerellidae), or holoptic, as found in the Teloganellidae and more apotypic families of the Ephemerelloidea (the historical broad concept of Tricorythidae).

Recently, one of us (JPB) collected numerous larvae in Madagascar that are generically similar to the single female larva referred to above. Fortunately, the series contained male larvae, and the more mature of those clearly possess dioptic compound eyes. This places them undoubtedly in the family Teloganodidae and most likely in the genus *Manohyphella* as discussed above. It has also allowed us the opportunity to describe these larvae at the generic level, offer some hypotheses regarding generic relationships within the Teloganodidae, and provide detailed information regarding habitat and ecology in Madagascar. The generic description and methods of cladistic analysis are comparative with those used in the monographic revision of the Teloganodidae (McCafferty & Wang 1997).

In addition, there are apparently species level differences between the originally studied single female larva taken in 1971 and the more recently collected material. We therefore also describe herein these two species. We do this cognizant that one of the two may eventually prove to be the unknown larvae of *M. keiseri*. We maintain that describing and establishing a working taxonomy for a possibly imperiled fauna in Madagascar outweighs the inconvenience of some minor nomenclatural change that might possibly be required in the future.

2. *Manohyphella*

2.1. Larval description

- Head

Head capsule (Fig. 1) with margin lacking well-developed fringe of setae; setal fringe weakly developed laterally only.

Labrum (Fig. 2) short and broad; distal margin broadly emarginate, with dense, fine, moderately long cilia-like setae; dorsal surface with somewhat irregular transverse row of long, hair-like setae (longer and thicker than marginal setae) at approximate midlength of labrum.

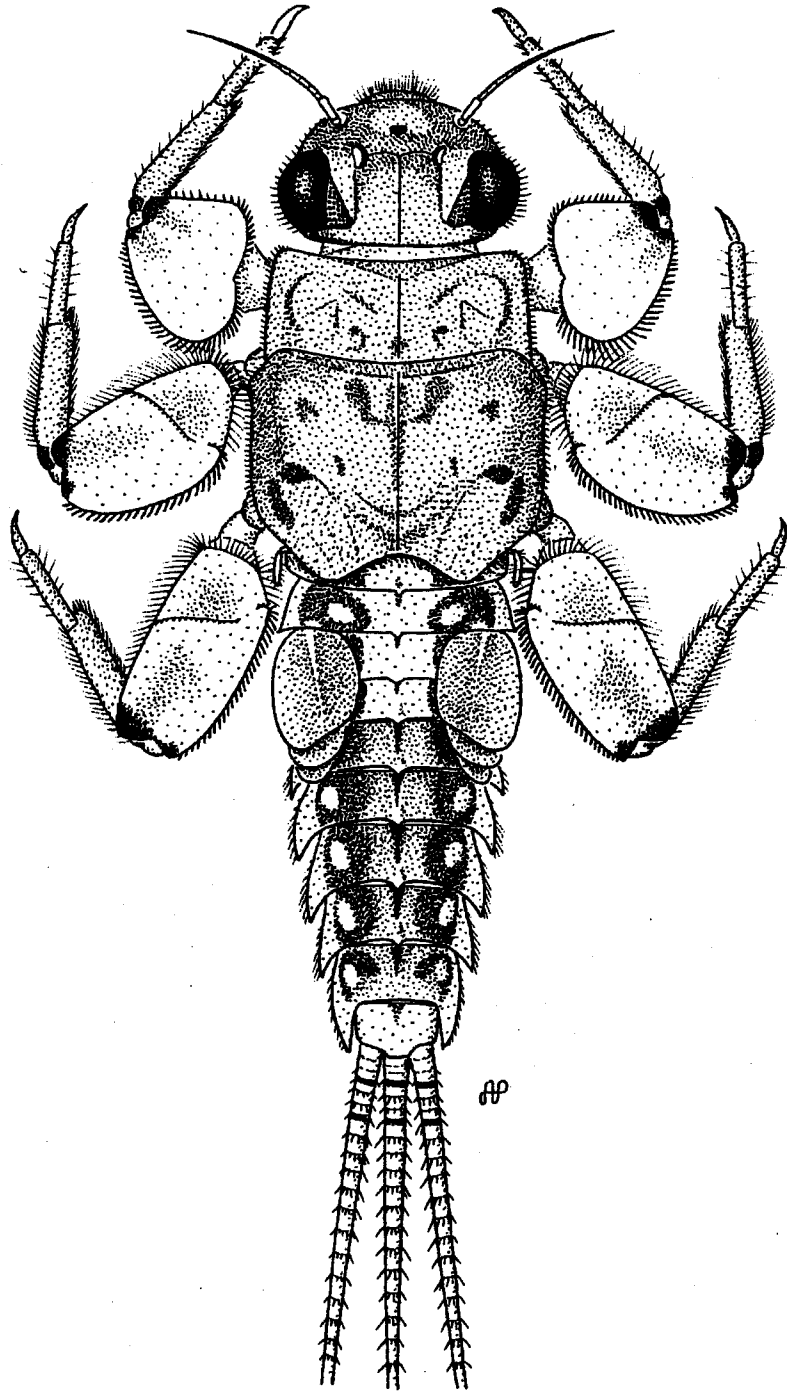


Fig. 1. *Manohypella animosa*, dorsal habitus of male larva.
Fig. 1. *Manohypella animosa*, habitus dorsal de larve mâle.

Mandibles (Figs. 3, 4, 11) narrow, somewhat broadened apically; inner and outer incisors separate and divergent; tuft of few to several long, hair-like setae present mediolaterally (such setae sometimes broken off to various degrees in well-worn mandibles, and possibly becoming fewer in numbers with age or among species); angulate mandible (Fig. 4) with small patch of setae near base of mola at medial margin; prosthema with long, multiple branches.

Maxillae (Fig. 5) without palps or lateral nodules; dark, transverse, mediolateral suture-like line continuing from slight lateral sulcus and developed for approximately one-half width of galealaciniae; apical spine of galealaciniae with thin blade-like development medially.

Labium as in Figure 6, with relatively well-developed glossae and paraglossae (not highly fused); paraglossae somewhat bluntly pointed medioapically.

Hypopharynx (Fig. 7) with lingua and superlinguae subequal in length; lingua distally somewhat truncate to slightly cone-shaped; superlinguae broadly rounded distally.

- Thorax

Prosternum without medial, bilobular, spiny process.

Forefemora (Figs. 1, 8) very broad; midfemora (Figs. 1, 9) broad, with or without transverse row of setae; hindfemora (Figs. 1, 10) somewhat broad, with or without transverse row of setae.

Tarsal claws (Figs. 8, 10) with row of sparse, minute, blunt denticles.

- Abdomen

Gills small, single, fibrilliform on abdominal segment 1 (Fig. 1); lamellate gills on abdominal segments 2-5; gills 2 (Fig. 1) operculate, parallel sided, and appearing either broadly rounded or pointed, somewhat falcate, or obliquely truncate distally.

Terga with single, posteromedial tubercles (variable but best developed on terga 3-8) (Figs. 1, 13), and with posterolateral processes well developed on segments 5-9 (Fig. 1).

Median caudal filament well developed (Fig. 1).

2.2. Larval diagnosis

The larvae of *Manohyphella* differ from all other known larvae of Teloganodidae by having a mediolateral tuft of well-developed setae on the mandibles, whereas other genera either have no setae in this position or only one bristle-like seta in this position. It should be kept in mind that because of their position, these setae are subject to breakage, although stubs are

usually apparent. Nevertheless, *Manohyphella* larvae also differ from all other known genera by having a combination of a broad midfemora and a moderately broad hindfemora. Only the South African genus *Les-tagella* Demoulin (McCafferty & Wang 1997 : Fig. 7) has forefemora as broadened as those of *Manohyphella*. The shape of the operculate gills in *Manohyphella* is also slightly different than that of other genera, being at least somewhat quadrate. In addition, only the South African genus *Lithogloea* Barnard (McCafferty & Wang 1997 : Fig. 6) has posterolateral abdominal processes as well developed as in *Manohyphella*.

Manohyphella is most similar to the South African fauna of Teloganodidae rather than the Indian/Oriental fauna of Teloganodidae with respect to such characteristics as having a well-developed median caudal filament (see McCafferty & Wang 1997 : Figs. 8 and 9), not having a singular bristle-like seta mediolaterally on the mandibles (see McCafferty & Wang 1997 : Figs. 26-28), and having relatively well-developed and well-separated glossae and paraglossae (not fused subdistally) (see McCafferty & Wang 1997 : Figs. 62-64). *Manohyphella* also lacks the well-developed head capsule fringe of setae typical of the Indian/Oriental fauna, but which is also present in the South African genus *Les-tagella* (McCafferty & Wang 1997 : Figs. 7-10).

3. *Manohyphella animosa* McCafferty & Benstead, n. sp.

3.1. Description

Larva (Fig. 1)

Body Length 5.0-6.0 mm (middle instar). General coloration cream with brown (often diffuse) markings dorsally, pale ventrally.

— Head

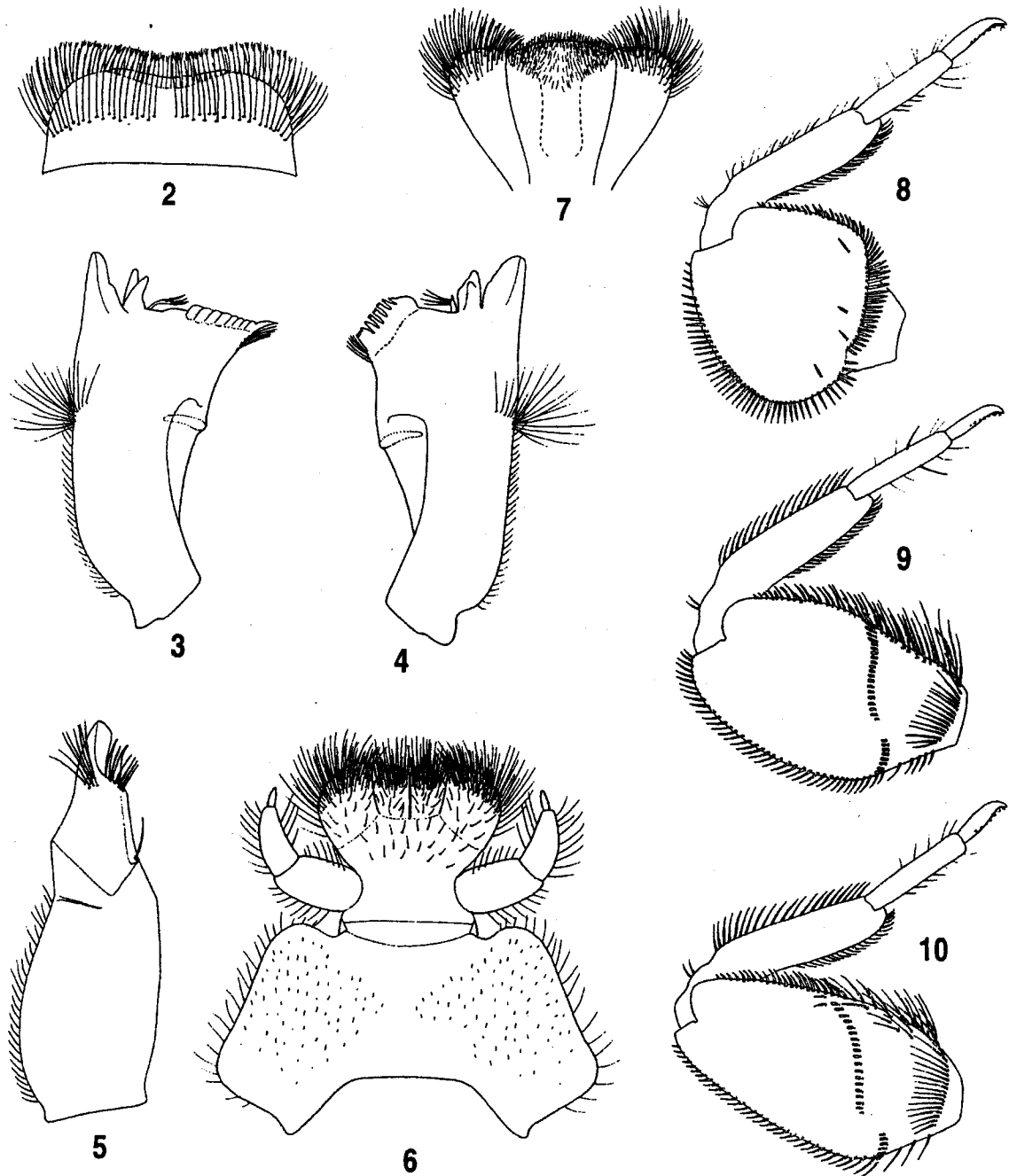
Markings variable, sometimes entirely brown, but often paler between compound eyes and immediately anterior to median ocellus (Fig. 1).

Mandibles (Figs. 3, 4) with mediolateral cluster of hairlike setae profuse, with 10 or more setae; lateral margin basad of cluster with sparse row of short, hairlike setae continuing to base.

Submentum (Fig. 7) rounded at distolateral corners, and lateral margin with sparse row of fine, short, hairlike setae.

— Thorax

Femora (Fig. 1) with dark spots distally; forefemoral marginal armature consisting of moderately long, sharp, spinelike setae (Fig. 8); transverse row similar



Figs. 2-10. Larval structures of *Manohypella animosa*. 2 : labrum (dorsal). 3 : planate mandible. 4 : angulate mandible. 5 : maxilla. 6 : labium. 7 : hypopharynx. 8 : left foreleg. 9 : left midleg. 10 : left hindleg.

Figs. 2-10. Structures larvaires de *Manohypella animosa*. 2 : labre (vue dorsale). 3 : mandibule plane. 4 : mandibule angulée. 5 : maxille. 6 : labium. 7 : hypopharynx. 8 : patte antérieure gauche. 9 : patte intermédiaire gauche, 10 : patte postérieure gauche.

but somewhat blunt apically ; mid- and hindfemora (Figs. 1, 9, 10) with dorsal, transverse row of short, spatulate setae (row disrupted subposteriorly).

— Abdomen

Terga (Fig. 1) with narrow, dark, prominent markings at middle of anterior margin and becoming attenuated posteriorly, best developed on terga 4-8 (Fig. 1). Small medioposterior tubercles on terga 1-8, low and posterodorsally oriented (best seen in lateral view, and often difficult to detect on more anterior terga).

Adult : unknown.

3.2. Material examined

Holotype : Male larva, Madagascar, Vatoharanana stream, Parc National de Ranomafana, 21° 17.407' S, 47° 25.677' E, VI-29-1998, J. P. Benstead. Paratypes : four male and nine female larvae, same data and deposition as holotype (some parts on slides). Additional material : one female larva, Madagascar, Mariavatra stream, Ranomafana N. P., S 21° 15.629' E 47° 25.149', VI-19-1998, J. P. Benstead. All types deposited in the type collection of the Purdue Entomological Research Collection (PERC), West Lafayette, Indiana.

3.3. Etymology

The species epithet alludes to the fullness of life or spirit, from the Latin *animosus*.

4. *Manohyphella sphyxia* McCafferty & Benstead, n. sp.

4.1. Description

Larva

Body : Length 7.2 mm (middle instar larva). General coloration tan with suffuse brown markings

— Head

Vertex light brown with medium brown speckling.

Mandibles (Fig. 11) with mediolateral cluster with fewer than 10 setae ; lateral margin basad of cluster devoid of setae except for minute, short, spatulate setae mainly along basal curvature.

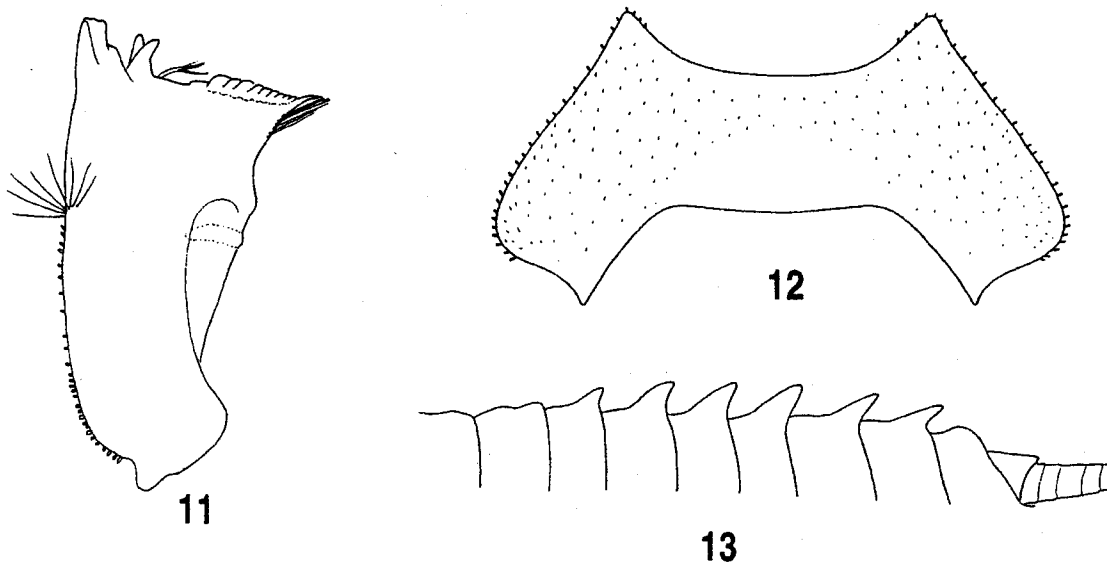
Submentum (Fig. 12) bluntly pointed at distolateral corners, and lateral margin with sparse row of minute, short, spatulate setae.

— Thorax

Femora without distal spots dorsally ; forefemoral marginal armature consisting of moderately long, spinelike setae interspersed with longer, more hairlike setae, especially along posterior margin ; mid- and hindfemora without dorsal, transverse row of setae.

— Abdomen

Terga without median markings except small medioanterior spots on terga 1-4. Medioposterior tubercles well developed and vertically prominent on terga 3-8 (Fig. 13).



Figs. 11-13. Larval structures of *Manohyphella sphyxia*. 11 : planate mandible. 12 : submentum. 13 : abdomen (lateral view).
Figs. 11-13. Structures larvaires de *Manohyphella sphyxia*. 11 : mandibule plane. 12 : submentum. 13 : abdomen (vue latérale).

Adult : unknown

4.2. Material examined

Holotype : Female larva, Madagascar, Fianarantsoa Prov., Tsaratango R., 9 km E Ranomafana, XI-6-1971, G.F. and C.H. Edmunds, and F. Emmanuel (mouthparts slidemounted) ; deposited at PERC.

4.3. Etymology

The specific epithet alludes to flight and refuge, from the Greek *phyxios*.

5. Cladistics

By using the character polarities and the highly parsimonious cladogram of the Teloganodidae presented by McCafferty & Wang (1997), a meaningful hypothesis of the relationship of *Manohypella* to other genera and its cladistic position within the Teloganodidae can be formulated. Within the clade representing the Teloganodidae *sensu stricto*, one branch of the basal dichotomous branching is to *Ephemerellina* Lestage and the other is to a lineage consisting of all other genera. *Manohypella* does not share the apomorphy of having a spinous bilobular process on the prosternum that defines the *Ephemerellina* branch ; however it does share two of the three synapomorphies that were used to define the second, more inclusive lineage. These

consist of the labrum having dorsal setae in medial transverse rows and the narrowing of the mandibles. It does not share with the remainder of the second group the reduction of the setal patch occurring at the base of the mola on the medial margin of the angulate mandible. This character state distribution together with the autapomorphies associated with *Manohypella*, such as the mediolateral setal tuft on the mandibles, the broadened midfemora, and the shape of the operculate gill, provide considerable evidence that *Manohypella* represents a distinct initial branch within the second grouping. Genera resulting from the branch opposite *Manohypella* share the synapomorphy of the reduction of the setal patch on the angulate mandible and include *Nadinetella* McCafferty & Wang, *Lithogloea*, *Lestagella*, *Macafertiella* Wang, and *Teloganodes* Eaton (Fig. 14).

The cladistic basis of the branching sequence involving *Nadinetella*, *Lithogloea*, *Lestagella*, *Macafertiella*, and *Teloganodes* (Fig. 14) may be found in McCafferty & Wang (1997). The hypothesized cladistic position of *Manohypella* is considered most probable because *Manohypella* demonstrates no homoplasy with respect to the synapomorphies associated with subsequent clusters of the latter generic lineages. Furthermore, it demonstrates only one or two possible convergences with respect to autapomorphies associated with

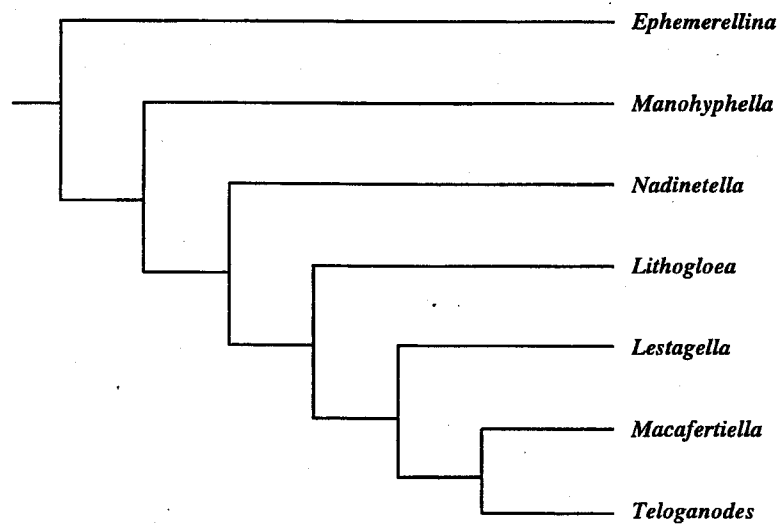


Fig. 14. Cladogram of the genera of Teloganodidae (character state data given in text and in McCafferty & Wang [1997]).

Fig. 14. Cladogramme des genres de Teloganodidae (état des caractères donnés dans le texte et dans McCafferty & Wang [1997]).

the latter individual generic lineages. The well-developed posterolateral processes of the abdomen in *Lithogloea* and *Manohyphella* are considered convergent. The development of such processes is subject to convergence in many lineages throughout the pannote mayflies (McCafferty & Wang 2000), and therefore it is not surprising to find such a convergence within the Teloganodidae. The expanded forefemora of *Manohyphella* and *Lestagella* may also be considered a convergence, another characteristic commonly evolved throughout diverse taxa of Pannota.

6. Biogeography

McCafferty & Wang (1997) regarded Teloganodidae to be of Old World Gondwanan origin and to have participated in vicariant biogeography demonstrated by a trans-Indian Ocean track. They also stated that because of this, "one might expect Teloganodidae (esp. Teloganodinae) to be a reasonable candidate for distribution in Madagascar." The confirmation of *Manohyphella* as a member of Teloganodidae *sensu stricto* bears out that earlier prediction.

If the cladogram of Teloganodidae genera (Fig. 14) is modified into an area cladogram, some further historical biogeographic hypotheses result. McCafferty & Wang (2000) provided cladistic evidence that the origin of Ephemerellidae (essentially a Laurasian group) and all other families of the Ephemerelloidea (essentially a Gondwanan group) coincided with the breakup of Pangaea, approximately 150 million years ago (see e.g., Brown & Lomolino 1998). From this and the known distribution of Teloganodidae, the family may be assumed to have been present in Gondwana prior to any breakup of Madagascar, the Indian subcontinent, and Africa. The earliest sequentially derived generic lineage, represented by *Ephemerellina*, is restricted to southern Africa as are some other subsequent generic lineages within the family (*Nadinetella*, *Lithogloea*, *Lestagella*). These African lineages, with the possible exception of *Lestagella*, may have been established prior to any breakup of Gondwana. It was previously argued that they represent ancient relict groups in Africa (see McCafferty & Wang 1997). *Manohyphella* represents another early branched, and probably ancient, lineage, which in this case is restricted to Madagascar and possibly also consisting of very few species. The relatively apotypic sister lineages represented by *Macaferiella* and *Teloganodes* are found only in the Indian/Oriental region.

Because of the disparate cladistic positions of the Madagascar and Indian/Oriental lineages, it can not be

said with any certainty that vicariance mediated the evolution of both of these elements. For example, given the cladistic relationships, it would be logical to presume that the *Manohyphella* lineage was already present prior to continental breakup and then became isolated in Madagascar as a fortuitous by-product of the spatial isolation of Madagascar. Nonetheless, the origin of the Indian/Oriental lineage (*Macaferiella*/*Teloganodes*) may indeed have been mediated by vicariance at the time of continental breakup. This hypothesis is supported by the sister relationship of the apotypic southeastern African genus *Lestagella* with the *Macaferiella*/*Teloganodes* lineage, as discussed by McCafferty & Wang (1997). The possible geological timing of such vicariant events involving the trans-Indian Ocean track, especially that which is congruent with the very common congeneric occurrences of baetid genera in Africa and Madagascar, were discussed by McCafferty (1999). The close biogeographic relationship of Madagascar and southern Africa, as indicated by mayflies in general, may lend support to the hypothesis that the *Manohyphella* lineage originated much earlier than the time of the breakup of Madagascar, or Madagascar + Indian subcontinent, from Africa.

7. Ecology

7.1. Methods

Larvae of *Manohyphella animosa* were sampled from six streams within Ranomafana National Park (RNP) and its periphery (Fig. 15) from April through July in 1998. Three streams were within the forest protected by RNP (see also Fig. 16), and three drained a largely deforested peripheral, agricultural zone. Detailed physical parameters associated with each of these streams are given in Table 1. All streams were located between 700 and 1100 m elevation. The general environment within the park consisted of primary and secondary pre-montane rainforest. The general environment of the peripheral area consisted of swidden agriculture, secondary (fallow) vegetation, riparian rice paddies, and remnant forest lots.

Larvae were taken by Surber sampler in riffle-cobble habitats. Densities were compared between the six streams and between land use categories where streams occurred using an analysis of variance (ANOVA). Land use categories (forest vs. agriculture) and stream (nested within land use) were both considered fixed effects in the analysis (SAS Institute Inc. 1994).

Foreguts were removed from five *M. animosa* larvae taken from Vatoharanana Stream and ranging in body length from 2.0 to 3.0 mm. Contents were slide-moun-

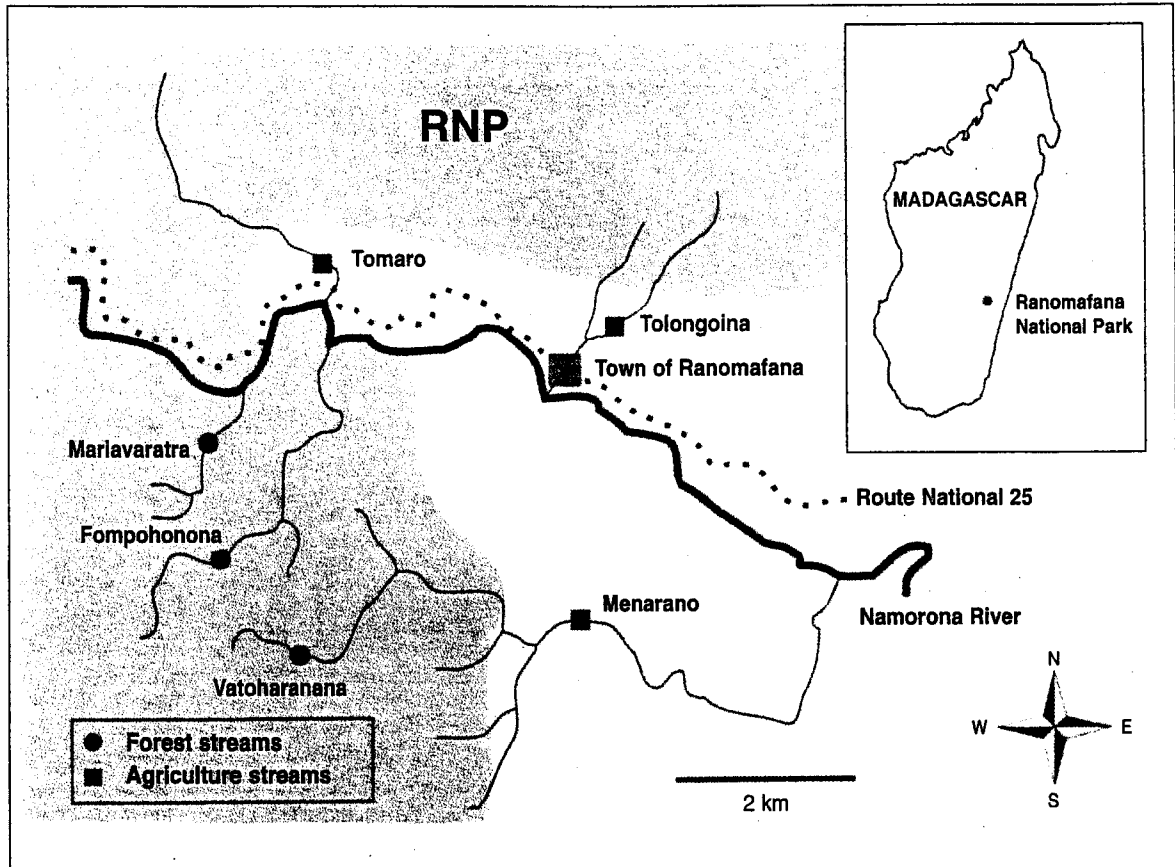


Fig. 15. Map of location of Ranomafana National Park and six streams included in the ecological study. Only part of the park is shown (shaded area) ; the peripheral zone extends 3 km from the park boundary.

Fig. 15. Carte du Parc National Ranomafana et localisation des six cours d'eau de l'étude écologique. Une partie seulement du parc est figurée (zone ombrée) ; la zone périphérique s'étend sur 3 km à partir de la frontière du parc.

ted in glycerol and sealed with varnish. Diet categories represented were determined as either amorphous detritus (non-cellular), leaf and wood detritus, diatoms, filamentous algae, or animal material. Contents were quantified by measuring the relative area of each diet category represented under a phase contrast microscope equipped with video camera and PC using Image-Pro Plus image analysis software (version 3.0.1 for Windows). At least 50 gut particles were identified and measured from each of the five guts. Gut content data are expressed as the mean relative proportion (by area) of the diet categories represented.

7.2. Results and discussion

Densities of *Manohypella animosa* larvae (Fig. 17) varied greatly among forest streams (3-150m⁻²) but were consistently low (< 3m⁻²) in agriculture streams. Differences in mean densities between forest and agri-

culture streams and between all streams were highly significant (Table 2). Vatoharanana Stream, where highest densities of larvae were found, has experienced

Table 2. Results of analysis of variance of the effects of land use and stream identity on density of *Manohypella animosa*, Ranomafana National Park, 1998.

Tableau 2. Résultats de l'analyse de variance des effets du milieu terrestre environnant (forêt, agriculture) et des types de rivière sur la densité de peuplement de *Manohypella animosa*, Parc National Ranomafana, 1998.

Factor	df	SS	MS	F	P
Stream [Land use]	4	130243.28	32560.82	35.51	< 0.0001
Land use	1	44521.38	44521.38	48.56	< 0.0001
Error	54				

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Table 1. Physical description of stream reaches sampled in Ranomafana National Park and peripheral zone, eastern Madagascar, April-July 1998.

Tableau 1. Caractéristiques physiques des portions de rivières échantillonnées dans le Parc National Ranomafana et sa zone périphérique, à l'est de Madagascar, Avril-Juillet 1998.

Stream	Mean width (m)	Mean maximum depth (m)	Mean temperature (° C)	Mean conductivity (μ S cm^{-1})	Substratum	Mean canopy cover (%)	Land use
<i>Forest</i>							
Mariavaratra	6.0	0.31	17.0	14.7	Cobble, with boulders and gravel/sand	71	Selectively logged during mid-1980s
Fompohonona	5.3	0.38	17.0	20.5	Cobble, with sand and boulders	74	Primary forest; some human disturbance
Vatoharanana	9.6	0.51	17.0	15.3	Boulders, cobble and sand	83	Primary forest; some human disturbance
<i>Agriculture</i>							
Tomaro	13.7	0.72	18.5	12.6	Cobble	0	Rice agriculture
Tolongoina	7.2	0.56	17.3	13.6	Boulders, cobble, gravel and sand	14	Rice and sugar cane agriculture
Menarano	9.7	0.48	17.5	13.6	Cobble and sand	0	Rice and cassava agriculture

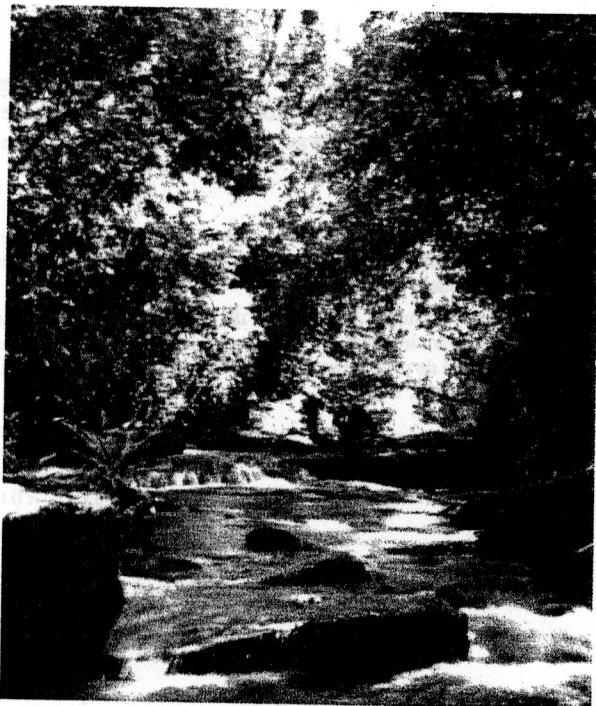


Fig. 16. Vatoharanana Stream at ca. 1100 m within Ranomafana National Park, Madagascar.

Fig. 16. Cours d'eau Vatoharanana à environ 1100 m d'altitude dans le Parc National Ranomafana, Madagascar.

the lowest level of historical disturbance from selective logging. This and the very low densities associated with the agriculture streams suggest that *M. animosa* may be sensitive to catchment disturbance. Many forest specialist aquatic insect species in Madagascar are known to decline in agricultural streams (Gibon et al. 1996, Gibon & Elouard 1996, Benstead, unpublished), whereas some other species such as some baetid and leptophlebiid mayflies typically increase.

The distribution of this particular mayfly may be influenced by gradient characteristics of the stream that produce a series of waterfalls along its course. Vatoharanana Stream is located at the highest elevation of the six streams (1100 m) and has a series of various sized bedrock steps giving rise to waterfalls (fig. 16). Mayflies of the family Teloganodidae have generally been associated with such upper catchment streams in both Sri Lanka (Hubbard & Peters 1984) and South Africa (McCafferty & Wang 1997) to such an extent that they have been referred to as the "waterfall mayflies" (McCafferty & Wang 1997).

Assuming *M. animosa* (and probably *Manohyphella* in general) is highly restricted to these types of streams, it will be especially susceptible to potential perturbations in Madagascar. For example, a high proportion of microendemic, forest stream specialist species in eastern Madagascar have been shown to be ex-

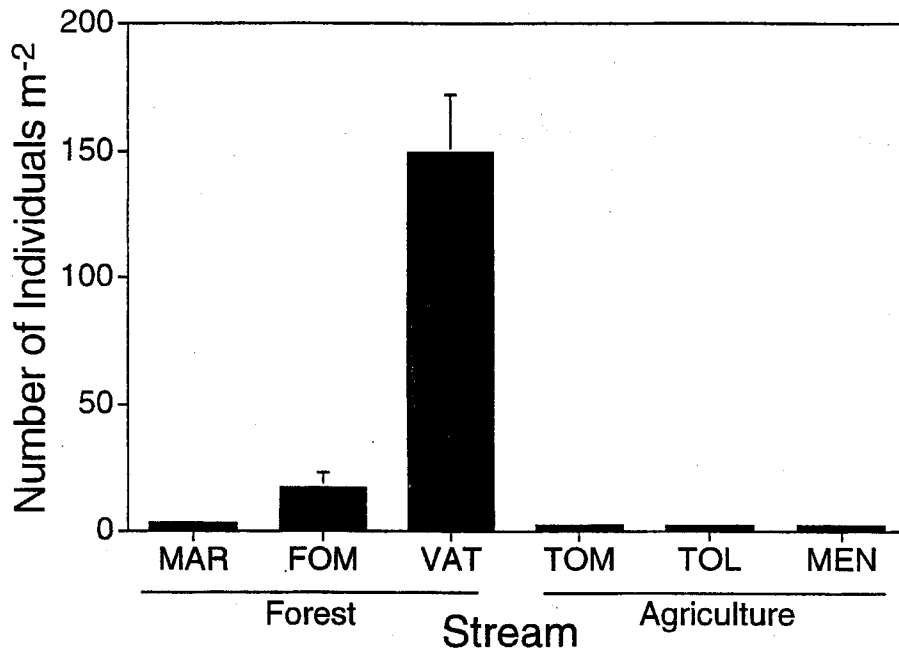


Fig. 17. Mean densities (± 1 SE) of *Manohypella animosa* larvae in the three forest streams and three agricultural streams, Ranomafana National Park and peripheral zone, Madagascar, 1998. Stream names are abbreviated (first three letters of those listed in Table 1). $N = 10$ Surber samples.

Fig. 17. Densités moyennes (± 1 Erreur Standard) des larves de *Manohypella animosa* dans les trois cours d'eau en forêt et les trois cours d'eau en terrains agricoles, Ranomafana National Park et sa zone périphérique, Madagascar, 1998. Les noms de cours d'eau sont abrégés (trois premières lettres de ceux-ci listées dans le tableau 1). $N = 10$ prélèvements au Surber.

tremely vulnerable to catchment deforestation in the region (Gibon & Elouard 1996, Gibon et al. 1996, Benstead et al. 2000).

Gut content analysis showed the diet of *M. animosa* to be dominated by amorphous detritus (Fig. 18). The makeup and proportion of the diet suggest that the larvae are primarily deposit feeders and to a lesser degree algal feeders. Thus, the larval microhabitat probably includes the bottoms and possibly the partially exposed sides of stones in current.

Only a few related mayflies of the superfamily Ephemerelloidea have been studied with respect to their diets. These include species in the families Ephemerellidae and Austremerellidae. *Ephemerella infrequens* McDunnough was reported by Hawkins (1985) to be a diatom scraper, detritus shredder and collector-gatherer. *Ephemerella needhami* McDunnough was shown by McShaffrey & McCafferty (1990) to brush fine detritus and to a lesser degree scrape diatoms and bite off the tips of filamentous algae. Five species of *Eurylophella* were reported as detritus and diatom fee-

ders by Sweeney & Vannote (1981). *Austremerella* sp. (most likely *A. picta* Riek) was reported to be a leaf shredder by Chessman & Boulton (1999).

8. Functional morphology

Mandibles generally appear morphologically suited for biting or shredding in *Austremerella*, *Ephemerella*, *Eurylophella* and *Manohypella*. In addition, the maxillae are well suited for brushing or scraping in *Manohypella*, *Ephemerella*, and *Eurylophella* because of their extensive apical armature (Fig. 5) (see also McShaffrey & McCafferty 1990, McCafferty & Wang 2000); however, the maxillary armature of *Austremerella* is relatively reduced (see McCafferty & Wang 1997) and may be related to such larvae being primarily leaf shredders. In *Manohypella*, the apical spine of the galealaciniae has become blade-like medially and is thus very reminiscent of the outer incisors of the mandibles. Both of these structures appear suited to scraping encrusted diatoms and may indeed account for that part of the observed diet of *M. animosa* (Fig. 18).

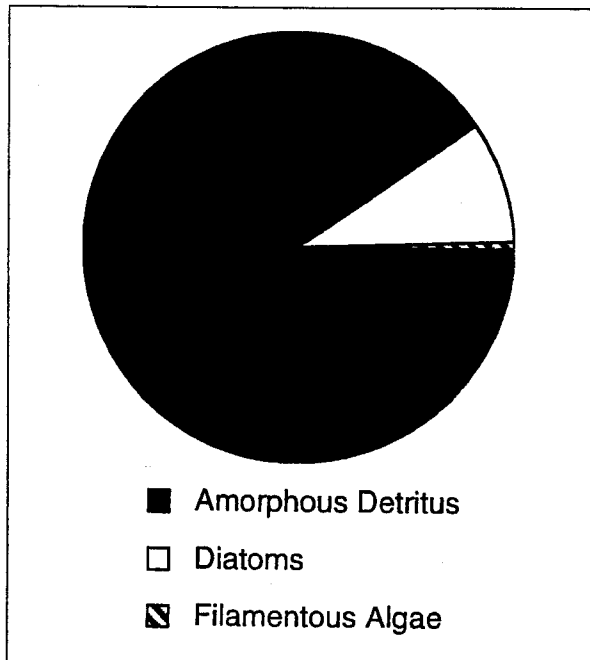


Fig. 18. Mean relative proportions of food categories in guts of *Manohyphella animosa* larvae collected from Vatoharanana Stream, Ranomafana National Park, Madagascar, June 1998. $N = 5$ guts.

Fig. 18. Proportions moyennes relatives des catégories trophiques dans les tubes digestifs de larves de *Manohyphella animosa* récoltées dans le cours d'eau Vatoharanana dans le Parc National Ranomafana, Madagascar, Juin 1998. $N = 5$

Based on findings of the functional morphology study of McShaffrey & McCafferty (1990), it is possible that *Manohyphella* larvae are capable of having a broader spectrum of diet than is indicated from the present study. Along with the brushing of fine detritus, the scraping of periphyton, and the biting of filamentous alga, McShaffrey & McCafferty (1990) also observed opportunistic carnivory in *E. needhami*. In *Manohyphella*, however, biting or shredding may be rare and fortuitous or non-existent, as suggested by our gut analyses and which is apparently the case in some *Eurylophella*.

Although feeding ecology and behavioral data are not documented for other Teloganodidae, the genera *Nadinetella*, *Macafertiella*, and *Teloganodes* appear also to have maxillae fitted for brushing or scraping fine detritus and diatoms. We predict that at least fine detritus, and possibly diatoms, make up a considerable portion of the diet of these latter genera.

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