

Complementary description of the genus *Manohyphella* Allen, 1973 (Insecta: Ephemeroptera: Teloganodidae), with some comments on its ecology in the Andasibe area (East Coast, Madagascar)

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Academic editor: Burgert Muller | Received 9 April 2015 | Accepted 11 March 2016 | Published 1 April 2016

<http://zoobank.org/91CB1013-08C4-44A1-AA55-87CB0644B5AA>

Citation: Oliarinony R, Elouard J-M, Sartori M (2016) Complementary description of the genus *Manohyphella* Allen, 1973 (Insecta: Ephemeroptera: Teloganodidae), with some comments on its ecology in the Andasibe area (East Coast, Madagascar). African Invertebrates 57(1): 1–14. doi: 10.3897/afrinvertebr.57.8449

Abstract

Based on a large collection of material from the East Coast of Madagascar, we redescribe the endemic genus and species *Manohyphella keiseri* Allen, 1973. The male imago is described for the first time and details on the nymphal stage is provided, especially on the gill formula. The species *M. animosa* McCafferty & Benstead, 2002 and *M. sphyxia* McCafferty & Benstead, 2002 are considered as subjective junior synonyms of *M. keiseri* Allen, 1973. Notes on the life cycle of the species in the Andasibe area is presented, as well as data about the density of the populations. *M. keiseri* is an inhabitant of pristine running waters in rainforests and is therefore a good indicator for habitat quality.

Keywords

Synonymy, *Manohyphella*, morphology, life cycle, ecology

Introduction

The genus *Manohyphella* (type species *Manohyphella keiseri* Allen, 1973) was first proposed for some female imagos captured on the East Coast of Madagascar. They were characterized by the peculiar shape of the hind wing, with a pointed costal process located in the posterior half of the wing (Allen 1973). At the time, the genus was placed in the subfamily Teloganodinae within the family Ephemerellidae. Teloganodinae was later raised to the family level (McCafferty and Wang 1997), and its composition circumscribed in a subsequent paper (McCafferty and Wang 2000).

The female of *Manohyphella* was the only stage known until McCafferty and Benstead (2002) which described the nymph and proposed two new species, *M. animosa* and *M. sphyxia*, mentioning that one of them could in fact be the true nymph of *M. keiseri*.

During research lead by the LRSAE in Madagascar from 1991 to 1999 (see Elouard and Gibon 2001 for a review of the programme), numerous *Manohyphella* nymphs were collected, and one was successfully reared to the male imaginal stage. This gives us the opportunity to describe the male imago, and to bring complementary information on the nymphal stage, especially the gills. Due to the broad range of our *Manohyphella* collection, intraspecific variation is considered and some taxonomic changes proposed.

More recently, field work was conducted for one year in the area of Andasibe (East Coast) by Ranalison Oliarinony, where populations of *Manohyphella*, among other macroinvertebrates, were sampled each month. We present some ecological data concerning the genus, especially its life cycle.

Material and methods

Material examined (all from Madagascar)

The examined material is deposited in the collections of the Musée cantonal de Zoologie, Lausanne (MZL) and in the collections of the Florida A & M University, Tallahassee (FAMU).

Manampatrana Basin: Andringitra, Sahanivoraky, Sahanivoraky River, 47°00'41"E, 22°13'33"S, Elevation: 1400 m (Point P0167), 19.11.1993, J.-M. Elouard coll., 1 ♂ reared with its exuvia (both partially on slide); Sahavatoy River Tributary, 46°58'29"E, 22°13'00"S, 1250 m (P0173), 23.11.1993, J.-M. Elouard coll., 1 larvae; Mahazoalala, Manampatrana River, 47°18'19"E, 22°41'04"S, 130 m (P0448), 18.06.1995, M.R. Andriamihaja coll., 2 ♀♀ (one partially on slide) (MZL).

Betaolana Basin: Betaolana (camp 1), Ambolokopatrika River, 49°26'28"E, 14°32'15"S, 800 m (P0872), 08.10.1999, E. Doumenq coll., 2 larvae (one partially on slide); same locality and collector (P0875), 10.10.1999, 3 larvae (one partially on slide) (MZL)

Ampary Basin: Anjanaharibe (camp 1), Analambe River, 49°26'53"E, 14°47'00"S, 1200 m (P0897), 27.10.1999, E. Doumenq coll., 1 larva; same locality and collector (P0899), 31.10.1999, 3 larvae (MZL).

Lokoho Basin: Marojejy (Parc National), Manantenina River, 49°46'29"E, 14°24'26"S, 425 m (P1008), 25.11.1999, E. Doumenq coll., 1 larva; Anjanaharibe (camp 2), Ambatomainity River, 49°27'42"E, 14°44'42"S, 1260 m (P1020), 07.12.1999, E. Doumenq coll., 1 larva (MZL)

Namorona Basin: Ranomafana, Ambatoaranana River, 47°27'26"E, 21°15'23"S, 77 m (P0643), 08.11.1996, J.-L. Gattolliat & C. Rochat coll., 1 larva (MZL).

Vatoharanana, stream, Ranomafana National Park, 21°17,407'S, 47°25,677'E, 29.06.1998, 4 larvae (one partially on slide); same place, but 21°15,629'S/47°25,149'E, 11.01.1998, 1 ♀ subimago; same locality, 30.12.1998, 1 ♀, 1 ♂, all J.P. Benstead's coll. (FAMU).

Rianila Basin: Antanambotsira, Antanambotsira River, 48°25'29"E, 18°52'32"S, 950 m (P2103), 14.09.2001, 3 larvae, Andasibe (Périnet), Réserve Mantadia, Rianasoa River, 48°25'56"E, 18°49'47"S, 920 m (P2112), 15.06.2001, 4 larvae; (P2113), 09.07.2001, 3 larvae; (P2114), 15.08.2001, 3 larvae; (P2115), 13.09.2001, 5 larvae; (P2116), 10.10.2001, 5 larvae; (P2117), 14.11.2001, 1 larva; (P2118), 29.11.2001, 9 larvae (one partially on slide); (P2120), 20.02.2002, 3 larvae; (P2121), 17.04.2002, 2 larvae; (P2122), 16.05.2002, 1 larva; (P2123), 05.06.2002, 2 larvae; Andasifahatelo, Madiofasina River, 48°26'20"E, 18°55'14"S, 870 m (P2124), 13.06.2001, 4 larvae; (P2126), 14.08.2001, 6 larvae; (P2127), 11.09.2001, 17 larvae; (P2128), 09.10.2001, 2 larvae; (P2129), 13.11.2001, 5 larvae; (P2130), 27.11.2001, 1 larva; (P2131), 14.01.2002, 1 larva; Andasibe (Périnet), Réserve Mantadia, Belakato River, 48°25'08"E, 18°49'23"S, 920 m (P2136), 13.06.2001, 1 larva; (P2137), 09.07.2001, 1 larva; (P2138), 15.08.2001, 6 larvae; (P2139), 12.09.2001, 2 larvae; (P2141), 14.11.2001, 2 larvae; (P2142), 29.11.2001, 7 larvae; (P2143), 18.01.2002, 4 larvae; (P2147), 04.06.2002, 1 larva; Andasibe (Périnet), Réserve Mantadia, Beanamalao River, 48°46'05"E, 18°49'32"S, 920 m (P2148), 15.06.2001, 10 larvae; (P2149), 13.09.2001, 3 larvae; (P2150), 29.11.2001, 8 larvae; Andasibe (Périnet), Réserve Mantadia, Andranomanamponga River, 48°25'55"E, 18°48'56"S, 920 m (P2151), 13.06.2001, 1 larva; (P2152), 12.09.2001, 1 larva; (P2153), 29.11.2001, 1 larva; Ambavaniasy, Irihitra River, 48°32'09"E, 18°57'01"S, 520 m (P2178), 10.06.2001, 15 larvae; (P2179), 18.09.2001, 3 larvae; (P2180), 26.11.2001, 4 larvae; Ambavaniasy, Analambalo River, 48°30'02"E, 18°57'23"S, 750 m (P2181), 12.06.2001, 12 larvae; (P2182), 17.09.2001, 15 larvae; (P2183), 25.11.2001, 8 larvae, all R. Oliairiny coll. (MZL).

Ecology and life cycle

Six streams belonging to the Rianila watershed (7820 km²) were studied. They are all located in the Eastern Domain, once entirely covered with rainforest, and now heavily altered by human activities. Three sites (Belakato BT, Madiofasina MA, Rianasoa RA) are located in the Mantadia National Park, in primary forests, whereas three others (Antanambotsira AA, Sandrasoa SA, Sahaparasasy SY) are located in degraded, open canopy areas composed of *Tavy* (traditional form of slash-and-burn agriculture,

mainly for rice culture) and *Savoka* (fallow fields). All localities belong to second or third order streams. Characteristics of the localities are given in Table 1.

Monthly samplings were performed in each locality from June 2001 until June 2002, with the exception of November 2001 (bimonthly samplings) and March 2002 (no samplings due to heavy rains at the end of the wet season). A Surber net of 0.1 m², mesh size of 250 µm was used with three replicates at each site. Material was then fixed in ethanol for further studies. Head width (HW) of all specimens was measured to the nearest 0.1 mm using a stereomicroscope and an eyepiece micrometer. Mature larvae (recognizable by their black wing pads) were sexed and measurements used to investigate sizes at emergence. Density is expressed as mean number of individuals m⁻², and biomass was derived from mean density and length-mass relationships as proposed by Benke et al. (1999) for the genus *Serratella* ($DW = \ln(0.7255) + 3.325 \cdot \ln HW$). Results are expressed in mg dry weight (DW) m⁻².

Results

Manohyphella keiseri Allen, 1973

Manohyphella keiseri Allen, 1973, Pan-Pacific Entomology 49: 160–162; terra typica: Madagascar, Ranomafana

Manohyphella animosa McCafferty & Benstead, 2002, Annals Limnology 38: 44–46; terra typica: Madagascar, Ranomafana, **syn. n.**

Manohyphella sphyxia McCafferty & Benstead, 2002, Annals Limnology 38: 46–47; terra typica: Madagascar, Ranomafana, **syn. n.**

Description. Male imago. Body length: 6.5–7.1 mm; forewing length: 6.8–8.1 mm; hindwing length: 1.11–1.15 mm.

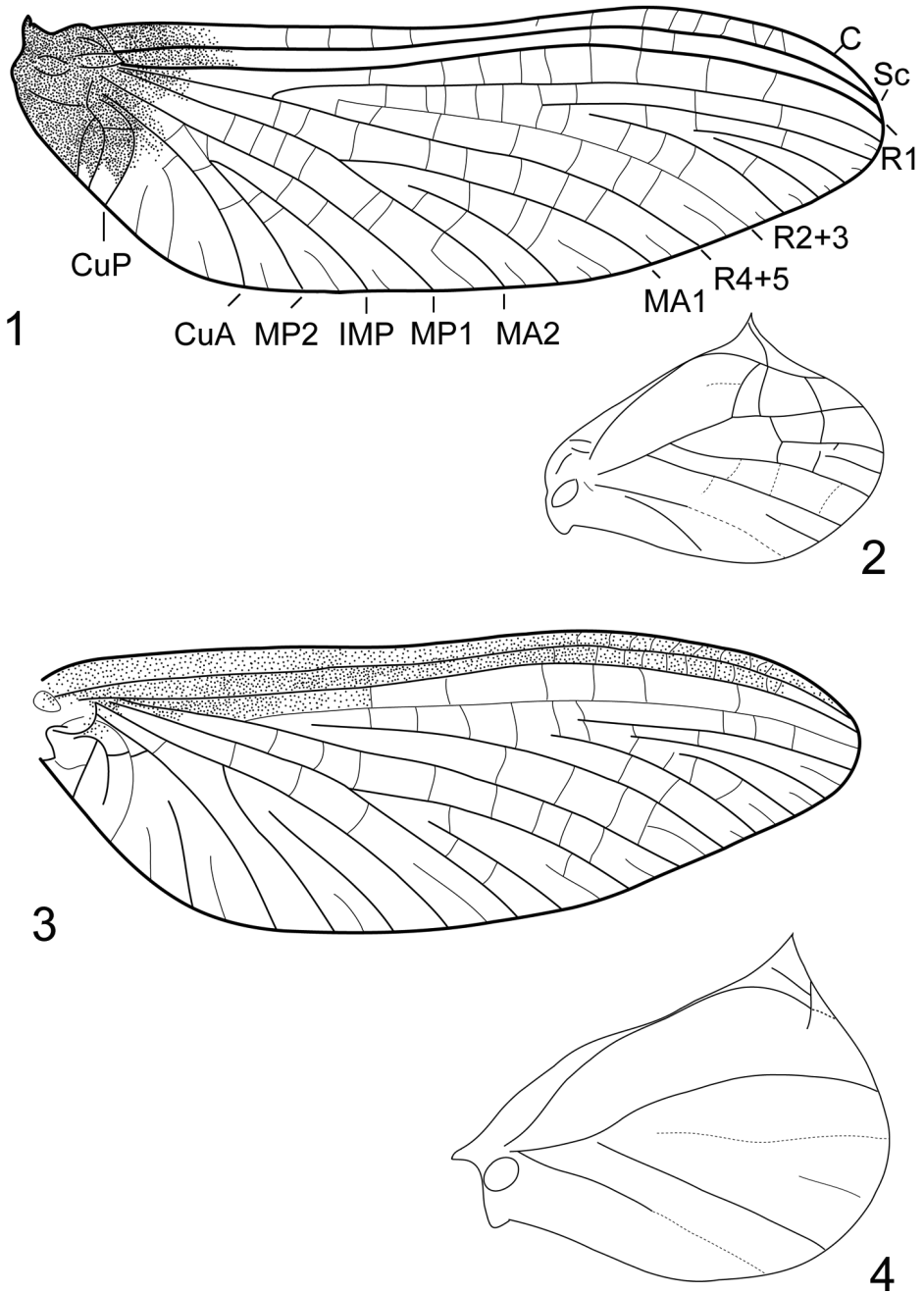
Head: frons dark brown; ocelli whitish with blackish stem; upper part of compound eyes light grey, lower part dark grey; antennae whitish.

Pronotum: light brown, with some blackish maculae and a black sagittal line; foreleg with coxa and trochanter light brown, femur medium brown, tibia dark brown in the basal half, light brown in the apical one, tarsi yellowish brown; leg formula: femur 1.4 mm, tibia 2.5 mm, tarsus 2.15 mm (ta₁ 0.9 mm, ta₂ 0.8 mm, ta₃ 0.3 mm, ta₄ 0.15 mm); tarsal claw dissimilar.

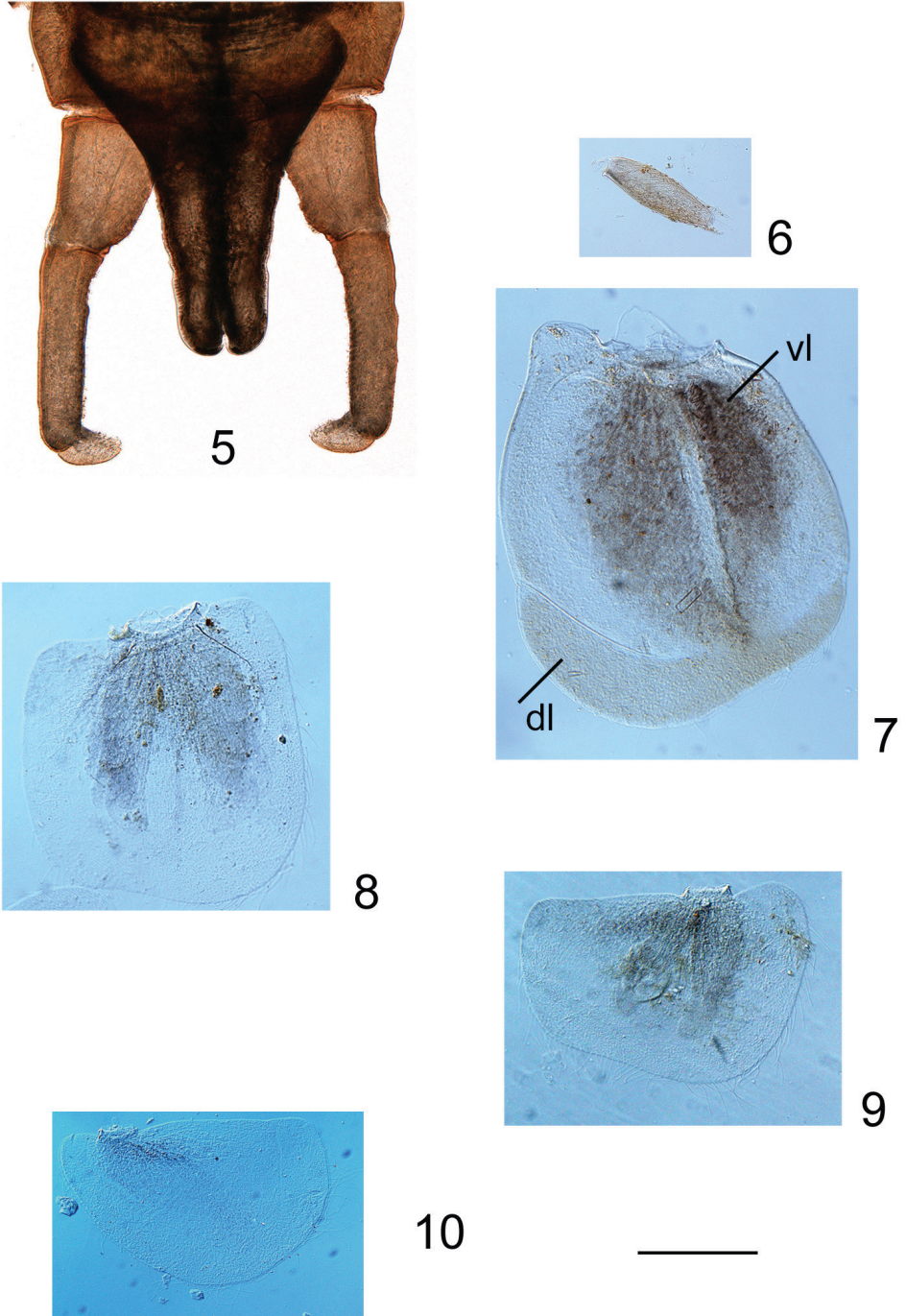
Meso-metathorax: medium brown, washed with grey; coxa and trochanter washed with black, femur medium brown with two longitudinal blackish stripes, femoro-tibial articulation blackish, tibia and tarsus light brown; tarsal claw dissimilar. Forewing (Fig. 1) translucent with base tinted with dark brown; longitudinal veins medium to light brown, crossveins translucent; a single intercalary between IMP and MP2, one between MP2 and CuA, and three between CuA and CuP; hindwing (Fig. 2) entirely dark brown, costal process pointed and located ca 1/3 along the tip of the wing; mesoscutellum with well-developed posterior processes.

Table 1. Environmental characteristics of the six study sites in the Andasibe area (Madagascar).

Code	Locality	Belakato	Madiofasina	Rianasoa	Antanambotsira	Sandrasoa	Sahaparas
		BT	MA	RA	AA	SA	SY
Coordinates	18°49'23"S/48°25'08"E	18°55'14"S/48°26'20"E	18°49'47"S/48°25'57"E	18°52'32"S/48°25'29"E	18°55'47"S/48°31'01"E	18°52'30"S/48°22'47"E	
Altitude (m. a.s.l.)	920	870	920	950	710	920	
Canopy cover (%)	90	70	60	0	3	7	
Slope (%)	3	8	5	2	2	3	
Channel width(m)	2.78	2.51	4.11	3.28	0.46	3.63	5.09 ± 0.93
Water depth (m)	0.18	0.14	0.14	0.01	0.14	0.13	0.16 ± 0.02
Velocity (m/sec)	0.47	0.44	0.51	0.09	0.43	0.46	0.38 ± 0.11
pH	7.07	7.23	7.03	0.12	7.10	7.13	7.40 ± 0.10
Water T (°C)	16.00	16.17	15.83	1.53	20.33	19.50	19.33 ± 2.25



Figures 1–4. *Manobyphella keiseri* Allen, 1973 adults. **1** male forewing **2** male hindwing **3** female forewing **4** female hindwing. Abbreviations: **C** Costa **Sc** Subcosta **R** Radius **MA** Media anterior **MP** Media posterior **IMP** Main intercalary vein in media posterior **CuA** Cubitus anterior **CuP** Cubitus posterior.



Figures 5–10. *Manohypella keiseri* Allen, 1973 adult (**5**) and larva (**6–10**). **5** male genitalia in ventral view **6** gill I **7** gill II **8** gill III **9** gill IV **10** gill V. Scale bar: 0.2 mm (**6–10**). Abbreviations: **dl** dorsal lamella **vl** ventral lobes.

Abdomen: tergites greyish brown, colour intensity increasing toward the tip; presence of two rounded and whitish spots in postero-lateral position of each segment, especially well marked on segments VI–IX; abdominal sternites light grey.

Genitalia (Fig. 5): styliger plate light brown, with a rounded process in the middle of the posterior margin; gonopods light brown, three-segmented, the first one stout, just over half the length of segment II; segment III ovoid and short; inner margin of gonopods bearing stout and short scale-like setae; penes lobes medium brown stout and almost completely fused except at the tip, shorter than the gonopods; no spines or ornamentation present. Cerci broken.

Female imago. Body length: 6.1–6.2 mm; forewing length: 8.7–9.8 mm; hindwing length: 0.97–1.02 mm.

Similar to the male, except as follows: legs uniformly light brown; forewing (Fig. 3) with subcostal field entirely brownish, hind wing (Fig. 4) light brown, with costal process located ca $\frac{1}{5}$ of the tip of the wing; abdominal patterns visible but less contrasted, sternites greyish brown; subanal plate slightly incised in the middle; cerci entirely whitish.

Female subimago. Similar to the adult female, except general coloration reddish brown, wings entirely medium brown, subanal plate regularly rounded.

Nymph (Fig. 11). The species has been described by McCafferty and Benstead (2002), with the following important complements:

Patch of setae on the outer margin of the mandibles variable in number and often broken, their insertion only visible at high magnification. Maxilla with a spoon-like tooth, and with two stout and curved dentisetae; patch of setae at the base of the galea composed of 2–5 long, thin setae. Labium with submentum well developed, antero-lateral corners more or less rounded; base of the 3rd segment of the labial palp as wide as the articulation with the 2nd segment.

Gills (Figs 6–10) present on segments I–V. Gill I (Fig. 6) small, finger-like and one segmented, covered with long and thin setae. Gill II (Fig. 7) with a plate like dorsal lobe, and a ventral lobe constituted of costal and anal branches, dorsal gill more or less quadratic, with a distinct longitudinal ridge. In the distal $\frac{1}{4}$ of the dorsal lobe, a weak line well visible and almost reaching the middle of the plate, probably allowing the larva to lift the distal part of the gill. Dorsal plate of gill III (Fig. 8) quadratic, outer margin concave and with long, thin setae. Dorsal plate of gill IV (Fig. 9) transverse, with long, thin setae on the margin. Gill V (Fig. 10) identical to the previous one, smaller and without ventral lobe. Single postero-median tubercles on tergites variable in size and orientation depending on the developmental stage of the larva. Cerci and terminal filament with rows of stout, long setae.

Ecology. *Manohyphella keiseri* larvae were almost exclusively found in the three forested localities (BT, MA, RA) and were virtually absent from the Savoka open canopy localities (4 specimens captured in the three localities in one year), confirming that the species is strictly bound to the forest cover. Populations in BT were not dense enough to proceed to life cycle analyses. Mean densities in MA and RA over the investigated period were 12.50 ± 17.93 and 10.56 ± 11.18 ind. m⁻² respectively. Mean biomass was 8.17 and 7.07 mg DW m⁻² respectively.



Figure 11. *Manohypella keiseri* Allen, 1973 from top to bottom: medium size female larva from Ranomafana area (P0643), medium size male larva from Marojejy area (P1020), full grown male larva from Andasibe area (P2183). Scale bar: 1 cm.

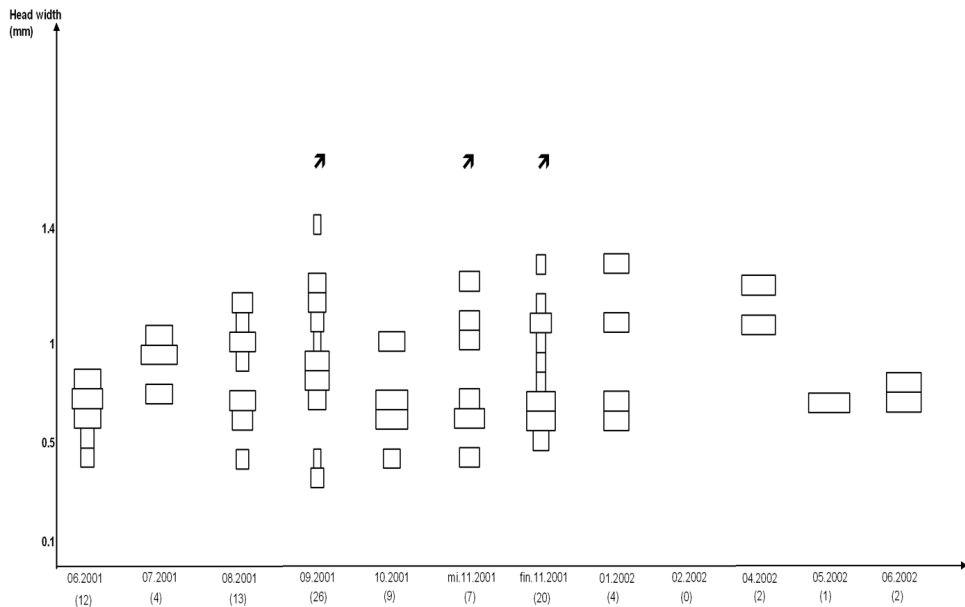


Figure 12. Life cycle of *M. keiseri* in Andasibe area; arrows indicate mature larvae (emergence); number of specimens examined are in brackets below the sample dates.

The life cycle exhibits a seasonal pattern which is not characteristic of tropical species (Fig. 12). Mature nymphs were found between September and November, at the end of the dry season.

Discussion

Morphological description

Relationships of *Manohyphella* with other Teloganodidae have been already discussed by McCafferty and Benstead (2002) as well as by Sartori et al. (2008) who included what they called *M. animosa* in their phylogenetic reconstruction of the Oriental lineage. *Manohyphella* is clearly more closely related to the Afrotropical lineage than to the Oriental one: presence of a well developed terminal filament, patch of setae on the outer margin of the mandibles, are two important characters shared between all Afrotropical genera (*Ephemerellina* Lestage, 1924, *Lestagella* Demoulin, 1970, *Lithogloea* Barnard, 1932, *Nadinetella* McCafferty & Wang, 1998), including *Manohyphella*. Very recently, two new teloganodid genera have been described from India (Selvakumar et al. 2014), which also possess a well developed terminal filament. One of them (*Jano-hyphella* Selvakumar, Sivaramakrishnan & Jacobus, 2014) does not belong to Teloganodidae (Kluge et al. 2015); the other one, *Indoganodes* Selvakumar, Sivaramakrishnan & Jacobus, 2014, does not bear patches of setae on the outer margin of the mandibles,

abdominal tergites bear poorly developed median tubercles, incisors of the mandibles are not spoon-shaped, and the shape of the legs is much more slender compared to *Manohyphella*.

Here we describe for the first time the gills composition and it appears that *Manohyphella* possesses a unique combination of characters among Teloganodidae (Kluge 2004, table 8, page 297). *Manohyphella* bears gills on segments I–V, the first one finger-like, gills II–IV with an entire dorsal lobe and a ventral lobe and a gill V with only an entire dorsal lobe. The closest relative is *Nadinetella crassi* (Allen & Edmunds, 1963) from the Cape Province in South Africa which possesses almost the same formula except that gill V bears a ventral lobe.

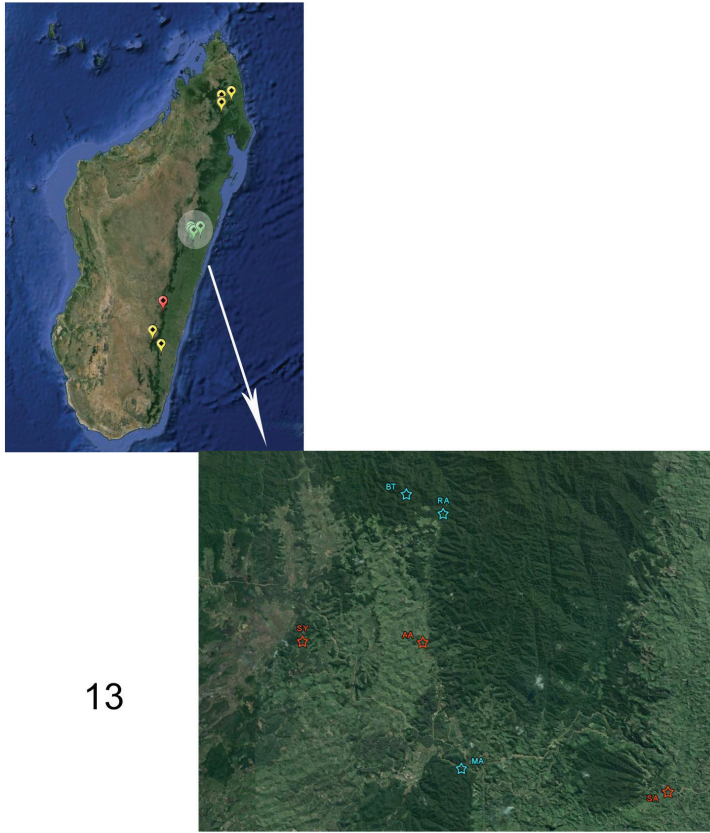
As mentioned by Allen (1973), the forewing venation in the median and cubital fields seems constant among the material examined and differs from all other Teloganodidae. The male genitalia are also different from the other Afrotropical ones, being less stocky compared to *Lithogloea harrisoni* Barnard, 1932, without divergent apical lobes, as in *Nadinetella crassi* and more stout at base compared to those of *Ephemerellina barnardi* Lestage, 1924 or *Lestagella penicillata* (Barnard, 1940) (Pereira-da-Conceicao and Barber-James 2013).

The wide geographical range where *Manohyphella* has been found allows us to consider the morphological variation encountered in the nymphs. McCafferty and Benstead (2002) separated *M. animosa* from *M. sphyxia* mainly by the shape of the postero-lateral corners of the submentum, as well as by the shape of the tubercles on the tergites. We have been through all material available and found both characters subject to variations; the tubercles vary in structure depending on the developmental stage, whereas the submentum presents different development of the postero-lateral corners, from clearly rounded to more acute; moreover this structure is delicate and subject to being distorted during slide mounting, hence changing its normal shape. Comparison of morphological characters of other mouthparts, and legs showed no clear-cut separation allowing attribution of some populations to different species.

It is moreover amazing to see that the three nominal species have been described from the same area (Ranomafana National Park and surroundings), one of them, *M. sphyxia* based only on a single female nymph. Our winged material from Manampatrana perfectly fits the generic and specific diagnosis proposed by Allen (1973), and is similar to the type material (deposited in the Naturhistorisches Museum, Basel, Switzerland) of *M. keiseri*. Therefore, we conclude that a single species is present in the available material and consequently, *M. animosa* McCafferty & Benstead, 2002 and *M. sphyxia* McCafferty & Benstead, 2002 are considered as subjective junior synonyms of *M. keiseri* Allen, 1973. To date, *Manohyphella* is therefore a monospecific endemic genus of Madagascar.

Ecology and life cycle

Our results concerning habitat preferences are in accordance with those obtained by Benstead et al. (2003) in Ranomafana area. *M. keiseri* is an inhabitant of pristine tropi-



13

Figure 13. Map of known specimens of *M. keiseri*, with detailed map of the Andasibe area. Yellow pins: new localities; red pin: type locality (Ranomafana); green pins: localities in Andasibe area. Code of the localities according to Table 1.

cal forested streams obviously very sensitive to habitat degradation. This characteristic is probably found in other teloganodid species, as demonstrated by Mantel et al. (2010) who show that South African Teloganodidae in general were among the most sensitive taxa to the impact of dams. Densities in our study sites are higher than in Benstead et al. (2003) study (5.3 ± 4.3 ind. m^{-2}). *M. keiseri* biomass is lower than those of other mayflies studied (Oliarinony unpubl. results), especially Baetidae which can be two to four times higher. As these are the first quantitative results for the family Teloganodidae, no comparison can be made with other species in South Africa or in Asia.

It is difficult to interpret the cycle in detail because the number of specimens is not high enough. Our graph (Figure 12) suggests a seasonal life cycle with adults emerging at the end of the dry season. Aseasonality in the tropics is well documented and common in aquatic life histories (Yule and Pearson 1996; Salas and Dudgeon 2003). The presence of young larvae in September, together with mature ones, could indicate either recruitment from a previous generation (i.e. at least a bivoltine cycle) or a de-

layed hatching of the last generation of the year before. Thus, we cannot exclude that *M. keiseri* is univoltine in the study area.

Conclusion

M. keiseri is a typical taxon of running waters flowing in intact tropical rainforest of the East Coast of Madagascar (Fig. 13). Its patchy distribution reflects the range of the remains of the tropical forest, except for the Montagne d'Ambre where the species has never been found despite numerous samplings. Its range is similar to those of *Probosciodoplocia vayssierei* Elouard & Sartori, 1997 (Euthyplociidae), *Dabulamanzia gladius* Gattolliat, 2000 (Baetidae), or *Ranorythus violettai* Ollarinony & Elouard, 1997 (Tricorythidae). Although microendemism is important among Malagasy mayflies (Vuataz et al. 2013), the monospecificity of widely distributed genera is not unique, such as *Nesoptiloides electroptera* (Demoulin, 1966), *Edmulmeatus grandis* Lugo-Ortiz & McCafferty, 1997, *Spinirythus martini* Ollarinony & Elouard, 1998 for example (Elouard and Gibon 2001).

Easy to identify at the nymphal stage and with a distribution restricted to pristine environments, *M. keiseri* is therefore a good bioindicator for environmental assessments.

Acknowledgements

We want to thank the late Dr Michel Brancucci and Dr Daniel Burkhardt (Naturhistorisches Museum Basel) for giving us the opportunity to study the type material of *M. keiseri* deposited in their collection. Janice G. Peters (Florida A & M University, Tallahassee, USA) provided us with important comparative material. Ranalison Ollarinony thanks the University of Lausanne for a research grant during her stay in Switzerland. Comments by Luke Jacobus (Columbus, USA) and Helen Barber-James (Grahamstown, South Africa) greatly helped to improve the manuscript.

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