

## ***Massartella hirsuta* sp. nov. (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) and new data on mayflies of Guyana Highlands**

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Description and figures of the larva and egg of *Massartella hirsuta* sp. nov. (Ephemeroptera: Leptophlebiidae) from the south-eastern part of Grand Sabana region (Venezuela) are presented. Diagnostic characters distinguishing the larvae of this species from other known *Massartella* species include a heavy row of setae along the entire outer margin of the mandibles. This character, among others, will also distinguish the new species from undescribed species of *Massartella* from the sandstone table mountains. Two well-defined species groups of the genus *Massartella* can be distinguished in the Guyana Highlands: (1) *M. venezuelensis* group including *M. venezuelensis* and *M. hirsuta* sp. nov., and (2) *M. devani* group containing *M. devani* and undescribed taxa from Mt. Roraima and Mt. Chimantá plateaus. The first group seems to be distributed in uplands (~1000 m a.s.l.), while the second group appeared to be restricted to the thermal refugia above 2000 m a.s.l. The origin of *Massartella* species in Guyana Highlands is discussed.

**Keywords:** mayfly larva; egg; table mountains; vertical displacement; Neotropical zoogeography; South America

### **Introduction**

The area of north-eastern South America extending between the Orinoco River to the north and the Amazon River to the south is occupied by the large Guyana Shield. The shield represents a large black water area notorious for the poorness of its productivity. Tea-coloured waters flow from nutrient poor, sandy soils. The streams are low in minerals, acid (pH 3.5–5.5) and may contain high concentrations of organic compounds leached from vegetation (Lánczos, Schlögl, Šmída and Brewer-Carías 2007). The mayfly fauna of this area is characterised by high endemism (Domínguez, Molineri, Pescador, Hubbard and Nieto 2006). The Gran Sabana region is located in the Venezuelan part of the Guyana Shield, at the headwaters of the Caroní River (Orinoco River basin). The region is characterised by peculiar flat-topped table mountains, the tepuis, separated from surrounding wide lowlands and uplands by the sheer cliffs. Tepuis are composed of quartzites and sandstones of the Precambrian Roraima Group, overlaying the igneous-metamorphic Guyana Shield (South American old core, Gibbs and Barron 1993).

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The Gran Sabana is part of an undulated erosion surface and forms an “altiplano” (upland) inclined to the south, with altitudes ranging from about 750 to 1450 m a.s.l. (Briceño and Schubert 1990). From this level the tepuis emerge. They are acknowledged islands supporting high endemism (Huber 2005; Rull 2007). The ecological community of their summits is considered a distinct and discontinuous biogeographical province called Pantepui. Pantepui ranges from 1500 to 3000 m a.s.l and covers an area of about 5000 km<sup>2</sup> (Berry, Holst and Yatskievych 1995; Huber 1995). Some of the tepuis have been thoroughly explored by scientific expeditions, and the others are virtually unknown. Nevertheless, no valid mayfly records have been published from the flat-topped mountain summits until now. One unique piece of evidence of mayflies was recently published by Charles Brewer-Carías from a stream in a newly discovered gigantic cave in Chimantá massive (Šmída, Brewer-Carías and Audy 2005). The author mentioned “one species of *Ephemera* flying in dimness near where the river emerges from the cave”; this obviously was not a member of the genus *Ephemera*, but some unidentified mayfly. The present paper provides first reliable records of mayflies from the table mountains.

The genus *Massartella* includes four species and belongs to the family Leptophlebiidae (Ephemeroptera), the most diverse South American mayfly family with 41 known genera (Dominguez et al. 2006). The genus *Massartella* was established by Lestage (1930) and re-described by Peters and Edmunds (1972). According to the generic description of Pescador and Peters (1990), supplemented by Derka (2002), the larvae of *Massartella* can be distinguished from all the other genera of Leptophlebiidae by the following combination of characters: (1) clypeus is as wide as the labrum; (2) length of labrum is approximately 1/2 maximum width, and lateral margins are slightly expanded apically; (3) mandibles have a slightly curved outer margin with a median setae turf; (4) glossae are ventrally curved, and submentum has several long lateral spines; (5) claws have denticles which are progressively larger apically except apical denticle is much larger; (6) abdominal terga have series of short lateral spines, and broad posterior spines and long feather-like setae; (7) abdominal gills occur on segments 1–6, and are alike, plate-like and have well developed dorsal and ventral lamellae. The dorsal lamella can be apically terminated in a slender process; (8) the eggs have chorion covered with fibrous filaments, and are adorned with hexagonal or circular structures.

The genus *Massartella* is disjunctly distributed in south-eastern Brazil and north-eastern Argentina and the Guyana Shield along the Venezuela–Brazil–Guyana border (Pescador and Peters 1990; Derka 2002). Two described and one undescribed *Massartella* species are known from the Brazilian Shield. *Massartella alegrettae* Ulmer, 1943 is known only from a male imago and subimago. *Massartella brieni* (Lestage, 1924), inhabiting high mountainous rivers and streams of south-eastern Brazil, is the more common species with all stages described. Two immature larvae unassociated with adults and unassigned to any particular species were collected in north-eastern Argentina (Pescador and Peters 1990). Pescador and Peters (1990) described a new species *Massartella venezuelensis* from the northern part of the Guyana region of Venezuela, and Derka (2002) described *Massartella devani* from a stream at the Roraima foothills. Venezuelan *Massartella* populations represent the most northern geographic limits among the Patagonia Shield, South Andean, cold-adapted leptophlebiid genera of the Neotropics (Savage 1987).

This paper aims to (1) describe a new species of *Massartella*, (2) provide first reliable data on mayflies from flat-topped table mountains, the tepuis, and

(3) advance hypotheses concerning the zoogeography and origin of some *Massartella* species.

## Taxonomy

### *Massartella hirsuta* sp. nov.

*Material examined. Holotype.* Mature larva, SE Venezuela: Bolivar state, Paraitepui de Roraima village environs, right side tributary of Kanaupán River where it is crossed by a tourist pathway from Paraitepui village to the Río Tek, c. 1100 m a.s.l., 17. November 2008.

*Paratypes.* One immature larva, same data as holotype, two immature larvae, the same locality as holotype, 20 January 2006.

Type material is preserved in alcohol and deposited in the senior author collection (T. Derka, Comenius University, Bratislava, Slovakia) and in the Museum of Zoology, Lausanne, Switzerland.

### *Larva* (in alcohol)

Body length 14 mm. Dorsum of head yellowish, venter brownish-yellow; a wide longitudinal brown band in centre divided by pale yellow band between median ocellus and labrum; a brown band rising from the anterior base of eyes and covering both anterolateral parts of head (outer margins of mandibles) (Figure 1). Antennae pale yellow. Ocelli and eyes dark brown or black.

*Mouthparts* (Figures 2–5). Labrum with a broad anteromedian emargination with five denticles, dorsally and laterally covered by very long and relatively dense setae (Figure 2); mandibles yellowish with darker brown spots, outer margins of mandibles completely covered by a dense row of long setae (Figure 3); maxillary palps pale yellow, all segments with long setae (Figure 4); labial palps pale yellow, segment 1 of labial palp with long, fine setae and long, thick setae, segment 2 with long, thick setae, segment 3 with numerous long thick setae and one row of peg-like setae (Figure 5).

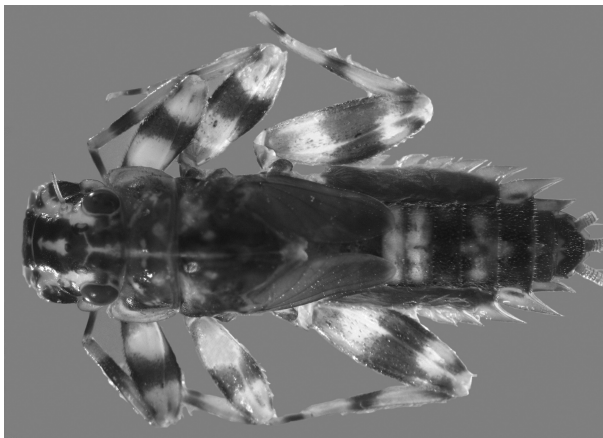
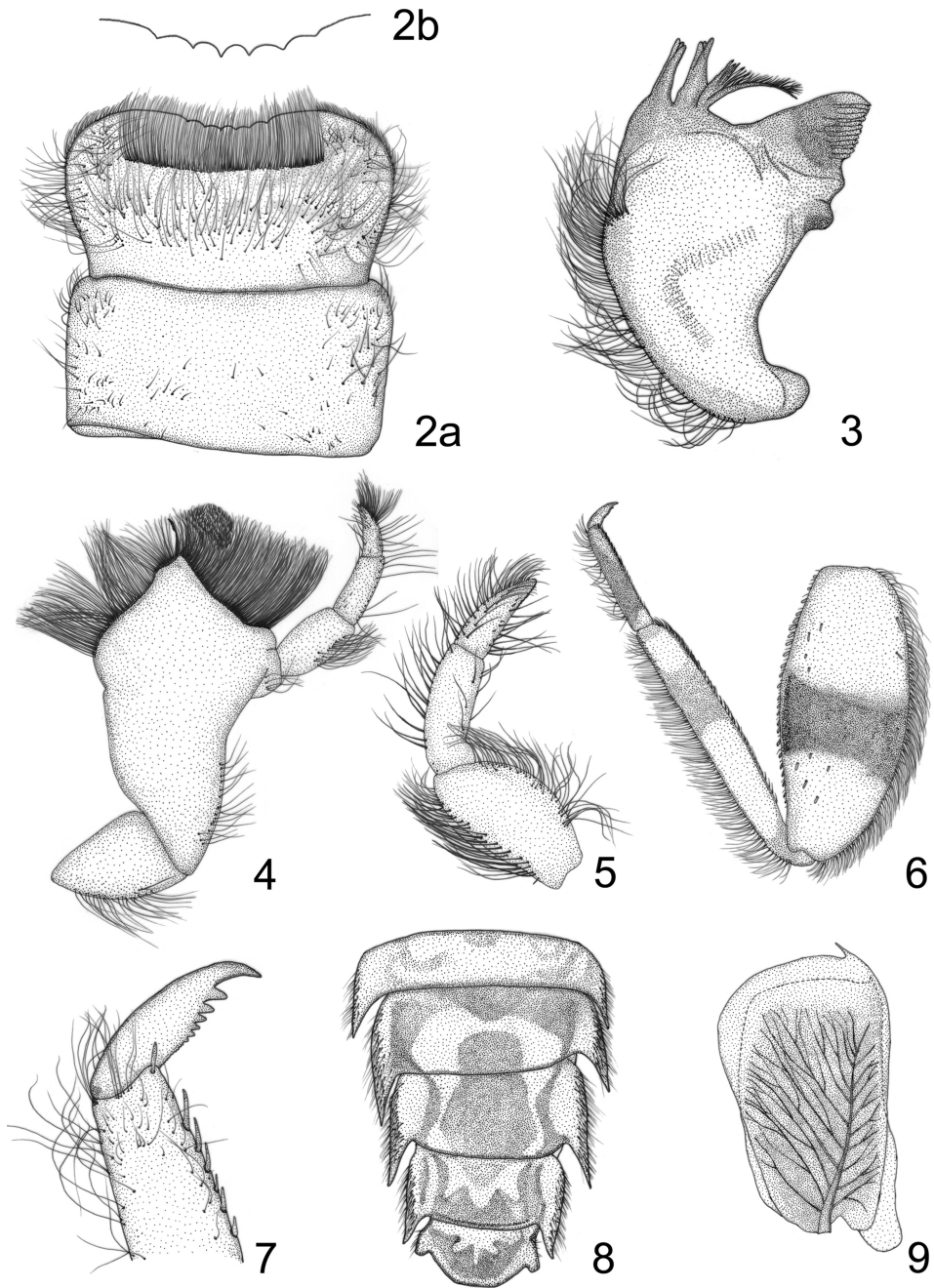


Figure 1. *Massartella hirsuta* sp. nov., dorsal habitus of holotype larva.



Figures 2–9. *Massartella hirsuta* sp. nov., dorsal view. (2a) Labrum; (2b) enlarged anteromedian emargination of labrum; (3) left mandible; (4) maxilla; (5) labial palp; (6) foreleg; (7) foreclaw; (8) abdomen; (9) fourth gill plate.

*Thoracic nota.* Brown with large pale yellow spots (Figures 1 and 8). Sterna yellowish with dark margins.

*Legs* (Figures 1, 6 and 7). Yellow; trochanter with brown spot; femora relatively wide, with broad transverse median brown band, and distal and apical

light brown bands (not always visible), dorsally covered with scattered to numerous lanceolate setae, inner margins with numerous short thick setae, outer margins with thick long setae and a row of dense long finer setae; tibiae reddish brown with transverse darker brown band, smaller brownish area close to femoral articulation, outer margins with a dense row of very long fine setae, tarsi yellow with wide brown spots, outer margins with a row of long fine setae (Figures 1 and 6); tarsal claws with 4–7 denticles, basal denticles greatly reduced (Figure 7).

*Abdomen* (Figures 1, 8 and 9). Terga yellow with dark brown maculae; sterna glabrous, yellow with brown markings along margins; posterolateral spines of 5th to 9th segments long, up to 2/3 of maximum median length of each segment, numerous thick setae along margins of terga.

*Gills* (Figure 9). Membrane grey, tracheae dark grey; dorsal portion of gill lamellae with weakly developed apical process. Caudal filaments yellow, brown at the base, brown annulation on every 2nd to 4th joint.

### *Egg*

Eggs are elongate oval. The chorion is covered with fibrous filaments and adorned with circular structures (Figure 10).

*Male and female imago*. Unknown.

*Male and female subimago*. Unknown.

### *Etymology*

Hirsutus in Latin means hairy, hirsute. This species is the most hirsute of five known *Massartella* species.

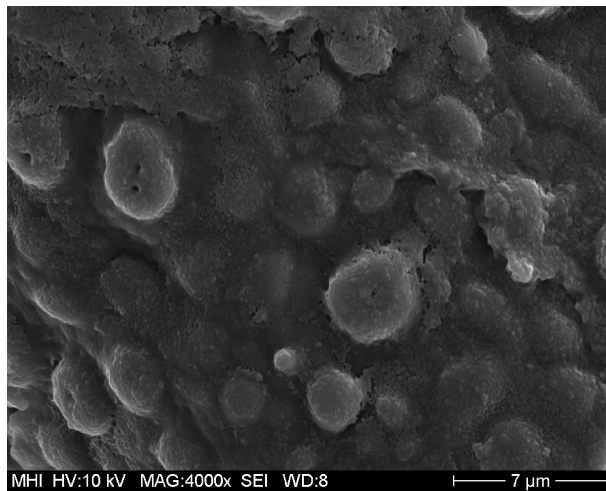


Figure 10. Scanning electron micrograph of *Massartella hirsuta* sp. nov. Egg, detail of chorionic surface.

### Biology

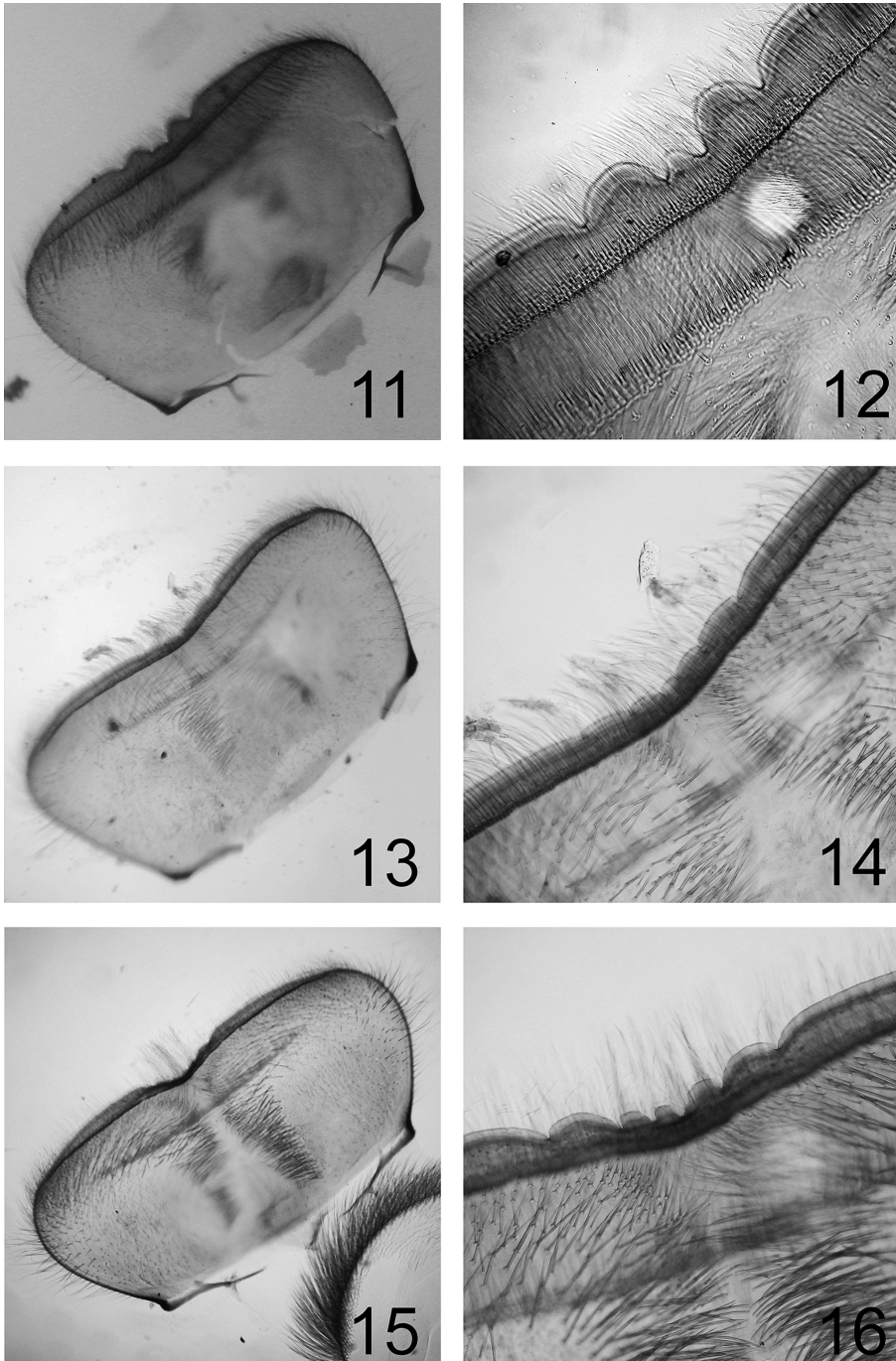
The larvae were collected in a small, shallow, 1.0 m wide stream at an altitude of about 1100 m a.s.l. The stream was partially shaded by a gallery forest with a water temperature of 21.4°C (measured at midday). The bottom was composed of stones, gravel and wood debris. The stream flows through the hilly secondary savannas. The population density of *M. hirsuta* was presumably very low because only few larvae were captured, in spite of high sampling effort.

### *Massartella* larvae from table mountains (Pantepui)

Other species of *Massartella* larvae were found at the Mt. Roraima and Mt. Chimantá plateaus, respectively. Mt. Roraima is located in SE Venezuela at the conjunction of Venezuelan, Guyana and Brazilian borders. The elevation of the sandstone plateau platform oscillates between 2600 and 2700 m a.s.l. Mt. Roraima is separated from surrounding uplands by vertical cliffs 300–500 m high and covers an area of about 34 km<sup>2</sup> (Šmída, Audy and Vlček 2003). The *Massartella* larvae were found in a small cave (diameter c. 1 m) at 2700 m a.s.l. in January 2007. The larvae dwelt under sandstone and crystal stones in relatively cold water with a constant temperature of about 14°C. Anisopteran dragonfly larvae and caddisfly larvae from the family Helicopsychidae were found at the same site. In general, streams at the Roraima plateau are extremely oligotrophic (pH = 5.05, electrical conductivity = 19 µS/cm, PO<sub>4</sub>-P < 0.01 mg/l and NO<sub>3</sub>-N < 0.05 mg/l; Lánčzos et al. 2007).

Chimantá massif is located about 100 km west from Mt. Roraima. It is a spectacular complex of tepui summits with total surface of about 1470 km<sup>2</sup> with summits ranging from 1700 to 2700 m a.s.l. (Huber 1992). The summits are isolated from surrounding uplands by cliffs ranging from 400 to more than 1000 m. In the Chimantá massif the biggest quartzite cave in the world – Cueva Charles Brewer – was discovered (Šmída et al. 2005). Mayfly larvae were collected in the river at the cave entrance in February 2007. The altitude of the site is 2100 m a.s.l. Parameters measured by Lánčzos et al. (2007) are similar to the Mt. Roraima streams (temperature = 13.6°C, electrical conductivity = 20 µS/cm, pH = 4.58, PO<sub>4</sub>-P = 0.14 mg/l, NO<sub>3</sub>-N < 0.05 mg/l).

*Massartella* larvae from both Mt. Roraima and Mt. Chimantá are morphologically very similar to *M. devani*. However, differences in general shape of labrum and number of denticles of anteromedian emargination of labrum are evident (Figures 11–16). Anteromedian emargination of labrum has five denticles similar to all *Massartella* species except *M. devani*. Similar to *M. devani* they lack apical process on the dorsal portion of gill lamellae and eggs are adorned with circular anchoring structures (see Derka 2002 for details). Interestingly, in spite of the fact that populations of *M. devani* and the species from Mt. Roraima are isolated only by a 400 m high vertical cliff, specimens from Roraima plateau are morphologically more similar to those from Chimantá than to *M. devani* inhabiting Roraima foothills. The specimens from Roraima and Chimantá will probably be assigned to a new species, different from *M. devani*. However, more specimens are needed for detailed morphological study. Because of morphological similarity, even more detailed study supported by molecular data will be needed in order to say whether Roraima and Chimantá populations belong to the same species or not.



Figures 11–16. Photographs of labra of *Massartella* larvae. (11) General shape of *M. devani* labrum; (12) enlarged denticles of anteromedian emargination of *M. devani* labrum; (13) general shape of labrum of *Massartella* from Chimantá; (14) enlarged denticles of anteromedian emargination of labrum of *Massartella* from Chimantá; (15) general shape of labrum of *Massartella* from Roraima; (16) enlarged denticles of anteromedian emargination of labrum of *Massartella* from Roraima.

## Discussion

The larvae of *M. hirsuta* can easily be distinguished from other *Massartella* species by outer margins of mandibles completely covered by a dense row of long setae (Figure 3). The following combination of characters will distinguish the larvae of *M. hirsuta* from those of *M. brieni*: (1) labrum covered with numerous fine long setae (Figure 2); (2) femora wide, with broad transverse median brown band, outer margins of femora, tibiae and tarsi with a row of dense long fine setae (Figure 6); (3) dorsal portion of gill lamellae with weakly developed apical process (Figure 9); (4) abdominal sterna glabrous, posterolateral spines of 5th to 9th segments long, up to 2/3 of maximum median length of particular segments (Figures 1 and 8). The larvae of *M. hirsuta* can be distinguished from those of *M. venezuelensis* by the relative length and shape of posterolateral spines of abdominal segments (compare Figures 1 and 8, and Figure 35 in Pescador and Peters 1990). Specimens of *M. hirsuta* can be easily distinguished from *M. devani* and specimens from Roraima and Chimantá by the following combination of characters: (1) labrum covered with numerous fine long setae (Figure 2); (2) all segments of maxillary palps with long setae (Figure 4); (3) outer margins of femora, tibiae and tarsi with a row of dense long fine setae (Figure 6); (4) abdominal sterna glabrous, posterolateral spines of segments long, up to 2/3 of maximum median length of segment (Figure 8); (5) dorsal portion of gill lamellae with apical process (Figure 9). The distinction between larvae of *M. hirsuta* and *M. devani* can also be based on the number of denticles of anteromedian emargination of labrum.

The eggs of *M. hirsuta* are similar in general shape to other *Massartella* species. Circular structures covering the chorion are not very different from those of *M. devani* (Derka 2002). In contrast, chorionic surface structures of *M. brieni* are clearly hexagonal (Pescador and Peters 1990).

Two morphologically and ecologically clearly different groups can be distinguished within the Guyana Highlands *Massartella* representatives: (1) *M. venezuelensis* group including *M. venezuelensis* and *M. hirsuta*, and (2) *M. devani* group including specimens from Roraima and Chimantá. The *M. venezuelensis* group can be morphologically characterised by long posterolateral spines of abdominal segments, an apical process on the dorsal portion of gill lamellae and generally hairy body parts (maxillary and labial palps, legs, posterolateral spines of abdominal segments). The *M. devani* group is typical in that it lacks an apical process on the dorsal portion of gill lamellae, has relatively short posterolateral spines on abdominal segments, and has a less hairy body. Ecological differences are obvious. The *M. venezuelensis* group seems to be distributed in uplands (~1000 m a.s.l), while the *M. devani* group appeared to be restricted to the thermal refugia above 2000 m a.s.l. Cold and extremely oligotrophic springs in the tepuis basal slopes and/or shaded springs at the plateaus of the highest tepuis are typical habitats of the *M. devani* group.

## Zoogeography

The leptophlebiid fauna of southern South America, southern Africa, Madagascar, Australia and New Zealand have historically been postulated to have close affinities and *Massartella* was traditionally viewed as an ancient genus (e.g. Tsui and Peters 1975; Pescador and Peters 1980). Tsui and Peters (1975) hypothesised



that the evolution of *Massartella* probably occurred after the Paleocene when Australia became separated from Antarctica. According to these authors, the possible dispersal route could be eastern Australia – eastern Antarctica – Antarctic Peninsula – southern South America. Pescador and Peters (1980) placed *Massartella* to the *Penaphlebia* lineage restricted to South America and Australia. Recent DNA analyses placed the genus *Massartella* to Paleoaustral group of Atalophlebiinae and supported presumably ancient connections between the leptophlebiid faunas of Australia and South America (O'Donnell and Jockusch 2008). The genus is exclusively associated with the Brazilian and Guyana Shields and completely absent from cold streams in the Andes (Pescador and Peters 1990; Derka 2002; Domínguez et al. 2006). Thus, the Guyana representatives must have colonised Guyana Highlands from the Brazilian Shield via today's Amazon basin.

The unique biota of the Guyana highlands had been formerly considered an example of long-lived species originated by ancient evolution in isolation since Cretaceous (the Lost World hypothesis), around 80–100 Ma (Maguire 1970). These organisms were viewed as remnants of formerly widespread ancient biota, originated by vicariance and linked to the fragmentation of a continuous erosion surface into isolated, flat-topped table mountains. However, recent studies supported by molecular data attributed pre-Quaternary differentiation mainly to tectonic, eustatic and orogenic events, which occurred during the late-Tertiary (Nores 2004), while Quaternary speciation has been related primarily to climatic cycles (Hewitt 2000). Floristic studies in the Guyana region revealed relationships that were compatible with the vertical displacement hypothesis, which proposes intermittent biotic mixing between highlands and lowlands due to the Quaternary glacial/interglacial alternation (Steyermark and Dunsterville 1980; Huber 1988).

The Guyana Highlands had been probably colonised by *Massartella* invaders before the interruption of connection between Guyana and Brazilian Shields during the Miocene–Pliocene marine incursion (c. 5 Ma) or even earlier, before establishment of the Amazon drainage (10 Ma) (see Nores 1999; Hubert and Renno 2006, for a review). An alternative hypothesis may highlight a late Miocene or early Pleistocene dispersal from the Brazilian Shield with diversification within the region occurring in the Quaternary. The disturbance-vicariance hypothesis has been proposed to explain observed patterns of Amazonian diversity (Bush 1994; Haffer 1997; Colinvaux 1998). According to this hypothesis, eastward spread of Andean cool-adapted organisms would have been possible, thanks to the climate cooling that marked the initiation of the Late Cenozoic glacial cycles, which favoured the invasion of the Amazon lowlands by mountain taxa. The Pleistocene temperature fluctuations ( $\pm 7.7^\circ\text{C}$ ) may have also facilitated the northward spread of cool adapted taxa from Brazilian uplands to Amazonia and Guyana uplands. In both cases, the present Guyana population may be considered a dispersal relict and continued gene flow between Guyana and Brazilian Shields is unlikely.

The *M. venezuelensis* species group seems to have more ecological affinities with the species inhabiting the Brazilian Shield than to the *M. devani* species group. The *M. venezuelensis* group was found inhabiting streams in altitudes of about 1000 m a.s.l. and therefore has higher dispersion possibilities than species of the *M. devani* group. Similarly, *M. brieni* distributed in south-eastern Brazil has wider altitudinal distributional range (800–1600 m a.s.l., Pescador and Peters 1990). The latest palynological findings in the Guyana Highlands indicate downward biotic

migrations of c. 1100 m altitude during glacials, and subsequent interglacial upward shift, in response to colder and warmer climates, respectively (Rull 2004, 2006). Glacial phases have been notably longer than interglacial ones, so it is believed that boreal continents have been glaciated for approx. 80% of the time since the beginning of the Quaternary (Willis and Whittaker 2000). From this point of view, interglacials can be seen as short disturbance periods in normal glacial conditions. In theory, there have been roughly 40 opportunities for biotic interchanges between the tepui summits in the last 2.5 Ma (Rull 2004, 2005). Rull and Nogué (2007) performed paleotopographical reconstruction of the available space for migration during the Last Glacial Maximum which occurred around 21,000 year BP. They showed that most migration pathways among tepuis were opened for vascular plant species with lower altitudinal limits of distribution  $\leq 1500$  m a.s.l., and closed for species with lower altitudinal limits  $\geq 2300$  m a.s.l. Therefore, during glacials, biotic mixing and hybridisation is expected in the lowlands. At the mountaintops cold-adapted species and communities are expected to have occurred, and vicariance prevailed (Rull 2005). We can hypothesise that the *M. venezuelensis* species group inhabiting warmer streams in uplands is probably the ancestral group which migrated northward from the south and have managed to cross lowland barriers between Brazilian and Guyana Shields. During glacials they might have spread to the lowlands of the Guyana Shield. Thus, the wide distributional area of species of the *M. venezuelensis* group in Guyana uplands and findings of more undescribed species are expectable. The *M. devani* species group may be therefore derive from the *M. venezuelensis* group. The *M. devani* species group representatives may be considered relicts of wider glacial distribution of a common ancestor recently restricted to thermal refugia in cold spring streams at higher altitudes. Other opinions consider interglacials such short timespan events (11,000 years or less), which do not promote complete speciation. Some evidence for this period being too brief for bursts of widespread speciation is the lack of diversification among populations separated by 11,000 years of Holocene warmth (Bush 2005). It can be particularly true for the *M. devani* group, with morphologically very similar populations from Roraima and Chimantá summits, today effectively isolated by geographical barriers. Such morphological similarity may indicate recent separation, probably after the last glacial maximum. We can only speculate that *M. devani* might have separated earlier, during one of the previous interglacials. Further investigations at tepui summits will probably lead to findings of more *Massartella* populations (species) from *M. devani* species group, at least in the eastern sector of the Guyana Highlands. In the future, molecular methods should be applied in order to explain the origin and evolution of the genus *Massartella* in the Guyana Highlands.

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### References

- Berry, P.E., Holst, B.K., and Yatskievych, K. (1995), *Flora of the Venezuelan Guayana, Vol. 1. Introduction*, St. Louis: Missouri Botanical Garden Press.

- Briceño, H.O., and Schubert, C. (1990), 'Geomorphology of the Gran Sabana, Guayana Shield, Venezuela', *Geomorphology*, 3, 125–141.
- Bush, M.B. (1994), 'Amazon speciation, a necessarily complex model', *Journal of Biogeography*, 21, 5–17.
- Bush, M.B. (2005), 'Of orogeny, precipitation, precessions and parrots', *Journal of Biogeography*, 32, 1301–1302.
- Colinvaux, P.A. (1998), 'A new vicariance model for Amazon endemics', *Global Ecology and Biogeography Letters*, 7, 95–96.
- Derka, T. (2002), '*Massartella devani*, a New Mayfly Species from Venezuela's Highlands (Ephemeroptera: Leptophlebiidae: Atalophlebiinae)', *Aquatic Insects*, 24, 309–316.
- Domínguez, E., Molineri, C., Pescador, M.L., Hubbard, M.D., and Nieto, C. (2006), 'Ephemeroptera of South America', in *Aquatic Biodiversity in Latin America (ABLA)* (Vol. 2), eds. J. Adis, J.R. Arias, G. Ru-Delgado and K.M. Wantzen, Sofia-Moscow: Pensoft.
- Gibbs, A.K., and Barron, C.N. (1993), 'The geology of the Guyana Shield', *Oxford Monographs on Geology and Geophysics*, 22, 1–246.
- Haffer, J. (1997), 'Alternative models for vertebrate speciation in Amazonia: an overview', *Biodiversity and Conservation*, 6, 451–476.
- Hewitt, G.M. (2000), 'The genetic legacy of the Quaternary ice ages', *Nature*, 405, 907–913.
- Huber, O. (1988), 'Guyana highlands vs. Guyana lowlands, a reappraisal', *Taxon*, 37, 595–614.
- Huber, O. (1992), *El macizo del Chimantá. Un ensayo ecológico tepuyano*, Caracas: Oscar Todtmann, pp. 1–343.
- Huber, O. (1995), 'Geographical and physical features', in *Flora of the Venezuelan Guayana: Volume 1. Introduction*, eds. P.E. Berry, B.K. Holst and K. Yatskievych, St Louis: Missouri Botanical Garden Press, pp. 1–61.
- Huber, O. (2005), 'Diversity and vegetation types in the Guayana Region, an overview', *Biologiske Skrifter*, 55, 169–188.
- Hubert, N., and Reno, J.F. (2006), 'Historical biogeography of South American freshwater fishes', *Journal of Biogeography*, 33, 1414–1436.
- Láncoz, T., Schlögl, J., Smida, B., and Brewer-Carías, Ch. (2007), 'Preliminary results of the Tepuy 2007 expedition to the Venezuelan table mountains – water geochemistry and its relation to the genesis of the quartzite karst', in *Hydrogeochémia 07*, Bratislava: Slovenská Asociácia Hydrogeológov, pp. 136–141.
- Lestage, J.A. (1930), 'Notes sur le genre *Massartellanov.* gen. de la famille des Leptophlebiidae (Ephemeroptera) et le genotype *Massartella brieni* Lest.', *Une Mission Biologique Belge au Brésil*, 2, 249–258.
- Maguire, B. (1970), 'On the flora of the Guyana Highland', *Biotropica*, 2, 85–100.
- Nores, M. (1999), 'An alternative hypothesis to the origin of Amazonian bird diversity', *Journal of Biogeography*, 26, 475–485.
- Nores, M. (2004), 'The implications of Tertiary and Quaternary sea level rise events for avian distribution patterns in the lowlands of northern South America', *Global Ecology and Biogeography*, 13, 149–161.
- O'Donnell, B.C., and Jockusch, E.L. (2008), 'Phylogenetic relationships of leptophlebiid mayflies as inferred by *histone H3* and *28S ribosomal DNA*', *Systematic Entomology*, 33, 651–667.
- Pescador, M.L., and Peters, W.L. (1980), 'Phylogenetic relationships and zoogeography of cool-adapted Leptophlebiidae (Ephemeroptera) in southern South America', in *Advances in Ephemeroptera Biology*, eds. J.F. Flannagan and K.E. Marshall, Winnipeg, Manitoba: Plenum Press, pp. 43–56.
- Pescador, M.L., and Peters, W.L. (1990), 'Biosystematics of the Genus *Massartella* Lestage (Ephemeroptera: Leptophlebiidae: Atalophlebiinae) from South America', *Aquatic Insects*, 12, 145–160.
- Peters, W.L., and Edmunds, G.F., Jr. (1972), 'A revision of the generic classification of certain Leptophlebiidae from southern South America (Ephemeroptera)', *Annals of the Entomological Society of America*, 65, 1398–1414.
- Rull, V. (2004), 'An evaluation of the Lost World and Vertical Displacement hypotheses in the Chimantá Massif, Venezuelan Guayana', *Global Ecology and Biogeography*, 13, 141–148.

- Rull, V. (2005), 'Biotic diversification in the Guayana Highlands: a proposal', *Journal of Biogeography*, 32, 921–927.
- Rull, V. (2006), 'Quaternary speciation in the Neotropics', *Molecular Ecology*, 15, 4257–4259.
- Rull, V., and Nogué, S. (2006), 'Potential migration routes and barriers for vascular plants of the Neotropical Guyana Highlands during the Quaternary', *Journal of Biogeography*, 34, 1–16.
- Savage, H.M. (1987), 'Biogeographic classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon geological centers of ancestral origin and ecology', *Studies on Neotropical Fauna and Environment*, 22, 43–52.
- Steyermark, J.A., and Dunsterville, G.C.K. (1980), 'The lowland floral element on the summit of Cerro Guaiquinima and other corros of the Guayana highland of Venezuela', *Journal of Biogeography*, 7, 285–303.
- Šmída, B., Audy, M., and Vlček, L. (2003), 'Expedícia Roraima, Venezuela. Jaskyňa Kryštálové oči (Cueva Ojos de Cristal)', *Bulletin of the Slovak Speleological Society, Supplement*, 3, 1–178.
- Šmída, B., Brewer-Carías, Ch., and Audy, M. (2005), 'Speleoexpedície do vnútra masívu Chimantá (Venezuela) v roku 2004. Cueva Charles Brewer – Najväčšia kvarcitová jaskyňa sveta', *Bulletin of the Slovak Speleological Society*, 2, 1–190.
- Tsui, P.T.P., and Peters, W.L. (1975), 'The comparative morphology and phylogeny of certain gondwanian Leptophlebiidae based on the thorax, tentorium, and abdominal terga (Ephemeroptera)', *Transactions of the American Entomological Society*, 101, 205–595.
- Willis, K.J., and Whittaker, R.J. (2000), 'The refugial debate', *Science*, 281, 1406–1407.