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A NEW FOSSIL MAYFLY SPECIES OF THE GENUS *BORINQUENA* TRAVER, 1938 (INSECTA: EPHEMEROPTERA: LEPTOPHLEBIIDAE: ATALOPHLEBIINAE) FROM MIOCENE DOMINICAN AMBER

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Abstract.— The Neotropical mayfly genus *Borinquena* Traver, 1938 so far comprises three described extant species from the Caribbean basin. Furthermore, three fossil species from Dominican amber have been described in this genus. Based on a single male imago, *Borinquena schawallfussi* **sp. nov.** is described in this contribution as the fourth fossil species of *Borinquena* from Miocene Dominican amber. The new species clearly differs from all other fossil and recent representatives of the genus *Borinquena* in forewing colouration and venation, hind wing shape and venation, and in the shape of penis lobes and their ventral spines.

Key words.— Mayflies, Hagenulini, Neotropics, new species, Dominican amber, Miocene.

INTRODUCTION

The genus *Borinquena* was established by Traver (1938) for two Puerto Rican species, namely *B. carmencita* Traver, 1938 and *B. contradicens* Traver, 1938. Later on, Peters (1971) described the extant species *Borinquena traverae* from Dominica and placed it in a separate, new subgenus *Australphlebia* Peters, 1971 due to its lack of hind wings. In the same contribution, Peters mentioned another undescribed species of *Australphlebia* from St. Lucia, also characterized by the absence of hind wings. Pescador *et al*. (1993) provided information about yet another undescribed species of *Borinquena* from Puerto Rico. Two more species of *Borinquena* (*Australphlebia*) were reported by McCafferty (1985: 10) from Costa Rica, however with no details on the life stages of the material examined. Finally, Kluge (1994: 261) described a new Cuban species *Hagenulus* (*Borinquena*) *sextus* Kluge, 1994, based on imagines and associated larvae, thus treating *Borinquena* as subgenus of *Hagenulus*. Hofmann & Peters (1999) described *Hagenulopsis guadeloupensis* Hofmann & Peters, 1999, a species phenetically very similar to *Australphlebia traverae* and

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determined the synonymy of *Hagenulopsis* Ulmer, 1920 with *Australphlebia*. This point of view was later supported by Peters & Domínguez (2001).

All so far known fossil species of the genus *Borinquena* were described by Staniczek (2003) from Miocene Dominican amber. *Borinquena maculata* Staniczek, 2003 and *B. parva* Staniczek, 2003 are known from male imagines, while another species described as *Borinquena* (?) *caeciliana* Staniczek, 2003, was described from a well-preserved female imago. In this context, Staniczek (2003) also revised the distinguishing characters of *Borinquena*, redefined its diagnosis, and classified this taxon as distinctive genus. From the same deposits, a new monotypic genus *Hagenulites* Staniczek, 2003 with type species *H. hitchingsi* Staniczek, 2003 was also described (Staniczek 2003). Additionally, the phylogenetic relationships within the tribe Hagenulini Kluge, 1994 were reviewed and discussed in detail.

Godunko & Krzemiński (2009) described additional characters of *B. parva* from a well-preserved male adult specimen housed in the collection of the American Museum of Natural History (New York City, USA), and enhanced the diagnosis of this species. This specimen later was also briefly mentioned by Penney & Green (2011) and Penney *et al.* (2012) in connection with a phoretic association with Collembola. It should also be noted that the earliest reference to representatives of the subfamily Atalophlebiinae Peters, 1980 in Dominican amber, including the genera *Careospina* Peters, 1971 and *Borinquena*, had been published by Poinar (1992).

Thus, at present there are three recent species of *Borinquena* described from the Caribbean basin, namely *B. carmencita* and *B. contradicens* from Puerto Rico, and *B. sexta* from Cuba. With *B. caeciliana*, *B. maculata* and *B. parva* there are another three fossil species known from Miocene Dominican amber.

The objective of the present contribution is to describe the fourth fossil species, *B. schawallfussi* sp. nov., based on a male imago, and to present diagnostic characters distinguishing it from other recent and fossil Miocene representatives of the genus.

All records of recent and fossil species of *Borinquena* are restricted to the Greater Antillean, but notably no extant species of *Borinquena* is reported from Hispaniola. Closely related taxa previously included in this genus (i.e. *Australphlebia* Peters, 1971) or placed within *Hagenulus* Eaton, 1882 s.l. are restricted to Central and South America.

Material and methods

Line drawings were made using a Leica M205C stereo microscope with attached camera lucida or directly from photographs taken through a Leica Z16 APO Microscope, processed with Helicon Pro to obtain combined photographs with extended depth of field and subsequently enhanced with Adobe Photoshop CS5. Additional photographs were made with a Leica MZ FL III microscope with attached Leica DC 200. The holotype of the described species is deposited at the Institute of Systematics and Evolution of Animals (ISEA), Museum of Natural History, Polish Academy of Science, Kraków, Poland. Morphological terminology follows Tsui & Peters (1972), Kluge (1994, 2004), Staniczek (2003), and Godunko & Krzemiński (2009).

Systematic palaeontology

Order **Ephemeroptera** Hyatt and Arms, 1890

Family **Leptophlebiidae** Banks, 1900

Subfamily **Atalophlebiinae** Peters, 1980

Tribe **Hagenulini** Kluge, 1994

Genus ***Borinquena*** Traver, 1938

Borinquena schawallfussi sp. nov.
(Figs 1–9)

Holotype: Male imago, nr. ISEA/MP/2763, Miocene Dominican amber, in the collection of the Museum of Natural History, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences (Kraków, Poland). There is also one specimen of Auchenorrhyncha (Fulgoromorpha: Cixiidae: ? Bothriocerinae) present as syninclusion.

Diagnosis. The new species can be distinguished from other fossil and recent representatives of the genus *Borinquena* by the combination of following characters:

Forewing (Figs 3, 6): (i) anterior part between C and R translucent and hyaline; (ii) few cross veins surrounded by dark clouds; (iii) cubital field with two intercalaries, iCu_1 basally attached to CuP, and iCu_2 basally approximated to iCu_1, but detached from it. *Hind wing* (Fig. 7): (iv) not shortened, with relatively long and acute costal projection; (v) venation reduced to two longitudinal and two intercalary veins, not connected with wing base; *genitalia* (Figs 4–5, 8–9): (vi) styliger plate not elongated and narrow; (vii) posterior margin of styliger plate with shallow indentation mediodistally and small projection centrally; (viii) inner margin of first segment of gonostyli distally without visible hairs; (ix) penis lobes pointed apically, divided, nearly parallel sided except slightly convergent tips; (x) ventral spines of penis lobes relatively large, placed at an angle about 65–70° to the longitudinal axis of lobes.

Description of holotype.

Partly damaged specimen, well visible from dorsal and lateral sides. Most part of right forewing, tip of left forewing, tarsi of right hind leg, and most part of caudal filaments lost. For measurements see Table 1; for general view of specimen see Fig. 1.

Head yellowish to light brown. Frons with three well-developed ocelli; median one much smaller than lateral ocelli. Compound eyes contiguous medially, with two distinct portions; upper portion brownish, flattened, with square facets; lower portion paler. Antennae yellowish, with slightly darker first two segments (Fig. 2).

Thorax mainly unicolour, light brown to brown, with irregular smudges on meso- and metathorax; lateral sides light brown. Arrangement of mesonotal sutures similar to those described by Tsui & Peters (1972) and Kluge (1994) (Fig. 2).

Legs yellowish to light brown, partly translucent; forelegs with slightly darker tip of tibia and tarsi, covered with irregular blackish spots. Patello-tibial suture distinct in all legs. Tarsi four-segmented. Ratio of foreleg tarsal segments I/II/III/IV = 1/0.84/0.51/0.18. All tarsal claws dissimilar with one hooked and one blunt claw.

Forewings hyaline, translucent. Wing venation is described based on almost completely preserved left forewing. Longitudinal and cross venation well visible, yellowish to light brown; cross venation not rich, all cross veins surrounded by dark brownish clouds; field between C and R uncoloured, translucent, and hyaline (Figs 3, 6). Costal field with at least 9 simple cross veins; vein RS forked less than $^1/_4$ [approximately 0.21] of distance between base and wing margin; vein MA forked less than half [0.35] of vein length, asymmetrical, with slightly sagged MA_2; vein MP forked less than $^1/_3$ [0.27] of distance from base to wing margin, with nearly symmetrical fork; iCu_1 basally attached to CuP; iCu_2 basally approximated to iCu_1, but detached from it; A_1 and A_2 parallel to CuP (Figs 3, 6).

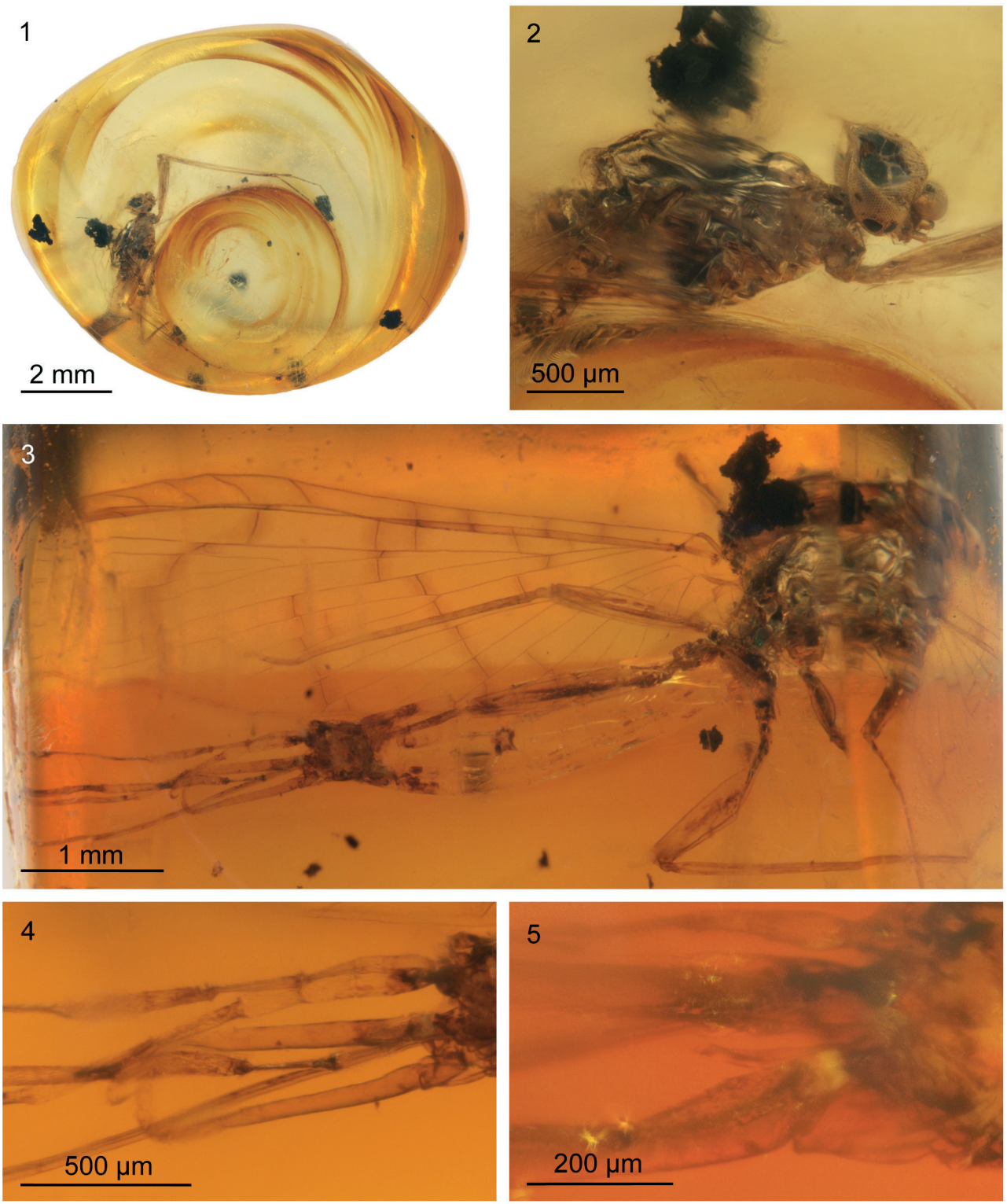
Hind wings very small, 1.87× longer than wide (without costal projection), translucent, with relatively long and acute costal projection (Fig. 7). Venation reduced to two longitudinal veins, two additional intercalary veins not connected with wing base; two upper veins with common stem basally, forked at $^1/_4$ of entire length, and inserting by two branches at the base of costal projection; one of these branches secondarily branched closely to wing margin (Fig. 7).

Genitalia yellowish to brownish. Styliger plate hardly visible ventrally, not elongated, narrow, approximately two times longer than wide; posterior margin of styliger with shallow indentation mediodistally and small projection medially. Bases of gonostyli medially close to each other, distinctly longer than wide. Gonostyli each with three segments; segment I extremely

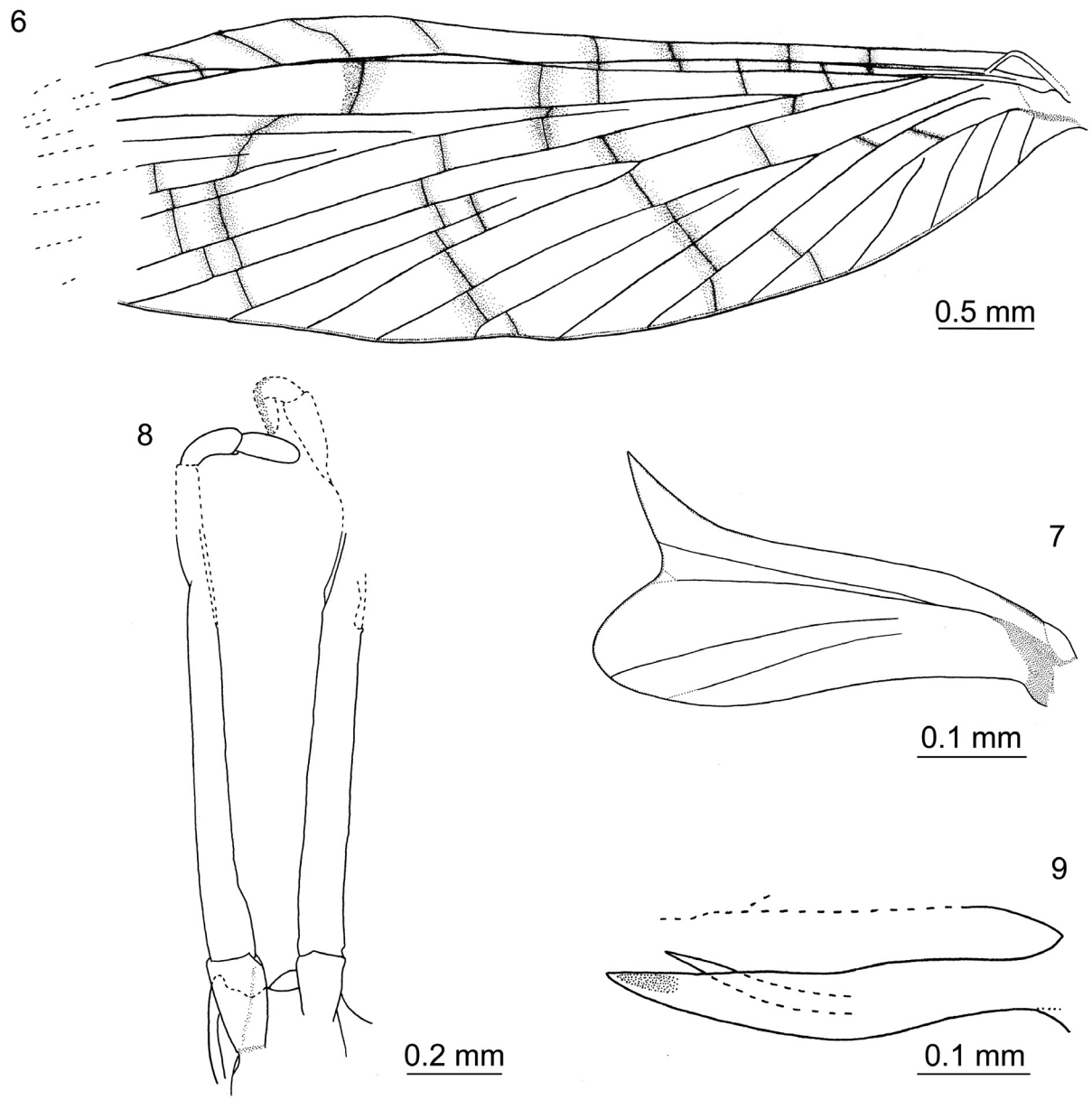
Table 1. Measurements of *Borinquena schawallfussi* sp. nov., holotype, male imago, ISEA/MP/2763.

Characters	Measurements (mm)
Length of body	5.38
Length of right foreleg	6.46
Length of femur	1.33
Length of tibia	2.60
Length of tarsus	2.53
Segment I	1.00
Segment II	0.85
Segment III	0.50
Segment IV	0.18
Length of left foreleg	6.61
Length of femur	1.38
Length of tibia	2.63
Length of tarsus	2.60
Segment I	1.03
Segment II	0.85
Segment III	0.53
Segment IV	0.19
Length of right middle leg	3.82
Length of femur	1.33
Length of tibia	2.10
Length of tarsus	0.39
Segment I	0.10
Segment II	0.09
Segment III	0.07
Segment IV	0.13
Length of left middle leg	3.87
Length of femur	1.30
Length of tibia	2.13
Length of tarsus	0.44
Segment I	0.10
Segment II	0.10
Segment III	0.09
Segment IV	0.15
Length of right hind leg	4.28
Length of femur	1.50
Length of tibia	2.33
Length of tarsus	0.45
Segment I	0.12
Segment II	0.11
Segment III	0.10
Segment IV	0.12
Length of left hind leg	3.65*
Length of femur	1.45
Length of tibia	2.20*
Length of tarsus	–
Segment I	–
Segment II	–
Segment III	–
Segment IV	–
Length of right forewing	1.75*
Length of left forewing	5.38*
Length of right hind wing	0.50
Length of left hind wing	0.50
Length of right cercus	2.25*
Length of left cercus	2.43*
Length of paracercus	2.38*

* – preserved part



Figures 1–5. *Borinquena schawallfussi* sp. nov., holotype, male imago, nr. ISEA/MP/2763, Miocene Dominican amber, collection MNH ISEA PAS, photographs. (1) total view of specimen in piece of amber; (2) lateral view of head and thorax, right side; (3) lateral view of abdomen and forewing, right side; (4) end of abdomen with gonostyli, cerci, and paracercus, dorsal view; (5) right penis lobe, dorsal view.



Figures 6–9. *Borinquena schawallfussi* sp. nov., holotype, male imago, nr. ISEA/MP/2763, Miocene Dominican amber, collection MNH ISEA PAS, line drawings. (6) right forewing, ventral view; (7) right hind wing, ventral view; (8) gonostyli, dorsal view (penis lobes and cerci are not depicted); (9) right penis lobe, dorsal view.

elongated, straight, with slightly curved inner margin, distally slightly arcuated; lacking of visible hairs on inner margin of first segment distally. Segments II and III of gonostyli short, approximately of equal length. Ratio of gonostyli segments I/II/III = 1.00/0.14/0.13 (Figs 4, 8).

Penis lobes divided by distinct V-shaped incision; main part of lobes subparallel, only tip of lobes slightly convergent; ventral spine well developed on each of lobe, relatively large, placed at an angle about 65–70° to longitudinal axis of lobe (Figs 5, 9). Left penis lobe hardly distinguishable, similar to right lobe (Fig. 9).

Abdominal segments completely preserved, abdominal segments partly flattened; segments I–VII translucent, segments VIII–X yellowish to light brown; small posterolateral projections on segments IX and X (Fig. 3). Caudal filaments partly preserved, brown to dark brown; preserved part of paracercus of same thickness as cerci (suggesting that paracercus was fully developed).

Discussion

The systematic position of *B. schawallfussi* sp. nov. within the genus *Borinquena* can be clearly confirmed by the following combination of male imaginal characters: (i) first segment of gonostyli distinctly elongated and straight; (ii) penis lobes divided, at least basally tubular (see Traver 1938: 17; Peters 1971: 26; Kluge 1994: 261; Staniczek 2003: 17). Additionally, shape of hind wings with well-developed costal process is similar to those in all other species of *Borinquena*. Except of *B. parva*, all other recent and fossil taxa of this genus (including *B. schawallfussi* sp. nov.) are also characterized by the presence of a more or less protruding subapical spine on the ventral side of each penis lobe.

Forewing venation of *B. schawallfussi* sp. nov. generally similar to the majority of other species of *Borinquena*: Costal field with several unbranched cross veins, similar to those in other recent and fossil species (except for Miocene *B. caeciliana*), lack of cross veins in costal and subcostal fields (Staniczek 2003: 13). Small differences between the new species and other representatives of the genus can be found in the locations of RS, MA, and MP vein furcations. In *B. schawallfussi* sp. nov., the furcation of each of these veins is much closer to the wing base than in other species of *Borinquena* (Figs 3–4). *B. schawallfussi* sp. nov. can be characterized by the presence of two cubital intercalaries: iCu_1 basally attached to CuP; and iCu_2 basally approximated to iCu_1, but separated from it. In this character, the new species clearly differs from the fossil species *B. caeciliana,* known as female subimago only (Staniczek 2003: 14, fig. 21).

Significant differences among the recent and fossil taxa of *Borinquena* also exist in colouration of forewings. Costal and subcostal field except of clouded cross veins uncoloured, translucent and hyaline in *B. schawallfussi* sp. nov., in contrast to only slightly darker fields in fossil *B. maculata*, and in contrast to costal field and basal part of subcostal field brownish shaded in the extant *B. sexta* (compare our Figs 3–4 to Kluge 1994: 263, 264: fig. 57; and Staniczek 2003: 8, 9: figs 10, 11).

Cross veins are few, surrounded by dark brownish clouds in the new species, in contrast to numerous cross veins without any surrounding clouds in all recent species of *Borinquena* and in fossil *B. parva*, or few cross veins without any accompanying clouds in *B. caeciliana* (Staniczek 2003: 12, 14, figs 16, 17, 20, 21; Godunko & Krzemiński 2009: 133, fig. 7). Only one fossil species, *B. maculata*, is also characterized by presence of dark clouds surrounding cross veins (Staniczek 2003: 8, 9, fig. 11).

The shape of hind wings of *B. schawallfussi* sp. nov. generally matches all other species of *Borinquena*. However, the new species can be easily separated from extant *B. carmencita* and *B. sexta* by its larger distal part of hind wing. The shape of costal projection in *B. schawallfussi* sp. nov. is different from fossil *B. caeciliana* (compare our Fig. 5 with Staniczek 2003: 14, 15, figs 21, 24d).

The hind wing venation of the new species (Fig. 7) is closest to Miocene *B. maculata* and *B. parva* (Staniczek 2003: 15, fig. 24b, c; Godunko & Krzemiński 2009: 133, fig. 8), and is characterised by a basally bifurcated vein anteriorly, and additional veins posteriorly. Among extant species of *Borinquena,* a similar arrangement of hind wing venation is recognized both in the Puerto Rican *B. contradicens* and Cuban *B. sexta* (compare our Fig. 7 to Traver 1938, plate III, fig. 50; Peters 1971: 37, fig. 71; Kluge 1994: 263, fig. 53).

The genitalia of *B. schawallfussi* sp. nov., particularly the shape of gonostyli, closely resemble other species of *Borinquena* (see above). Nevertheless, the new species can be easily separated from some recent and fossil representatives by the shape of styliger, including a shallow indentation mediodistally and a small projection centrally. In the extant *B. carmencita*, and in the Miocene *B. maculata* and *B. parva,* the styliger is without central projection, but with medially concave posterior margin. The shape of the styliger plate in *B. schawallfussi* sp. nov. closely resembles two recent species, i.e. *B. contradicens* and *B. sexta*.

More significant differences between all taxa referred above can be found in the shape and structure of their penis lobes. The new species clearly occupies an intermediate position between the Miocene *B. maculata* and *B. parva* (compare our Figs 7, 9 to Staniczek 2003: 8, 9, 12, 13: figs 12, 18, 19; Godunko & Krzemiński 2009: 133, 134, figs 9, 10): (**i**) penis lobes are tubular-like only basally, pointed apically, deeply incised and nearly parallel sided, except slightly convergent tips in *B. schawallfussi* sp. nov. (in contrast to tubular, curved, and clearly convergent lobes of *B. parva*, and in contrast to tubular and largely fused lobes in *B. maculata*); (ii) ventral spines of penis lobes are more robust and positioned at different angle, whereas in the Miocene species *B. maculata* the ventral spines are small and oriented perpendicularly to the longitudinal axis of lobes, and in *B. parva* spines are completely missing. The presence of ventral penial spines in *B. schawallfussi* sp. nov. thus adds additional support to the assumption that the lack of spines in *B. parva* represents a secondarily developed trait within the genus (Staniczek 2003: 17). Some similarity of the shape of penis lobes can be also traced between *B. schawallfussi* sp. nov. and the extant species *B. contradicens* and *B. sexta*. However, the penis lobes of the latter species are clearly less separated, partially fused, in contrast to distinctly divided lobes of the new species.

Extant species of *Borinquena* inhabit tropical rain forest streams and show peak emergence from October through December, but adults of *B. carmencita* were also found throughout the year in fewer numbers (Pescador *et al*. 1993). We may assume that fossil species of *Borinquena*, including *B. schawallfussi*, had a similar phenology.

Etymology. The new species is named in honour of the mythical German entomologist Dr. Wolfmut Schawallfuss, actually a portmanteau name amalgamised from two former long-time curators of the SMNS, Dr. Wolfgang Schawaller and Dr. Helmut Schmalfuss. The names of both scientists were frequently muddled up by visitors and SMNS staff alike to a point that eventually some colleagues assumed the existence of a certain "Dr. Schawallfuss" at the SMNS.

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References

Hofmann, C. and W. L. Peters. 1999. *Hagenulopsis guadeloupensis* Hofmann & Peters. *In*: Hofmann, C., Sartori, M. & Thomas, A. (Eds). Les Ephéméroptères (Ephemeroptera) de la Guadeloupes (Petites Antilles français). Mémories de la Société Vaudoise des Sciences Naturelles, 20: 82–93.

Godunko, R. J. and W. Krzemiński. 2009. New fossil findings of the mayfly genera *Balticobaetisca* Staniczek & Bechly, 2002 (Ephemeroptera: Baetiscidae) and *Borinquena* Traver, 1938 (Leptophlebiidae: Atalophlebiinae). Aquatic Insects, 31 (Suppl. 1), 125–136.

Kluge, N. J. 1994. A revision of Leptophlebiidae of Cuba (Insecta, Ephemeroptera). Zoosystematica Rossica, 2(2): 247–285.

Kluge, N. J. 2004. The phylogenetic system of Ephemeroptera. Dortrecht, Kluwer, 1–442.

McCafferty, W. P. 1985. New records of Ephemeroptera from Middle America. International Quarterly of Entomology, 1(1): 9–11.

Penney, D. and D. I. Green. 2011. Fossils in Amber: Remarkable Snapshots of Prehistoric Forest Life. Siri Scientific Press, 98–99.

Penney, D., McNeil, A., Green, D. I., Bradley, R., Jepson, J. E., Whithers, P. J. and R. F. Preziosi. 2012. Ancient Ephemeroptera–Collembola symbiosis predicts contemporary phoretic associations. PLoSONE, 7(10): e47651.

Pescador, M. L., Masteller, E. C. and K. M. Buzby. 1993. Composition and Phenology of Ephemeroptera from Tropical Rainforest Stream at El Verde, Puerto Rico. Journal of the Kansas Entomological Society, 66(2): 151–159.

Peters, W. L. 1971. A revision of the Leptophlebiidae of the West Indies (Ephemeroptera). Smithsonian Contributions to Zoology, 62: 1–48.

Peters, W. L. and E. Domínguez. 2001. The identity of *Hagenulopsis minuta* Spieth (Leptophlebiidae: Atalophlebiinae). *In*: Dominguez, E. (Ed.). Trends in research in Ephemeroptera and Plecoptera. Proc. IX Int. Conf. on Ephemeroptera & XIII Int. Symp. on Plecoptera, Kluwer Academic/Plenum Press, New York, 353–358.

Poinar, G. O. 1992. Life in Amber. Stanford University Press. Stanford/Connecticut, 350 pp.

Staniczek, A. H. 2003. New fossil mayflies from Dominican amber (Insecta: Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Stuttgarter Beiträge zur Naturkunde (Ser. B. Geologie und Paläontologie), 341: 1–22.

Traver, J. R. 1938. Mayflies of Puerto Rico. Journal of Agriculture of the University of Puerto Rico, 22: 5–42, pl. 1–3.

Tsui, P. T. P. and W. L. Peters. 1972. The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera). Journal of Zoology, 168(3): 309–367.

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