Stuttgarter Beiträge zur Naturkunde
Serie B (Geologie und Paläontologie)

Herausgeber:

Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 341	22 pp., 24 figs.	Stuttgart, 15. 12. 2003

New fossil mayflies from Dominican amber (Insecta: Ephemeroptera: Leptophlebiidae: Atalophlebiinae)

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With 24 Figures

Abstract

New fossil Hagenulini (Insecta: Ephemeroptera) from Dominican amber are described: *Hagenulites hitchingsi* n.g., n.sp., *Borinquena maculata* n.sp., *Borinquena parva* n.sp., and *Borinquena (?) caeciliana* n.sp. are the first fossil records for these taxa. The diagnosis of *Borinquena* is redefined and the phylogenetic implications of these findings are discussed.

Zusammenfassung

Neue fossile Hagenulini (Insecta: Ephemeroptera) aus dem Dominikanischen Bernstein werden beschrieben: *Hagenulites hitchingsi* n.g., n.sp., *Borinquena maculata* n. sp., *Borinquena parva* n.sp. und *Borinquena (?) caeciliana* n.sp. sind die ersten Fossilnachweise für diese Taxa. Die Diagnose von *Borinquena* wird neu definiert und die phylogenetischen Implikationen dieser Neufunde werden diskutiert.

1. Introduction

The mayfly family Leptophlebiidae is distributed worldwide and is one of the most diverse mayfly taxa. Within the Leptophlebiidae there are three subfamilies presently distinguished (KLUGE 1994b), among which the monophyletic Atalophlebiinae are mainly distributed in the southern hemisphere, due to their Gondwanian origin (SAVAGE 1987). There are several fossil records of Leptophlebiidae (HUBBARD & SAVAGE 1981, HUBBARD 1987, KEILBACH 1982, SPAHR 1992, KLUGE 1993, PETERS & PETERS 2000, WEITSCHAT & WICHARD 2001). However, some of these fossils (e.g. *Xenophlebia*, DEMOULIN 1968, *Conovirilus*, MCCAFFERTY 1997) can only be tentatively placed within the Leptophlebiidae (see KLUGE 1993 and PETERS & PETERS 2000). Others (e.g. *Cretoneta*, TSHERNOVA 1971) have now been transferred to other families (see KLUGE 1993). The fossil records of Atalophlebiinae are very scarce (RIEK 1954). Although abundant in the Neotropical fauna not a single species of Atalophlebiinae has yet been formally described from Dominican amber.

This is surprising given the fact that amber from the Dominican Republic is considered one of the most important deposits for fossil insects. Only POINAR (1992) briefly mentions leptophlebiids from Dominican amber. A search for mayflies within the amber collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS), the Florida State Collection of Arthropods (FSCA), and additional sources yielded numerous undescribed species of Hagenulini. The latter is a tribe within the Atalophlebiinae (KLUGE 1994a) to which extant leptophlebiid mayflies of the West Indies belong (PETERS 1971, SAVAGE 1987).

Methods

All drawings were made with a camera lucida on a Wild M5 binocular microscope. Photographs were made with a Nikon Coolpix 995 digital camera on the same microscope using a photo adapter. Photographs were digitally processed in Adobe Photoshop 5.0 to combine several original photos with different depths of field. The anatomical terminology is based on PETERS (1971) and KLUGE (1994c).

Acknowledgements

I am most grateful to Mrs J. G. PETERS (Laboratory of Aquatic Entomology, Florida A&M University, Tallahassee, Fla., USA) for making available Hagenulini from Dominican amber and for many valuable comments on an earlier draft of this manuscript. I also thank Dr G. BECHLY and Dr G. BLOOS (both SMNS, Stuttgart) for careful proof-reading of this manuscript, and Mr T. HITCHINGS (Canterbury Museum, Christchurch, New Zealand) for his help with the English.

2. Systematic Palaeontology

Class Insecta LINNAEUS, 1758
Pterygota BRAUER, 1885
Order Ephemeroptera HYATT & ARMS, 1890
Family Leptophlebiidae BANKS, 1900
Subfamily Atalophlebiinae PETERS, 1980
Tribe Hagenulini KLUGE, 1994

Genus *Hagenulites* n. g.

Type species: *Hagenulites hitchingsi* n. sp.

Derivation of name: Named after the similarity with the extant genus *Hagenulus*. The suffix *–ites* denotes that this genus is only known from fossils.

Diagnosis. – Same as type species since monotypic.

Hagenulites hitchingsi n. sp.

Figs. 1-7, 24a

Holotype: Male specimen no. SMNS DO-3276-M in the amber collection of the Staatliches Museum für Naturkunde Stuttgart, Germany.

Type locality: Dominican Republic, precise mine unknown.

Type horizon: Tertiary, Eocene to Miocene (SCHLEE 1990) but precise age is unknown, Dominican amber.

Derivation of name: Named in honour of ephemeropterist Terry R. Hitchings of Canterbury Museum, Christchurch, New Zealand.

Fig. 1. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, lateral habitus, photo. Scale 30 mm.

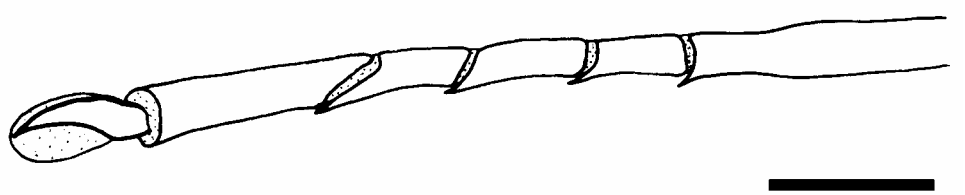

Fig. 2. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, right hind leg. Scale 0.1 mm.

Fig. 3. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, right forewing, photo. Scale 14 mm.

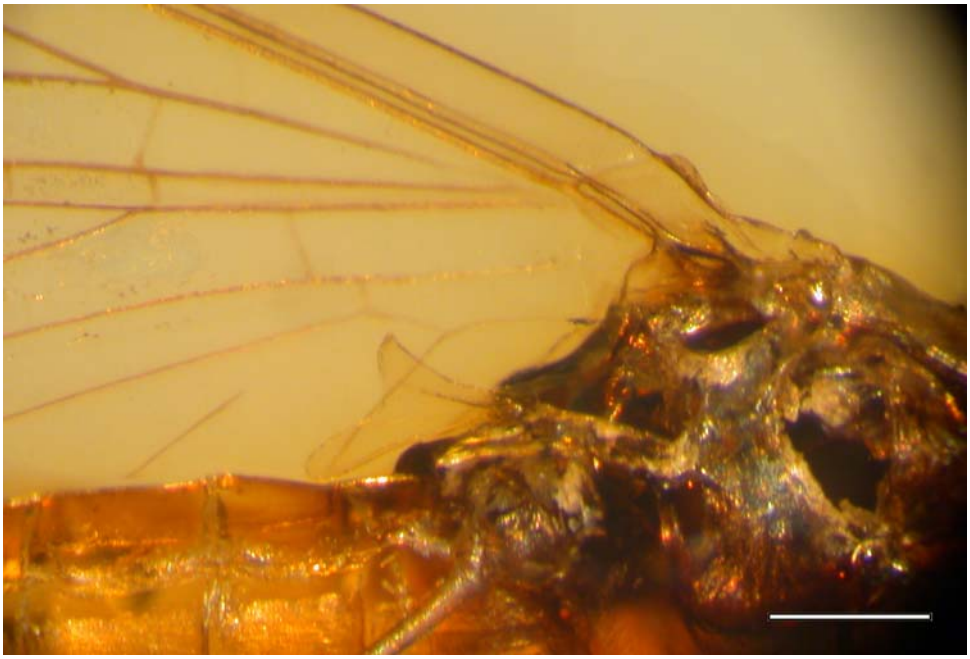

Fig. 4. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, right hind wing, photo. Scale 0.4 mm.

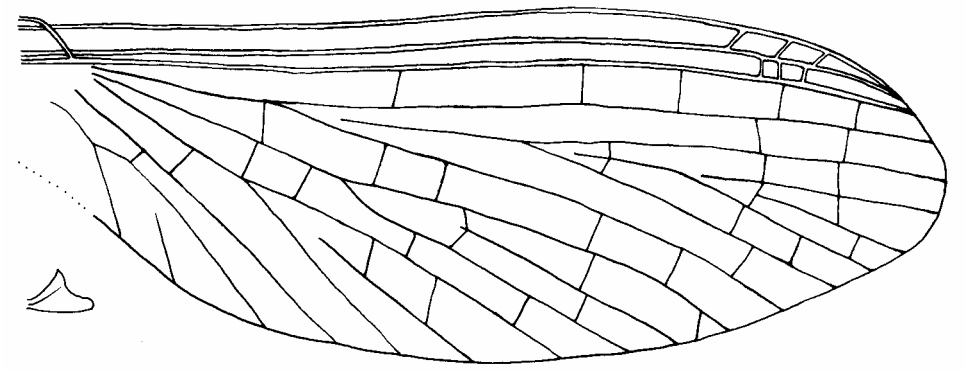

Fig. 5. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, reconstructed wings. Without scale.

Diagnosis.–*Hagenulites hitchingsi* n. sp. is characterised by the following combination of characters: hind wing with acute costal projection, forewing with asymmetrical fork of MA (MA1 basally straight, MA2 basally curved) and symmetrical fork of MP, dissimilar imaginal claws, ICu1 basally attached to CuP, anal veins lacking, forewings entirely hyaline, crossveins not surrounded by dark clouds, costal and subcostal field of forewing with only few crossveins in the pterostigmatic region, hind wing with only one longitudinal vein, first segment of forceps basally broad, its inner margin forming an angular bend, penes apically divergent, each with ventromedial subapical spine.

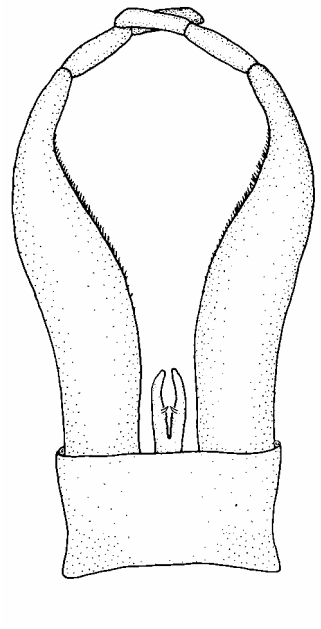

Fig. 6. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, genitalia in ventral view, photo.Scale 0.4 mm.

Fig. 7. *Hagenulites hitchingsi* n. sp., male holotype SMNS DO-3276-M, reconstructed genitalia in ventral view. Without scale.

Description. – A male imago preserved in Dominican amber (Fig. 1). Body length: 5 mm (without forceps and cerci). Right fore and middle leg broken. Right hind leg crippled, with miniaturised trochanter and femur, tibia and tarsus not developed. Right cercus entirely missing, left cercus and terminal filament partially broken off and not preserved.

Head. – Frons with three ocelli, median ocellus much smaller than the lateral ones. Compound eyes medially well separated and with two portions, anterodorsal portion with square facets. Length of antenna about 1.4x the length of head.

Thorax. – Small prothorax. Prosternum of triangular shape. Mesosternum with flat basisternum, the latter with median impression in its posterior half. Furcasternum medially well separated.

Legs (fig. 2). – Claws dissimilar with one hooked and one blunt claw. Tarsi with four separate tarsomeres. Length of middle leg 3.2 mm.

Wings (Figs. 3-5). – Forewing (Figs 3, 5): Length 4.4 mm. Wing entirely hyaline, without clouding. Costal field and subcostal field only apically with crossveins. Vein Rs forked less than one-fourth of distance frome base to margin, vein MA forked less than half of distance from base to margin, fork asymmetrical, MA2 sagged, vein MP forked at about one third of distance from base to margin, fork symmetrical, ICu1 basally attached to CuP, ICu2 basally detached from ICu1, anal veins lacking.

Hind wing (Figs. 4, 5): Length 0.4 mm, maximum width (without costal projection) 0.1 mm, with long acute costal projection, not extending past apex of hind wing, reduced venation with only one unforked longitudinal vein (apart from C), inserting at about half length of costal projection. Below costal projection slight longitudinal shading of wing, hind margin of wing thickened.

Male genitalia (Figs. 6, 7): styliger plate fused, forceps with three segments, length of forceps 0.6 mm. First segment of forceps long, in its distal half arcuated and

medially with short hairs. Segments two and three of forceps of equal length and short. Penes divided, divergent basally, converging apically and with ventral subapical spines.

Abdomen (Figs. 1, 2, 6): distinct posterolateral spines only on segments IX and X. Caudal filaments apically broken off and missing.

Genus *Borinquena* TRAVER, 1938

The genus *Borinquena* comprises three extant described species that are confined to the Greater Antilles. *B. carmencita* and *B. contradicens* are endemic to Puerto Rico (TRAVER 1938) and *B. sexta* is only known from Cuba (KLUGE 1994a). A forth de-scribed species, *Borinquena traverae* PETERS, 1971 has been transferred to *Hagenu-lopsis* by PETERS & DOMINGUEZ (2001). The male adult stages of *Borinquena* have a characteristic forceps: the basal straight part of its first segment is extremely elon-gated. This is a main diagnostic character of this taxon and also an autapomorphic character. The female adult stages have an extremely elongated egg guide that pro-trudes beyond the end of the abdomen. According to Kluge (1994a) the larvae of *Borinquena* can be distinguished from other Hagenulini by their elongated third segment of the labial palp. So far no fossil species of *Borinquena* has been described.

Borinquena maculata n. sp.
Figs. 8-12, 24b

Holotype: Male imago no. SMNS DO-3904-M in the amber collection of the Staatliches Museum für Naturkunde Stuttgart, Germany.

Type locality: Dominican Republic, precise mine unknown.

Type horizon: Tertiary, Eocene to Miocene (SCHLEE 1990) but precise age is unknown, Dominican amber.

Derivation of name: maculatus, lat. spotted, refers to the clouded cross veins of the forewings.

Diagnosis. – *Borinquena maculata* n. sp. is characterized by the following combination of characters: hind wing with acute costal projection and two longitudinal veins, one of which is forked, forewing with asymmetrical fork of MA (MA1 basally straight, MA2 basally curved), ICu1 basally attached to CuP, forewing crossveins of male surrounded by dark clouds, dissimilar imaginal claws, first segment of forceps basally extremely elongated and straight, penes tubular and parallel, with ventral subapical spine.

Description. – A male imago preserved in Dominican amber (Fig. 8). Body length: 5.5 mm (without forceps). The animal is embedded together with several other, still undescribed inclusions (Ephemeroptera: Baetidae; Diptera: Cecidomyidae, Bibionidae; Coleoptera: larva; Auchenorrhyncha) in an egg-shaped piece of amber (length 3.5 mm, width 2 mm). The specimen is only visible from its ventral side. The apex of the right forewing, the apical parts of the terminal filaments, and the tarsi of the forelegs are not preserved.

Head. – Frons with three ocelli, median ocellus much smaller than the lateral ones. Compound eyes with two portions, anterodorsal portion with square facets,

Fig. 8. *Borinquena maculata* n. sp., male holotype SMNS DO-3904-M, habitus in ventral view, photo. Scale 18 mm.

Fig. 9. *Borinquena maculata* n. sp., male holotype SMNS DO-3904-M, head in ventral view, photo. Scale 0.4 mm.

medially contiguous (Fig. 9). Length of antennal flagellum about twice the length of head.

Thorax. – Small prothorax. Prosternum of triangular shape. Mesosternum with flat basisternum, the latter with median impression in its posterior half. Furcasternum medially well separated.

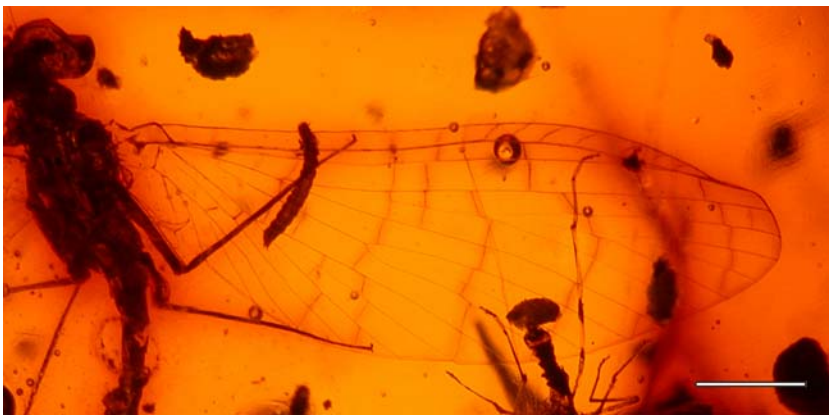

Fig. 10. *Borinquena maculata* n. sp., male holotype SMNS DO-3904-M, left forewing from ventrally, photo. Scale 0.8 mm.

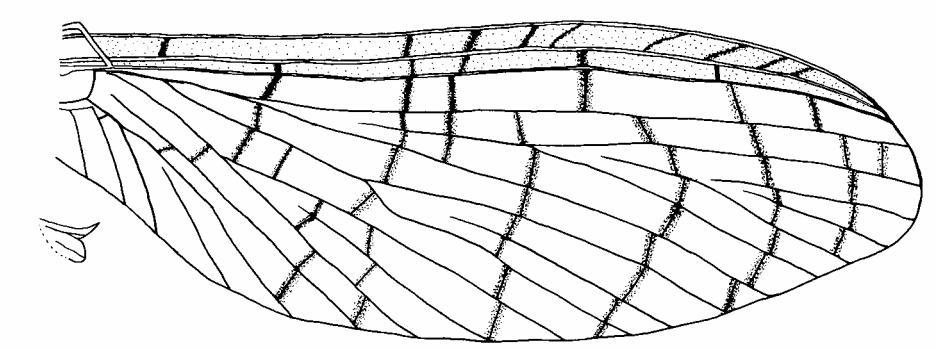

Fig. 11. *Borinquena maculata* n. sp., male holotype SMNS DO-3904-M, reconstructed wings. Without scale.

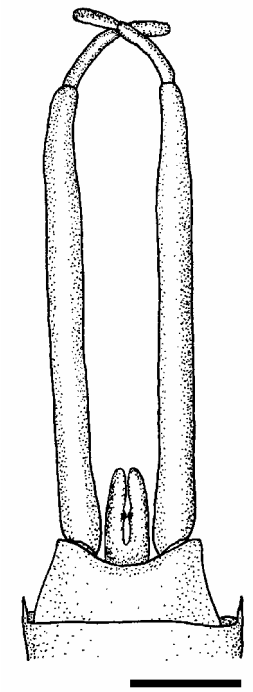

Fig. 12. *Borinquena maculata* n. sp., male holotype SMNS DO3904-M, genitalia in ventral view.

Legs. – All claws dissimilar with one hooked and one blunt claw. Preserved tarsi of fore and middle legs each with four separate tarsomeres. Length of middle leg 3.2 mm, hind leg 3 mm.

Wings. – Forewing (Figs. 10, 11): Length 5 mm, maximum width 2 mm. Costal field with crossveins. Vein Rs forked less than one-fourth of distance frome base to margin, vein MA forked less than half of distance from base to margin, fork asymmetrical, MA2 sagged, vein MP forked less than one third of distance from base to margin, fork symmetrical, ICu1 basally attached to CuP, ICu2 basally detached from CuP, A1 and A2 parallel to CuP. All short cross veins surrounded by dark clouds.

Hind wing (Fig. 11): Length 0.6 mm, maximum width (without costal projection) 0.16 mm, with long acute costal projection, reduced venation with only two longitudinal veins, both of which inserting at the base of costal projection, so the costal field does not extend apically beyond costal projection. Base of hind wings and accordingly base of longitudinal veins covered by middle femora and thus not visible.

Male genitalia (Fig. 12). – Styliger plate fused, mediodistally with slight indentation, length of styliger plate along median line about one third of maximum width. Forceps with three segments, length 1 mm. Basal segment of forceps extremely elongated, thin and straight, only in its very distal part medially slightly arcuated, its inner margin forming a slight curve. Segments two and three of forceps very short. Penes divided, tubular, parallel and straight, slightly convergent apically, with a pair of small subapical spines ventrally.

Abdomen (Fig. 8). – Distinct posterolateral spines only on segments IX and X. Caudal filaments apically broken off and missing.

Borinquena parva n. sp.

Figs. 13-19, 24c

Holotype: Male imago, amber collection of the Florida State Collection of Arthropods, coll. Woodruff

Type locality: Dominican Republic, precise mine unknown.

Type horizon: Tertiary, Eocene to Miocene (SCHLEE 1990) but precise age is unknown, Dominican amber.

Derivation of name: parvus, lat. small, refers to the small body size of this species.

Diagnosis. –*Borinquena parva* n. sp. is characterized by the following combination of characters: hind wing with acute costal projection, forewing with asymmetrical fork of MA (MA1 basally straight, MA2 basally curved), dissimilar imaginal claws, ICu1 basally attached to CuP, forewing crossveins of male not surrounded by dark clouds, first segment of forceps extremely elongated and straight, penes divided, apically convergent, without ventromedial spines.

Description. – A male imago preserved in Dominican amber (Fig. 13, 14). Body length: 3 mm (without forceps). Abdomen and forceps dorsally covered by thick layers of filamentous fungus hyphen. Both fore legs and left middle leg crippled, with miniaturised trochanteres and femora, tibiae and tarsi not developed. Left hind leg, cerci and terminal filament broken off and not preserved.

Head. – Frons with three ocelli, median ocellus much smaller than the lateral ones. Compound eyes with two portions, anterodorsal portion with square facets, medially contiguous (Fig. 15). Length of antenna about 1.4x the length of head.

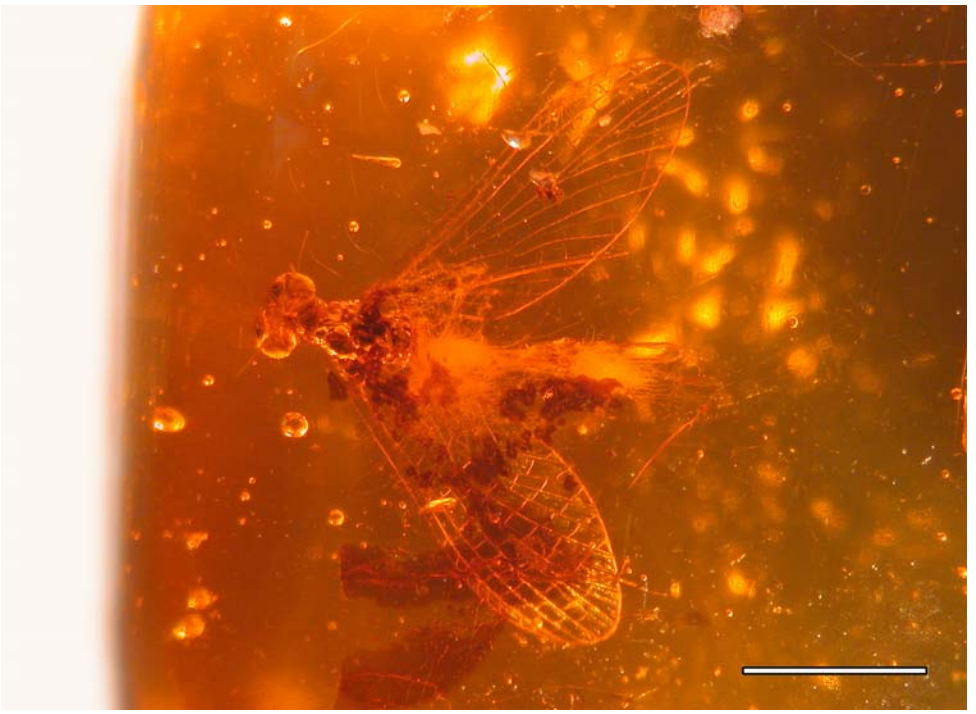

Fig. 13. *Borinquena parva* n. sp., male holotype, FSCA, habitus in dorsal view, photo. Scale 18 mm.

Fig. 14. *Borinquena parva* n. sp., male holotype, FSCA, habitus in ventral view, photo. Scale 18 mm.

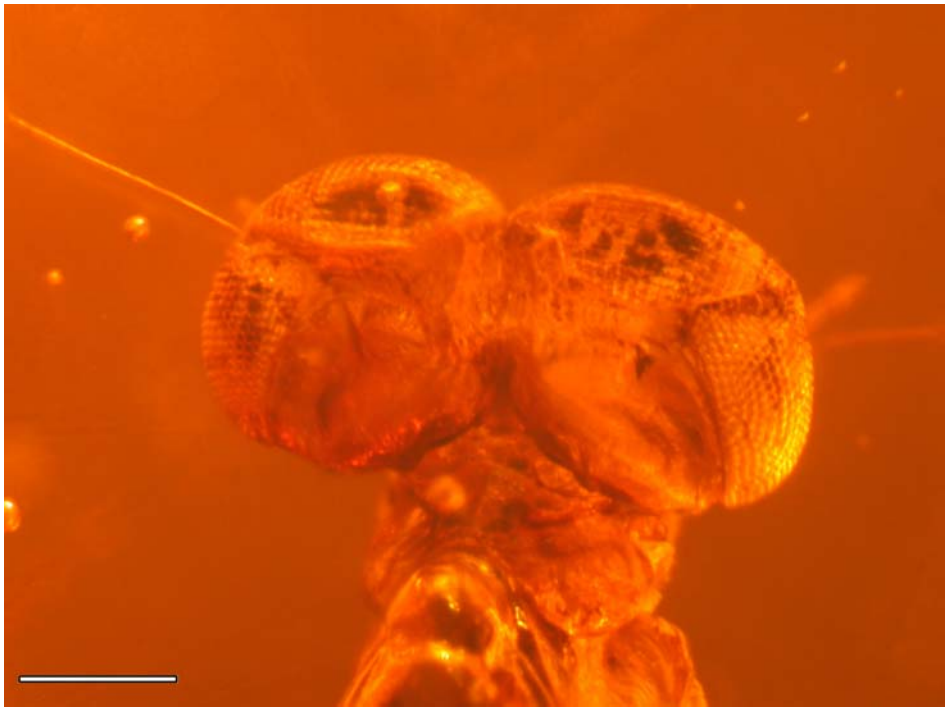

Fig. 15. *Borinquena parva* n. sp., male holotype, FSCA, head in dorsal view, photo. Scale 0.2 mm.

Fig. 16. *Borinquena parva* n. sp., male holotype, FSCA, right forewing in dorsal view, photo. Scale 0.8 mm.

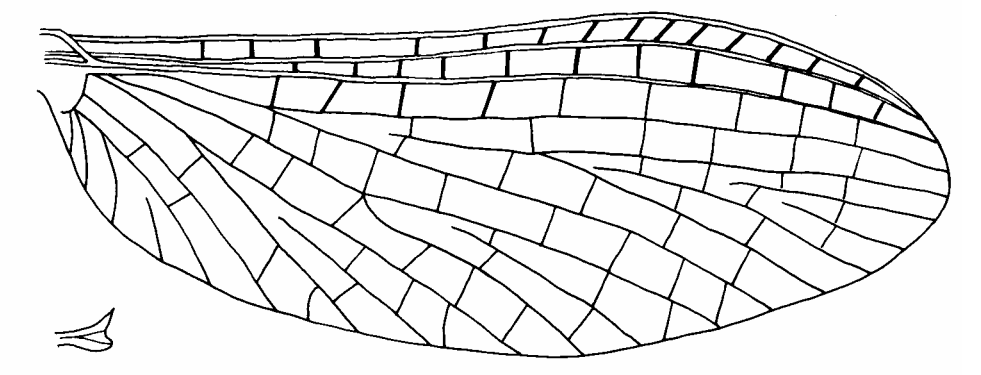

Fig. 17. *Borinquena parva* n. sp., male holotype, FSCA, reconstructed wings. Without scale.

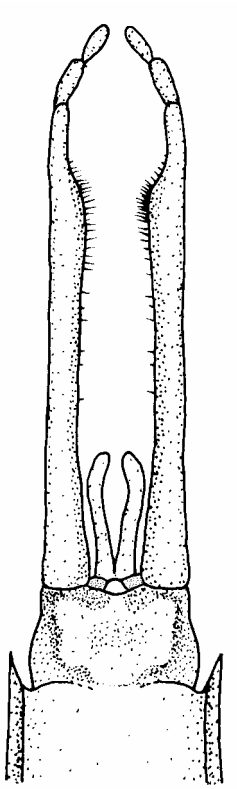

Fig. 18. *Borinquena parva* n. sp., male holotype, FSCA, genitalia in ventral view, photo. Scale 0.2 mm.

Fig. 19. *Borinquena parva* n. sp., male holotype, FSCA, reconstructed genitalia in ventral view. Without scale.

Thorax. – Small prothorax. Prosternum of triangular shape. Mesosternum with flat basisternum, the latter with median impression in its posterior half. Furcasternum medially well separated.

Legs. – Preserved claws dissimilar with one hooked and one blunt claw. Preserved tarsi of middle and hind leg each with four separate tarsomeres. Length of middle leg 2.8 mm.

Wings. – Forewing (Fig 16, 17): Length 4 mm, maximum width 1,6 mm. Wing entirely hyaline, without clouding. Vein Rs forked less than one-fourth of distance frome base to margin, vein MA forked less than half of distance from base to margin, fork asymmetrical, MA2 sagged, vein MP forked less than one third of distance from base to margin, fork symmetrical, ICu1 basally attached to CuP, ICu2 basally detached from CuP, A1 and A2 parallel to CuP.

Hind wing (Fig. 17): Length 0.3 mm, maximum width (without costal projection) 0.1 mm, with long acute costal projection, reduced venation with only one longitudinal forked vein, its anterior branch inserting at the base of costal projection.

Male genitalia (Figs. 18, 19). – Styliger plate fused, apically with slight medial indentation, length of styliger plate along median line about two thirds the maximum width. Forceps with three segments, length 1 mm. Basal segment of forceps extremely elongated, thin and straight, only in its very distal part medially slightly arcuated, its inner margin forming a slight angular bend. First segment in its apical half medially with short hairs. Segments two and three of forceps very short. Penes divided and divergent, apically converging, without subapical spines.

Abdomen (Figs 13, 14, 18 and 19). – Distinct posterolateral spines only on segments IX and X. Caudal filaments apically broken off and missing.

Borinquena (?) caeciliana n. sp.
Figs. 20-23, 24d

Holotype: Female subimago no. SMNS DO-5384-H in the amber collection of the Staatliches Museum für Naturkunde Stuttgart, Germany.

Type locality: Dominican Republic, precise mine unknown.

Type horizon: Tertiary, Eocene to Miocene (SCHLEE 1990) but precise age is unknown, Dominican amber.

Derivation of name: Named in honour of my late mother, Cäcilie Staniczek.

Diagnosis. – *Borinquena (?) caeciliana* n. sp. is characterized by the following combination of characters: hind wing with acute costal projection, forewing with asymmetrical fork of MA (MA1 basally straight, MA2 basally curved), dissimilar imaginal claws, ICu1 basally attached to CuP, costal field of forewing with few cross veins apically, long egg guide protruding beyond end of abdomen and with two distal broadenings, one of which is located subapically on dorsal side of the egg guide, the second one is located apically on the ventral side of the egg guide.

Description. – A female subimago preserved in Dominican amber (Fig. 20). Body length: 3.5 mm (without cerci). All legs preserved, right cercus and terminal filament entirely missing. Head and thorax in-between the border of two amber layers and only partly visible.

Legs. – Claws dissimilar with one hooked and one blunt claw. Tarsi with four separate tarsomeres. Length of middle leg 2.8 mm.

Wings. – Forewing (Figs. 20, 21): Length 5 mm. Wing entirely hyaline, without clouding. Costal field and subcostal field basally without crossveins. Vein Rs forked less than one-fourth of distance frome base to margin, vein MA forked at about half of distance from base to margin, fork asymmetrical, MA2 sagged, vein MP forked at about one third of distance from base to margin, fork symmetrical, ICu1 basally attached to CuP, A1 parallel to CuP.

Fig. 20. *Borinquena (?) caeciliana* n. sp., female subimago, holotype, SMNS DO-5384-H, habitus in dorsal view, photo. Scale 22 mm.

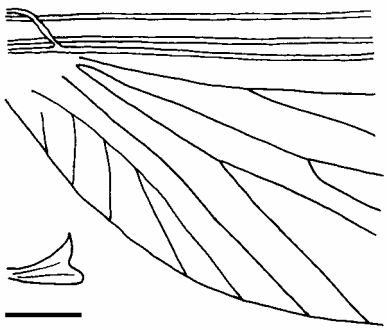

Fig. 21. *Borinquena (?) caeciliana* n. sp., female subimago, holotype, SMNS DO-5384-H, forewing base and hind wing. Scale 0.4 mm.

Hind wing (Figs. 21, 24): Length 0.4 mm, maximum width (without costal projection) 0.1 mm, with long acute costal projection, not extending past apex of hind wing, reduced venation with two distinct unforked longitudinal veins.

Female genitalia (Figs. 22, 23). – Abdominal sternites VII and VIII caudally extended to form a long egg guide extending beyond the apex of abdomen. Egg guide with a small subapical projection on its dorsal side and a ventral apical extension.

Abdomen (Figs. 20, 22, 23). – Distinct posterolateral spines only on segments IX and X. Terminal filament and right cercus basally broken off and missing.

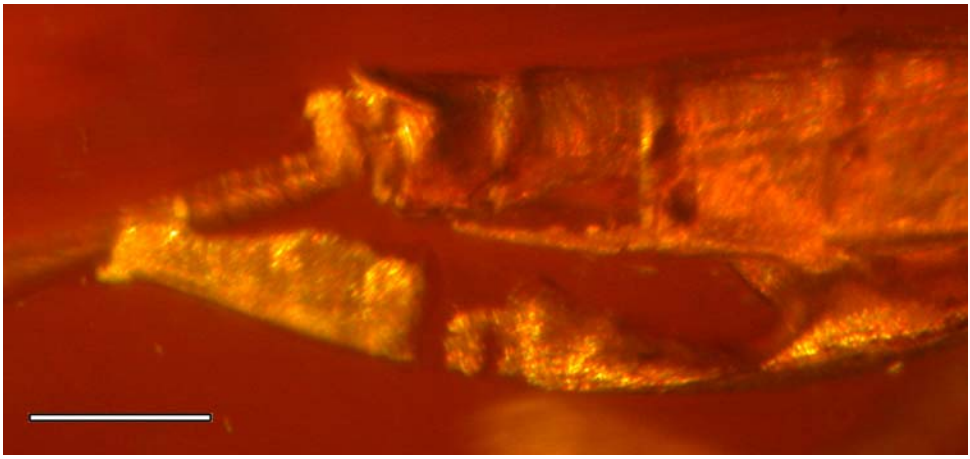

Fig. 22. *Borinquena (?) caeciliana* n. sp., female subimago, holotype, SMNS DO-5384-H, genitalia in lateral view, photo. Scale 0.2 mm.

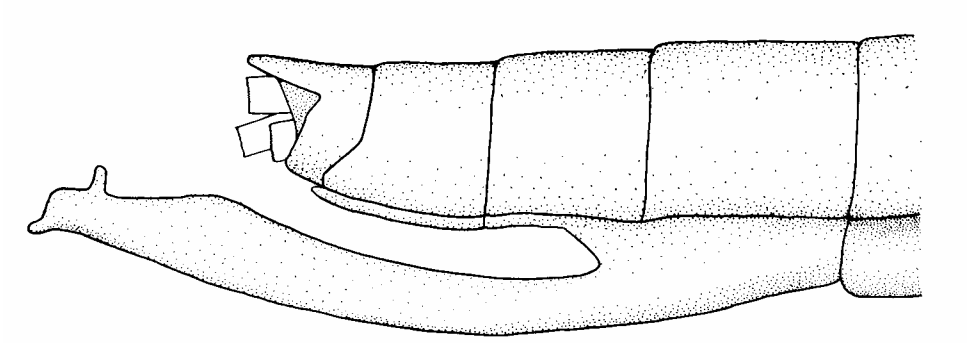

Fig. 23. *Borinquena (?) caeciliana* n. sp., female subimago, holotype, SMNS DO-5384-H, reconstructed egg guide. Without scale.

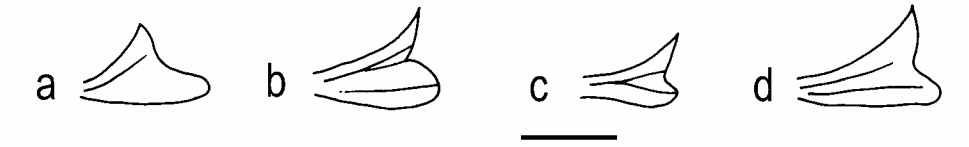

Fig. 24. Hind wings of (a) *Hagenulites hitchingsi* (b) *Borinquena maculata* (c) *Borinquena parva* (d) *Borinquena (?) caeciliana*. Scale 0.4 mm.

3. Discussion

In the past there have been different assumptions on the phylogenetic relationships of the atalophlebiid genera that occur in the Caribbean archipelago. SAVAGE (1987) suspected closer phylogenetic affinities between the genera of the "super-*Ha-genulopsis* lineage" namely *Careospina* and *Traverina* (*Careospina* lineage), *Neoha-genulus* and *Hagenulus* (*Hagenulus* lineage), *Hagenulopsis*, *Borinquena* and *Askola* (*Hagenulopsis* lineage). FLOWERS & DOMINGUEZ (1991) in a cladistic analysis did not support this phylogeny. They suggested a paraphyletic *Hagenulus* s. str. as well as a closer relationship of species of *Hagenulus* s.str. with

the *Hermanella* lineage sensu SAVAGE (1987). The characters to support the latter hypotheses are the presence and specific position of a dorsal row of labral setae, the elbowed shape of the second segment of the labial palp, the attachment of ICu and the acute costal projection in the winged stages. According to KLUGE (1994a), the cladistic analysis of FLOWERS & DOMINGUEZ (1991) suffered from incorrect coding of some crucial characters, e.g. errors in the character states of the MP fork in the genera *Hagenulus*, *Careospina* and *Traverina*. In their analysis neither *Borinquena*, *Hagenulopsis*, nor *Traverina* were taken into account, so the significance of the resulting cladogram was somewhat limited. KLUGE (1994a) in a detailed critical discussion rejected the results of FLOWERS & DOMINGUEZ (1991), and also PETERS (1971) and SIVARAMAKRISHNAN & PETERS (1984) regarded the larval filter feeding adaptations of the *Hermanella* lineage on the one hand and of the *Hagenulus* lineage on the other as convergent development. DOMINGUEZ et al. (2001) in another cladistic analysis nevertheless maintained the paraphyly of the Hagenulini. However, they did not discuss the controversial findings of KLUGE (1994a) at all. KLUGE (1994a) recognised the monophyly of the "super-*Hagenulopsis* lineage" *sensu* SAVAGE and the "*Farrodes* lineage", defined these genera as tribe Hagenulini, and listed autapomorphic characters for this group. Among these characters are the symmetrical MP of the forewing, the long acute costal projection of the hind wing and the termination of its Sc close to the base of the costal projection. However, all these characters are also present in other taxa of the Leptophlebiidae, so the monophyly of this entire group remains debatable.

KLUGE distinguished three subgroups by the different basal attachment of vein ICu (KLUGE 1994a). The first one is represented by the genera *Farrodes* and *Homothraulus*, in which ICu is basally separated from the cubital veins. In *Askola froehlichi*, ICu is basally attached to CuA. The third group, the taxon *Hagenulus s. l.*, can be defined amongst other characters by the attachment of ICu to CuP. *Borinquena*, in addition to *Careospina*, *Traverina*, *Poecilophlebia*, *Turquinophlebia*, and *Hagenulus* s.str., is classified as subgenus of *Hagenulus* s. l. by KLUGE (1994a). Other authors (DOMINGUEZ et al. 2001; PETERS & DOMINGUEZ 2001) maintained the subordinate taxa of *Hagenulus* s. l. as genera. The latter concept is followed herein as well, and with respect to a still lacking comprehensive phylogenetic analysis of the Neotropical Leptophlebiidae, the Hagenulini are herein restricted to the unambiguously monophyletic taxon *Hagenulus* s.l. (sensu KLUGE 1994a).

The taxonomy of *Borinquena*

The taxon *Borinquena* was established by TRAVER (1938), who described two Puerto Rican species, *B. contradicens* and *Borinquena carmencita*, and designated the latter species as genotype. PETERS (1971) added the Dominican species *Borinquena traverae* to the genus, established the new subgenus *Australphlebia* to accommodate the loss of the hind wings in this species, and redefined the diagnosis of *Borinquena* accordingly. KLUGE (1994a) added a new Cuban species *Hagenulus (Borinquena) sexta* and once again redefined the diagnosis of *Borinquena*. The genus *Hagenulopsis* was established by ULMER (1920) for the Brazilian species *Hagenulopsis diptera*. TRAVER (1944) added a second species, *H. minuta*. HOFMANN et al. (1999) described a very similar species to *Australphlebia traverae* as *Hagenulopsis guadeloupensis* and confirmed the synonymy of *Hagenulopsis* with *Australphlebia*, that was proposed by PETERS & DOMINGUEZ (2001). Fossil species

of these genera have not been formally described up to now, although POINAR (1992) mentions the presence of *Careospina* and *Borinquena* from Dominican amber.

As KLUGE (1994a) discusses, there are few diagnostic characters that separate the adult stages of *Borinquena* from *Hagenulus* s.str. However, the unique and unusually long straight first segment of the forceps is a striking autapomorphic as well as diagnostic character of this taxon (see Appendix, character 8). Besides the extant species, this character is also present in *B. maculata* and *B. parva*. Consequently these new fossil species are placed within *Borinquena*. Aside from the elongated basal part of the first forceps segment, all extant species of *Borinquena* (at least in the males) can be distinguished by the absence of dark clouds on the cross veins of the forewings, but not *Borinquena maculata* (char. 11). Therefore the reduction of the clouding pattern in *Borinquena* cannot be retained as a diagnostic feature of this taxon any longer. Likewise, the presence of a subapical ventral spine on the penis lobes was regarded as diagnostic character of *Borinquena*, but *B. parva* is the first species of the genus that lacks this spine (char. 10). Such a penis spine is also present in the imagines of *Hagenulus, Neohagenulus and Hagenulopsis*, but with the exception of *Hagenulus morrisonae*. As KLUGE (1994a) discusses, in the subimago of *H. morrisonae* a penis spine is still present and only lost in the imago. It is most likely that the missing penis spine in *B. parva* is also a secondary development within this genus. Otherwise the penis morphology of *B. parva* is remarkably plesiomorphic with respect to the other species of the genus: the penis lobes are not tubular, parallel and partially fused as in most other species of *Borinquena* and all species of *Hagenulus*, but they are entirely separated (char. 9). The partially fused penis of the Cuban species *B. sexta* resembles an intermediate state between *B. parva* and the other species of this genus.

The phylogenetic affinities of *Borinquena*

KLUGE (1994a) regards *Hagenulus* s. str. as sistergroup of *Borinquena* based on the presence of a long female egg guide. At the same time he assumes that this character may be “a plesiomorphy or parallelism with some other Atalophlebiinae”. Under the assumption that the elongated egg guide would be “a plesiomorphy with other Atalophlebiinae”, a sistergroup relationship between *Hagenulus* and *Borinquena* would not be substantiated by a single character. This leads to the question of the definition of the term “egg guide” and its homology within Ephemeroptera. A true ovipositor made up of derivates of the gonopodes VIII and IX was reduced early in the stem lineage of mayflies. In the groundplan of Ephemeroptera a true ovipositor is lacking, and the paired female gonopores are located in the abdominal sternal membrane between segments VII and VIII. This can still be observed in the majority of mayfly species that have no egg guide at all, just the posterior end of the sternite VII is slightly produced backward to form an egg valve. This character state is also distributed in many Leptophlebiidae and is regarded as the groundplan condition of this taxon. In few other taxa of Ephemeroptera, this sternite VII can be markedly elongated to form an egg guide that may even extend beyond sternum VIII (e.g. *Nesameletus austrinus*, HITCHINGS & STANICZEK 2003). A secondary egg guide formed at least by an elongated sternum VII is also present in different taxa of Leptophlebiidae. Within the Atalophlebiinae, such an egg guide is present in a variety of species with only distant phylogenetic affinities, for instance within the New Zealand genera *Isothraulus*, *Tepakia*, and *Zephlebia* (TOWNS & PETERS 1996), the New Caledonian genera *Tindea*,

Peloracantha, and *Coula* (PETERS & PETERS 1979), and the African genus *Maheathraulus* from Mahé Island, Seychelles (PETERS et al. 1964). In most of these species the egg guide is only very short and only reaches segment VIII. Within the Hagenulini, a short egg guide is present in *Traverina*, *Careospina* and *Neohagenulus*. In some taxa of Leptophlebiidae the egg guide is clearly bipartite: Its ventral part is formed by the extension of the sternum VII, and its dorsal part by an extension of the anterior part of sternum VIII, that together form a secondary ovipositor. A detailed comparative study of the egg guides within Leptophlebiidae has not yet been undertaken, and the composition of the egg guides in the different species is not well known. A bipartite egg guide has been described within both Leptophlebiinae (e.g. *Habrophlebiodes*, see BERNER & PESCADOR 1988) and Atalophlebiinae. Within Hagenulini, such a bipartite egg guide is also present at least in Hagenulini (see PETERS 1971 and KLUGE 1994a). In all the described species of *Hagenulus* the two components of the egg guide are easy to distinguish (PETERS 1971), but in other taxa the dorsal part is not clearly visible. Likewise, in *Borinquena (?) caeciliana* the involvement of sternum VIII is only basally perspicuous. The egg guide is generally short in most taxa of the Hagenulini. In *Hagenulopsis*, whose assignment to the Hagenulini is debatable (see below), the egg guide reaches almost the end of the abdomen. In *Askola* a long egg guide is present, but only in *Borinquena* and *Hagenulus* it extends beyond the last abdominal segment. With respect to this character distribution within Leptophlebiids, an extremely elongated egg guide is regarded as a synapomorphic character of *Hagenulus* and *Borinquena*. This extremely elongated egg guide, "the elongated male forceps, the tubular penes with subapical spine and the similar larva to *Borinquena"* were the reasons for PETERS (1971) to assume a closer relationship between *Hagenulus* and *Borinquena*.

KLUGE (1994a) debated the inclusion of *Hagenulopsis* within the Hagenulini. However, the subimaginal characters KLUGE (1994a) proposes as autapomorphies for the Hagenulini are not investigated in *Hagenulopsis.* It may indeed be possible that the elongated egg guide and the tubular penes point to a closer relationship of *Hagenulopsis* with *Borinquena* and *Hagenulus*, but on the other hand PETERS (1969) assumed a sistergroup relationship between *Askola* and *Hagenulopsis*, probably because of the lack of hind wings and the presence of the elongated egg guide in both genera. This issue requires a comparative investigation with more material that was not available to me. In any case the attachment of ICu to MA in the forewing of the Hagenulini must be interpreted as autapomorphic character of this taxon.

The taxonomic position of *Borinquena (?) caeciliana*

Unfortunately the female adult stages of *Hagenulus* and *Borinquena* cannot be distinguished with certainty. The females of both genera have extremely elongated egg guides. In *B. (?) caeciliana* the egg guide is dorsally equipped with a characteristic subapical projection. Similar projections are also present in *Borinquena carmencita* and *B. sexta*. Also *Hagenulus caligatus*, *H. morrisonae*, and *H. eatoni* have dorsal subapical projections (PETERS 1971). As this type of egg guide occurs in *Hagenulus* and *Borinquena*, a safe placement of this female specimen is impossible. However, the distribution of these characters may indicate the presence of an egg guide with a projection in the groundplan of *Borinquena* + *Hagenulus*. This projection is formed by the sternum VIII and marks the dorsal opening of the egg guide (J. PETERS, pers. comm.).

In extant species the female imagines of *Borinquena* do not have clouded crossveins. *B. (?) caeciliana* is only known from the subimaginal state, but the subimaginal wings of the other species of *Borinquena* and *Hagenulus* are little known and omitted in most of the descriptions. Other diagnostic characters that could separate the two taxa are restricted to the larvae. However, *Borinquena (?) caeciliana* has significantly reduced hind wings with not more than two veins. A hind wing reduction to such an extent is, in extant species, only found within *Borinquena*: While all extant species of *Hagenulus* have hind wings with more than two veins, in *B. carmencita* the hind wing is as small and reduced as in *B. (?) caeciliana*. A placement within *Hagenulopsis* can be excluded because the apex of the egg guide in *B. (?) caeciliana* is blunt as in all species of *Borinquena* and *Hagenulus* (PETERS 1971), whereas the apex of the egg guide in *Hagenulopsis* is acutely pointed (HOFMANN et al. 1999). The degree of hind wing reduction is certainly a weak character, so it only justifies a tentative placement within *Borinquena* until new material may allow a definite assignment within the hagenulid taxa. The possibility that *B. (?) caeciliana* may represent the female of either *B. maculata* or *B. parva* can be most probably ruled out by a comparison of the hind wings (fig. 24). It is also likely that *B. (?) caeciliana* does not represent the female of *Hagenulites hitchingsi*, although both specimens have similarities in their wing venation. In both species the basal costal and subcostal field lacks crossveins. The hind wing venation of both specimens is significantly reduced, but the hind wing of *B. (?) caeciliana* has an additional weak longitudinal vein (Figs.21, 24). Moreover, the costal projection in the hind wing of *H. hitchingsi* is located in the middle of the hind wing, while the costal projection of *B. (?) caeciliana* is close to the apex of the hind wing. Finally ICu2 is basally attached to ICu1 in *B.* (?) *caeciliana* (Fig. 21), but in *H. hitchingsi* ICu2 is dislocated (Fig. 5).

The taxonomic and phylogenetic position of *Hagenulites hitchingsi*

The asymmetrical MA fork, the symmetrical MP fork, the acute and long costal projection of the hind wings, the dissimilar claws and the basal attachment of ICu to MP in the forewing clearly mark *H. hitchingsi* as a taxon within the Hagenulini. However, *H. hitchingsi* shows none of the autapomorphic characters of any of the hitherto described genera (see also appendix 1): It lacks the membraneous medial connection of the penis lobes as it is present in *Neohagenulus*. The hyaline wings and the lack of an apical process of the penes exclude it from *Poecilophlebia* and from *Turquinophlebia*. It differs from *Careospina* and *Traverina* by the presence of a ventral subapical penis spine. Finally it also lacks the significantly extended first forceps segment of *Borinquena*. According to KLUGE (1994a), *Hagenulus* s. str. is only defined by larval autapomorphies, but a look at the male genitals reveals that all hitherto described species of *Hagenulus* share tubular penis lobes that are more or less parallel and medially approximated. The penis lobes of *Hagenulites hitchingsi* however are only parallel in their proximal half. In *Borinquena*, the sistergroup of *Hagenulus*, multiple character states can be observed (see appendix 1, char. 9). This gives me reason to assume that the parallel tubular penes in both genera is a parallel development, and hence the tubular penes could be regarded as an autapomorphic character of *Hagenulus*. This would definitely exclude *Hagenulites hitchingsi* from *Hagenulus* s. str. To accommodate this, the new genus *Hagenulites* has been established for *H. hitchingsi*. While it is obvious that *H. hitchingsi* is an in-group

taxon of *Hagenulus* s.l., its precise phylogenetic position remains doubtful, as the larvae, subimagines and female imagines are still unknown.

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Appendix 1: Matrix of selected characters of the discussed taxa:

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Askola froehlichi	0	0	0	2	3	1	0	1	3	0	2	0	1	0
Borinquena (?) caeciliana	0	0	1	1	1	3	?	?	?	?	?	1	?	?
Borinquena carmencita	0	0	1	1	1	3	1	0	3	1	2	0	0	0
Borinquena contradicens	0	0	1	1	0	3	1	0	2	1	2	0	0	0
Borinquena maculata	0	0	1	1	1	?	1	0	3	1	0	1	1	?
Borinquena parva	0	0	1	1	1	?	1	0	3	0	2	0	1	?
Borinquena sexta	0	0	1	1	0	3	1	0	2	1	2	0	0	0
Careospina hespera	0	0	1	0	0	0	0	0	0	0	2	0	0	0
Hagenulites hitchingsi	0	0	1	1	2	?	0	0	2	1	2	1	0	?
Hagenulopsis diptera	0	0	1	2	3	2	0	0	2	1	0	0	0	0
Hagenulopsis guadeloupensis	0	0	1	2	3	2	0	0	3	1	2	1	0	0
Hagenulopsis minuta	0	0	1	2	3	2	0	0	2	1	2	1	1	0
Hagenulopsis traverae	0	0	1	2	3	2	0	0	3	1	2	1	0	0
Hagenulus caligatus	0	0	1	1	0	3	0	0	3	1	1	0	0	1
Hagenulus eatoni	0	0	1	1	0	3	?	?	?	?	?	0	?	?
Hagenulus jamaicensis	0	0	1	1	0	3	0	0	3	1	1	1	0	?
Hagenulus morrisonae	0	0	1	1	0	3	0	0	3	0	2	1	0	1
Hagenulus rangelae	0	0	1	1	0	?	0	0	3	1	2	0	0	?
Neohagenulus julio	0	0	1	0	0	0	0	0	1	1	2	0	1	0
Poecilophlebia pacoi	0	0	1	0	0	0	0	0	0	1	0	1	1	0
Traverina cubensis	0	0	1	0	0	0	0	0	0	0	2	0	1	0
Turquinophlebia grandis	0	0	1	0	0	0	0	0	3	1	2	0	1	0

1. forewing with MA fork not fixed in position (usually asymmetrical) (0) or MA fork symmetrical (1)
2. forewing with symmetrical (0) or asymmetrical MP fork (1)
3. ICu basally attached to CuA (0) or attached to CuP (1)
4. acute costal projection of hind wing short (0) or long (1) or hind wing missing (2)
5. hind wing with more than two (0) or with two (1) or with single vein (2) or wing entirely missing (3)
6. female egg guide short (0) or elongated, extending near middle to sternum IX (1) or elongated, extending past middle of sternum IX with apex acutely pointed (2) or elongated, extending past sternum IX with blunt apex (3)
7. basal part of forceps segment 1 straight and extremely elongated: (0) no (1) yes
8. distal part of forceps not (1) tapering (0)
9. penis lobes entirely separated (0) or basally with membraneous connection (1) or basally approximated (2) or entirely approximated (3)
10. penes ventrally each without subapical spine (0) or with spine (1)
11. crossveins of male forewings clouded (0) or clouded only in costal and subcostal field (1) or not clouded (2)
12. costal field of forewings basally with (0) or without (1) crossveins
13. eyes of male medially separated (0) or contiguous (1)
14: forelegs of larva without (0) or with (1) filter hairs