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## A new genus of long-horned caddisfly from the Amazon basin (Trichoptera: Leptoceridae: Grumichellini)

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### Abstract

*Amazonatolica hamadae*, new genus, new species (Leptoceridae: Grumichellini), is described from the Amazon basin of Brazil. The adult male and female, larva, pupa and case are described and illustrated. The biology and habitat of the new species is unusual for members of its tribe in that it occurs attached to vegetation in acidic, lowland streams.

**Key words:** Trichoptera, Leptoceridae, Grumichellini, new genus, new species, Brazil, South America, Amazon, Neotropics, caddisfly, larva, pupa

### Introduction

The Leptoceridae, or long-horned caddisflies (named for the very long, slender adult antennae), is the second largest family in the order Trichoptera, with a total of 1,567 species worldwide (Morse 2003), 148 in the Neotropics (Flint et al 1999), and 41 in Brazil (Paprocki et al. 2004) (the latter figures represent a fraction of the actual fauna as many new species are known from the Neotropics). The family contains two subfamilies, the largely southern hemisphere Triplectidinae and the more cosmopolitan Leptocerinae (Morse 1981, Morse & Holzenthal 1987), containing 14 and 30 genera, respectively. The Grumichellini, one of 3 triplectidine tribes, has its greatest diversity in the Neotropics, where two genera are known, *Atanatolica* Mosely 1936, with 17 described species and *Grumichella* Müller 1879, containing 4 described species (Holzenthal 1988). Two other grumichelline genera, comprising a total of only 3 species, are known from the Australasian Region. *Triplexa villa* Mosely 1953 (in Mosely & Kimmins 1953), occurs in south-eastern Australia and *Gracilipsodes psocopterus* Sykora 1967, and *Gracilipsodes similis*

Ward 2001, are endemic to New Caledonia; the latter genus was recently resurrected from synonymy with *Triplexa* (Ward 2001). Holzenthal (1988) discussed the phylogeny and biogeography of the tribe and St. Clair (1994) presented additional morphological and behavioral observations.

Larvae of all 4 genera of Grumichellini (Triplectidinae) are known (Holzenthal 1988, St. Clair 1994, Ward 2001) and share strikingly similar morphologies and behaviors. The larvae frequent the splash zones of waterfalls, similar fast flowing sections of streams, or the thin film of water flowing over bedrock outcrops. In some cases, at least in some *Atanatolica*, larvae are found out of the flow of water, where they are kept wet by intermittent splashes of water, but often are found several meters from the water source in essentially terrestrial conditions (Holzenthal 1988). The stout legs and strong tarsal claws of the larvae, as well as their long slender bodies and cases, apparently aid their purchase on the substrate and affect the direction of water flow around the larva. In addition, the legs of *Grumichella* are broader and flatter than in the other genera, perhaps acting as stationary hydrofoils to hold the larvae in place in the current. Larvae feed by scraping the thin film of periphyton growing on the substrate. The Neotropical genera, especially *Grumichella*, can be extremely abundant in their preferred habitat, where 100s of individuals per square meter can be observed in hygropetric (the surface film of water on rocks) or similar habitats.

To date, at least in Latin America, all known species in both Neotropical grumichelline genera (*Atanatolica*, *Grumichella*) are confined to areas of high topographic relief where stream gradients are sufficient to provide the proper habitats for the larvae. The greatest diversity of species occurs in the northern Andes of Colombia and Venezuela south to Bolivia and then again in the mountains of southeastern Brazil. Stream gradient, rather than elevation seems to be the determining factor as species are known from both high and low elevation streams.

In February of 2000 the junior author and her thesis advisor, Dr. Neusa Hamada, collected immatures of an unusual caddisfly from a tributary of the Amazon River near Manaus, Brazil, and from the Reserva Adolpho Ducke, within the city of Manaus itself! They determined the larvae to belong to the Grumichellini, close to *Atanatolica*, and sent illustrations and specimens, including adult males and females and immatures, to the senior author for verification. In the present paper, we assign these to a new genus and species, *Amazonatolica hamadae*, most closely related to *Atanatolica* and *Triplexa*, and describe the adult and larval stages, case, and biology.

## Materials and methods

Techniques and procedures used in the preparation and examination of specimens are those outlined by Blahnik & Holzenthal (2004) and Holzenthal & Andersen (2004). Terminology for genitalia and wing venation follows that presented by Holzenthal (1988).

Type material is deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA), the University of Minnesota Insect Collection, St. Paul, Minnesota, USA (UMSP), the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP), and the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH).

## Systematics

### *Amazonatolica*, new genus

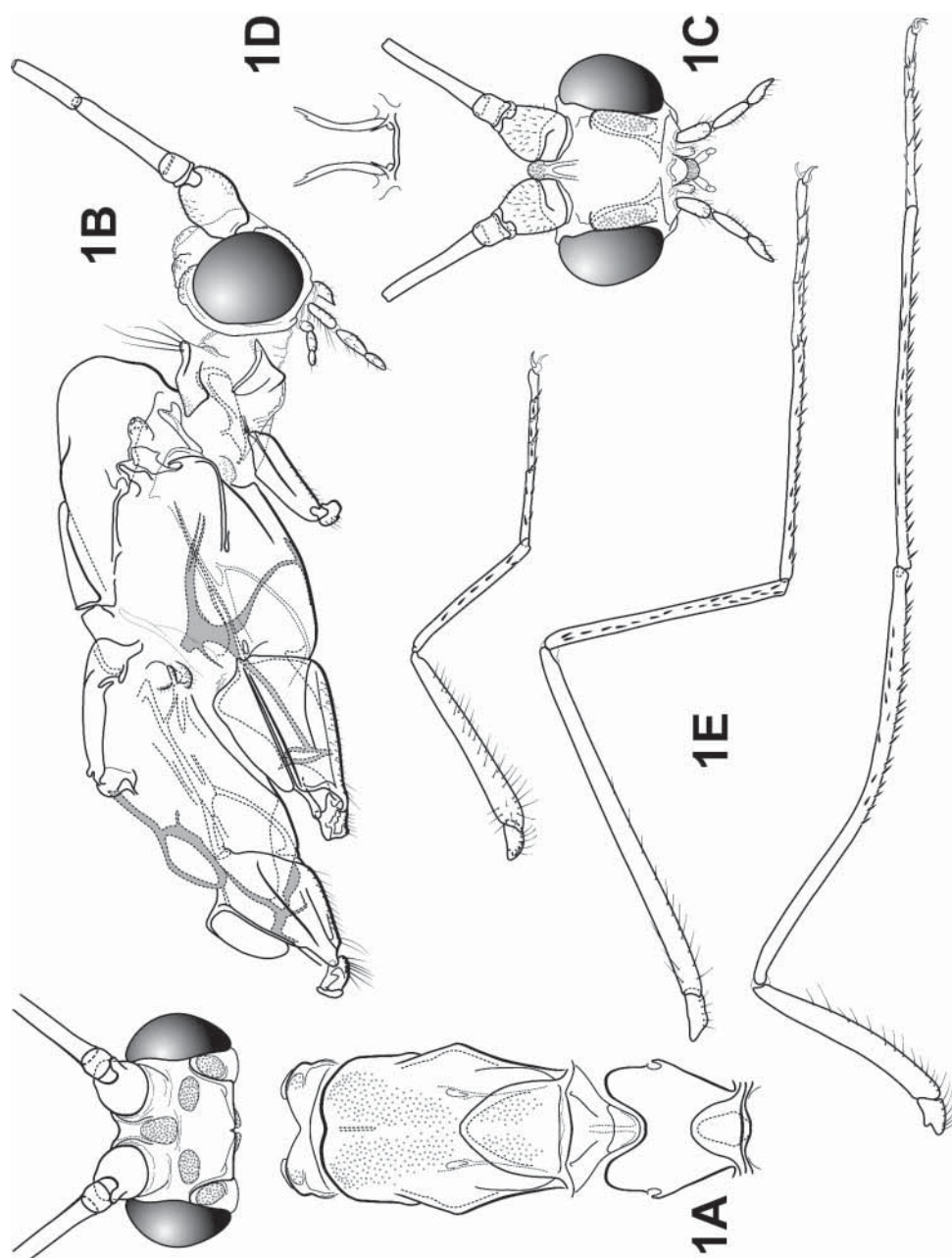
Figs. 1–9

Type species: *Amazonatolica hamadae*, new species, original designation.

Adult: body, wings, and appendages pale stramineous, denuded (all specimens in alcohol). Head: frontal setal wart elongate oval (Fig. 1C), anteromesal, anterior, and posterolateral setal warts subequal, oval (Fig. 1A); intraocular distance about 2X diameter of eye (Fig. 1A); malar space very narrow (Fig. 1B); tentorium (Fig. 1D): anterior arms slender, slightly curved, tentorial bridge straight, very narrow, dorsal arms vestigial; antennal scape short (Figs. 1B, C), cylindrical, unmodified, with vestiture of short, fine setae; mouthparts (Figs. 1B, C): labrum very small; mandibles minute, slender; maxillary galea a small setose lobe, maxillary and labial palps 3-segmented in both sexes; haustellum present, very short. Thorax (Figs. 1A, B): prothorax small, meso- (especially) and metathorax very large; mesopleural katapisternum very narrow (Fig. 1B); pronotal setal wart small, mesoscutum and mesoscutellum with fine, diffuse setae (Fig. 1A); legs very slender (Fig. 1E), foreleg shortest, hind leg longest, hind leg femur short, slightly bowed, hind leg tibia long, bowed, hind leg basitarsus 2X longer than tarsal segments 2–5 combined; all tibiae lacking spurs (i.e., tibial spur formula 0, 0, 0), but tibiae and tarsi bearing small, black spines; tarsal claws small. Forewings (Figs. 2A, 3A) narrow in both sexes; forks I and V present in male (Fig. 2) (as interpreted by Holzenthal 1988); I, III, and V present in female; forewing forks I (both sexes) and III (female) petiolate, with stems equal in length to their forks; fork V deep, sessile; discoidal and thyridial cells long, subequal in male, discoidal cell 2/3 length of thyridial cell in female. Hind wings (Figs. 2B, 3B) narrow, but especially so in female; pointed apically; only fork V present; wide space between R1 and Rs.

Male (Fig. 4): Abdominal segment IX annular, narrow. Segment X simple; without processes. Preanal appendage long, digitate, setose, shorter than abdominal segment X. Inferior appendage long, bipartite; primary segment with long, digitate apicodorsal portion and broader basal portion; basal portion with broad, triangular, sclerotized mesal shelf; apicodorsal portion bearing short, stout, spine-like setae on mesal surface; second article of inferior appendage (harpago) long, spatulate, apex rounded. Phallic apparatus simple, phallobase tubular; phallicata absent (or fused apically with phallobase); parameres absent; endophallic membranes present apicoventrally; phallotremal sclerites present.

Female (Fig. 5): Tergum IX lightly sclerotized, with dorsal setae; sternum IX lightly sclerotized, rounded, covered with fine microtrichia. Appendage of segment X short, broadly rounded apically, heavily setose. Valve prominent, flaplike, apex irregular, heavily setose. Tergum X produced into thin, ventrally directed, apically excavated, sclerotized plate below appendages of segment X and between valves. Vaginal apparatus oval, with central, key-hole shaped sclerites.



**FIGURE 1.** *Amazonatolica hamadae*, new species. Adult head and thorax: A—dorsal; B—lateral; C—frontal; D—tentorium, dorsal; E—fore-, mid-, and hind legs, lateral.

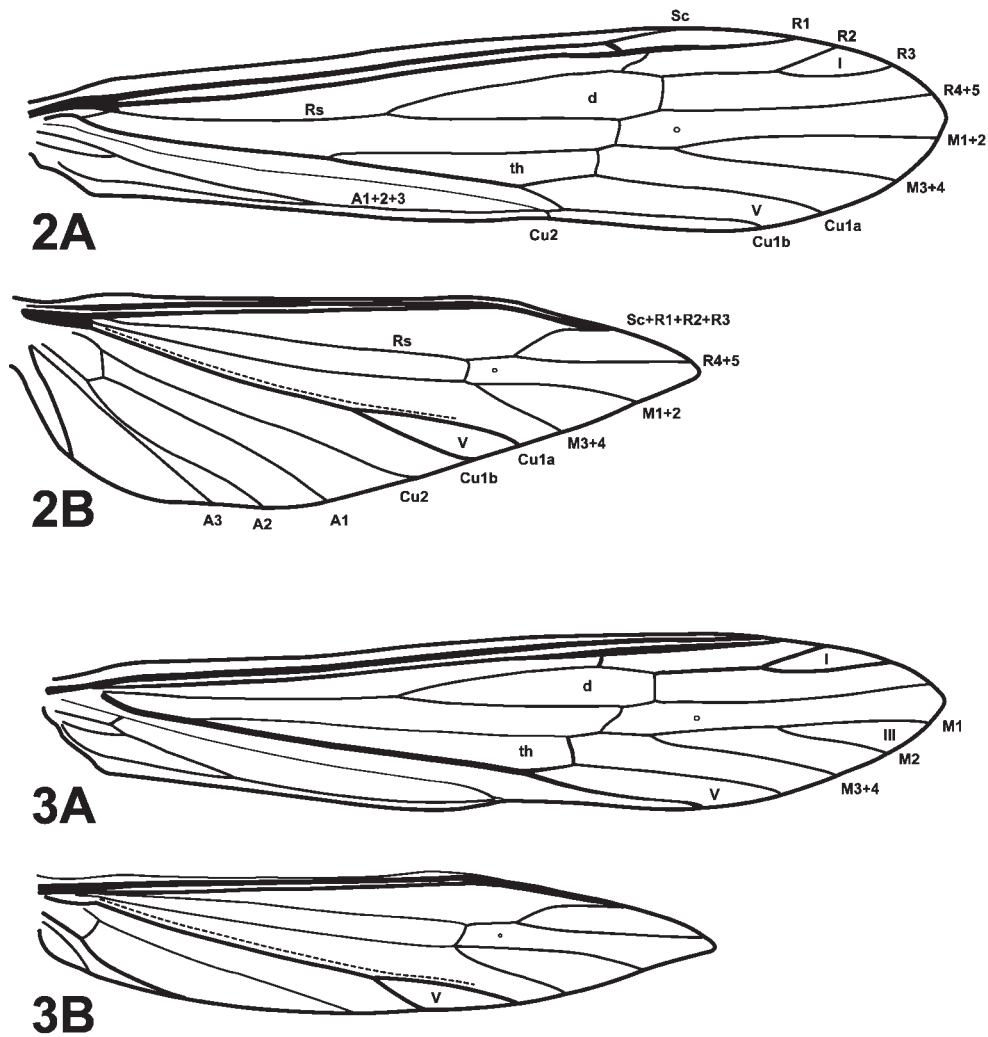
Larva: Length of final instar larva 7.5–8 mm (n=6). Head (Figs. 6B, 8): pale stramineous; elongate oval; antennae atypical for family, very short, situated close to anterior margin of head capsule; ventral apotome small, triangular, but venter of head semimembranous, unpigmented and ventral ecdysial line obscure (Fig. 8); head setal pattern (Fig. 8) atypical for family, numerous short, pale, secondary setae on labrum and at head primary setal positions 1–3, 7–11, and 15–17; primary seta 12 apparently absent; mandibles (Fig. 7D) scraper-like, symmetrical, broadly triangular, with shallow apical teeth and deep mesal concavity bearing apical brush of peglike setae and basal brush of long, slender setae. Thorax (Figs. 6A, B): pale yellow; pronotum wider than long, apical margin straight, covered with many short, fine secondary setae, pronotal cuticle (Fig. 7E) (also, but to a lesser extent, head and mesonotum) sparsely papillate; mesonotal sclerites completely covering dorsum of mesonotum, somewhat expanded laterally, anterolateral corners rounded, anterior half covered with many fine, secondary setae, pale yellow, with darker pigmentation along ecdysial line and distinctive dark spot at ventrolateral corner; metanotal *sal* and *sa2* sclerites completely fused, forming a single large median plate with posterolateral corners extended and directed mesad, very lightly pigmented except for darker pigmented areas along ecdysial line; *sa3* sclerites elongate oval, very lightly pigmented; metanotal setae as in Fig. 6B; foretrochantin horn-shaped (Fig. 7F); meso- and metapleural sclerites large; thoracic sterna without setae; legs short, stout (7A–C); foreleg shortest, hind leg longest; hind tibia broad, triangular in cross section, greatly expanded apicoventrally, lacking macrosetae, but covered with fine microtrichia; tarsal claws short, stout, with short basal seta. Abdomen (Fig. 6A): unusually long and slender; segment I with lateral hump sclerite (Fig. 7H), but without dorsal hump sclerite; abdominal fringe and lateral tubercles absent; gills absent; dorsal sclerite of segment IX (Fig. 7I) with posterolateral corners irregularly extended, with 1 pair of long apicolateral seta and 2 pairs of very short mesal setae; anal proleg (Fig. 7G) with narrow ventral plate in addition to lateral sclerite and ventral sole plate and bearing long apicolateral setae; band of uniformly small spines adjacent to anal opening; 6 anal papillae present, single dorsal papilla, 2 pairs of mesal papillae, and 1 ventral papilla; anal claw prominent, with single, stout, dorsal accessory hook.

Larval Case (Fig. 6C): Composed entirely of silk; long, slender, tapered, gently curved, transparent. Length of final instar case 10–11 mm (n=6).

Pupa: Head (Fig. 9B): sparsely setose, with pair of short setae on vertex, pair of long frontal setae, and single, pale setae below each eye; labrum oval, with 2 pairs of long basal setae, and 3 pairs of much shorter, paler lateral and apical setae; mandibles small, each with single, large, apical tooth, inner margins smooth. Abdomen (Fig. 9A): long, slender; abdominal segment I with elongate, narrow, faint sclerite, bearing single, fine seta; abdominal hook plates III, IV, Va and Vp, VI present, small, oval, bearing 2–3 or 4 (plate Vp) small spines; lateral abdominal setal fringe absent; gills absent; dorsum of segment VIII with pair of small, narrow, irregular sclerites; segment IX narrow, tapered, very membranous, with single pair of lateral setae; anal processes slender, flexible, each bearing 3 setae

along length (Fig. 9A). Anterior silken membrane of pupal case (Fig. 9C) imperfectly tri-perforate.

**Etymology.** The genus name is a combination of the word *Amazona* for the Amazon River and the suffix *-tolica* taken from the name of the related genus *Atanatolica*.



**FIGURE 2.** *Amazonatolica hamadae*, new species. Male wings: A—forewing; B—hind wing.

**FIGURE 3.** *Amazonatolica hamadae*, new species. Female wings: A—forewing; B—hind wing.

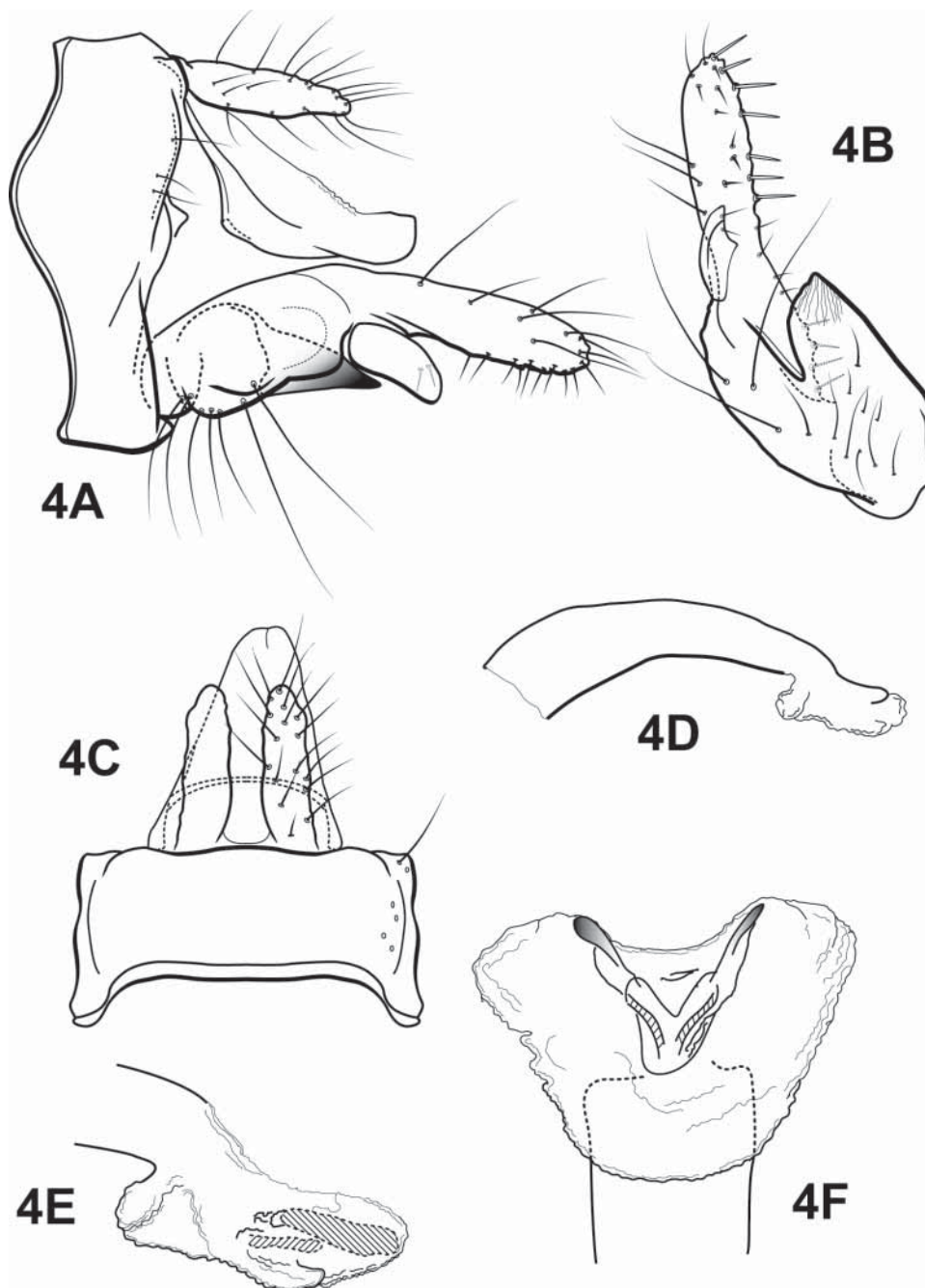
### *Amazonatolica hamadae*, new species

Figs. 4–5

This new species can be distinguished from other members of the Grumichellini by several features as discussed below (Phylogenetic Considerations). It can be easily separated from other Latin American members of the tribe by its 0,0,0 tibial spur formula, 3-segmented



maxillary palp, absence of fork III in the hind wing of both sexes, and by the male genitalia with its combination of simple tergum X, prominent harpago, and the broad, triangular, sclerotized mesal shelf of the inferior appendage.



**FIGURE 4.** *Amazonatolica hamadae*, new species. Male genitalia: A—lateral; B—inferior appendage, ventral; C—segments IX & X, dorsal; D—phallus, lateral; E—apex of phallus, enlarged, lateral; F—apex of phallus, enlarged, ventral.

Adult: Forewing length 7 mm (n=3) male; 6 mm (n=5) female. Color (in alcohol) pale stramineous (denuded, although in a mature female pharate pupa, the wings appear to be a darker brown, with a large patch of white setae apically).

Male (Fig. 4): Abdominal segment IX annular, narrow; anterior and posterior margins sinuate; in dorsal view quadrate; sparse setae present posterolaterally. Segment X saddle-shaped, simple, lightly sclerotized, lacking setae or secondary processes, covering the phallic apparatus dorsally; in lateral view, narrow basally, directed ventrad, broader mesally, truncate apically; in dorsal view, triangular, apex slightly and narrowly cleft. Pre-anal appendage long, digitate, setose, shorter than segment X. Inferior appendage long, bipartite, consisting of primary segment and second article (harpago); primary segment with basal and apical regions; basal region broad, sclerotized, with rounded basoventral corner, bearing very long setae; with broad, triangular, sclerotized mesal shelf, its apex rugose; apical region digitate, more lightly sclerotized, bearing very long setae dorsally and laterally, and short, stout, spinelike setae on mesal surface; second article of inferior appendage (harpago) long, spatulate, apex rounded, with pair of short apicomesal setae. Phallic apparatus simple, phallobase tubular, wide basally with wide opening, tapering apically; phallicata absent; parameres absent; endophallic membranes present apicoven-trally; phallotremal sclerites present, large, V-shaped.

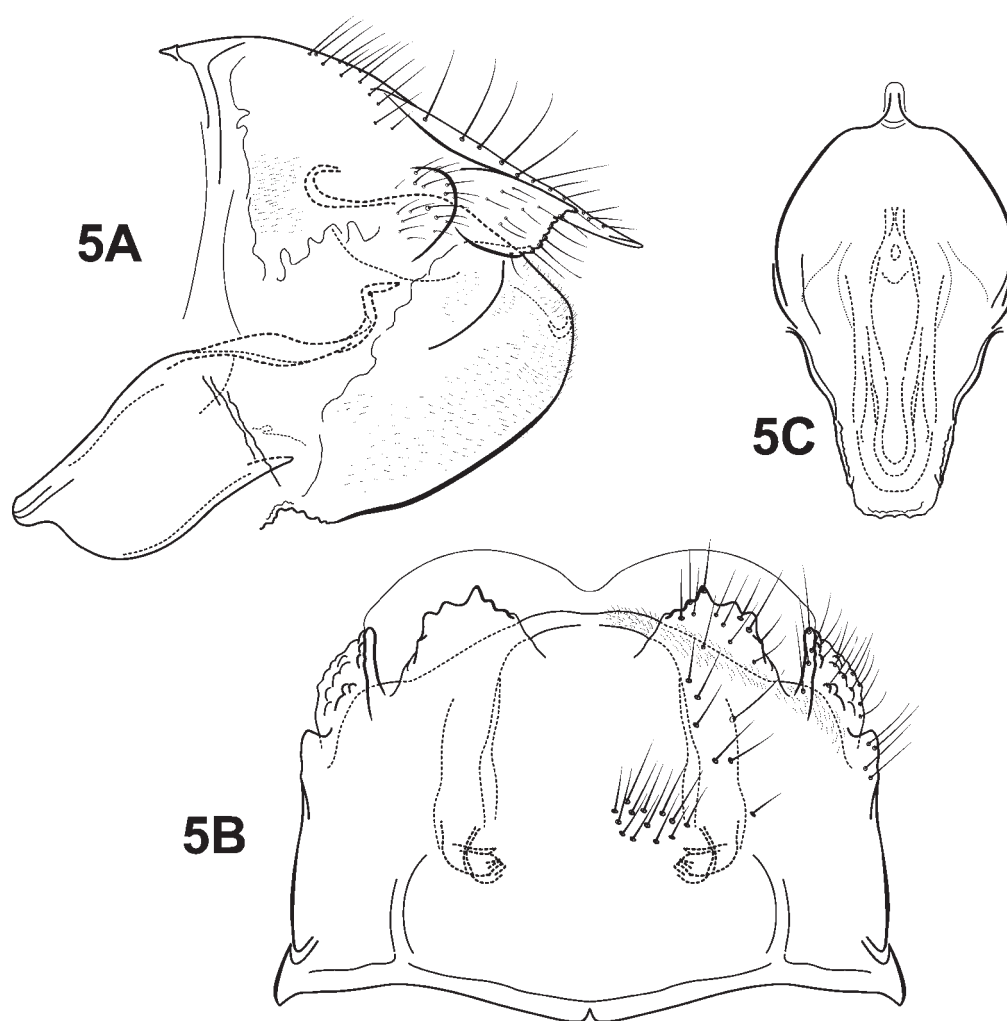
Female (Fig. 5): Tergum IX lightly sclerotized, with patch of dorsal setae and more sparsely distributed, longer dorsolateral setae; sternum IX lightly sclerotized, rounded, bulbous, covered with fine microtrichia. Appendages of segment X short, broad, thumb-shaped, heavily setose, situated dorsolaterally. Valve prominent, flaplike, apex irregular, heavily setose. Tergum X produced into thin, ventrally directed, apically excavate, sclero-tized plate below appendages of segment X and between valves. Vaginal apparatus, in ventral view, oval, broadest mesally, narrowing anteriorly, with central, key-hole shaped sclerites; in lateral view, saddle-shaped.

**Holotype male: BRAZIL: Amazonas:** Manaus, Reserva Florestal Adolpho Ducke, 02°57'S, 59°57'W, Igarapé Barro Branco (sede), vi.2001, J. Vidal (INPA).

**Paratypes: BRAZIL: Amazonas:** Manaus, highway ZF3, Fazenda Dimona, igarapé [small stream] at km 6, 02°19'67"S, 60°04'66"W, 07–11.iv.2002, J.L. Nessimian — 6 males, 20 females (INPA); Fazenda Dimona, (PDBFF), km 172, BR 174, igarapé do acampamento, 02°19'40"S, 60°04'39"W, 07.iv.2002, J.L. Nessimian — 1 male, 1 female (UMSP); same, except 02°20'19.5"S, 60°06'09.5"W, 12.iv.2002 — 1 male, 6 females (NMNH); Reserva Florestal Adolpho Ducke, Igarapé do Bolívia, acampamento, 02°57'S, 59°57'W, 19.iv.2002, A.M.O. Pes — 1 male, 8 females (INPA); Igarapé do Acará, 22.vii.2002, J. Vidal, J.M.F. Ribeiro — 2 males, 2 females (MZUSP); Igarapé Barro Branco (sede), vi.2001, J. Vidal — 20 females (INPA); Presidente Figueiredo, Igarapé da Onça, Balneário Sossego da Pantera, 02°05'57"S, 60°01'02"W, 04.v.2000. A.M.O. Pes, J. O. da Silva — 1 female (INPA); same, except 06.iv.2000, A.M.O. Pes, J. O. da Silva — 2 males, 3 females (INPA); Presidente Figueiredo, Igarapé da Pantera, km 20, AM 240,



02°02'S, 59°50'W, 14.xii.2001, A.M.O. Pes, J.O. da Silva, J. Bosco — 2 females (INPA); same, except 03-04.v.2000 — 2 females (UMSP); Presidente Figueiredo, Igarapé do Sr. José, ramal/km 24, AM [highway] 240, 02°01'06"S 59°49'27"W, 24-27.ii.2000, A.M.O. Pes, U.C. Barbosa — 1 male, 5 females (INPA); same, except 05.iv.2000. A.M.O. Pes, J.O. da Silva — 1 male, 3 females (INPA); same, except 04-05.iv.2000. A.M.O. Pes, J.O. da Silva — 5 females (INPA); same, except 03-04.vii. 2000. A.M.O. Pes, J.O. da Silva — 2 females (INPA): same, except 03-04.vii. 2000. A.M.O. Pes, J.O. da Silva, J. Bosca — 1 male, 4 females (UMSP); same, except 31.v. 2000. A.M.O. Pes, J.O. da Silva — 4 males, 9 females (INPA); same, except 02-03.viii. 2000. A.M.O. Pes, J.O. da Silva — 1 female (INPA).



**FIGURE 5.** *Amazonatolica hamadae*, new species. Female genitalia: A—lateral; B—dorsal; C—vaginal apparatus, ventral.

**Additional Material Examined: BRAZIL: Amazonas:** Igarapé do Tinga, 18.iii.2004, A.M.O. Pes — 3 larvae, 4 pre-pupae (INPA); Presidente Figueiredo, Igarapé

da Onça, Balneário Sossego da Pantera, 02°05'57"S, 60°01'02"W, 14.xii.2001, A.M.O. Pes, on aquatic plants — 25 larvae (INPA); same, except 14.iii.2002, A.M.O. Pes, on aquatic plants — 25 larvae (12 examined for gut contents), 6 pupae (INPA); Presidente Figueiredo, Igarapé da Pantera, km 20, AM 240, 02°02'S, 59°50'W, 14.xii.2001, A.M.O. Pes — 3 larvae, 2 pupae (UMSP); Manaus, Reserva Florestal Adolpho Ducke, Igarapé do Bolívia, acampamento, 02°53'S, 59°58'W, 20.iv.2002, A.M.O. Pes — 3 pupae (UMSP); Igarapé Barro Branco, 02°53'S, 59°58'W, 30.i.2002, A.M.O. Pes — 6 larvae (NMNH). **Bahia:** Barreiras (divisa com Tocantins), Rio Boró, 12°17'56.5"S, 45°50'55.5"W, 18.viii.2002, N. Hamada — 4 larvae (INPA). **Rondônia:** Vilhena, igarapé pequeno na ponte da estrada velha entre Nova Conquista e Colorado do Oeste [small stream at bridge on old road between Nova Conquista and Colorado do Oeste], 12°54'35.4"S, 60°14'48.5"W, 11.vii.2002, N. Hamada — 13 larvae (INPA).

Distribution. BRAZIL: Amazonas, Bahia, Rondônia.

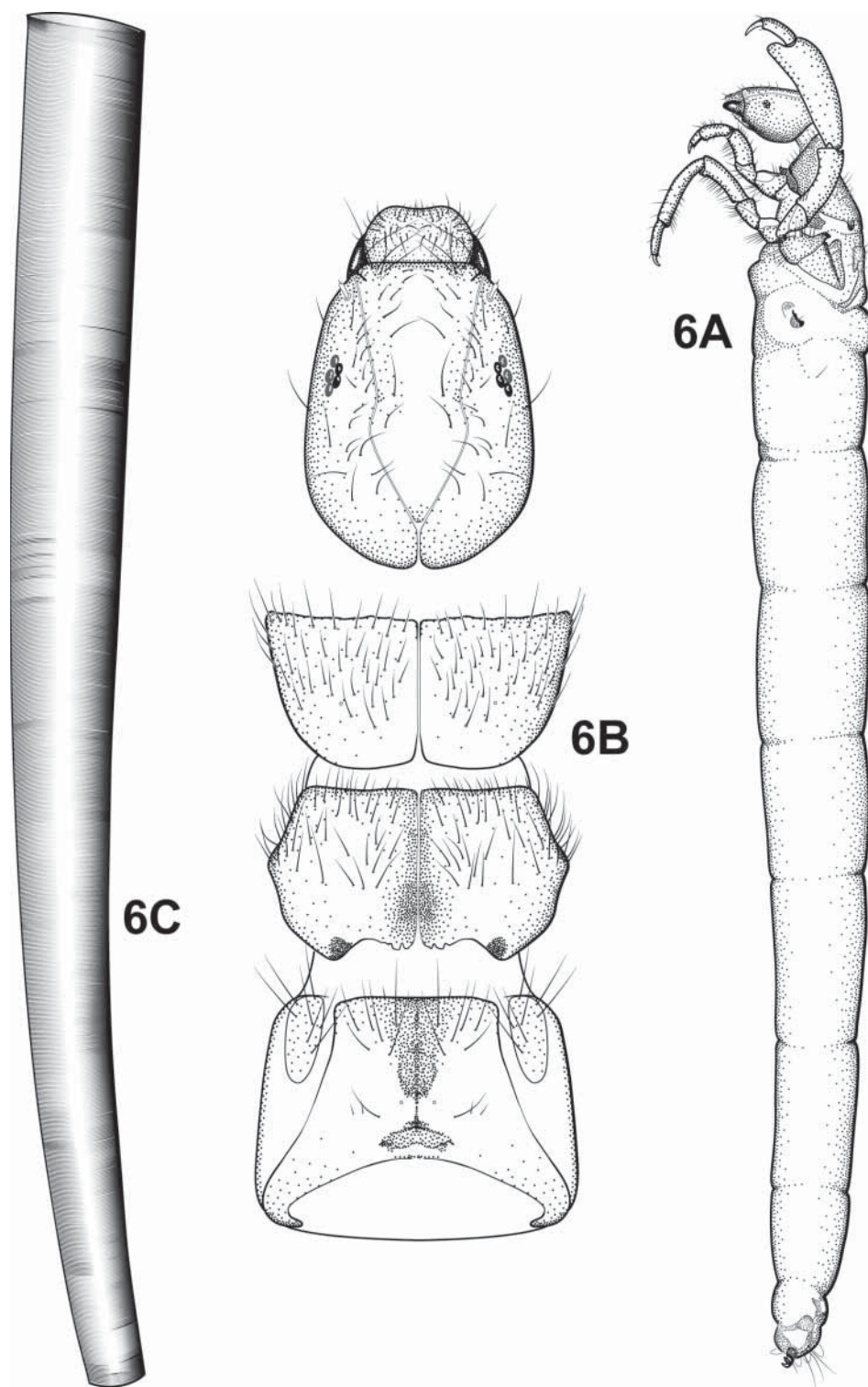
Etymology. We take great pleasure in naming this species in honor of Dr. Neusa Hamada, INPA, in recognition of her contributions to this study and to our knowledge of the Trichoptera fauna of the Amazon basin.

### Habitat and biology

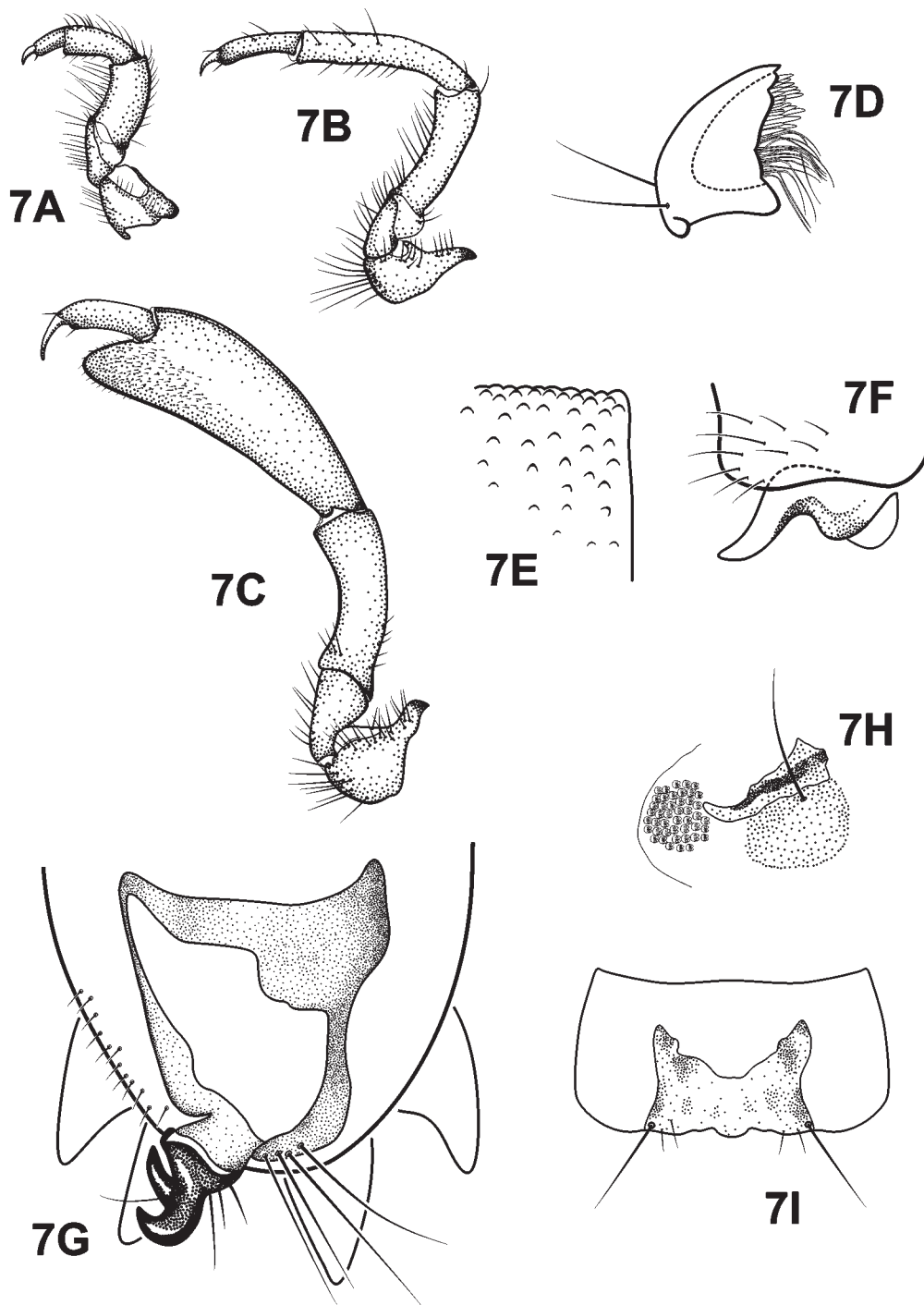
Gut contents of larvae (n=12) contained vascular plant tissue and algae typical of the phytoplankton found in the black water streams of the Rio Negro Basin (Chlorophyceae and Diatomacea: *Eunotia* spp.) as well as unidentified zooplankton.

*Amazonatolica hamadae* larvae inhabit acidic black water streams typical of central Amazonia. Many occurred within the Reserva Florestal Adolpho Ducke (INPA) an area of undisturbed *terra firme* forest area, with little light penetration and streams from 1st to 3rd order). Larvae of *A. hamadae* were found on the aquatic herb *Thurnia sphaerocephala*, (Rudge) J.D. Hooker (Thurniaceae) which is abundant in these streams, but also among the roots of riparian vegetation trailing in the water. Larvae were found in more lentic areas of the stream, but preferred areas of moderate current. Larvae aggregated under mature leaves of the aquatic plants for pupation.

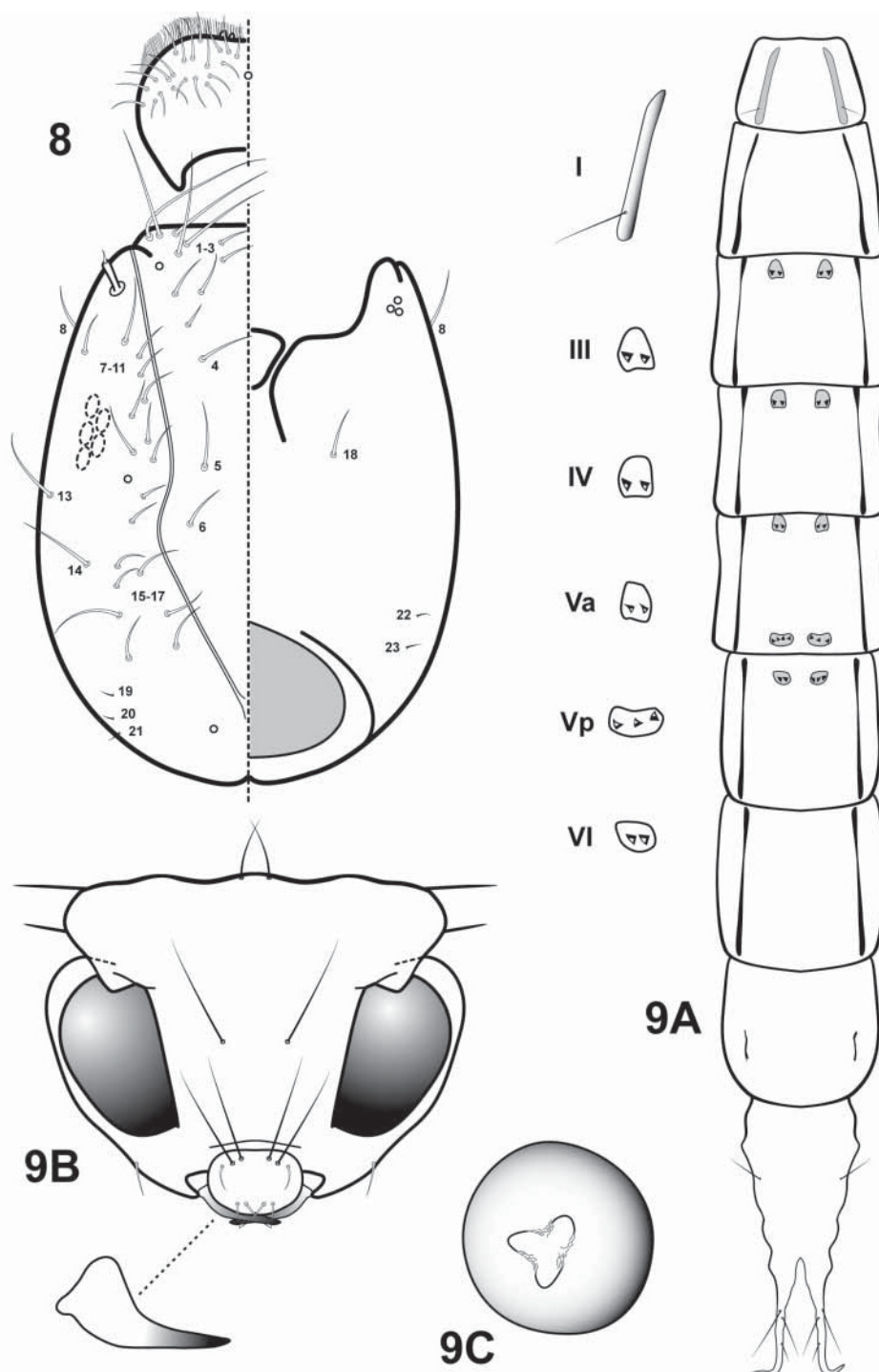
Pes (2001) reported the presence of *A. hamadae* (as *Atanatolica*) from Presidente Figueiredo County, Amazonas, among aquatic vegetation in streams flowing through open areas and having bedrock streambeds (Igarapé do km 24, AM 240 [47 larvae], Igarapé das Lages [1 larva], Igarapé do km 28, AM 240 [13 larvae]). The larvae were more common in areas of current, but especially so during the dry season. Larvae (63) were also found in a disturbed stream, Igarapé da Comunidade Marcus Freire, which was impacted by sedimentation, lacked stones in the stream bed, and had a great abundance of the aquatic plant *Tonina fluvialis* Aubl. (Eriocaulaceae). Physiochemical characteristics of the water from the collection sites were: width 3.25–11 m, depth 0.28–0.93 m, discharge 0.57–5.98(m<sup>3</sup>s<sup>-1</sup>), velocity 0.27–1.41 (ms<sup>-1</sup>), temperature 24–26°C, pH 4–4.7.



**FIGURE 6.** *Amazonatolica hamadae*, new species. Larva: A—lateral; B—head and thorax, dorsal; C—case, lateral.



**FIGURE 7.** *Amazonatolica hamadae*, new species. Larva: A—foreleg, lateral; B—midleg, lateral; C—hind leg, lateral; D—mandible, dorsal; E—anteromesal corner of pronotum, detail of cuticle; F—fore trochantin, lateral; G—abdominal segments IX & X, lateral; H—lateral hump scutellum, lateral; I—tergum IX, dorsal.



**FIGURE 8.** *Amazonatolica hamadae*, new species. Larval head and labrum setal pattern, left half dorsal, right half, ventral.

**FIGURE 9.** *Amazonatolica hamadae*, new species. Pupa: A—abdomen, abdominal hook plates, enlarged; B—head, frontal, mandible enlarged; C—anterior silken membrane of pupal case.



The larvae from Rondônia were collected from a stream in *terra firme* pasture (width 3 m, depth 0.24 m, discharge  $0.38 \text{ m}^3\text{s}^{-1}$ , velocity  $0.54 \text{ ms}^{-1}$ , temperature  $22^\circ\text{C}$ , pH 4) and those from Bahia from among aquatic vegetation in a large, sandy bottomed river flowing through open *cerrado* forest (width 20 m, depth 1.20 m, discharge  $6.7 \text{ m}^3\text{s}^{-1}$ , velocity  $0.82 \text{ ms}^{-1}$ , temperature  $24^\circ\text{C}$ , pH 4.3) (N. Hamada, pers. comm.).

### Phylogenetic considerations

Morse (1981) erected the tribe Grumichellini for the Neotropical genera *Atanatolica* and *Grumichella* and established its monophyly based on the shared possession of a 0,2,2 adult tibial spur formula. Later, Morse & Holzenthal (1987) restated the tibial spur character as “mesotibial preapical spurs absent” and added a second synapomorphy for the tribe, lateral pronotal warts absent. At the same time, Morse & Holzenthal transferred *Triplexa* to the Grumichellini as the sister genus to *Atanatolica*, based on the shared possession of apical processes on segment X and mesal setae on the apex of the inferior appendage in the male genitalia. The later relationship was first suggested by Holzenthal (1985) and confirmed by St. Clair (1994). Finally, Holzenthal (1988) and St. Clair (1994) listed over a dozen additional apomorphies for the Grumichellini, all derived features found in the larval stage.

*Amazonatolica* clearly falls within the Grumichellini, with which it shares in the adult stages a reduced tibial spur formula (0,0,0 in *Amazonatolica*, Fig. 1E) and the absence of lateral pronotal warts (Fig. 1A). In the larval stage, the labrum and head have many secondary setae (Fig. 8), although there are only single setae at positions 4 and 5, rather than multiple secondary setae in these positions, as in *Atanatolica* and *Grumichella* (Holzenthal 1988, figs. 2A, 53A, respectively). Furthermore, it is difficult to determine if head seta 12 is absent in the new genus (synapomorphy 4 of Holzenthal, 1988). Head secondary setation is also listed as a feature of both *Triplexa* (St. Clair 1994) and *Gracilipsodes* (Ward 2001). The pro-, meso-, and metanota in all 5 genera also possess numerous secondary setae (not only in *Atanatolica* as mistakenly indicated by Holzenthal, 1988, synapomorphy 35). Mandibles of the new genus are trowel-like as in other grumichellines, with a central concavity filled with a setal brush (Fig. 7D; Holzenthal 1988, fig. 52D; Ward 2001, fig. 13). Larval antennae are short (synapomorphy 6 of Holzenthal 1988), but are much closer to the anterior margin of the head capsule rather than midway between the anterior margin and the eye, as indicated by St. Clair (1994) and Ward (2001) for other grumichellines. All grumichellines, including *Amazonatolica*, have metanotal *sa1* and *sa2* sclerites fused, forming a broad dorsal plate with the posterolateral corners extended laterad and recurved mesad (Fig. 6B) (synapomorphies 7-9 of Holzenthal 1988). In addition, metanotal *sa3* is long and oval in all genera (synapomorphy 10 of Holzenthal 1988). The larval legs, especially the hind legs, of *Amazonatolica* are broad and stout, appearing most similar to those of *Grumichella* (synapomorphy 11 of Holzenthal 1988, fig. 52A). The abdominal gills are

reduced in all genera (absent in *Amazonatolica*, Fig. 6A) and the lateral fringe is absent (synapomorphies 12 and 14 of Holzenthal 1988). Finally, the meso- and metanotal pleural sclerites are broad and platelike in all genera (synapomorphy 13 of Holzenthal 1988).

Within the Grumichellini, Holzenthal (1988) established monophyly of *Grumichella* and *Atanatolica* based on 20 and 13 characters, respectively, from larval, pupal, and adult stages (synapomorphies 15–34 and 35–47 of Holzenthal 1988, respectively). With *Grumichella*, *Amazonatolica* shares the short, clear head and labral setae (Fig. 8; Holzenthal 1988, fig. 53A), but in *Amazonatolica* the setae are very faint and difficult to see except at high magnification. The hind legs of both genera are broad, but they are much flatter in *Grumichella* than they are in *Amazonatolica*, and while the anal claw has a dorsal accessory hook in the new genus, it is not as long and slender as in *Grumichella*; these similarities are likely primitive for the tribe and related to the habitat requirements of the larvae. In the pupa, both *Grumichella* and *Amazonatolica* have small mandibles and labrums, but in the latter genus the labrum bears setae. All other apomorphies listed by Holzenthal (1988) for *Grumichella* remain unique for the genus. Of particular note are the long, narrow frontal setal warts and the wide malar space of *Grumichella* (syapomorphies 33 and 34 of Holzenthal 1988, respectively); in *Amazonatolica*, the malar space is very narrow and the frontal setal warts are not elongate, but similar in shape to those of *Atanatolica* (representing the primitive condition).

With *Atanatolica*, *Amazonatolica* seems only to share the long, straight anal processes of the pupa, but these processes are less sclerotized and flexible in the Amazonian genus. In the male genitalia, the mesal surface of the inferior appendage bears stout, spine-like setae, a character also shared with *Atanatolica*, *Gracilipsodes*, and *Triplexa*, and thus one that could be interpreted as a synapomorphy for a clade including these genera and *Amazonatolica*. However, the absence of apical, digitate processes on tergum X of *Amazonatolica*, interpreted here as the primitive state, sets the new genus apart from the other 3 genera. In the female genitalia, *Amazonatolica* shares none of the synapomorphies listed by Holzenthal (1988) for *Atanatolica* and is unlike the females of *Triplexa* (Mosely & Kimmins 1953, fig. 156) and *Gracilipsodes* (Ward 2001, figs. 2–5). Based on these characters, relationships among the genera of Grumichellini are inferred as *Grumichella* (*Amazonatolica*, *Atanatolica*, *Gracilipsodes*, *Triplexa*).

Several derived characters render *Amazonatolica* unique within the Grumichellini. In the adult, the maxillary palps are reduced to 3 segments, the tibial spurs are absent on all legs (tibial spur formula 0,0,0), and fork III is absent in both the male and female hind wings. These characters are unique not only within the Grumichilline, but within the entire Triplectidinae.

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