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Phylogeny and revision of the Neotropical genus *Grumichella* Müller (Trichoptera: Leptoceridae), including nine new species and a key

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The systematics of the Neotropical caddisfly genus *Grumichella* Müller (Leptoceridae: Grumichellinae) are reviewed. Diagnoses, descriptions and illustrations are provided for four previously described species, *G. aequiunguis* Flint, 1983, *G. flaveola* (Ulmer, 1911), *G. pulchella* (Banks, 1910) and *G. rostrata* Thienemann, 1905, and nine new species: ***G. blahniki* sp. nov.** (Peru), ***G. boraceia* sp. nov.** (Brazil), ***G. cressae* sp. nov.** (Venezuela), ***G. jureia* sp. nov.** (Brazil), ***G. leccii* sp. nov.** (Brazil), ***G. muelleri* sp. nov.** (Brazil), ***G. paprockii* sp. nov.** (Brazil), ***G. parati* sp. nov.** (Brazil) and ***G. trujilloi* sp. nov.** (Venezuela). The monophyly of the genus is corroborated (16 synapomorphies) and the phylogenetic relationships of its included species, based on analysis of 66 adult, larval, and pupal characters, are inferred as (*G. aequiunguis* ((*G. boraceiae* (*G. leccii*, *G. parati*)) (*G. rostrata* ((*G. flaveola*, *G. pulchella*) (*G. muelleri*, *G. paprockii*)) (*G. jureia* (*G. trujilloi* (*G. cressae*, *G. blahniki*)))))). A taxonomic key to the males of the species is presented.

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ADDITIONAL KEYWORDS: biodiversity – caddisflies – Grumichellinae – phylogenetic relationships – review – systematics.

INTRODUCTION

The cosmopolitan family Leptoceridae Leach, 1815, is the second largest in Trichoptera, with 52 genera and 2037 described species (Holzenthal, Morse & Kjer, 2011). Traditionally, the family has been classified in two subfamilies, Leptocerinae Ulmer, 1903 and Triplectidinae Ulmer, 1906. The Leptocerinae are cosmopolitan and the Triplectidinae are distributed primarily in the Australian and Neotropical regions, with a putative member in southern Africa (De Moor, 1997). Three synapomorphies for Triplectidinae were presented by Morse (1981) and Morse & Holzenthal (1987): the loss of the primitive phallic parameres, the marked reduction of the phallicata and the presence of a large tooth on each pupal mandible (Calor & Holzenthal, 2008). Morse (1981) also divided the Triplectidinae into three tribes, Triplectidini, Hudsonemini and Grumichellini. The tibial spur formula in Triplectidinae ranges from 0,0,0 to 2,2,4.

According to Morse (1981), the monophyly of Leptocerinae is based on the loss of one branch of the median vein (undivided M_{1+2}[fork III]) in the hind wing, the loss of the sectoral crossvein in the hind wing and the reduction of the adult tibial spur formula from 2,4,4

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to 2,2,4 (or the absence of mid-tibial pre-apical spurs). The first two characters are not exclusive to this subfamily and also are present in members of Grumichellini, as pointed by Holzenthal & Pes (2004) and Malm & Johanson (2008, 2011).

Within the subfamily Triplectidinae, the tribe Grumichellini was established based on a reduction in adult tibial spur formula to 0,2,2, at least for *Grumichella* and *Atanatolica* (Morse, 1981). Morse & Holzenthal (1987) re-analysed this diagnostic character and defined it as 'absence of mesotibial preapical spurs'. They added a second synapomorphy, absence of lateral pronotal tubercle in adults. Later, Holzenthal (1988a) reviewed the tribe Grumichellini and increased the number of synapomorphies supporting its monophyly to 21 based largely on larval morphology.

Morse & Holzenthal (1987) proposed *Atanatolica* as the sister genus of *Triplexa*, but they included only three grumichelline genera in their analysis. Later, Calor & Holzenthal (2008) proposed a phylogenetic hypothesis for the tribe Grumichellini when describing a new genus, *Osflintia*, from Peru. The monophyly of Grumichellini was corroborated by the following 14 characters: absence of lateral setal warts on the pronotum; second article of the inferior appendage very reduced; presence of stout, spine-like setae on the mesal surface of the inferior appendage; forewing fork V starting before crossvein *m-cu*; dilated apical region of inferior appendage of male genitalia; larval labrum with many secondary setae; larval head with many secondary setae; two setae on outer margin of larval mandibles; larval mandibles without teeth, trowel-like; larval antennae short; larval *sa*2 sclerites extended laterad; larval metanotal *sa*3 sclerite long; larval metapleural sclerites broad, plate-like; and larval gills restricted to anteriormost abdominal segments (Calor & Holzenthal, 2008). A Neotropical clade (*Amazonatolica*, *Grumichella*, *Osflintia* and *Atanatolica*) was recovered as monophyletic and was supported by three synapomorphies: forewing fork V starting after crossvein *m-cu*; posterolateral corners of larval *sa*2 sclerites curved mesad; and larval lateral fringe absent. The Neotropical genera were arranged in two monophyletic clades. One with *Osflintia* and *Atanatolica* as sister genera, and the other with *Amazonatolica* and *Grumichella* as sister genera (Calor & Holzenthal, 2008).

Malm & Johanson (2011) conducted a phylogenetic analysis of the family based on sequence data from five genes, including mitochondrial COI and four nuclear genes (CAD, EF-1α, IDH and POL). The phylogeny they obtained was in general congruence with the framework based on morphology, but there were differences in the resulting classification. The monophyly of each of the two subfamilies, Triplectidinae and Leptocerinae, was corroborated, but only with the exclusion of one tribe each from the morphological assessment of Morse and Holzenthal's prior work (Grumichellini and Leptorussini). Consequently, Grumichellini and Leptorussini were elevated to subfamily status (Fig. 1B) by Malm & Johanson (2011). Malm & Johanson (2011) recovered the grumichelline genera as collectively monophyletic and sister to the subfamily Leptocerinae. This relationship is supported by shared morphological character states (e.g. a reduced tibial spur formula, 0,0,0 or 2,2,2, and the absence of the discoidal cell in the hind wings, except in *Triplexa*). The genitalia of grumichellines resemble those of Triplectidinae (e.g. both lacking phallic

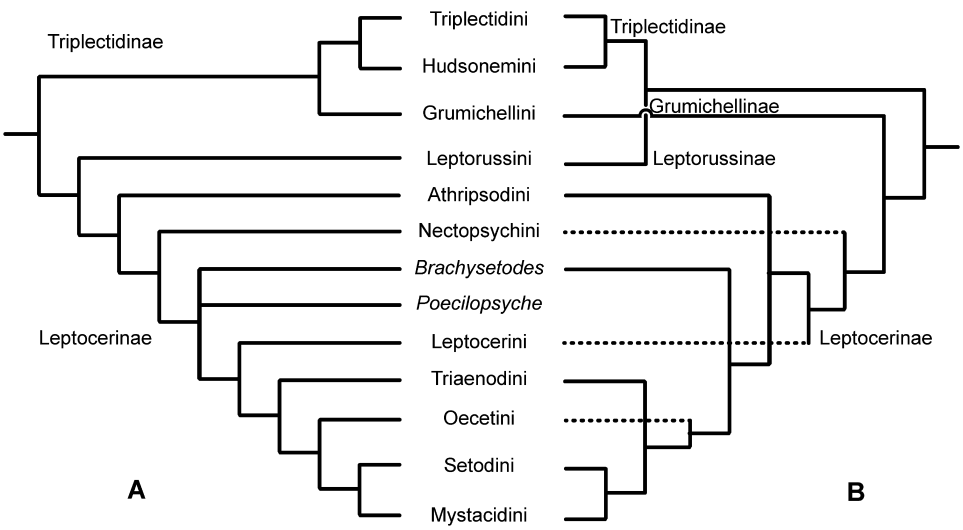

Figure 1. Phylogeny of Leptoceridae tribes (and two non-associated genera). A, morphological approach with two subfamilies (Morse, 1981; Morse & Holzenthal, 1987). B, molecular approach with four subfamilies (Malm & Johanson, 2011).

parameres, vs. present in Leptocerinae), which may be a plesiomorphic trait. Accordingly, Malm & Johanson (2011) proposed the elevation of the tribe to subfamily status: Grumichellinae Morse, 1981.

As currently circumscribed, the subfamily Grumichellinae comprises six genera, four in the Neotropical region (*Amazonatolica*, *Atanatolica*, *Grumichella*, *Osflintia*) and two in the Australian region (*Triplexa* and *Gracilipsodes*). The genus *Grumichella* comprises four described species (*G. aequiunguis*, *G. flaveola*, *G. pulchella* and *G. rostrata*) with a distribution in South America from Venezuela south to Argentina, and additional records in Paraguay and south-eastern and southern Brazil (Holzenthal, 1988a). Here, the systematics of the genus are reviewed, and a phylogeny of the species is proposed. Additionally, nine new species are described and illustrated from Brazil, Peru and Venezuela, and an identification key for males is presented.

MATERIAL AND METHODS

Material examined was borrowed from the Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA), National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH), University of Minnesota Insect Collection, St Paul, MN, USA (UMSP), Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP), and the Museu de Zoologia, Universidade Federal da Bahia, Salvador, Bahia, Brazil (UFBA). The holotypes and type series will be deposited in MZUSP, UFBA and UMSP, as indicated in the 'Material examined' section in each description.

Methods used in the collection, preparation, examination, illustration and description of the species were those discussed by Holzenthal & Andersen (2004), Blahnik & Holzenthal (2004), Blahnik, Holzenthal & Prather (2007) and Calor & Mariano (2012). The morphological terminology used in this paper follows that described and figured by Schmid (1980) and adopted by Holzenthal (1988a). The descriptions and key were produced using the software package DELTA (Dallwitz, Paine & Zurcher, 1999; Coleman, Lowry & Macfarlane, 2010) to increase the consistency and accuracy of the descriptions and the key.

For the phylogenetic analyses, the putative ingroup included all species of *Grumichella*, and outgroups included all other genera of Grumichellinae (*Amazonatolica*, *Atanatolica*, *Gracilipsodes* and *Triplexa*) and members of other clades of Leptoceridae (*Hudsonema*, *Nectopsyche*, *Oecetis*, *Triaenodes* and *Triplectides*). This combination of taxa was used to polarize character states (via a posteriori rooting of the ingroup), test the monophyly of the subfamily Grumichellinae, and infer the relationships among the ingroup clades. The choice of taxa was based on the previous phylogenetic hypotheses of Leptoceridae (Morse, 1981; Malm & Johanson, 2011), Triplectidinae (Morse & Holzenthal, 1987) and Grumichellinae (Holzenthal, 1988a; Holzenthal & Pes, 2004; Calor & Holzenthal, 2008; Malm & Johanson, 2008).

Morphological characters from both adults and immature stages were included in the data matrix (Appendix 1). The data matrix was constructed using the software NDE (Page, 2001) and included 66 characters (29 adult characters, 24 larval characters and 13 pupal characters) and 22 taxa (Appendix 2). Parsimony analyses were implemented in TNT 1.1 (Goloboff, Farris & Nixon, 2008) under equal and implied weighting (Goloboff, 1993, 1995). Branch and bound and heuristic searches were conducted, with the final analyses carried out using stepwise taxon addition with 1000 random addition sequences (RAS) and tree-bisection-reconnection (TBR) branch swapping, 500 replicates and 100 trees saved in each replicate. The analyses under implied weighting were run with different values of k. The fit range was from 1 to 100 (1–10, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100). This procedure was implemented to evaluate potential topological changes under different k values (Prendini, 2000; Salles *et al*., 2014). These searches were conducted using the implicit enumeration command in TNT 1.1. Additionally, a sensitivity analysis was completed to compare the results from equal and implied weighting under different parameters. In this way, the sensitivity analysis (*sensu* Giribet & Wheeler, 2007) was implemented to support the topological choice from our different results, demonstrating by the different 'support' parameters of the clades the robustness of the topology.

SYSTEMATICS

LEPTOCERIDAE LEACH, 1815

GRUMICHELLA MÜLLER, 1879

Grumichella Müller, 1879: 407 (Type species: *Grumichella rostrata* Thienemann, 1905, first included species). – Holzenthal, 1988a:88 [male, female, larva, pupa, revision, phylogeny, distribution]. – Flint, Holzenthal & Harris, 1999: 128 [catalog]. – Morse, 1981: 259 [classification, phylogeny]. – Morse & Holzenthal, 1987: 140 [classification, phylogeny]. – Calor & Holzenthal, 2008: 255 [phylogeny]. – Malm & Johanson, 2011: 3, 7 [classification, phylogeny].

Leptocellodes Ulmer, 1911: 21 [Type species: *Leptocellodes flaveola* Ulmer, 1911, original designation (the designation of *G. flaveola* Ulmer, 1911 as type species by Ulmer (1955) is not valid (ICZN 1985, Art. 69(a) *sensu* Holzenthal, 1988a)]; – Ulmer, 1955: 499 [to synonymy].

Grumichella Müller, 1879 (= *Leptocellodes* Ulmer, 1955) comprises 13 species, including the nine new

species described here: *G. aequiunguis* Flint, 1983; *G. blahniki* sp. nov.; *G. boraceia* sp. nov.; *G. cressae* sp. nov.; *G. flaveola* (Ulmer) Holzenthal, 1988a, *G. jureia* sp. nov.; *G. leccii* sp. nov.; *G. muelleri* sp. nov.; *G. paprockii* sp. nov.; *G. parati* sp. nov.; *G. pulchella* (Banks) Holzenthal, 1988a; *G. rostrata* Thienemann, 1905; *G. trujilloi* sp. nov.

Müller (1879a, b, 1880a, b, 1888, 1921) illustrated the larvae of an unknown species and discussed its biology. Pupae and cases of two species, *G. rostrata* and *G. aequiunguis*, were described by Thienemann (1905). Roback (1966) described and illustrated the larvae of *G. flaveola* from Peru, but included it under 'unknown family 2'. Ulmer (1955) also described immature forms of the genus. Morse (1981) erected the tribe Grumichellini to accommodate *Grumichella* and *Atanatolica* in his family classification. Holzenthal (1988a) reviewed the genus, redescribed the four valid species, and described the larvae and pupae, including those of eight probable unknown species of larvae (Holzenthal's 'species A–H'). He also corroborated the monophyly of *Grumichella* based on 20 synapomorphies and proposed the phylogenetic relationships among two species groups: *G. pulchella* and *G. rostrata* groups. The first species group, composed of *G. flaveola* and *G. pulchella*, is characterized by nine spots on the forewings. The *G. rostrata* group, comprising *G. aequiunguis* and *G. rostrata*, bears only two spots on forewings. Holzenthal & Pes (2004), in their description of *Amazonatolica*, another Grumichellini genus, discussed other characters and the phylogenetic position of *Grumichella*. Calor & Holzenthal (2008) described another related genus, *Osflintia*, and proposed a phylogeny of Grumichellini, placing *Osflintia* as sister-genus of all other grumichelline genera.

Biological remarks: Müller (1879a, b) provided the first records of the habitat of larvae, including their occurrence in small waterfalls and rock surfaces in fast flowing waters of small mountain streams. These observations were corroborated by others authors (e.g. Holzenthal, 1988a; Flint *et al*., 1999). In our fieldwork, the larvae (and pupae) were often collected from aggregations of more than 50 individuals positioned side by side or in a small clump (e.g. Parque Estadual de Campos do Jordão, São Paulo State, Brazil). Müller (1879a, b) also observed the use of the posterior silken projection on the larval cases to help to hold the larva in the current. The ability of larvae to maintain position in fast flow is aided by the stout legs with modified tarsal claws, as emphasized by Holzenthal (1988a) and by other authors observing larvae of other grumichelline genera (St. Clair, 1994; Ward, 2001). Müller (1879a, b) 'speculated' that the water current prevented the pupae from crawling out of the case, and that the anterior attachment pedicle of the case needed to be severed by the emerging pupae. The loose case then drifted to slack current, where the adult could emerge (Holzenthal, 1988a). In laboratory rearings and rarely in natural habitats (e.g. *G. boraceia* sp. nov.), a behaviour of flotation and drift was observed in the fifth instar larvae, with air bubbles inside the anterior portions of cases (our pers. observ.).

The use of abandoned larval cases by other genera of caddisflies is not uncommon, especially in *Triplectides* (Holzenthal, 1988b; Flint *et al*., 1999; Crisci-Bispo, Bispo & Froehlich, 2004; Calor & Froehlich, 2008), and includes observations by A.R.C. and by P.A. Rueda-Martín (pers. commun.) in Brazil and Argentina, respectively, of *Marilia* (Odontoceridae) occupying *Grumichella* cases.

Grumichella aequiunguis Flint, 1983 (Fig. 2)

Grumichella aequiunguis Flint, 1983: 68, figs 246–248 [Type locality: Argentina: Misiones, Arroyo Piray Mini, rt. 17, W Dos Hermanas, 23.xi.1973, O. S. Flint, Jr, type 100540; NMNH; male]. – Holzenthal, 1988a:91 [male, female, larva, pupa, case, distribution]. – Flint, Holzenthal & Harris, 1999: 128 [catalog]. – Blahnik, Paprocki & Holzenthal, 2004: 5 [distribution]. – Paprocki, Holzenthal & Blahnik, 2004: 12 [distribution]. – Dumas *et al*., 2009: 368 [distribution]. – Paprocki & França, 2014: 57 [distribution].

Diagnosis: Grumichella aequiunguis can be diagnosed by the following characters: 2 brown spots on male forewing; male genitalia bearing long, wide, rhomboid 2nd article of inferior appendage, with an excavate mesal surface, subequal in length to apicodorsal portion of 1st article; larval abdominal sternum I with 25–30 long setae. It is most similar to *G. boraceia* sp. nov., but differs in having a pointed rather than blunt apex of the 2nd article of the inferior appendage, which is not excavate.

Adult: Head and body yellowish.

Male: Forewing length: 8–9 mm. Forewing light golden brown, with 2 small brown spots, 1 at midlength, 1 at apex of anal area (arculus). Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin broadly rounded; pleural region sparsely setose; tergum IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, clavate, apex rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin slightly concave, ventral margin abruptly convex; segment X in dorsal view, rectangular, with posterolateral borders well developed, lateral margins subparallel, with apicodorsal shelf, shelf almost rectangular, 1/3 as wide as apex of segment X, without

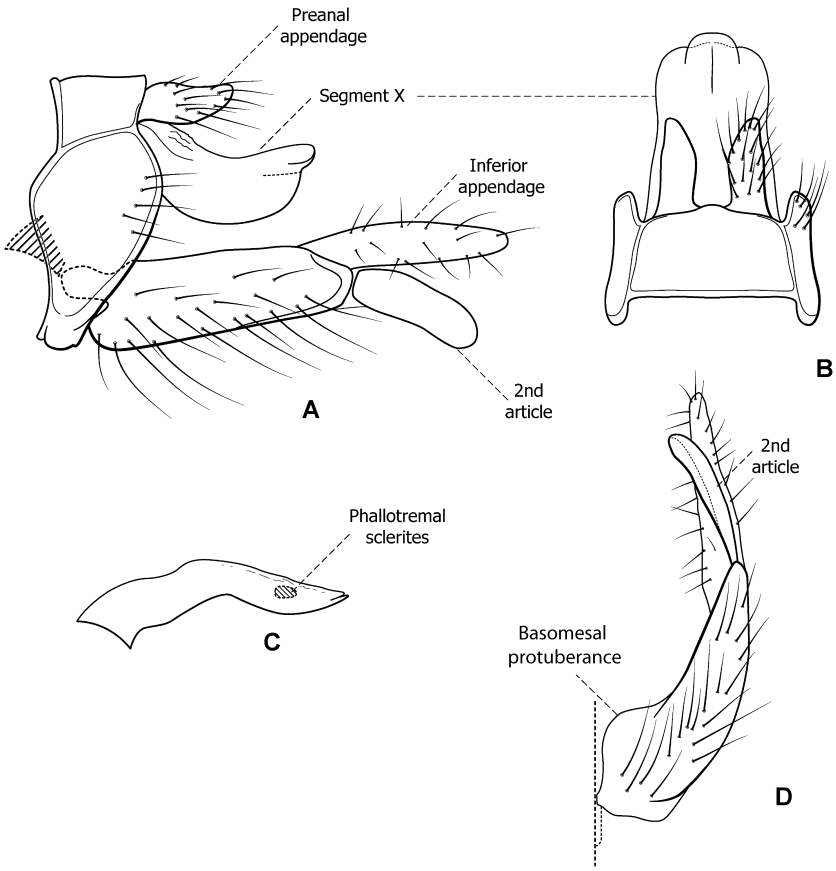

Figure 2. *Grumichella aequiunguis*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

sulcus apically, but bearing a small fold. Inferior appendage concave in ventral view, with basal region tuboid, not enlarged; rounded basally, heavily setose, bearing a small basomesal protuberance; middle region of inferior appendage with constriction before apicodorsal region; 2nd article subequal in length to apicodorsal portion of 1st article, broad along apical 2/3, mesal surface excavate, apex blunt, slightly curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, narrow, posterodorsally directed lateral flanges, apices acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 7–8 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Larva: Head dark brown, almost black, thoracic sclerites dark brown, almost black, legs dark brown, almost black. Length of larva 7 mm. Abdominal sternum I with 25–30 long setae. Lateral hump sclerite very small.

Larval case: Length 10 mm; constructed entirely of rings of dark brown silk, gently curved, tapered, narrow, without diagonal sutures (or sutures indistinct), posterior end with ventral, dorsally directed projection, visible externally, posterior aperture C-shaped.

Pupa: Segment IX very slender; anal process long, narrow, slender, unpigmented or slightly yellowish, apically upturned, hooked.

Pupal case: With ventral silken pedicel, pedicel short; anterior silken membrane with an eccentric, horizontal, slit-like opening.

Distribution: Argentina, Brazil, Paraguay.

Material examined: **ARGENTINA: Misiones:** Ao. Piray Mini W., Dos Hermanas, 23.xi.1973, O.S. Flint Jr, 1 male, paratype (NMNH). **BRAZIL: Paraná:** Rio Cascata, Graciosa, road to Morretes, 10.i.1998, UV light, Holzenthal, Melo & Almeida, 25°20′13″S, 48°53′58″W, elevation (el.) 750 m, 3 males (UMSP); **Minas Gerais:** Parque Estadual de São Gonçalo do Rio Preto, Rio Preto, 12.x.2000, UV light, Paprocki, Amarante & Salgado, 18°07′50″S, 43°20′15″W, el. 791 m, 11 males (UMSP); same data, except Córrego das Éguas, 14.x.2000, UV light, Paprocki, Amarante & Isaac, 18°08′43″S, 43°22′09″W, el. 891 m, 3 males (UFBA); Parque Estadual Itacolomi, Rio Belchior, 19.ix.1998, UV light, Paprocki & Amarante, 20°25′02″S, 43°25′38″W, el. 725 m, 1 male, 10 females (UMSP).

GRUMICHELLA FLAVEOLA (ULMER, 1911) (FIGS 3, 4)

Leptocellodes flaveola Ulmer, 1911: 22 [Type locality: Bolivia: Yungas, Bogota; ZMHU; male]. – Jörgensen, 1919: 397 [male]. – Mosely, 1949: 41 [redescription, male]. – Fisher, 1966: 9 [catalog]. – Holzenthal, 1988a:91 [male, female, larva, pupa, case, distribution]. – Flint, Holzenthal & Harris, 1999: 128 [catalog]. – Munõz-Quesada, 2000: 279 [distribution].

Notanatolica poujadei Navás, 1927: 73 [Type locality: Ecuador, Loja; MNHNP; male]. – Mosely, 1936: 107 [to synonym]. – Fisher, 1966: 9 [catalogue].

Unknown family 2, Roback, 1966: 256, 303, figs 254–266 [larva].

Grumichella flaveola (Ulmer). – Holzenthal, 1988a: 91 [new combination, male, female, larva, pupa, case, distribution]. – Flint, 1991: 93 [male]; – Flint, 1996: 417 [distribution]. – Flint, Holzenthal & Harris, 1999: 128 [catalogue].

Diagnosis: Grumichella flaveola can be diagnosed by the following characters: male forewings with 9 brown spots; male genitalia with 1st article of inferior appendage with small basomesal protuberance; 2nd article 1/2 to 1/3 of length of apicodorsal portion of 1st article; apex of 2nd article acuminate, curved mesal; larval abdominal sternum I with 2 pairs of short setae. It is most similar to *G. pulchella*, except for the quadrate apicodorsal portion of 1st article of the inferior appendage.

Adult: Head and body yellowish.

Male: Forewing length: 11–12 mm ($N = 5$). Forewing light golden brown, with 9 small brown spots (Fig. 3). Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin broadly rounded; in lateral view, pleural region setose; tergum IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, clavate, apex rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin abruptly concave at 2/3 length, with apex upcurved, ventral margin slightly convex; segment X in dorsal view, subtriangular, with posterolateral borders not developed, lateral margins sinuate, narrowing apically, with apicodorsal shelf, shelf almost rectangular, 1/3 as wide as apex of segment X, without sulcus apically. Inferior appendage nearly straight in ventral view, with basal region tuboid, not enlarged; slightly rounded basally, setose, bearing a small basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article shorter than apicodorsal portion of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata sharply down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 7–8 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners (Fig. 4). Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Larva: Head light brown, thoracic sclerites light brown, legs yellowish to brownish, with dorsal borders of middle and hind femora black. Length of larva 8 mm. Abdominal sternum I with 2 pairs of short, thin setae; lateral hump sclerite very small.

Larval case: Length 9 mm; constructed of alternating rings of clear and dark brown silk, nearly straight, tapered, wide, with 2 distinct diagonal sutures, 1 towards posterior end and 1 more or less at midlength, posterior end with ventral, dorsally directed projection, visible externally, posterior aperture C-shaped.

Pupa: Segment IX slender; anal process short, roughly trapezoidal in general shape, tapering posteriorly to narrow apex, with basodorsal, pigmented area shaped like a parallelogram, apically upturned, hooked.

Pupal case: With anteroventral silken pedicel, pedicel short; anterior silken membrane with 3 small openings arranged in a triangle.

Distribution: Argentina, Bolivia, Colombia, Ecuador, Peru, and Venezuela.

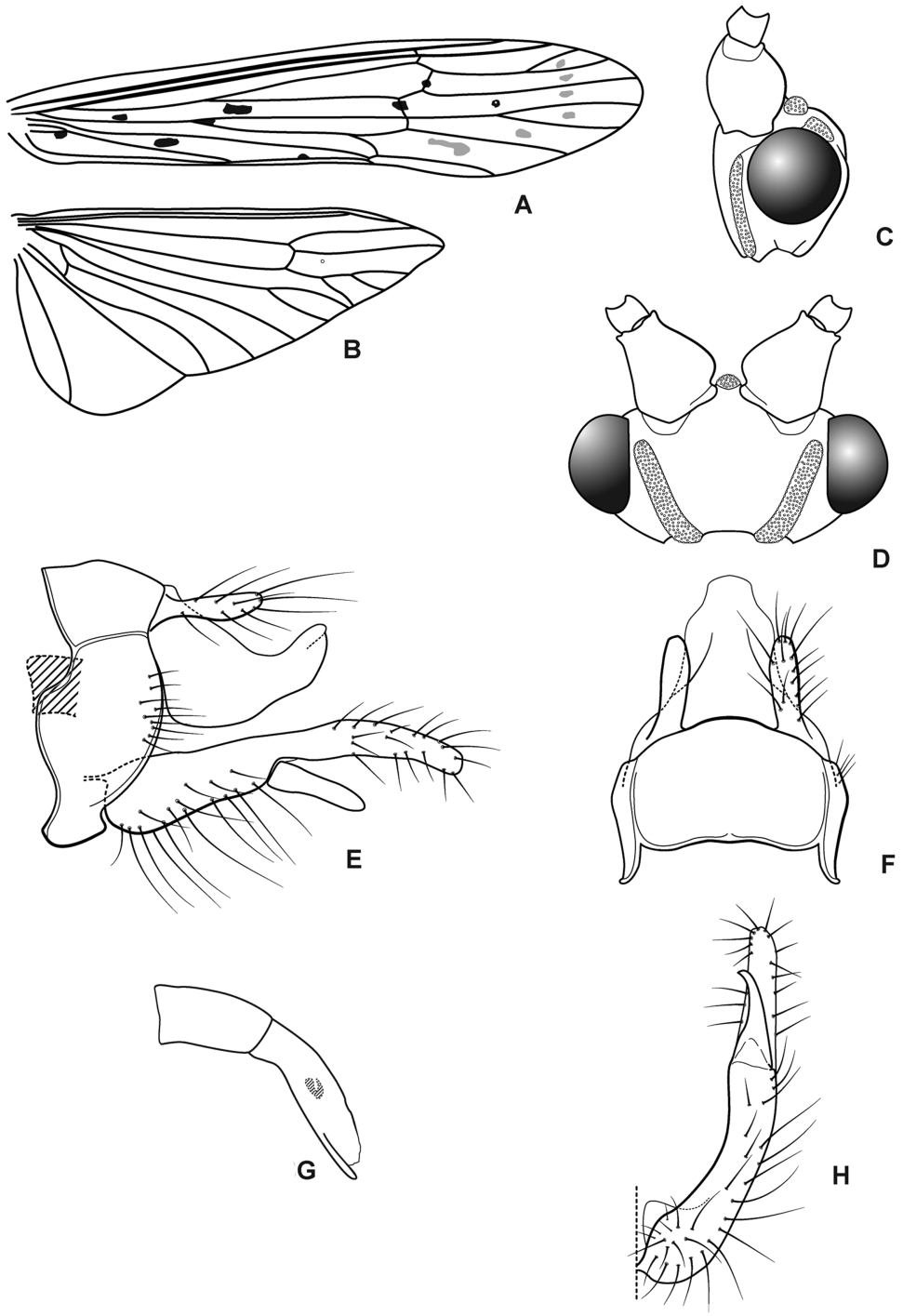

Figure 3. *Grumichella flaveola*, male. A, forewings. B, hind wings. C, head, lateral view. D, head, dorsal view. E, genitalia, lateral view. F, genitalia, dorsal view. G, phallus, lateral view. H, inferior appendage, ventral view.

Material examined: **ARGENTINA: Salta:** Rt. 59, Km 23.5, Cañada La Gotera, 16–17.x.1973, O.S. Flint Jr, 34 males, 6 females (NMNH). **BOLIVIA: La Paz:** Rio Coroico, el. 1200 m, 23–26.ix.1984, L.E. Pena G., 5 males (NMNH). **COLOMBIA: Antioquia:** Rio Medellin, 6 km, S. Caldas, 24.ii.1984, C.M. & O.S. Flint Jr; 1 male, 12 females (NMNH). **ECUADOR: Pastaza:** Mera, el. 1300 m, xii.1992, V.O. Becker col., 1 female, det. O.S. Flint Jr (NMNH); Puyo (12 km W), 9.v.1977, P.J. Spangler & D.R. Givens, 2 males (NMNH). **PERU:**

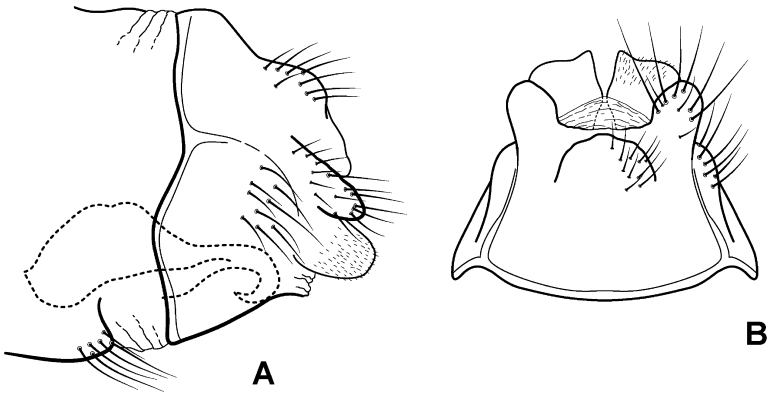

Figure 4. *Grumichella flaveola*, female. A, genitalia, lateral view. B, genitalia, dorsal view.

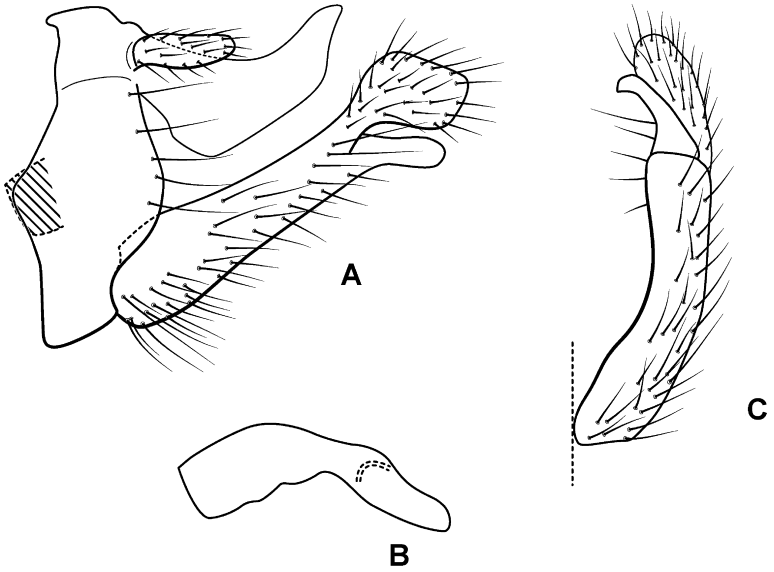

Figure 5. *Grumichella pulchella*, male. A, genitalia, lateral view. B, aedeagus, lateral view. C, inferior appendage, ventral view.

Dept. Cusco: Santa Isabel, Cosnipata Valley, ix.26 1951, F. Woytkowski; 1 male (NMNH). **VENEZUELA: Barinas:** Queb. San Juan in Sta. Rosa, Barinas, 08°27′52″N, 70°50′55″W, el. 1000 m, 4 males, 11 females (UMSP), 1 male, 2 females (UFBA).

GRUMICHELLA PULCHELLA (BANKS, 1910) (FIG. 5)

Leptocella pulchella Banks, 1910: 160 [Type locality: Colombia: Tolima, Canõn de Monte, Dec., type 11783; MCZ; male]. – Fisher, 1966: 60 [catalogue].

Leptocellodes pulchellus Ulmer, 1955: 499 [to synonym]. – Flint, 1967: 22 [male].

Grumichella pulchella Holzenthal, 1988a:93 [new combination]. – Flint, Holzenthal & Harris, 1999: 128 [catalogue]. – Munõz-Quesada, 2000: 279 [distribution].

Diagnosis: Grumichella pulchella can be diagnosed by the following characters: male forewings with 9 brown spots; male genitalia bearing apicodorsal portion of 1st article of inferior appendage quadrate; segment X acuminated, dorsal view. As discussed before, it is most similar to *G. flaveola*, but differs in the apicodorsal portion of the 1st article of the inferior appendage, which is not digitate.

Adult: Head and body yellowish.

Male: Forewing length: 11–12 mm. Forewing light golden brown, with 9 small brown spots. Abdominal segment IX annular; in dorsal view, with anterior margin straight, posterior margin broadly rounded; in lateral view, pleural region setose; tergum IX without dorsal

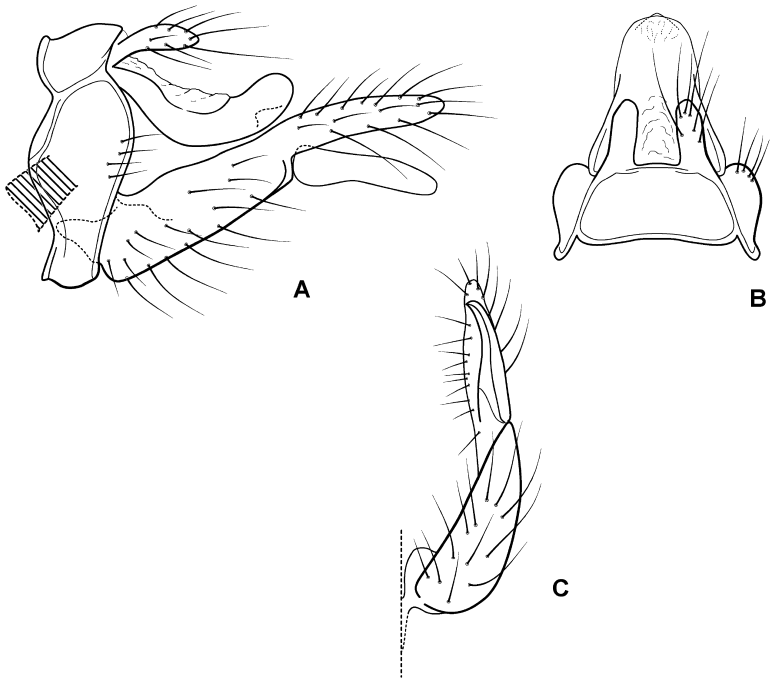

Figure 6. *Grumichella rostrata*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, inferior appendage, ventral view.

protuberances. Preanal appendage setose, at least 4× as long as wide; in lateral view, clavate, apex rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin abruptly concave at 2/3 length, with apex upcurved, ventral margin slightly convex; segment X in dorsal view, subtriangular, with posterolateral borders not developed, lateral margins sinuate, narrowing apically, with apicodorsal shelf, shelf narrow, attenuate, acutely upturned, 1/3 as wide as apex of segment X, without sulcus apically. Inferior appendage nearly straight in ventral view, with basal region tuboid, not enlarged; slightly rounded basally, setose, bearing a small basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article shorter than apicodorsal portion of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article quadrate, setose. Phallic apparatus simple, phallicata sharply down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Distribution: Colombia.

GRUMICHELLA ROSTRATA THIENEMANN, 1905 (FIG. 6)

Grumichella rostrata Thienemann, 1905: 49 (Type locality: no type nor type depository designated, but name based on material probably from Brazil, Santa Catarina, Gruta dos Macacos, near Blumenau according to Holzenthal, 1986; case, pupa). – Thienemann, 1909: 41, 42, 125 [larva, pupa]. – Fisher, 1966: 10 [catalogue]. – Holzenthal, 1988a:93–95 [male, female, larva, case, pupa, distribution]. – Flint, Holzenthal & Harris, 1999: 128 [catalogue]. – Paprocki, Holzenthal & Blahnik, 2004: 12 [distribution]. – Calor, 2011: 322 [distribution]. – Paprocki & França, 2014: 57 [distribution].

Diagnosis: Grumichella rostrata can be diagnosed by the following characters: male forewing with 2 or 3 brown spots; male genitalia bearing segment X flattened, lateral view; 2nd article of inferior appendage subequal to apicodorsal portion of 1st article; apex of 2nd article acuminated, curved mesad. *Grumichella rostrata* is most similar to *G. lecci* sp. nov., but differs in having segment X without sulcus apically, and the subequal lengths of the 2nd article of inferior appendage and the apicodorsal portion of the 1st article.

Adult: Head and body yellowish.

Male: Forewing length: 8–11 mm. Forewing light golden brown, with 2 or 3 small brown spots, bearing dark setae on posterodorsal margin. Abdominal segment IX annular; in dorsal view, with anterior margin slightly convex, posterior margin nearly straight; in lateral view, pleural region sparsely setose; tergum IX without protuberances dorsally. Preanal appendage setose, at

least 4× as long as wide; in lateral view, clavate, apex subacute. Segment X saddle-shaped; in lateral view flattened, dorsal margin abruptly concave at 2/3 length, with apex upcurved, ventral margin abruptly convex; segment X in dorsal view, rectangular, with posterolateral borders developed, lateral margins sinuate, with apicodorsal shelf, shelf rounded, 1/3 as wide as apex of segment X, without sulcus apically. Inferior appendage slightly concave in ventral view, with basal region tuboid, not enlarged; slightly rounded basally, setose, bearing a small basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article subequal in length to apicodorsal portion of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 6–9 mm. Forewing yellowish to brown or dark brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Larva: Head dark brown, almost black, thoracic sclerites dark brown, almost black, legs dark brown, almost black. Length of larva 6–7 mm. Abdominal sternum I with 25–30 long setae; lateral hump sclerite very small.

Larval case: Length 7–9 mm; constructed entirely of rings of dark brown silk, gently curved, tapered, wide, with 2 distinct diagonal sutures, 1 towards posterior end and 1 more or less at midlength, posterior end with ventral, dorsally directed projection, visible externally, posterior aperture C-shaped.

Pupa: Segment IX very slender; anal process long, narrow, slender, unpigmented or slightly yellowish, apically upturned, hooked.

Pupal case: With anteroventral silken pedicel, pedicel very long, thin; anterior silken membrane with an eccentric, horizontal, slit-like opening.

Distribution: Brazil.

Material examined: **BRAZIL: Bahia:** Elisio Medrado, Serra da Jibóia, Faz. Jequitibá, GAMBA, Córrego Caranguejo, 12°52′127″S, 39°28′324″W, el. 510m, 28.iii.2012, Quinteiro F.B., Duarte T. & Garcia I., 2 males (UFBA); Varzedo, Serra da Jibóia, Faz. Baixa da Areia Cai Camarão, 12°57′45″S, 39°27′12″W, Prop. Sr. Getulio, Córrego Cai Camarão, 24.x.2012, Gomes V., Campos R. & Vilarino A., 3 males (UFBA); **Minas Gerais:** Rio Tanque, *c.* 12 km (rd) from Ipoema, 16.v.1998, UV light, Holzenthal & Paprocki, 19°32′12″S, 43°26′53″W, el. 750 m, 1 male, 2 females (UMSP); Parque Estadual Itacolomi, Rio Belchior, 20.ii.1999, UV light, Paprocki & Amarante, 20°25′02″S, 43°25′38″W, el. 725 m, 2 males (UMSP); Córrego Pitanga, upstream of confluence with Rio Santo Antônio, 19.x.2000, UV light, Paprocki & Ferreira, 19°05′40″S, 42°39′54″W, el. 238 m, 3 males, 1 female (UMSP); Parque Estadual do Ibitipoca, Corrego dos Macacos, 19.ix.2001, UV light, Holzenthal, Blahnik, Neto & Paprocki, 21°42′33″S, 44°53′36″W, el. 1360 m, 45 males, 142 females (UMSP); Córrego das Aguas Pretas & tribs., *c.* 15 km S Aiuruoca, 21.xi.2001, UV light, Holzenthal, Blahnik, Neto & Paprocki, 22°03′42″S, 44°38′14″W, el. 1386 m, 5 males (UMSP); **Rio de Janeiro:** Parque Nacional do Itatiaia, Rio Campo Belo, 23.xi.2001, UV light, Holzenthal, Blahnik, Neto & Paprocki, 22°27′02″S, 44°36′49″W, el. 1300 m, 1 male, 1 female (UMSP); Parque Nacional do Itatiaia, Lago Azul, 09.vii.1965, Froehlich C.G., 8 larvae (MZSP); Parque Nacional do Itatiaia, Rio Campo Belo, trail to Veu da Noiva, 24.xi.2001, UV light, Holzenthal, Blahnik, Neto & Paprocki, 22°25′42″S, 044°37′10″W, el. 1310 m, 2 males (UMSP); **Santa Catarina:** Nova Teutonia, 27°11′S, 52°23′S, 29.x.1939, Fritz Plauman, 1 male (NMNH); **São Paulo:** Campos do Jordão, 28.i.1959 (Hotel Umuarama, riacho a jusante do lago, 22°45′44″S, 45°34′56″W, el. 1700 m), Froehliuch C.G., 1 pupa (MZUSP); Parque Estadual de Campos do Jordão, Rio Galharada, 4.iii.1996, UV light & sweeping, Holzenthal & Guahyba, 22°41′40″S, 45°27′47″W, el. 1530 m, 1 larva, 3 females (UMSP); Parque Estadual de Campos do Jordão, Campo do Meio, 6.iii.1996, UV light, Holzenthal & Guahyba, 22°41′45″S, 45°29′27″W, el. 1500 m, 1 pupa (UMSP); Parque Estadualde Campos do Jordão, Rio Galharada, 22.i.1998, UV light, Holzenthal, Froehlich & Paprocki, 22°41′40″S, 45°27′47″W, el. 1530 m, 5 males, 9 females (UMSP); Parque Estadual de Campos do Jordão, Cachoeira Galharada, 15.x.1998, UV light, Paprocki & Froehlich, 22°41′44″S, 45°27′43″W, el. 1620 m, 3 males, 18 females (UMSP); Parque Estadual de Campos do Jordão, Rio Galharada, 10.ix1999, Froehlich C.G., 40 larvae (MZUSP); Cachoeira do Paredão, Lajeado, Serra da Bocaina, 1.iii.2002, UV light, Holzenthal, Blahnik, Paprocki & Prather, 22°43′32″S, 44°37′16″W, el. 1550 m, 17 males, 92 females (UMSP); Cachoeira do Príncipe, Lajeado, Serra da Bocaina, 4.iii.2002, UV light, Holzenthal, Blahnik, Paprocki & Prather, 22°42′55″S, 44°37′25″W, el. 1560 m, 1 female (UMSP); Parque Estadual de Campos do Jordão, córrego Campo do Meio, 6.vi.2005, Calor A.R., *c.* 100 larvae

(UFBA); Parque Estadual de Campos do Jordão, Rio Galharada, acima da cachoeira, 28.iii.2007, luz UV/branca, Calor A.R., Mariano R. & Lecci L., 4 males, 2 females (UFBA); Parque Estadual de Campos doJordão, Rio Galharada, 31.iii.2007, luz UV/branca, Calor A.R., Mariano R. & Lecci L., 1 larva (UFBA).

GRUMICHELLA BLAHNIKI CALOR & HOLZENTHAL SP. NOV. (FIG. 7)

Diagnosis: Grumichella blahniki can be diagnosed by the following characters: male forewings with 12 brown spots; male genitalia bearing segment X not flattened, lateral view; 1st article of inferior appendage with well-developed basomesal protuberance; 2nd article of inferior appendage shorter than the apicodorsal portion of 1st first article; apex of 2nd article pointed, curved mesad; Cu1a and M3+4 veins fused before the border in male hind wings. It is most similar to *G. cressae* sp. nov., except for having tergum IX without protuberances dorsally, and segment X with the posterolateral borders not developed.

Adult: Head and body yellowish brown.

Male: Forewing length: 10–12 mm. Forewing light golden brown, with 12 small brown spots. Male genitalia as in Figure 7. Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin broadly rounded; in lateral view, pleural region

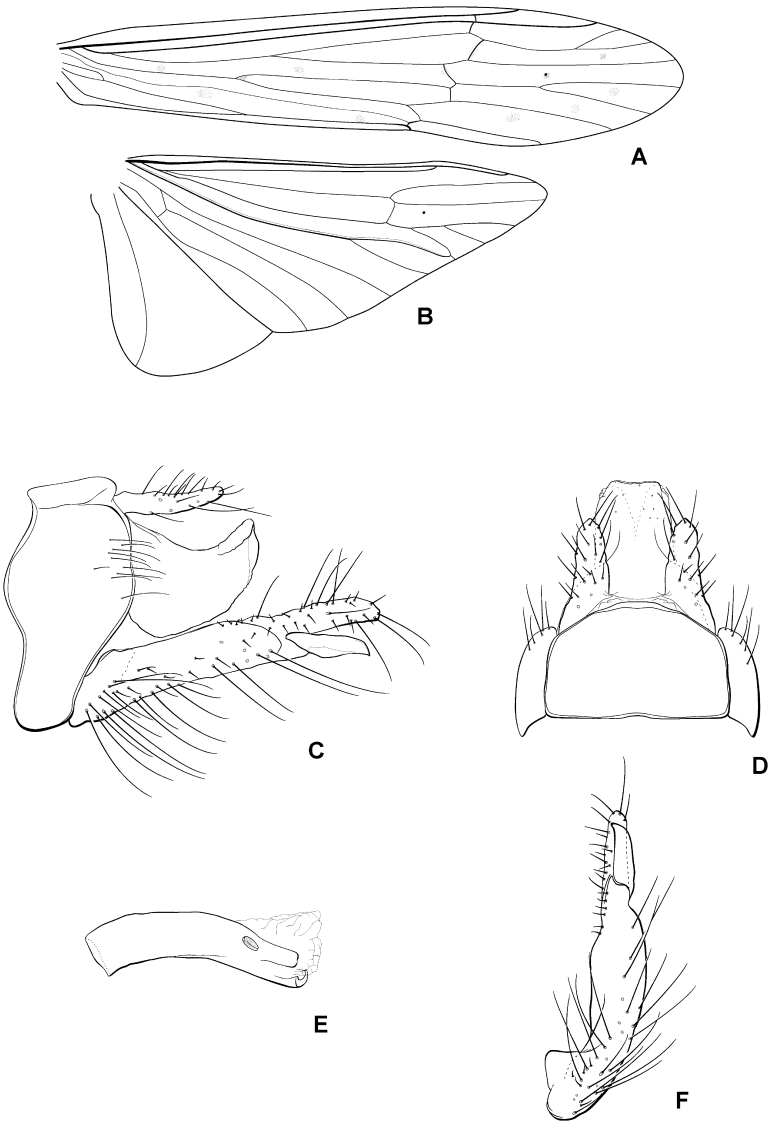

Figure 7. *Grumichella blahniki*, male. A, forewings. B, hind wings. C, genitalia, lateral view. D, genitalia, dorsal view. E, phallus, lateral view. F, inferior appendage, ventral view.

setose; tergum IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, digitate, apex subacute. Segment X saddle-shaped; in lateral view not flattened, dorsal margin slightly concave, apex upcurved, ventral margin abruptly convex; with posterolateral borders not developed, lateral margins subparallel after 1/3 length, with apicodorsal shelf, shelf rounded or almost rectangular, almost as wide as apex of segment X, with ventral sulcus apically. Inferior appendage slightly concave in ventral view, with basal region tuboid, not enlarged; rounded basally, heavily setose, bearing a small basomesal protuberance; middle region of inferior appendage with constriction before apicodorsal region; 2nd article shorter than apicodorsal portion of 1st article, broad, tapering throughout end, mesal surface not excavate, apex pointed, slightly curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 6–8 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Etymology: The specific epithet is in honor of Dr Roger Blahnik for his dedication to Neotropical caddisflies.

Distribution: Peru.

Holotype, male: **PERU: Paucartambo:** Pte. San Pedro, *c*. 50 km NW Pilcopata, el. 1600 m, 2–3.ix.1988, O.S. Flint Jr and N. Adams (NMNH).

Paratypes: same data as holotype, 6 males (NMNH), 2 males (UFBA), 2 males (UMSP).

GRUMICHELLA BORACEIA CALOR & HOLZENTHAL **SP. NOV.** (FIG. 8)

Diagnosis: Grumichella boraceia can be diagnosed by the following characters: male forewings with 3 brown spots; male genitalia bearing segment X not flattened, lateral view; 1st article of inferior appendage with small basomesal protuberance; 2nd article of inferior appendage subequal the apicodorsal portion of 1st article; apex of 2nd article acuminated, curved mesad; larval abdominal sternum I with 16–24 setae.This new species is most similar to *G. aequiunguis*, but differs in having the 2nd article of the inferior appendage with the mesal surface excavate, and with the apex blunt.

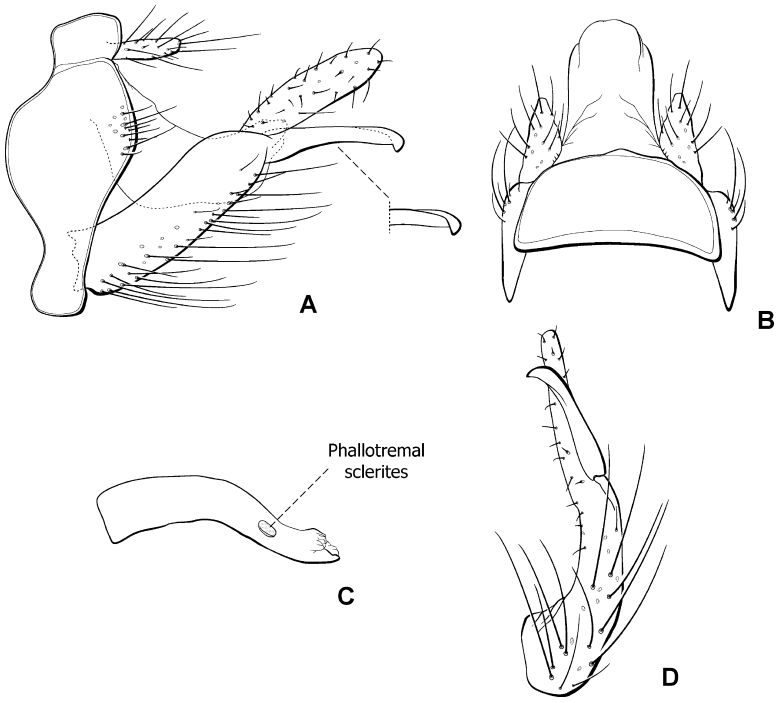

Figure 8. *Grumichella boraceia*, male. A, genitalia, lateral view (apex of 2nd article of inferior appendage, medial view). B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

Adult: Head and body yellowish brown.

Male: Forewing length: 9–10 mm. Forewing light golden brown, with 3 small brown spots, without dark setae on posterodorsal margin. Male genitalia as in Figure 8. Abdominal segment IX annular; in dorsal view, with anterior margin slightly convex, posterior margin broadly rounded, with medial protuberance; in lateral view, pleural region setose; tergum IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, digitate, apex rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin slightly concave, apex upcurved, ventral margin abruptly convex, with middle length straight; segment X in dorsal view, rectangular, with posterolateral borders well developed, lateral margins subparallel after 1/3 length, with apicodorsal shelf, shelf almost rectangular, but sometimes varying to rounded, 1/2 as wide as apex of segment X, without sulcus apically. Inferior appendage slightly concave in ventral view, with basal region enlarged; rounded basally, heavily setose, bearing a small basomesal protuberance; middle region of inferior appendage with constriction before apicodorsal region; 2nd article subequal in length to apicodorsal portion of 1st article, narrow, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 7–9 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Larva: Length of larva 6–9 mm. Abdominal sternum I with 16–24 setae. Lateral hump sclerite small.

Larval case: Length 7–11 mm; constructed entirely of rings of dark brown silk, gently curved, tapered, wide, with 2 distinct diagonal sutures, 1 towards posterior end and 1 more or less at midlength, posterior end with ventral, dorsally directed projection, visible externally, posterior aperture C-shaped.

Pupa: Segment IX very slender; anal process long, narrow, slender, unpigmented or slightly yellowish. With dark setae. Apically upturned, hooked.

Pupal case: With anteroventral silken pedicel, pedicel long; anterior silken membrane with an eccentric, horizontal, slit-like opening.

Etymology: The species name refers to 'Estação Biológica de Boracéia', Salesópolis, São Paulo, the research station of the Museu de Zoologia, Universidade de São Paulo. The word 'boracéia' means 'agglomeration of people' or, by derivation, 'party, dance'. It is treated as a noun in apposition.

Distribution: Brazil.

Holotype, male: **BRAZIL: São Paulo:** Salesópolis, Rio Claro, 19.iv.1998, UV light, Holzenthal, Melo & Froehlich, 23°38′08″S, 45°49′55″W, el. 800 m (MZUSP).

Paratypes: Same data as holotype, 2 males (UMSP), 2 males (UFBA); same data except Casa Grande, Ribeirão Coruja, 16.xi.1974, Froehlich C.G., 1 male, 1 female (MZUSP).

Additional material: Same data as holotype, except Casa Grande, Ribeirão Coruja, 16.xi.1974, Froehlich C.G., 1 female (MZUSP); same data, except Ribeirão do Campo, 16.ix.2007, Froehlich C.G., Domínguez E., Calor A.R. & Mariano R., 17 larvae, 43 pupae (UFBA).

GRUMICHELLA CRESSAE CALOR & HOLZENTHAL **SP. NOV.** (FIG. 9)

Diagnosis: Grumichella cressae can be diagnosed by the following characters: male forewings with 12 brown spots; male genitalia bearing segment X not flattened, lateral view; 1st article of inferior appendage with well-developed basomesal protuberance; 2nd article of inferior appendage shorter than apicodorsal portion of 1st article; apex of 2nd article acuminated and curved mesad. It is most similar to *G. blahniki* sp. nov., but differs in having segment X with posterolateral borders developed, and tergum IX bearing 1–2 small protuberances posterodorsally, which are absent in *G. blahniki* sp. nov.

Adult: Head and body yellowish brown.

Male: Forewing length: 9–10 mm. Forewing light golden brown, with 12 small brown spots. Male genitalia as in Figure 9. Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin nearly straight; in lateral view, pleural region heavily setose; tergum IX bearing a pair of small probuberances posterodorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, digitate, apex rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin slightly concave, apex

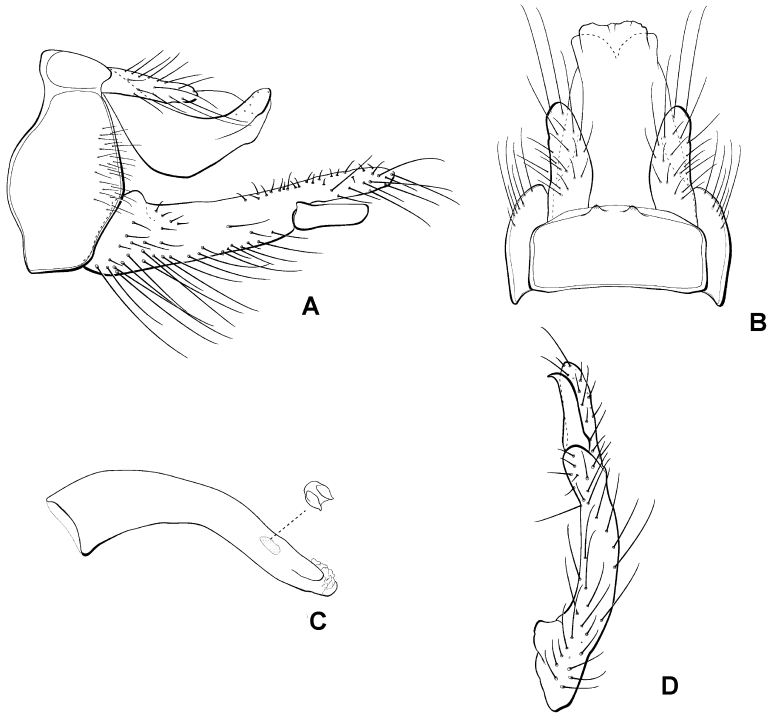

Figure 9. *Grumichella cressae*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

upcurved, ventral margin abruptly convex; with posterolateral borders developed, lateral margins subparallel after 1/3 length, with apicodorsal shelf, shelf almost rectangular, 2/3 as wide as apex of segment X, with ventral sulcus apically. Inferior appendage slightly concave in ventral view, with basal region tuboid, not enlarged; rounded basally, heavily setose, bearing a small basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article shorter than apicodorsal portion of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, narrow, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites relativelly large, almost spheric, with 2 posterolateral points.

Female: Head and body yellowish. Forewing length: 7–8 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Etymology: Named in honour of Dr Claudia Cressa, Universidad Central de Venezuela, who collected the specimens and in recognition of her contributions to Neotropical aquatic insect ecology.

Distribution: Venezuela.

Holotype, male: **VENEZUELA: Lara:** P. N. Dinira, Quebrada Buenos Aires, 09°36′24″N, 070°04′11″W, el. 1850 m, 19.i.2001, Holzenthal, Blahnik, Paprocki & Cressa (UMSP).

Paratypes: Same data as holotype, except 15 males (UMSP), 3 males (MZUSP), 3 males (UFBA).

Additional material: Same data as holotype, except 32 females (UMSP), 2 females (MZUSP), 2 females (UFBA).

GRUMICHELLA JUREIA CALOR & HOLZENTHAL **SP. NOV.** (FIG. 10)

Diagnosis: Grumichella jureia can be diagnosed by the following characters: male forewings with 3 brown spots, and dark setae in posterodorsal border; male genitalia bearing segment X with apicodorsal expansion, almost as wide as apical region, and dorsal sulcus on the segment X apex; 2nd article of inferior

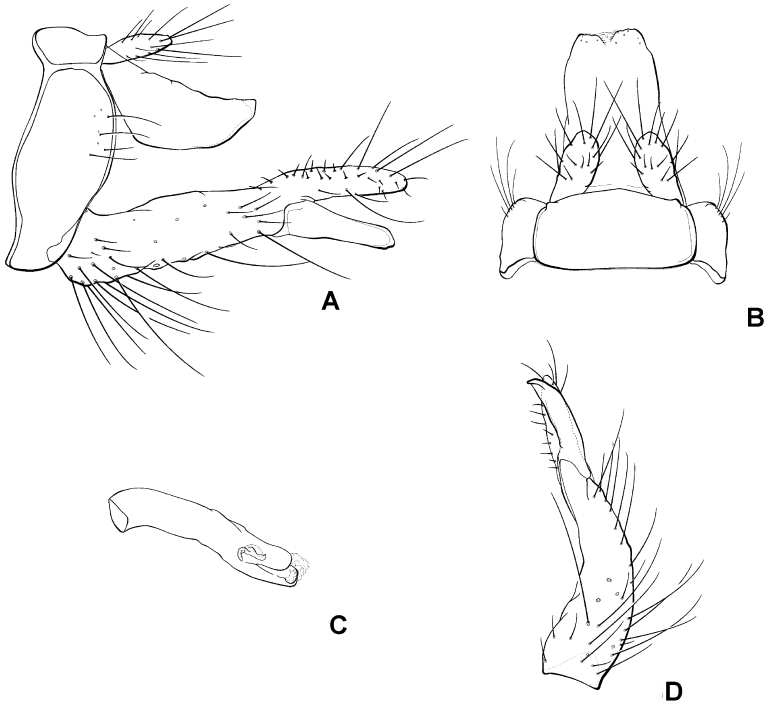

Figure 10. *Grumichella jureia*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

appendage subequal in length to apicodorsal portions of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, slightly curved mesad. It is most similar to *G. parati* sp. nov., but differs in the length of the 2nd article of the inferior appendage, and by the size of the posterolateral borders of segment X.

Adult: Head and body brownish.

Male: Forewing length: 9–10 mm. Forewing light golden brown, with 3 small brown spots, bearing dark setae on posterodorsal margin. Male genitalia as in Figure 10. Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin nearly straight; in lateral view, pleural region sparsely setose; tergum IX without protuberances dorsally. Preanal appendage setose, more or less 3× as long as wide; in lateral view, clavate, apex subacute or rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin nearly straight, ventral margin abruptly convex; segment X in dorsal view, rectangular, with posterolateral borders not developed, lateral margins subparallel, with apicodorsal shelf, almost as wide as apex of segment X, with dorsal sulcus apically. Inferior appendage slightly concave in ventral view, with basal region enlarged; slightly rounded basally, setose, not bearing a basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article subequal in length to apicodorsal portion of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, slightly curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites relativelly large, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 6–9 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Larval case: Length 7–9 mm; constructed of alternating rings of clear and dark brown silk, gently curved, tapered, wide, without diagonal sutures (or sutures indistinct), posterior end with ventral, dorsally directed projection, visible externally, posterior aperture C-shaped.

Pupa: Segment IX slender; anal process short, roughly trapezoidal in general shape, tapering posteriorly to

narrow apex, unpigmented or slightly yellowish. With dark setae. Apically upturned, hooked.

Pupal case: With anteroventral silken pedicel, pedicel short; anterior silken membrane with very small central opening surrounded by 4 radiating, slit-like openings.

Etymology: This name is a reference to the collecting site, the 'Estação Ecológica Juréia-Itatins'. The word 'juréia' means 'salient point, mountains' in the Tupi-guarani language. Treated as a noun in apposition.

Distribution: Brazil.

Holotype, male: **BRAZIL: São Paulo:** Estação Ecológica Juréia-Itatins, Córrego próximo à sede, 07.iv.2007, light, Roque F.O. (MZUSP).

Paratypes: Same data as holotype, except 1 male (MZUSP); 1 male (UMSP); 1 male (UFBA); same data, except 01.ii.2001, light, Mendes H.F., 1 male (UFBA).

Additional material: Same data as holotype, except 1 female (MZUSP); 1 pupa, 1 larva (UMSP); 3 pupae, 1 larva (UFBA).

GRUMICHELLA LECCII CALOR & HOLZENTHAL **SP. NOV.** (FIG. 11)

Diagnosis: Grumichella leccii can be diagnosed by the following characters: male forewings with 3 brown spots; male genitalia bearing segment X flattened, lateral view; 1st article of inferior appendage bearing a small basomesal protuberance; 2nd article longer than apicodorsal portion of 1st article, narrow, tapering throughout length, apex pointed, curved mesally; larval abdominal sternum I with 16–24 setae. It is most similar to *G. rostrata*, except for 2nd article of inferior appendage which is longer than the apicodorsal portion of 1st article, and segment X with small sulcus apically.

Adult: Head and body yellowish brown.

Male: Forewing length: 7–9 mm. Forewing light golden brown, with 3 small brown spots, without dark setae on posterodorsal margin. Male genitalia as in Figure 10. Abdominal segment IX annular; in dorsal view, with anterior margin slightly concave, posterior margin sinuate; in lateral view, pleural region sparsely setose; tergum IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, clavate, apex rounded. Segment X saddle-shaped; in lateral view flattened, dorsal margin slightly concave, apex upcurved, ventral margin abruptly

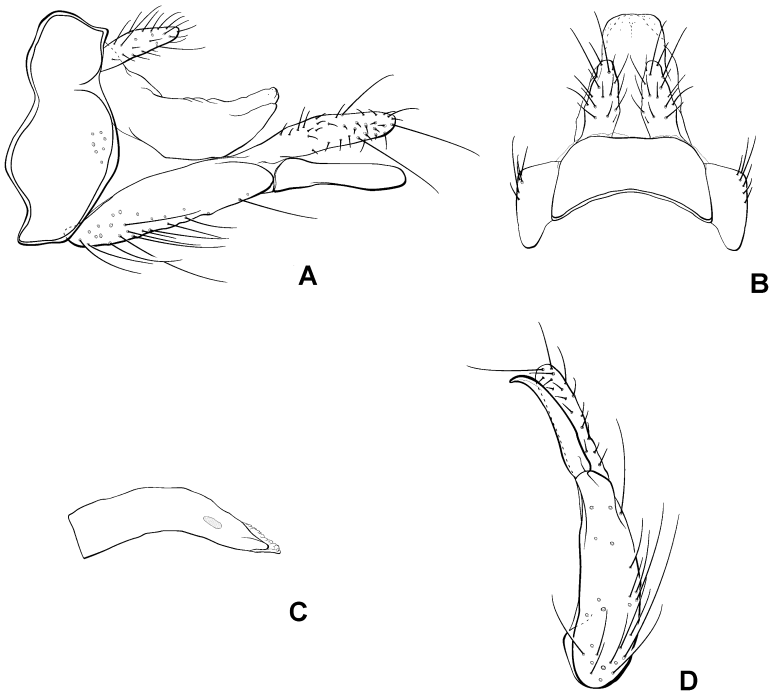

Figure 11. *Grumichella leccii*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

convex; segment X in dorsal view, subtriangular, with posterolateral borders developed, lateral margins sinuate, narrowing apically, with apicodorsal shelf, shelf almost rectangular, 1/2 as wide as apex of segment X, with ventral sulcus apically. Inferior appendage nearly straight in ventral view, with basal region tuboid, not enlarged; rounded basally, heavily setose, bearing a small basomesal protuberance; middle region of inferior appendage with constriction before apicodorsal region; 2nd article longer than apicodorsal portion of 1st article, narrow, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, narrow, posteromesally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 6–7 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Larva: Length of larva 6–8 mm. Abdominal sternum I with 16–24 setae. Lateral hump sclerite relatively large.

Larval case: Length 7–10 mm; constructed of rings of transparent silk, nearly straight, tapered, narrow, without diagonal sutures (or sutures indistinct), posterior end with ventral, dorsally directed projection, visible externally, posterior aperture C-shaped.

Pupa: Segment IX very slender; anal process long, narrow, slender, unpigmented or slightly yellowish. Without dark setae. Apically upturned, hooked.

Pupal case: With anteroventral silken pedicel, pedicel very long, thin; anterior silken membrane with an eccentric, horizontal, slit-like opening.

Etymology: Named in honour of Dr Lucas Silveira Lecci (Instituto Federal do Mato Grosso, Brazil), collector of this species, and also for his friendship and collaboration in the field.

Distribution: Brazil.

Holotype, male: **BRAZIL: São Paulo:** Jundiai, Serra do Japi, P.A. 11, stream before reservoir, 23°14′30″S, 46°57′16″W, 27.iii.2007, luz UV & branca, Calor A.R., Mariano R. & Lecci L.S. (MZUSP).

Paratypes: Same data as holotype, except 5 males (MZUSP), 5 males (UMSP); 27 males (UFBA); same data except Córrego da Ermida and small dam, 9.xii.1997, Froehlich C.G., 23°13′S, 46°56′W, 2 males (UMSP); same data, except Córrego da cachoeira Paraíso, 26.iii.2007, luz UV & branca, 23°14′S, 46°56′W, Calor A.R., Mariano R. & Lecci L.S., 1 male (UFBA).

Additional material: Same data as holotype, except 5 males, 5 females (UMSP), 27 males, 49 females (UFBA); same data, except Córrego da Ermida and small dam, 9.xii.1997, Froehlich C.G., 23°14′S, 46°56′W, 2 females (UMSP); same data, except riacho trilha da cachoeira Paraíso, 25.i.2007, luz, 23°14′30″S, 46°57′13″W, Lecci L.S., Nascimento E.& Polegatto C., 1 female (MZUSP); same data, except 2° riacho trilha da cachoeira Paraíso, 22.ii.2007, luz, 23°14′30″S, 46°57′13″W, Lecci L.S. & Nascimento E., 1 female (MZUSP); same data, except 2° riacho trilha da cachoeira Paraíso, 22.ii.2007, luz, 23°14′30″S, 46°57′13″W, Lecci L.S. & Nascimento E., 1 female (MZUSP); same data, except Córrego da cachoeira Paraíso, 26.iii.2007, luz UV & branca, 23°14′S, 046°56′W, Calor A.R., Mariano R. & Lecci L.S., 3 females (UFBA); same data, except P.A. 11, stream before the reservoir, 23°14′30″S, 46°57′15″W, el. 1022 m, 11.iii.2008, rede D, Lecci L.S. & Nascimento E., 21 pupae (UFBA).

GRUMICHELLA MUELLERI CALOR & HOLZENTHAL **SP. NOV.** (FIGS 12, 13)

Diagnosis: Grumichella muelleri can be diagnosed by the following characters: male forewings with 3 brown spots; male genitalia bearing segment X rectangular, with posterolateral border developed, dorsal view; without sulcus on the apex of segment X; 1st article of inferior appendage without basomesal protuberance; 2nd article of inferior appendage shorter than apicodorsal portion of 1st article; apex of 2nd article acuminated, curved mesad. This new species is most similar to *G. paprocki* sp. nov., but differs in having segment X with the posterolateral borders not developed, and the apicodorsal shelf on segment X from 2/3 to almost as wide as the apex of segment X.

Adult: Head and body yellowish brown.

Male: Forewing length: 6–7 mm. Forewing light golden brown, with 3 small brown spots, without dark setae on posterodorsal margin. Male genitalia as in Figure 12. Abdominal segment IX annular; in dorsal view, with anterior margin slightly concave, posterior margin slightly angulate; in lateral view, pleural region sparsely setose; tergum IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, clavate, apex acute. Segment X saddle-shaped; in lateral view not flattened, dorsal margin

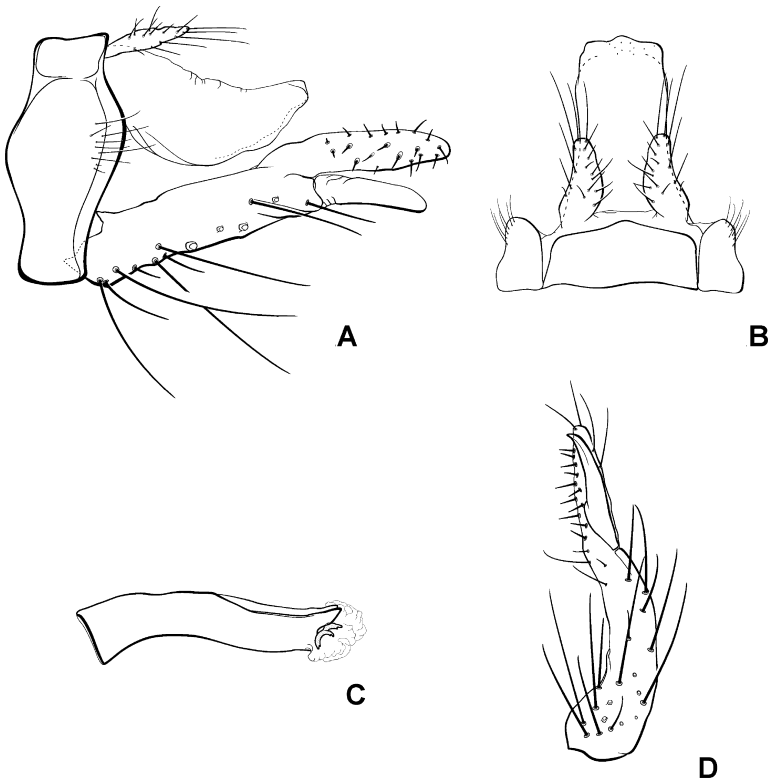

Figure 12. *Grumichella muelleri*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

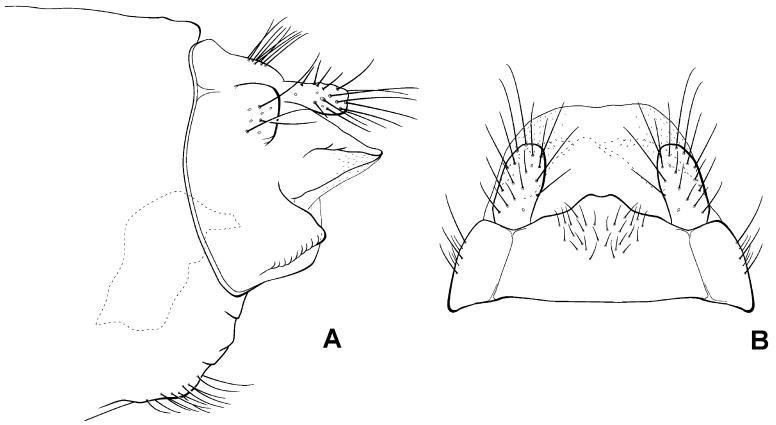

Figure 13. *Grumichella muelleri*, female. A, genitalia, lateral view. B, genitalia, dorsal view.

slightly concave, ventral margin abruptly convex; segment X in dorsal view, rectangular, with posterolateral borders not developed, lateral margins sinuate, with apicodorsal shelf, shelf almost rectangular, but sometimes varying to rounded, almost as wide as apex of segment X, without sulcus apically. Inferior appendage slightly concave in ventral view, with basal region enlarged; rounded basally, heavily setose, especially apically, not bearing a basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article shorter than apicodorsal portion of 1st article, broad basally, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata nearly straight; with pair of subequal, wide, posterodorsally directed lateral flanges, apices acuminate; phallotremal sclerites small, C-shaped.

Female: Head and body yellowish. Forewing length: 5–7 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia as in Figure 13, inseparable among the congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing a pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Etymology: The specific epithet is inhonor of the naturalist Fritz Müller, the 'prince of observers', according to Charles Darwin. Müller was a pioneer in studies of Neotropical caddisflies (among other taxa), including the description of the genus *Grumichella*. He was an important collaborator and supporter of Darwin's theory of evolution, especially by means of Müller's book 'Für Darwin' (1864) and its translations.

Distribution: Brazil.

Holotype, male: **BRAZIL: Santa Catarina:** Parque Ecológico Spitzkopf, confl. Rio Ouro & Rio Caeté, 25.ix.2003, UV light, Holzenthal, Paprocki & Calor, 27°00′21″S, 49°06′42″W, el. 140 m (MZUSP).

Paratypes: Same data as holotype, except 1male (UMSP), 1 male (UFBA).

Additional material: Same data as holotype, except 1 female (UMSP); same data, except Rio Caeté above 1st falls, 4.iii.1998, UV light, Holzenthal, Froehlich & Paprocki, 27°00′21″S, 49°06′42″W, el. 170 m, 2 females (UMSP), 1 female (UFBA).

GRUMICHELLA PAPROCKII CALOR & HOLZENTHAL **SP. NOV.** (FIG. 14)

Diagnosis: Grumichella paprockii can be diagnosed by the following characters: male forewing with 3 brown

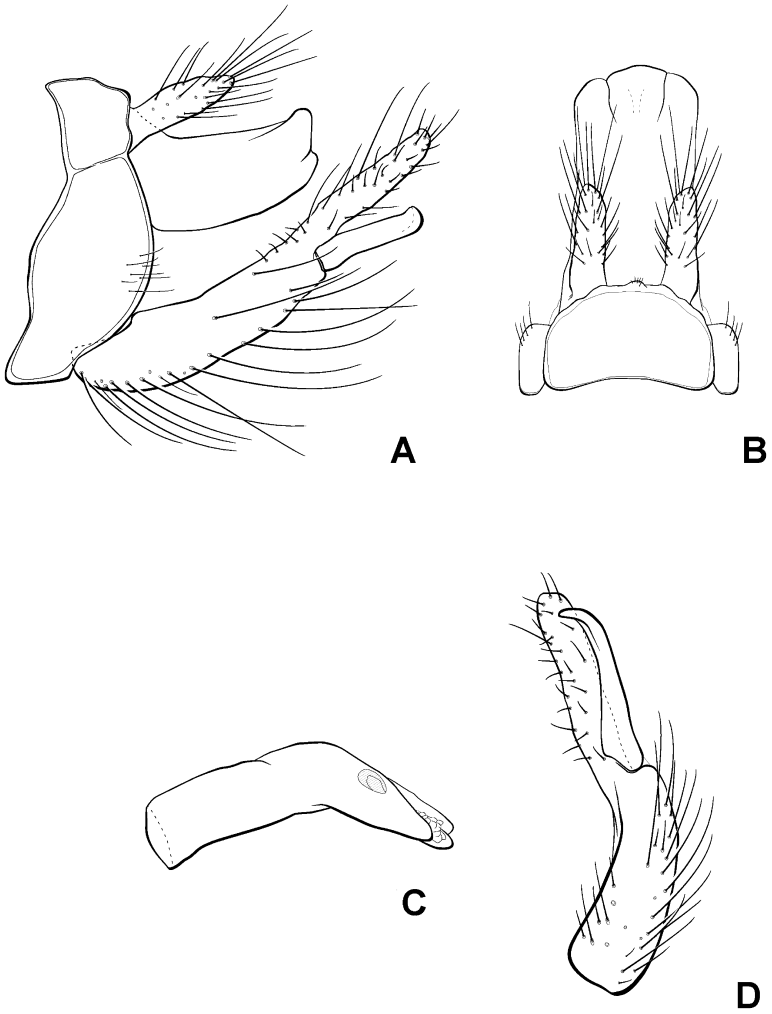

Figure 14. *Grumichella paprockii*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

spots; male genitalia bearing segment X not flattened, lateral view; 1st article of inferior appendage without basomesal protuberance; 2nd article of inferior appendage shorter than the apicodorsal portion of 1st article; apex of 2nd article acuminated, curved mesad. This new species is most similar to *G. muelleri*, but differs in having segment X with the posterolateral borders developed, and the apicodorsal shelf on segment X about 1/3 to 1/2 as wide as the apex of segment X.

Adult: Head and body yellowish brown.

Male: Forewing length: 8–9 mm. Forewing light golden brown, with 3 small brown spots, without dark setae on posterodorsal margin. Male genitalia as in Figure 14. Abdominal segment IX annular; in dorsal view, with anterior margin slightly concave, posterior margin broadly rounded, with medial protuberance; in lateral view, pleural region sparsely setose; tergum IX bearing 1 small probuberance posterodorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, digitate, apex subacute. Segment X saddle-shaped; in lateral view not flattened, dorsal margin slightly concave, apex upcurved, ventral margin slightly convex; segment X in dorsal view, rectangular, with posterolateral borders well developed, lateral margins subparallel, with apicodorsal shelf, shelf almost rectangular, but sometimes varying to rounded, 1/3 as wide as apex of segment X, with ventral sulcus apically. Inferior appendage concave in ventral view, with basal region tuboid, not enlarged; slightly rounded basally, setose, not bearing a basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article shorter than apicodorsal portion of 1st article, broad basally, tapering throughout length, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata sharply down-curved; with pair of subequal, wide, posteromesally directed lateral flanges, apices not acuminate; phallotremal sclerites small, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 6–7 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Etymology: Named in honour of Dr Henrique Paprocki, collector of this species and a colleague who encouraged this revision.

Distribution: Brazil.

Holotype, male: **BRAZIL: Minas Gerais:** Córrego da Serra de Ouro Fino, Valedo Tropeiro, 8.x.2000, UV light, Paprocki, Salgado & Isaac, 20°12′22″S, 43°38′35″W, el. 1000 m (MZUSP).

Paratypes: Same data as holotype, except Cachoeira do Abacaxi, Vale do Tropeiro, 7.xi.2001, UV light, Holzenthal, Amarante, Blahnik & Paprocki, 20°12′16″S, 43°38′10″W, el. 1120 m, 2 males (UMSP); Parque Estadual Itacolomi, Rio Belchior, 2.ii.1998, UV light, Holzenthal & Paprocki, 20°25′02″S, 043°25′38″W, el. 725 m, 3 males (UMSP), 2 males (UFBA); same data, except 24.i.1999, UV light, Amarante M.C., 20°25′02″S, 43°25′38″W, el. 725 m, 1 male (UMSP); same data, except 20.ii.1999, UV light, Paprocki & Amarante, 20°25′02″S, 43°25′38″W, el. 725 m, 2 males (UMSP).

Additional material: Same data as holotype, except 2 females (UMSP); Parque Estadual Itacolomi, Rio Belchior, 2.ii.1998, UV light, Holzenthal & Paprocki, 20°25′02″S, 043°25′38″W, el. 725m, 30 females (UMSP), 2 females (UFBA); same data, except 8.v.1998, UV light, Holzenthal & Paprocki, 20°25′02″S, 43°25′38″W, el. 725 m, 2 females (UMSP); same data except 20.xi.1998, UV light, Paprocki & Amarante, 20°25′02″S, 43°25′38″W, el. 725 m, 8 females (UMSP); same data except 17.xii.1998, UV light, Paprocki & Amarante, 20°25′02″S, 43°25′38″W, el. 725 m, 4 females (UMSP); same data except 24.i.1999, UV light, Amarante M.C., 20°25′02″S, 43°25′38″W, el. 725 m, 4 females (UMSP); same data except 20.ii.1999, UV light, Paprocki & Amarante, 20°25′02″S, 43°25′38″W, el. 725 m, 10 females (UMSP).

GRUMICHELLA PARATI CALOR & HOLZENTHAL **SP. NOV.** (FIG. 15)

Diagnosis: Grumichella parati can be diagnosed by the following characters: male forewing with 3 brown spots; male genitalia with segment X not flattened, lateral view; 1st article of inferior appendage without basomesal protuberance; 2nd article of inferior appendage longer than apicodorsal portion of 1st article; apex of 2nd article acuminated, curved mesad. It is most similar to *G. jureia* sp. nov., but differs in having the 2nd article of the inferior appendage longer than the apicodorsal portion of the 1st article, and segment X with the posterolateral borders developed.

Adult: Head and body yellowish brown.

Male: Forewing length: 8–9 mm. Forewing light golden brown, with 3 small brown spots, without dark setae on posterodorsal margin. Male genitalia as in Figure 15. Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin broadly rounded; in lateral view, pleural region setose; tergum

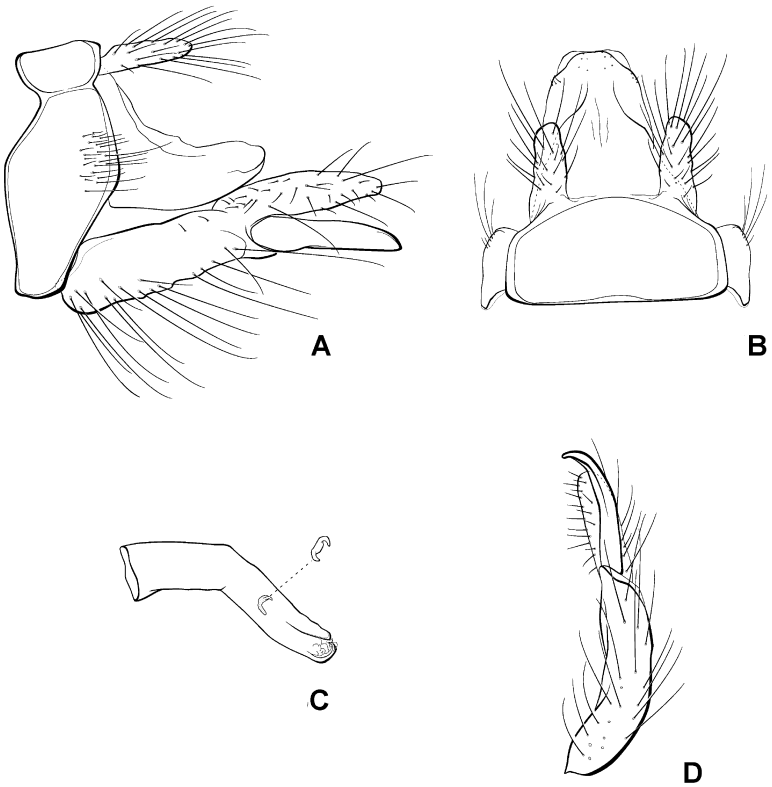

Figure 15. *Grumichella parati*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

IX without protuberances dorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, clavate, apex rounded. Segment X saddle-shaped; in lateral view not flattened, dorsal margin slightly concave, ventral margin abruptly convex, with middle length straight; segment X in dorsal view, subtriangular, with posterolateral borders developed, lateral margins sinuate, narrowing apically, with apicodorsal shelf, shelf slightly trapezoidal, 1/2 as wide as apex of segment X, without sulcus apically. Inferior appendage slightly concave in ventral view, with basal region tuboid, not enlarged; slightly rounded basally, setose, not bearing a basomesal protuberance; middle region of inferior appendage without constriction before apicodorsal region; 2nd article longer than apicodorsal portion of 1st article, narrow, tapering throughout length, mesal surface not excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata sharply down-curved; with pair of subequal, narrow, posterodorsally directed lateral flanges, apices acuminate; phallotremal sclerites small, U-shaped in dorsal view, with middle region enlarged.

Female: Head and body yellowish. Forewing length: 6–8 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Etymology: Parati'y in the Tupi-guarani language is a composite word formed by *parati*, a species of fish in the genus *Mugil* (Mugilidae) and *'y* (river). It is treated as a noun in apposition.

Distribution: Brazil.

Holotype, male: **BRAZIL: Rio de Janeiro:** Parati, Riacho Perequê-açu, Sitio Cachoeira Grande, 25.ix.2002, UV light, Blahnik, Prather, Melo, Froehlich, Silva, 23°13′14″S, 44°47′24″W, el. 120 m (MZUSP).

Paratypes: Same data as holotype, except 1 male (MZUSP), 13 males (UMSP), 2 males (UFBA); same data, except Trib. to Riacho Perequê-açu, 26.ix.2002, UV/mercury vapor lights, Blahnik, Prather, Melo, Froehlich, Silva, 23°12′50″S, 44°47′29″W, el. 190 m, 7 males (UMSP); same data except Rio das Flores, Macaéde Cima, 10 km SE Mury, 9.iii.2002, UV light, Holzenthal, Blahnik, Paprocki & Prather, 1 male

(UMSP); same data, except Encontro dos Rios Macaé/Bonito, 6 km S Lumiar, 10.iii.2002, Holzenthal, Blahnik, Paproki & Prather,22°23′29″S, 42°18′42″W, el. 600 m, 8 males (UMSP), 5 males (UFBA).

Aditonal material: Same data as holotype, except 1 female (MZUSP), 2 females (UMSP); same data, except trib. to Riacho Perequê-açu, 26.ix.2002, UV/mercury vapour lights, Blahnik, Prather, Melo, Froehlich, Silva, 23°12′50″S, 44°47′29″W, el. 190 m, 15 females (UMSP); same data, except Macaé, Rio Macaé, Macaé de Cima, 8.iii.2002, UV light, Holzenthal, Blahnik, Paproki & Prather, 22°23′41″S, 42°30′08″W, el. 1000 m, 15 females (UMSP); same data, except Rio das Flores, Macaé de Cima, 10 km SE Mury, 09.iii.2002, UV light, Holzenthal, Blahnik, Paprocki & Prather, 3 females (UMSP).

GRUMICHELLA TRUJILLOI CALOR & HOLZENTHAL **SP. NOV.** (FIG. 16)

Diagnosis: Grumichella trujilloi can be diagnosed by the following characters: male forewings with 12 brown spots; male genitalia bearing segment X flattened, lateral view; 1st article of inferior appendage bearing small basomesal protuberance; 2nd article of inferior appendage subequal in length to apicodorsal portion of 1st article; apex of 2nd article acuminated, curved mesad. *Grumichella trujilloi* is most similar to *G. cressae* and *G. blahniki*, but differs in having the 2nd article of inferior appendage shorter than the apicodorsal portion of the 1st article, and in having segment X, in lateral view, not flattened.

Adult: Head and body yellowish brown.

Male: Forewing length: 9–11 mm. Forewing light golden brown, with 12 small brown spots. Male genitalia as in Figure 16. Abdominal segment IX annular; in dorsal view, with anterior margin nearly straight, posterior margin sinuate; in lateral view, pleural region setose; tergum IX bearing a pair of small probuberances posterodorsally. Preanal appendage setose, at least 4× as long as wide; in lateral view, digitate, apex rounded. Segment X saddle-shaped; in lateral view flattened, dorsal margin slightly concave, apex upcurved, ventral margin convex; segment X in dorsal view, subtriangular, with posterolateral borders not developed, lateral margins sinuate, with apicodorsal shelf, shelf variable, acuminate to rounded, almost as wide as apex of segment X, with ventral sulcus apically. Inferior appendage slightly concave in ventral view, with basal region enlarged; subquadrangular basally, setose, bearing a small basomesal protuberance; 2nd article subequal in length to apicodorsal portion of 1st article, narrow, tapering throughout length, but constricted subapically or broad basally, tapering throughout length, mesal

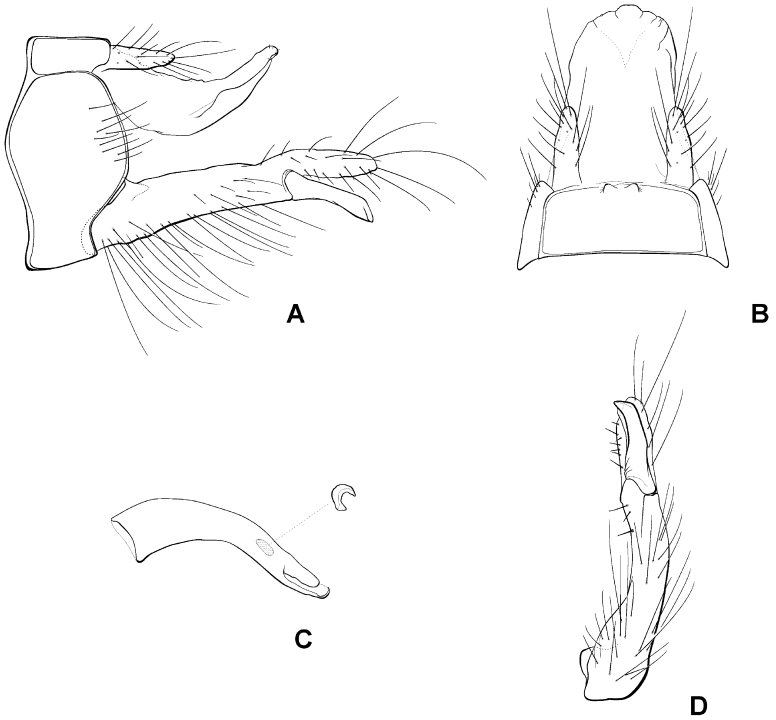

Figure 16. *Grumichella trujilloi*, male. A, genitalia, lateral view. B, genitalia, dorsal view. C, phallus, lateral view. D, inferior appendage, ventral view.

KEY TO MALES OF *GRUMICHELLA* MÜLLER

1. Forewing with 2–3 small brown spots . . . 2
   Forewing with 9–12 small brown spots . . . 9
2(1). Inferior appendage basally bearing a basomesal protuberance (Fig 2) . . . 3
   Inferior appendage basally not bearing a basomesal protuberance (Fig 14) . . . 6
3(2). Segment X, in lateral view, not flattened (Fig 2) . . . 4
   Segment X, in lateral view, flattened (Fig 6) . . . 5
4(3). 2nd article of inferior appendage with mesal surface not excavate; 2nd article with apex pointed (Fig 8) . . . ***Grumichella boraceia*** **sp. nov.**
   2nd article of inferior appendage with mesal surface excavate; 2nd article with apex blunt (Fig 2) . . . ***Grumichella aequiunguis*** **Flint**
5(3). 2nd article of inferior appendage subequal in length to apicodorsal portion of 1st article; segment X without sulcus apically (Fig 6) . . . ***Grumichella rostrata*** **Thienemann**
   2nd article of inferior appendage longer than apicodorsal portion of 1st article; segment X with small sulcus apically (Fig 11) . . . ***Grumichella leccii*** **sp. nov.**
6(2). 2nd article of inferior appendage shorter than apicodorsal portion of 1st article . . . 7
   2nd article of inferior appendage subequal in length or longer than apicodorsal portion of 1st article . . . 8
7(6). Segment X with posterolateral borders developed; apicodorsal shelf on segment X 1/3 to 1/2 as wide as apex of segment X (Fig 14) . . . ***Grumichella paprockii*** **sp. nov.**
   Segment X with posterolateral borders not developed; apicodorsal shelf on segment X 2/3 to almost as wide as apex of segment X (Fig 12) . . . ***Grumichella muelleri*** **sp. nov.**
8(6). 2nd article of inferior appendage subequal in length to apicodorsal portion of 1st article; segment X with posterolateral borders not developed (Fig 10) . . . ***Grumichella jureia*** **sp. nov.**
   2nd article of inferior appendage longer than apicodorsal portion of 1st article; segment X with posterolateral borders developed (Fig 15) . . . ***Grumichella parati*** **sp. nov.**
9(1). 2nd article of inferior appendage shorter than apicodorsal portion of 1st article; segment X, in lateral view, not flattened . . . 10
   2nd article of inferior appendage subequal in length or longer than apicodorsal portion of 1st article; segment X, in lateral view, flattened (Fig 11) . . . ***Grumichella trujilloi*** **sp. nov.**
10(9). Segment X with posterolateral borders developed; tergum IX bearing 1-2 small protuberances posterodorsally (Fig 9) . . . ***Grumichella cressae*** **sp. nov.**
   Segment X with posterolateral borders not developed; tergum IX without protuberances dorsally (Fig 7) . . . 11
11(10). Forewing with 12 small brown spots . . . ***Grumichella blahniki*** **sp. nov.**
   Forewing with 9 small brown spots . . . 12
12(11). Apicodorsal portion of 1st article of inferior appendage digitate (Fig 3) . . . ***Grumichella flaveola*** **Ulmer**
   Apicodorsal portion of 1st article of inferior appendage quadrate (Fig 5) . . . ***Grumichella pulchella*** **Banks**

surface excavate, apex pointed, curved mesally; apicordorsal portion of 1st article digitate, setose. Phallic apparatus simple, phallicata slightly down-curved; with pair of subequal, wide, posterodorsally directed lateral flanges, apices not acuminate; phallotremal sclerites relativelly large, U-shaped in dorsal view.

Female: Head and body yellowish. Forewing length: 6–7 mm. Forewing yellowish to brown, without dark setae on posterodorsal region. Genitalia inseparable from congeners. Abdominal segment IX lightly sclerotized, with dorsal plate, bearing pair of setose protuberances above appendages of segment X, appendages of segment X small; valves flat, thin, lightly sclerotized, with very short setae.

Etymology: The name of the species refers to the state of Trujillo, Venezuela, where the species was collected.

Distribution: Venezuela.

Holotype, male: **VENEZUELA: Trujillo:** Quebrada Potrerito, 7.5 km NE Bocono, 09°16′26″N, 70°13′06″W, el. 1530 m, 29–30.iv.1995, Holzenthal, Cressa, Gutic (UMSP).

Paratypes: Same data as holotype, except 2 males (UMSP), 1 female (MZUSP), 1 male (UFBA).

Additional material: Same data as holotype, except 5 females (UMSP), 1 female (MZUSP), 1 female (UFBA).

PHYLOGENETIC RESULTS

Phylogenetic analysis of the complete dataset (22 taxa and 66 characters) under equal weighting yielded 12

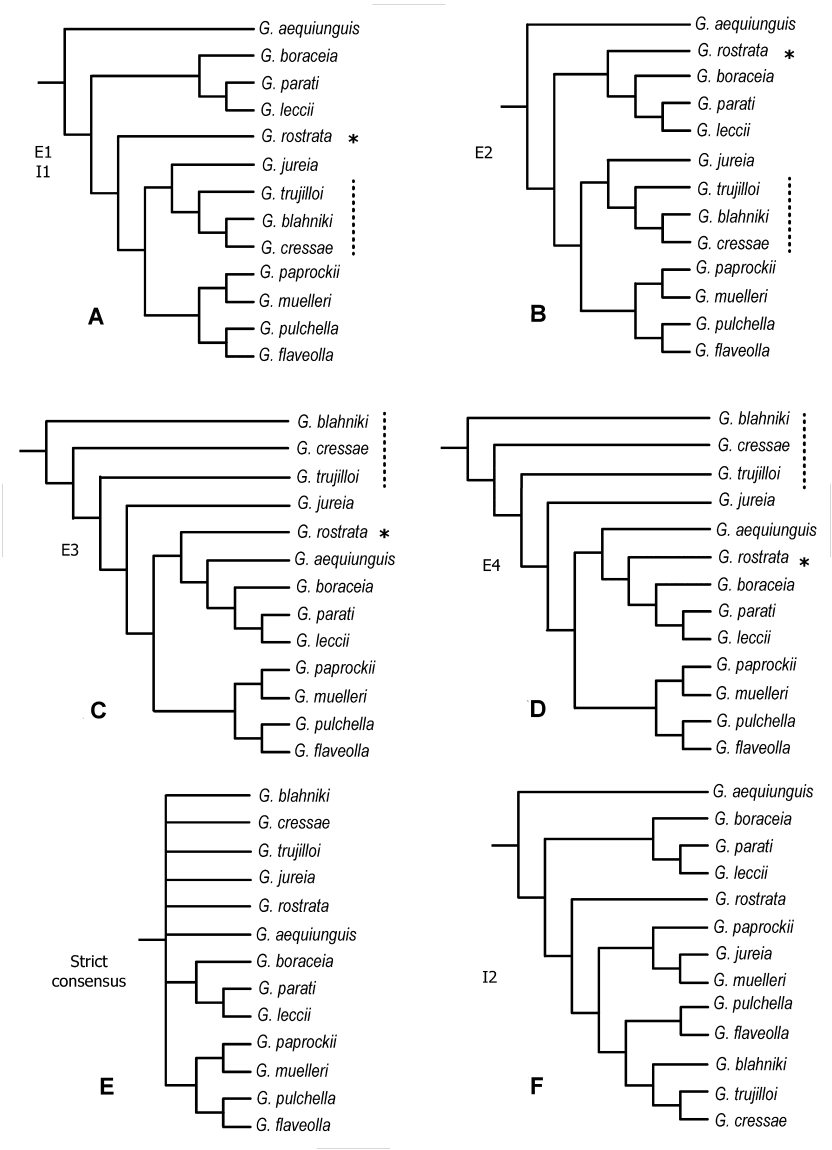

Figure 17. Phylogenetic results. A, most parsimonious tree from equal (E1) and implied weighting analyses (I1), using *k* values from 13 to 100. B–D, other three most parsimonious trees from equal analyses (E2, E3 and E4, respectively). E, tree representing the strict consensus from equal weighting analyses. F, tree from implied weighting analyses (I2) using *k* values from 1 to 12 (* indicating the type-species, *G. rostrata*; dashed line indicating *G. blahnik*, *G. cressa* and *G. trujilloi*).

trees, length 125 (see Fig. 17E for strict consensus), corroborating the monophyly of *Grumichella* (Fig. 17A–D; equal weighting results indicated as E1–E4 in figures). Among the 12 trees, only four show differences in the ingroup taxa relationships (Fig. 17). In comparing these four topologies, two trees (Fig. 17A, B) differ from each other only in the position of *G. rostrata* (indicated as * in the figure), while in the other two trees (Fig. 17C, D) *G. rostrata* and *G. aequiunguis* are in different positions in relation to the clade (*G. boraceiae* (*G. parati*, *G. lecci*)). The main differences occur when comparing the first two trees (Fig. 17A, B) and the second two trees (Fig. 17C, D) with respect to the position of the species *G. trujilloi*, *G. blahniki* and *G. cressae*. In the first set (Fig. 17A, B) the latter three species form a clade, while in the second set (Fig. 17C, D) they emerge as a paraphyletic grade at the base of those trees.

The phylogenetic analyses under implied weighting, with *k* values from 1 to 100, resulted in two topologies (Fig. 17A, F), with 2 *k* value ranges (1–12 and 13–100; implied weighting results indicated as I1 and

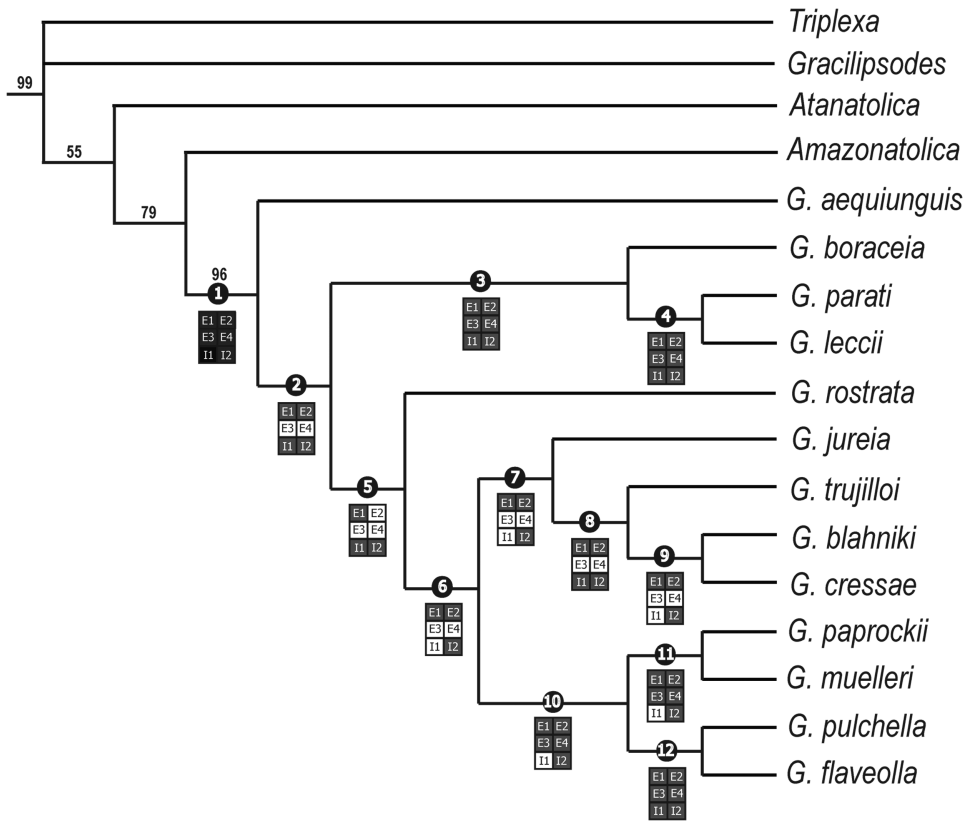

Figure 18. Phylogenetic relationship of *Grumichella* species. The plots (rectangles) on the nodes were divided into six parts, each representing different scenarios where the related clade was recovered. The four most parsimonious trees from equal weighting analyses are represented as E1, E2, E3 and E4. The two trees from implied weighting analyses using *k* values of 1–12 and 13–100 are represented as I1 and I2, respectively. Bootstrap values are presented in the basal nodes.

I2 in the figures), both also corroborating the monophyly of the genus. These topologies are only different in the phylogenetic relationships inside the clade (*G. jureiae*, *G. trujilloi*, *G. blahniki*, *G. cressae*, *G. paprockii*, *G. muelleri*, *G. pulchella*, *G. flaveola*), but the sister-group (*G. flaveola*, *G. pulchella*), and the clade (*G. trujilloi*, *G. cressae*, *G. blahniki*) occur in both topologies. Additionally, the resulting topology from the second range of *k* values is the same as resulting from equal weighting (Fig. 17A). Figure 18 shows the phylogenetic relationships of *Grumichella* species based on a topology from both equal weighting and implied weighting, under different parameters and analyses (E1–E4; I1–I2), and which clades were recovered or not (sensitivity analyses). Among the five possible trees from analyses under equal and implied weighting, the first tree (Fig. 17A) is more robust under different parameters, and contains the clades recovered from most analyses. Accordingly, this tree will be used to discuss the phylogenetic relationships among *Grumichella* species and, consequently, to understand character evolution in this group.

The monophyly of the genus *Grumichella* was supported by 16 synapomorphies (clade 1, Fig. 18), corroborating Holzenthal (1988a). However, the two species groups, as proposed by Holzenthal (1988a), were not totally recovered in our analyses. The synapomorphies of *Grumichella* are: from adults (character numbers as in list of characters, Appendix 1), (1) malar space wide; (2) front setal warts long and narrow; (7) 2–3 brown spots in male forewings; (12) segment X not flattened, lateral view; (14) presence of the apicodorsal protuberance on segment X; (19) absence of the stout, spine-like setae on the mesal surface of each inferior appendage; from larvae, (30) presence of frontoclypeal apotome with posterior, raised protuberance; (36) presence of carina bordering frontoclypeal suture on the head; (47) presence of peg-like setae row on the apex of posterior margin of tarsus; (48) tarsal claw curved; from pupae, (54) presence of dark spots on the front of the head; (55) vertex of head with raised projection; (57) labrum rudimentary; (58) absence of setae on labrum; (61) presence of abdominal hook plates with anterior sclerotized extension; (62) abdominal segment IX very long (Fig. 18).

The phylogenetic relationships of *Grumichella* species can be inferred as (*G. aequiunguis* ((*G. boraceiae* (*G. leccii*, *G. parati*)) (*G. rostrata* ((*G. flaveola*, *G. pulchella*)

(*G. muelleri*, *G. paprockii*)) (*G. jureia* (*G. trujilloi* (*G. cressae*, *G. blahniki*))))) (Fig. 18). Clade 2, recovered from both equal and implied weighting analyses, was supported by character 25(0), apex of 2nd article of the inferior appendage strongly curved mesad. This character is homoplastic (reversal) in *G. blahniki* and *G. jureia*. Groups 3 and 4 (Fig. 18) were recovered in all analyses, and contain (*G. boraceia* (*G. parati*, *G. leccii*)). There are two characters (15[2] apicodorsal protuberance on segment X with width 1/2 the width of apex of segment X, and 24[0] 2nd article of the inferior appendage slender) supporting clade 3, and one character (22[1] 2nd article of the inferior appendage longer than the apicodorsal portion) as a synapomorphy of the sister-group (*G. parati*, *G. leccii*). Calor & Holzental (2008, character 5) proposed the presence of '2nd article not reduced' as a synapomorphy of *Grumichella*. However, here this character was homoplastic (convergent) in clades 4, 9 and 10.

Clade 5 was also recovered from both the equal and the implied weighting analyses, and its monophyly is supported by character 64(1), anal process of pupae trapezoidal, a transformation from the 'tubular shape' proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 24, part). Inside clade 5, clade 6 was recovered from both the equal and the implied weighting analyses, but only from the second range of *k* values. Clade 5 was supported by character 63(0), anal process of pupae short, a transformation from anal process very long (and tubular) proposed as a synapomorphy of the genus by Holzenthal (1988a, character 24, part).

The monophyletic group (*G. jureia*, *G. trujillloi*, *G. blahniki*, *G. cressae*) was recovered in the equal and implied weighting analyses, but only from the second range of *k* values. This clade was supported by characters: 15(3), apicodorsal protuberance on segment X with almost the same width as apex of segment X; 16(0), presence of groove (or furrow) in the apicodorsal protuberance on segment X; and 29(1), phallotremal sclerites medium sized, a transformation from small size in other congeners. Clade 8 was recovered from both equal and implied weighting analyses, and was supported by character 7(2), 9–12 brown spots in the male forewings. This character was used by Holzenthal (1988a) to support the *G. pulchella* species group of *G. pulchella* and *G. flaveola*. The sister-group *G. blahniki* and *G. cressae* shares the synapomorphies 18(0), basodorsal protuberance on inferior appendage developed, and 22(2), 2nd article of the inferior appendage a little shorter than the apicodorsal portion.

Clade 10, including (*G. paprocki*, *G. muelleri*, *G. pulchella*, *G. flaveola*), was recovered from both equal and implied weighting analyses, but only from the second range of *k* values. The group is supported by two synapomorphies: 22(2), 2nd article of the inferior appendage a little shorter than the apicodorsal portion; and 28(1), phallicata strongly down curved. Clade 11 was also recovered from both equal and implied weighting analyses (from the second range of *k* values), and it is supported by character 17(1), absence (lost) of the basodorsal protuberance on inferior appendage. Clade 12 was recovered from all analyses, and is supported by character 7(2), 9–12 brown spots in male forewings. As commented before, the presence of two or nine brown spots in the forewings was used by Holzenthal (1988a) to separate the two putative species groups of the genus, in this case the *G. pulchella* species group.

DISCUSSION

The genus *Grumichella* comprises 13 species, including nine new species described here. The phylogenetic analyses corroborated the monophyly of *Grumichella*, as established by Holzenthal (1988a), and supported by 16 synapomorphies. Among the five possible trees from analyses using equal and implied weighting, the first tree is more robust under different parameters of the *k* value. Based on the clades recovered most among the analyses, the phylogenetic relationships of *Grumichella* species can be inferred as (*G. aequiunguis* ((*G. boraceiae* (*G. leccii*, *G. parati*) (*G. rostrata* ((*G. flaveola*, *G. pulchella*) (*G. muelleri*, *G. paprockii*)) (*G. jureia* (*G. trujilloi* (*G. cressae*, *G. blahniki*))))))). While our analysis supported the monophy of Holzenthal's (1988a) *pulchella* group, it did not support a monophyletic *rostrata* group.

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APPENDIX 1

Character list: 66 morphological characters (1–29 from adults, 30–53 from larvae and 54–66 from pupae), including all proposed morphological characters in the literature.

ADULT CHARACTERS

1. **Malar space:** (0) wide; (1) narrow. Malar space wide was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 34).
2. **Front setal warts:** (0) long and narrow; (1) short and wide. Front setal warts long and narrow was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 33).
3. **Pre-pronotal sclerites:** (0) absent; (1) present. The presence of pre-pronotal sclerites was proposed as a synapomorphy of the clade (Hudsonemini, Triplectidinae) by Morse & Holzenthal (1987, character 16).
4. **Lateral setal warts of pronotum:** (0) present; (1) absent. The absence of lateral setal warts on the pronotum was proposed as a synapomorphy of Grumichellini by Morse & Holzenthal (1987, character 19), and by Calor & Holzenthal (2008, character 1).
5. **Shape of anterolateral pronotal 'lobules':** (0) narrow; (1) wide/broad. The presence of broad

anterolateral pronotal lobules was proposed as a synapomorphy of the clade (Hudsonemini, Triplectidini) by Morse & Holzenthal (1987, character 17) and Calor & Holzenthal (2008, character 11).

6. **Mesoscutellar warts:** (0) absent; (1) single; (2) paired. The presence of a single mesoscutellar wart was proposed as a synapomorphy of *Grumichella* by Calor & Holzenthal (2008, character 3).
7. **Number of brown spots in male forewings:** (0) zero; (1) 2–3; (2) 9–12. The presence of two or nine brown spots in the forewing was used by Holzenthal (1988a) to separate the two putative species groups of *Grumichella*.
8. **One branch of the median vein (3rd cell) in the hind wings:** (0) absent (lost); (1) present. The loss of one branch of the median vein (third cell) in the hind wing is a synapomorphy of Leptocerinae (Morse, 1981; Morse & Holzenthal, 1987, character 9).
9. **Hind wing sectoral crossvein:** (0) present; (1) absent. The absence (or loss) of the hind wing sectoral crossvein was proposed as a synapomorphy of Leptocerinae by Morse (1981) and Morse & Holzenthal (1987, character 10).
10. **Forewing fork V:** (0) starting after crossvein *m-cu*; (1) starting before crossvein *m-cu*. Forewing fork V starting before crossvein *m-cu* was proposed as a synapomorphy of Grumichellini by Calor & Holzenthal (2008, character 13).

Male genitalic characters

11. **Tergum IX:** (0) without dorsal protuberances; (1) with 1 dorsal protuberance; (2) with paired dorsal protuberances.
12. **Segment X, lateral view:** (0) not flattened; (1) flattened.
13. **Number of the processes at apex of abdominal segment X:** (0) none; (1) 1 pair; (2) 2 pairs. Abdominal segment X with two pairs of apical, digitate processes and the presence of apical processes on segment X were proposed as synapomorphies of *Atanatolica*, and of the clade (*Atanatolica* + *Triplexa*) by Holzenthal (1988a, characters 41 and 20, respectively). Calor & Holzenthal (2008) treated this as a single character (character 4), and the presence of 'two pairs' was proposed as homoplastic in *Atanatolica* and *Triplexa*. The absence (loss) of processes at the apex of abdominal segment X was proposed as a synapomorphy of the clade (*Grumichella*, *Amazonatolica*) by Calor & Holzenthal (2008).
14. Apicodorsal protuberance on segment X: (0) present; (1) absent.
15. **Width of apicodorsal protuberance on segment X:** (0) 1/3 the width of the apex of segment X; (1) 2/3 the width of the apex of segment X; (2) 1/2 the width of the apex of segment X; (3) almost the same width as the apex of segment X.
16. Groove (or furrow) in apicodorsal proturberance on segment X: (0) present; (1) absent.
17. Basodorsal protuberance on inferior appendage: (0) present; (1) absent.
18. Basodorsal protuberance on inferior appendage: (0) developed; (1) undeveloped.
19. **Stout, spine-like setae on mesal surface of each inferior appendage:** (0) absent; (1) present. Stout, spine-like setae on the mesal surface of the inferior appendage (adult males) was considered as a synapomorphy of *Atanatolica* by Holzenthal (1988a, character 42). Morse & Holzenthal (1987, character 21) and Calor & Holzenthal (2008, character 6) proposed this same character as a synapomorphy of Grumichellini.
20. **Apical region of the inferior appendage:** (0) cylindrical; (1) apex dilated. Dilated apical region of the inferior appendage of male genitalia was proposed as a synapomorphy of Grumichellini by Calor & Holzenthal (2008, character 14), but with a reversal in the clade (*Osflintia*, *Atanatolica*, *Amazonatolica*, *Grumichella*).
21. **Second article of inferior appendage:** (0) present; (1) absent (or fused to first). The absence (or fusion) of the second article of each inferior appendage is a synapomorphy of Hudsonemini according to Holzenthal (1986) and Morse & Holzenthal (1987, character 22).
22. **Length of 2nd article of inferior appendage:** (0) subequal to the apicodorsal portion; (1) longer than the apicodorsal portion; (2) slightly shorter than the apicodorsal portion; (3) 1/2 length of the apicodorsal portion; (4) 1/5 length of the apicodorsal portion; (5) 1/6 or less than the apicodorsal portion. The reduced second article of each inferior appendage is a synapomorphy of *Atanatolica* according to Holzenthal (1988a, character 43). Calor & Holzenthal (2008, character 5) proposed the presence of '2nd article not reduced' as a synapomorphy of *Grumichella*.
23. Mesal surface of 2nd article of the inferior appendage: (0) not excavate; (1) excavate.
24. Thickness of 2nd article of the inferior appendage: (0) slender; (1) robust, strong.
25. Direction of the apex of 2nd article of the inferior appendage: (0) strongly curved mesad; (1) slightly curved mesad.
26. **Phallic parameres:** (0) absent; (1) present. The loss of primitive phallic parameres is a synapomorphy of Triplectidinae (Morse, 1981; Morse & Holzenthal, 1987, character 13).

27. Apical phallicata: (0) reduced; (1) not reduced. The reduced apical phallicata was proposed as a synapomorphy of Triplectidinae by Morse (1981) and Morse & Holzenthal (1987, character 14).

28. Curvature of phallicata: (0) almost straight; (1) strongly down-curved; (2) strongly up-curved.

29. Size of phallotremal sclerites: (0) small; (1) medium; (2) large.

LARVAL CHARACTERS

30. Frontoclypeal apotome with posterior, raised protuberance: (0) absent; (1) present. Frontoclypeal apotome with posterior, raised protuberance was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 16).

31. Number of secondary setae on the larval labrum: (0) with many secondary setae; (1) with very few secondary setae. Larval labrum with many secondary setae was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 2) and Calor & Holzenthal (2008, character 16). However, larvae of at least *Oecetis* also have many secondary setae on the labrum.

32. Number of secondary setae on the larval head: (0) with many secondary setae, especially in setal positions 1–5; (1) with very few secondary setae. Larval head with many secondary setae, especially primary setal positions 1–5, was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 3) and Calor & Holzenthal (2008, character 17).

33. Length of the secondary setae on the larval head: (0) long; (1) short. Presence of clear, short setae was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 15, part).

34. Number of setae on outer margin of larval mandibles: (0) none; (1) two. Two setae on outer margin of larval mandibles was proposed as a synapomorphy of Grumichellini by Calor & Holzenthal (2008, character 18).

35. Primary seta 12 on larval head: (0) absent; (1) present. Primary seta 12 apparently absent was proposed as a synapomophy of Grumichellini by Holzenthal (1988a, character 4). The loss of primary seta 12 on the larval head was inferred as a synapomorphy of *Atanatolica* by Calor & Holzenthal (2008, character 19).

36. Carina bordering frontoclypeal suture on the larval head: (0) present; (1) absent. The presence of a small carina bordering the frontoclypeal suture on the larval head was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 17).

37. Mandibular dentition of larvae: (0) without teeth (scraping); (1) with teeth (chewing). Mandibles without teeth, trowel-like, suggesting a scraper trophic function, was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 5) and Calor & Holzenthal (2008, character 20).

38. Length of larval antennae: (0) short; (1) long. Antennae short was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 6) and Calor & Holzenthal (2008, character 21).

39. Shape of the mesopleural sclerites: (0) broad, plate-like; (1) not broad. Mesopleural sclerites broad, plate-like was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 13). Calor & Holzenthal (2008, character 22) proposed this character as a synapomorphy of an inclusive clade of Grumichellini (all genera except *Triplexa*).

40. Metanotal *sa*1 plate (or right *sa*1 and left *sa*1 fused): (0) present (right and left *sa*1 fused); (1) absent (right and left *sa*1 not fused). Metonotal *sa*1 and *sa*2 fused, forming a broad dorsal plate was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, characters 7 and 8). Calor & Holzenthal (2008) modified this interpretation to be two separate characters (23 and 24), and the presence of metanotal *sa*1 plate (character 23) was not recovered as a synapomophy of Grumichellini. However, this was caused by a mistake (missing data vs. presence) in scoring the character in *Grumichella*. By re-running an amended matrix [23(0) in *Grumichella*], the presence of metanotal *sa*1 plate appears as a synapomorphy of Grumichellini (except *Gracilipsodes* and *Triplexa*).

41. Metanotal dorsal plate formed by *sa*2 sclerites fused to metanotal *sa*1 plate: (0) present (*sa*2 sclerites fused to metanotal *sa*1 plate); (1) absent (*sa*2 sclerites not fused to metanotal *sa*1 plate). As in the previous character, Calor & Holzenthal (2008) recovered the presence of metanotal dorsal plate (character 24) as a synapomophy of Grumichellini (except *Gracilipsodes* and *Triplexa*).

42. Metanotal *sa*2 sclerites: (0) extended laterad; (1) not extended laterad. A broad dorsal *sa*2 plate, with posterolateral corners extended laterad and recurved mesad was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 9). Calor & Holzenthal (2008) reinterpreted the morphological variation in this structure as two separate characters (25 and 26), and the 'posterolateral corners extended laterad' was recovered as a synapomorphy of Grumichellini.

43. **Apex of posterolateral corners of the metanotal *sa*2 sclerites:** (0) curved mesad; (1) curved laterad; (2) not curved. The posterolateral corners of the *sa*2 sclerites curved mesad was proposed as a synapomorphy of Grumichellini (except *Gracilipsodes* and *Triplexa*) by Calor & Holzenthal (2008, character 26).
44. **Length of metanotal sclerites *sa*3:** (0) short; (1) long. Long metanotal *sa*3 sclerites was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 10) and Calor & Holzenthal (2008, character 27).
45. **Shape of metapleural sclerites:** (0) broad, plate-like; (1) narrow. Metapleural sclerites broad, plate-like was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 13) and Calor & Holzenthal (2008, character 28).
46. **Shape of larval hind tibia:** (0) broad and stout; (1) slender and cylindrical. The character 'legs broad and stout' was proposed as a synapomorphy of Grumichellini, and the character 'larval legs, especially hind tibia and femur, broad and depressed' was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, characters 11 and 18, respectively). Calor & Holzenthal (2008) reinterpreted these characters as 'shape of larval hind tibia', and proposed the 'larval hind tibia broad and stout' as a synapomorphy of the clade (*Grumichella*, *Amazonatolica*).
47. **Row of peg-like setae on the apex of posterior margin of larval tarsus:** (0) present; (1) absent. The presence of a row of peg-like setae on the apex of posterior margin of larval tarsus was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 19).
48. **Direction of larval tarsal claw:** (0) slightly curved; (1) curved; (2) straight.
49. **Shape of the basal setae on tarsal claw of the larvae:** (0) peg-like; (1) thin spine-like. Basal setae peg-like was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a: character 21).
50. **Distribution of larval gills on abdominal segments:** (0) restricted to anterior-most abdominal segments; (1) not restricted to anterior-most abdominal segments. Gills restricted to the anterior-most abdominal segments was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 12) and Calor & Holzenthal (2008, character 30).
51. **Lateral fringe:** (0) absent; (1) present. Lateral fringe absent was proposed as a synapomorphy of Grumichellini by Holzenthal (1988a, character 14). Later, Calor & Holzenthal (2008) proposed this character as a synapomorphy of Grumichellini (except *Gracilopsodes* and *Triplexa*).
52. **Length of accessory teeth on larval anal claw:** (0) long; (1) short. Accessory teeth hook-like, long was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 22).
53. **Posterior extremity of larval case:** (0) without ventral projection; (1) with ventral projection.

Pupal characters

54. **Dark spots on frons of pupal head:** (0) present; (1) absent. Pupal heads distintly pigmented was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 30).
55. **Vertex of pupal head:** (0) with raised projection; (1) without raised projection. The vertex of pupal head bearing a projection was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 25).
56. **Number of long setae on the frons pupal head:** (0) 1 pair; (1) 2 pairs; (2) 4 pairs; (3) 6 pairs. Six pairs of long setae was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 26).
57. **Size of pupal labrum:** (0) rudimentary; (1) not rudimentary, normally sized. Labrum rudimentary was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 28).
58. Setae on pupal labrum: (0) absent; (1) present. Labrum without setae was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 29).
59. **Tooth on pupal mandibles:** (0) present; (1) absent. The presence of large tooth on each pupal mandible was proposed as a synapomorphy of Triplectidinae by Morse (1981) and Morse & Holzenthal (1987).
60. **Size of pupal mandibles:** (0) large; (1) small. Mandibles small was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 27).
61. **Pupal abdominal hook plates with anterior sclerotized extension:** (0) present; (1) absent. Presence of an anterior sclerotized extension on pupal abdominal hook plates was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, charater 23, part).
62. Length of abdominal segment IX of pupae: (0) short; (1) long; (2) very long.
63. **Length of anal process of pupae:** (0) short; (1) long; (2) very long. Anal process very long (and tubular) was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 24, part).

64. Shape of anal process of pupae: (0) tubular (and narrow); (1) trapezoidal; (2) almost conical. Anal process (very long and) tubular was proposed as a synapomorphy of *Grumichella* by Holzenthal (1988a, character 24, part).

65. Direction of the apex of anal process of pupae: (0) straight; (1) slightly curved; (2) strongly curved.

66. Length of pedicel of the pupal cases: (0) short; (1) long; (2) very long.

APPENDIX 2

Data matrix, 22 taxa and 66 characters (characters 1–29 from adults, characters 30–53 from larvae and 54–66 from pupae)

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Triaenodes	1	1	0	0	0	1	0	0	1	0	0	?	1	1	–	–	?	?	0	?	1	–	–	–	–	1	1	?	?	0	1	1	0
Nectopsyche	1	1	0	0	0	1	0	0	1	1	0	?	0	1	–	–	?	?	0	0	1	–	–	–	–	1	1	?	0	0	1	1	0
Oecetis	1	1	0	0	0	0	0	0	1	–	0	1	0	1	–	–	?	?	0	0	1	–	–	–	–	1	1	2	?	0	0	1	0
Triplectides	1	1	1	0	1	1	0	1	0	0	0	1	1	1	–	–	0	0	0	0	0	3	0	?	1	0	0	2	2	0	1	1	0
Hudsonema	1	1	1	0	1	1	0	1	0	0	0	1	1	1	–	–	0	1	0	–	1	–	–	–	–	0	0	0	2	0	1	1	0
Gracilipsodes	1	1	0	1	0	?	0	1	0	1	0	1	1	1	–	–	0	1	1	1	0	5	0	1	1	0	0	1	?	0	0	0	0
Triplexa	1	1	0	1	0	?	0	1	0	1	0	1	2	1	–	–	0	1	1	1	0	5	0	1	1	0	0	1	?	0	0	0	0
Amazonatolica	1	1	0	1	0	0	0	1	0	1	0	1	0	1	–	–	0	0	1	0	0	4	0	1	1	0	0	2	0	0	0	0	1
Atanatolica	1	1	0	1	0	2	0	1	0	1	0	1	2	1	–	–	0	0	1	0	0	5	0	?	1	0	0	?	1	0	0	0	0
G. aequiunguis	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	2	0	1	0	0	1
G. flaveola	0	0	0	1	0	1	2	1	0	1	0	0	0	0	0	1	0	1	0	0	0	2	0	1	0	0	0	1	0	1	0	0	1
G. pulchella	0	0	0	1	0	1	2	1	0	1	0	0	0	0	0	1	0	1	0	0	0	2	0	1	0	0	0	1	0	?	?	?	?
G. rostrata	0	0	0	1	0	1	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	2	0	1	0	0	1
G. boraceia	0	0	0	1	0	1	1	1	0	1	0	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1
G. muelleri	0	0	0	1	0	1	1	1	0	1	0	0	0	0	3	1	1	–	0	0	0	2	0	1	0	0	0	0	0	?	?	?	?
G. jureia	0	0	0	1	0	1	1	1	0	1	0	0	0	0	3	0	1	–	0	0	0	0	0	1	1	0	0	2	1	1	0	0	1
G. leccii	0	0	0	1	0	1	1	1	0	1	0	1	0	0	2	0	0	1	0	0	0	1	0	0	0	0	0	2	0	1	0	0	1
G. paprockii	0	0	0	1	0	1	1	1	0	1	1	0	0	0	0	0	1	–	0	0	0	2	0	1	0	0	0	1	0	?	?	?	?
G. parati	0	0	0	1	0	1	1	1	0	1	0	0	0	0	2	1	1	–	0	0	0	1	0	0	0	0	0	1	0	?	?	?	?
G. cressae	0	0	0	1	0	1	2	1	0	1	2	0	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	2	1	?	?	?	?
G. trujilloi	0	0	0	1	0	1	2	1	0	1	2	1	0	0	3	0	0	1	0	0	0	0	1	1	0	0	0	2	1	?	?	?	?
G. blahniki	0	0	0	1	0	1	2	1	0	1	0	0	0	0	3	0	0	0	0	0	0	2	0	1	1	0	0	2	0	?	?	?	?
Taxa	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Triaenodes	0	1	1	1	1	1	–	–	1	–	0	1	1	1	0	1	0	1	1	0	1	1	1	1	1	0	0	1	0	1	0	0	?
Nectopsyche	0	1	1	1	1	1	–	–	1	–	0	1	1	1	0	1	1	1	1	0	1	1	?	1	1	?	?	?	?	?	?	?	?
Oecetis	0	1	1	1	1	?	1	1	1	–	0	1	1	1	0	1	0	1	1	0	1	1	?	1	1	?	?	?	?	?	?	?	?
Triplectides	0	1	1	1	1	1	1	1	1	–	1	1	1	1	0	1	1	1	1	–	1	1	1	1	1	0	0	1	0	1	0	2	?
Hudsonema	0	1	1	1	1	1	1	1	1	–	0	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	?
Gracilipsodes	1	?	1	0	0	0	1	0	0	1	0	0	1	1	1	1	0	?	1	0	?	?	?	1	1	?	?	?	?	?	?	?	?
Triplexa	1	?	1	0	0	1	1	1	0	2	1	0	1	1	0	1	0	?	1	0	?	?	?	1	1	?	?	?	?	?	?	?	?
Amazonatolica	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	–	0	0	0	1	1	0	1	1	1	1	1	1	0	2	2	0
Atanatolica	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	1	1	1	1	2	1	1	1	0	1	1	?	0	2	0
G. aequiunguis	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	1	0	0	2	1	0	2	0
G. flaveola	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	1	0	0	2	0	1	2	0
G. pulchella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. rostrata	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	1	0	0	2	1	1	2	2
G. boraceia	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	1	0	0	2	1	0	2	1
G. muelleri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. jureia	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	1	0	0	2	0	1	2	1
G. leccii	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	3	0	0	1	0	0	2	1	0	2	2
G. paprockii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. parati	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. cressae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. trujilloi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
G. blahniki	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?