




Revisiting Brundin's collection, part I – larval description of three species of the genus *Podonomus* (Diptera: Chironomidae: Podonominae) with identification key for known larvae

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ABSTRACT

Podonomus is one of the richest genera of Podonominae, with 44 species described. With wide distribution in South America, *Podonomus* species are an important component of aquatic ecosystems such as streams and madicolous habitats. However, its larval stages have been historically overlooked, with only six species described. After visiting Brundin's collection, we were able to recover information on larvae of three species mentioned in his monograph. Here we describe the larvae of *P. apolobambae* and *P. setosus*, provide a broad description of the *P. albinervis* larva and present an identification key to the known larvae of the genus, including the other five species whose larvae are described, *P. amarali*, *P. fastigiatus*, *P. pepinellii*, *P. quito* and *P. tehuelche*.

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Introduction

In 1966, Lars Brundin published a monograph on Transantarctic relationships evidenced by chironomid midges, emphasising the subfamilies Podonominae, Aphroteniinae and Heptagyae (current Diamesinae). This publication was very original for the middle of the twentieth century because it was one of the first to include Hennig's cladistical methodology (Hennig 1966) in a biogeography framework, linking systematics and phylogeny of chironomids with the tectonics hypotheses of Wegener (1922). This monograph includes a unique revision of the genus *Podonomus* comprising the seven species then known, and the description of 29 new species and eight morphotypes. Since this publication, only eight new species of *Podonomus* have been described (Roback 1970; Roque and Trivinho-Strixino 2004; Siri and Donato 2012; Shimabukuro et al. 2017; Pinho and Shimabukuro 2018).

Brundin's monograph remains the most important contribution to our knowledge of Podonominae systematics, including detailed descriptions and illustrations of imago and pupae of most species. However, the larval life stage was not fully studied in that

work, with only a brief description of Podonominae larva in the general introduction and in the diagnosis of each genus. From the 29 species described in his monograph, Brundin mentioned the presence but did not describe the larvae of nine species, which he identified with certainty due to the presence of well-recognisable respiratory horns of the pupa in larval specimens. Indeed, when the pupa is associated with the adult stage, the presence of the prepupa generally guarantees the association of the larvae with the adult.

The larvae of *Podonomus apolobambae* Brundin (1966, p. 93, 230), *Podonomus albinervis* Brundin (p. 93, 232), *Podonomus dewertensis* Brundin (p. 93, 215), *Podonomus fittkaui* Brundin (p. 93), *Podonomus montanus* Brundin (p. 93, 218), *Podonomus nudipennis* Brundin (p. 93, 227, 228), *Podonomus reticulatus* Brundin (p. 93, 239), *Podonomus rivulorum* Brundin (p. 93) and *Podonomus setosus* Brundin (p. 93, 234) were identified but not formally described by Brundin. In fact, Brundin drew some parts of the larva of *P. setosus* (p. 91) and *P. apolobambae* (p. 94), but he did not provide any formal description.

Larvae of *Podonomus* genus can be distinguished from the other genera by the antennal segment 2 and 3 not annulated, procercus well sclerotised and generally dark all over, and in some species, the presence of long setae in the body. *Podonomus* larvae are still unknown for most species, with only six larvae properly described amongst the 44 species formally named (Prat et al. 2004; Siri et al. 2009; Siri and Donato 2012; Trivinho-Strixino et al. 2012). The larva of *P. quito* Roback was the first formally described larva of *Podonomus* (Roback 1970). Later, the larvae of *P. fastigians* Brundin (Roback and Coffman 1983), *P. tehuelche* Siri and Donato (Siri and Donato 2012) and *P. pepinellii* Roque and Trivinho-Strixino (Trivinho-Strixino et al. 2012) were fully described. Siri et al. (2009) erroneously reported that theirs was the first description of *P. fastigians* larva, by the omission of Roback and Coffman's (1983) previous description. Recently, *P. amarali* Pinho and Shimabukuro was described based on all development stages, including the larva (Pinho and Shimabukuro 2018).

While visiting Brundin's collection in 2014, held at the Naturhistoriska Riksmuseet (Swedish Museum of Natural History – SMNH) in Stockholm, Sweden, the first author was able to reexamine the *Podonomus* material belonging to Brundin's collection, including all slides and some of the wet samples. From the nine larvae mentioned in Brundin's monograph (1966), only *P. apolobambae*, *P. setosus* and *P. albinervis* were found in the collection.

Here, we describe the larvae of *P. apolobambae* and *P. setosus*, provide a broad description of *P. albinervis* larva and include a key to identify known *Podonomus* larvae. Moreover, the present study is a first effort towards increasing our knowledge of *Podonomus* larvae to contribute to ecological, systematic and biogeographic studies.

Materials and methods

Brundin (1966) mentioned the presence of larvae from nine species in his collection, but we were only able to find three of them at this time. The three species here described were confidently associated and identified by Brundin (1966, p. 93). In addition, we were able to confirm the identification of the slides by comparing some characters with the few drawings provided by Brundin (1966, p. 91 and 94). Larvae, pupae and males in slides were examined and photographed under magnification using a Nikon Eclipse 80i microscope with a Nikon D700 attached. High-resolution photos of each specimen were

made using stacking features. Larval structures (antenna, mandible and mentum) of these three species are also represented in drawings.

We found some incongruences between the labels on some slides (see [Figure 7](#) and Material examined sections) and the information in Brundin's monograph (Brundin 1966). The issue here lies with the dates in his monograph (not on the slides), because there is a mismatch between the dates listed in the description of the sampling localities (p. 67) and those in the Material examined (p. 230). We assume that Brundin collected *P. apolobambae* on the same day (5 March 1959) at both localities at the Cordillera Real in Bolivia, and not on 5 February 1959 as mentioned on page 230. In his monograph, Brundin only mentioned larvae of *P. apolobambae* occurring at the type locality: Nevado Huayana Potosí, 4300 m above sea level (asl), Cordillera Real, Bolivia, 5 March 1959. However, the slides containing *P. apolobambae* larvae ([Figure 7](#)) were labelled 'Podon. s. str. apolobambae Bolivia, Br. Huayna Potosí 4000 m 5/3 59 L.B. SA. 150', where he collected some males and some females (p. 230).

The terminology and abbreviations used in the descriptions follow Sæther (1980). Larval head capsule size is given as the postmentum length measured from the tip of the mentum to the postoccipital margin. This measure is less susceptible to deformation during slide mounting than any 'total' length. All measurements are given as ranges, with the smallest measurement followed by the largest.

The specimens used in the descriptions are the only ones we were able to find in Brundin's collection (BRD) and they vary in terms of preservation condition (both slides and wet samples). The collection is held at the Naturhistoriska Riksmuseet (Swedish Museum of Natural History) in Stockholm, Sweden. Additional specimens of *P. albinervis* were included from the collection of the Instituto de Limnología Dr. Raúl A. Ringuelet (ILPLA), which includes pupae reared from larvae, adult males reared from pupae and adult females reared from pupae; thus, complete association among all life stages were obtained.

Extra material was also examined to produce the key for the *Podonomus* larvae; *Podonomus pepinellii* specimens were obtained from the Reference Collection of the Laboratório de Ecologia de Insetos Aquáticos (LEIA) of the Universidade Federal de São Carlos (UFSCar), Brazil. Additional information was obtained from the following literature: Roback (1970), Roback and Coffman (1983), Siri et al. (2009), Siri and Donato (2012), Trivinho-Strixino et al. (2012), and Pinho and Shimabukuro (2018).

Results

Podonomus apolobambae Brundin, 1966

The description is based on two slides and one larva preserved in ethanol examined from the SMNH collection. Only the largest larva was used for the morphological measurements.

Larva (n = 3, except where otherwise stated; Figures 1, 2). Head capsule brown (in slide; [Figure 1a,d](#)), very dark in specimens from ethanol ([Figure 1e](#)). Head somewhat triangular, wider in its posterior part, dorsal length 337 µm (n = 1), ventral length 188 µm (n = 1).

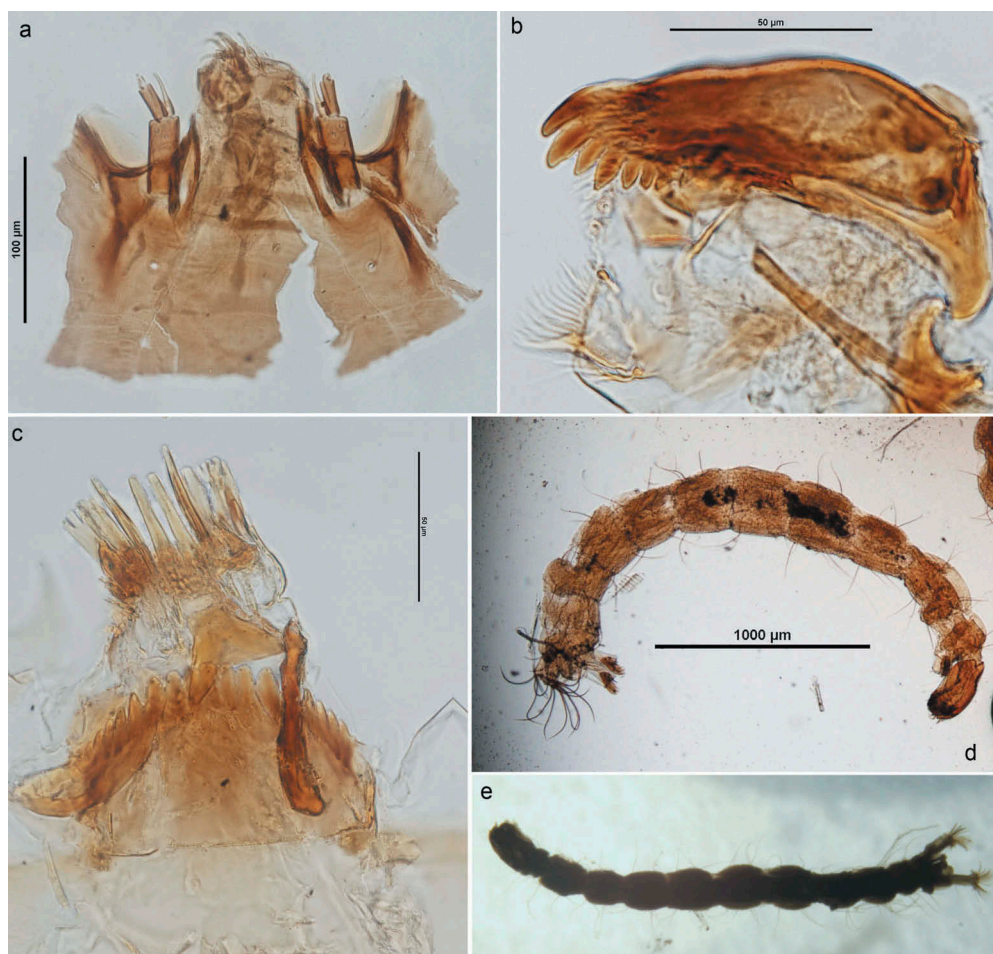


Figure 1. Photographs of *Podonomus apolobambae* Brundin, 1966 from Brundin's collection in the Swedish Museum of Natural History (SMNH). (a) Head, dorsal view; (b) mandible, lateral view; (c) mentum and prementum; (d) larva in slide, lateral view; (e) larva in ethanol, dorsal view.

Antenna (Figures 1a, 2a)

Segment lengths of A_1 – A_4 (μm) 46, 21, 8 and 3 ($n = 1$); ring organ situated at 0.57 from the base; flagellum 32 μm ; AR (basal segment/ flagellum) 1.58; antennal blade 30 μm long ($n = 1$), wider proximally and the extremity abruptly ending, reaching the third antennal segment; stylus 6 μm ($n = 1$).

Labrum

Mandible (Figures 1b, 2b) measuring 125 μm in length ($n = 1$), with outer margin bent in the middle, with seven teeth, one slightly small preapical outer, one apical, two large below, and three smaller inner teeth. Mentum (Figures 1c, 2c) 211 μm in width and 17 brownish teeth ($n = 1$), five central teeth light brown. Prementum (Figure 1c) localised behind the mentum, with a Y-like M appendage connected with 10 apicolateral

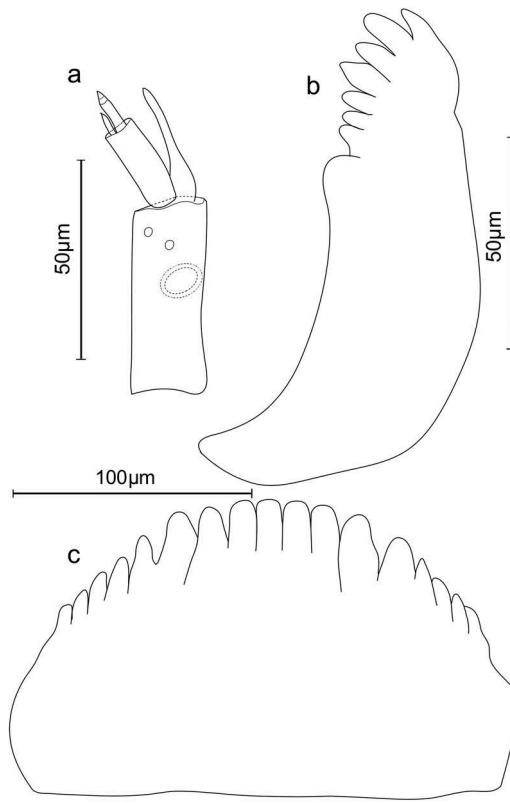


Figure 2. *Podonomus apolobambae* Brundin, 1966. (a) Antenna; (b) mandible; (c) mentum.

paramedian lamellae (one median pair unicuspid, two lateral pairs bicuspid and two outer pairs palmate).

Body

Abdomen with many long brown single setae and short setal tufts in all segments (Figure 1d,e). Procercus dark brown, bearing two strong dark setae and seven apical setae with equal sizes (Figure 1d). Posterior parapods 160 µm long ($n = 1$); claws of two types, dark brown distributed in two rows. Anal tubules short.

Comments. According to Brundin (1966), this species of the tropical Andes is close related to *fastigiatus* of the same areas and *nudipennis*. Numerous larvae were collected by Brundin together with the holotype, using stream nets, in a small stream with rich vegetation of mosses at Nevado Huayana Potosí, 4300 m asl, Cordillera Real, Bolivia, 5 February 1959.

Diagnosis. The larvae of *P. apolobambae* can be distinguished from other *Podonomus* species by the following combination of characters: long setae present in the abdomen; length of antennal segments (µm): 46, 21, 8 and 3; AR 1.58; blade on first antennal segment (30 µm long) presenting an enlarged basis and the extremity abruptly ending,

reaching the third antennal segment; stylus 6 μm , inserted in apical portion of second segment; mandible with seven teeth, preapical longer; mentum 211 μm wide, with 17 teeth, five central teeth of approximately the same size, and six pairs of lateral teeth; seven apical setae on procercus with similar sizes.

Material examined. Slide number **BRD 364**, labeled 'Pod. s. str. apolobambae Brundin-sp SA 150' with a larva lacking abdominal parts. Slide number **BRD 398**, labeled 'Podon. s. str. apolobambae Bolivia, Br, Huayna Potosí 4000 m 5/3 59 L.B. SA. 150' with two complete larvae and eight pupal exuviae (Figure 7).

Additional material examined: Slide number **BRD 361**, labeled 'Pod. s. str. apolobambae Br. SA 151' with pupal exuviae (Figure 7). Slide number **BRD 362**, labeled 'Podonomus s. str. apolobambae (Sill. I) Bv. SA 151' with three pupal exuviae and one pupa (Figure 7). Slide number **BRD 363**, labeled 'Pod. Sillac. I apolobambae Peru: Cord. Apolo-bamba Lag. Sillacunca' with a complete male (Figure 7). Slide number **BRD 401**, labeled 'Podon. s. str. apolobambae Bolivia, Br, Cor. Apoloba. Huayna Potosí 4000 m 5/3 59 L.B. SA. 150' with a male lacking wings.

***Podonomus setosus* Brundin, 1966**

The description is based in two larval heads mounted on one slide examined from the SMNH collection. No larva in ethanol was found at the SMNH.

Larva ($n = 2$, except where otherwise stated; Figures 3a–d, 4). Head capsule brown (in slide; Figure 3c,d). Head somewhat triangular, wider in its posterior part, dorsal length around 227 μm ($n = 1$), ventral length around 145 μm ($n = 1$).

***Antenna* (Figures 3c, 4a)**

Segment length of A_1 – A_4 (μm) 67, 30, 11 and 3 ($n = 1$); ring organ situated at 0.43 from the base; flagellum 42 μm ; AR = 1.55; antennal blade 33 μm long ($n = 1$) completely narrow and does not reach the third antennal segment; stylus 6 μm ($n = 1$).

Labrum

Labral setae and clypeal S3 as in Figure 3c. Mandible (Figures 3a,b, 4b) measuring 112 μm in length ($n = 1$), with outer margin slightly bent in middle, with seven teeth, one slightly small preapical outer, one large apical and five inner teeth, four small and one larger in the middle. Mentum (Figures 3b, 4c) with 75 μm in width and 15 teeth brownish, five central teeth approximately with the same size (last lateral teeth slightly larger), and five pairs of lateral teeth, the first lateral larger and separated from central and the other lateral teeth; three median teeth light brown ($n = 1$). Prementum (Figure 3b) localised behind the mentum, with a Y-like M appendage connected with 10 apicolateral paramedian lamellae (one median pair unicuspid, two lateral pairs bicuspid and two outer pairs palmate).

Body

An entire larva has not been found in the collection, only the two head capsules described here. Illustration provided by Brundin 1966 (fig. 18, p. 91) shows the presence



Figure 3. Photographs of *Podonomus setosus* Brundin, 1966 from Brundin's collection in the Swedish Museum of Natural History (SMNH). (a) Mandible, lateral view; (b) mentum, prementum and mandible; (c) head, dorso-lateral view; (d) head, dorsal view; (e) pupa, dorsal view.

of short setae on the abdominal segments, but it is not clear how it compares with the other *Podonomus* species.

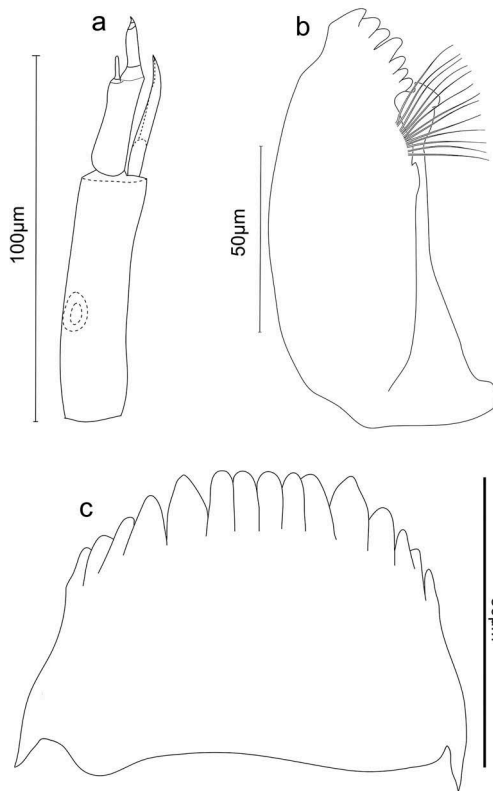


Figure 4. *Podonomus setosus* Brundin, 1966. (a) Antenna; (b) mandible; (c) mentum.

Comments. According to Brundin (1966), this species is close related to *albinervis* and to *inermis*. Larvae in great numbers were collected by him in the same stream on the same occasion together with the holotype, from Rio Rosario, Bahía Inútil, Tierra del Fuego, South Chile, 4 February 1959. Additionally, larvae of *P. setosus* were collected in Rio Fortuna, Bahía Inútil, Tierra del Fuego, South Chile, 6 February 1959 and in Rio Tres Brazos, near Punta Arenas, Terr. of Magellan, 3–22 February 1959.

Diagnosis. the larvae of *P. setosus* can be differentiated from those of its congeners by the combination of the following characters: large basal antennal segment, A_1-A_4 (μm): 67, 30, 11, 3; AR 1.55; blade on first antennal segment 33 μm completely narrow and does not reach the third antennal segment; stylus 6 μm , apically inserted on second segment; mandible with seven teeth, one slightly small preapical outer, one large apical and five inner teeth, four small and one large in the middle; mentum 75 μm wide, with 15 teeth, five central teeth approximately with the same size (last lateral teeth slightly larger), and five pairs of lateral teeth.

Material examined. Slide number **BRD 310**, labeled 'Podono. setosus BRUND. Larv-huvuaj R. Tres Brazos SA147' with two well preserved larvae (Figure 7).

Additional material examined: Slide number **BRD 384**, labeled 'Podono. s. str. setosus Br. (sp. Rosario) SA135' with a male pharate (Figures 3e, 7).

Podonomus albinervis Edwards, 1931

The description is based on two slides with five larvae from Brundin's collection at the SMNH, and on five slides and one wet specimen from the collection of the ILPLA.

Larva ($n = 7$, Figures 5a–d, 6). Total length 2.60–3.02 mm. Head capsule brown (in slide; Figure 5b), dark before cleared and somewhat subtriangular, wider in its posterior part. Dorsal and ventral length of the head 230–250 μm and 158–166 μm long, respectively. Postmentum dark, borders only slightly clearest.

Antenna (Figure 6a)

Antennal flagellomeres (A_1 – A_4): 50–54 μm ; 32 μm ; 8–12 μm ; 4 μm ; ring organ situated at 0.49–0.51 from the base. AR 1.05–1.10; blade on first antennal segment 30–34 μm long, approximately the same size as second segment; stylus 6 μm , slightly widened at apex, inserted in subapical portion of second segment. A_3 L/W ratio higher than 3. Length of the ventral head/total length of the antenna = 0.61–0.67; length of the total head/total length of the antenna = 0.39–0.42.

Labrum

Labral setae and clypeal S3 as in Figure 5b. Mandible (Figures 5a, 6b) 76–96 long, with seven teeth, the preapical one slightly longer. Mentum (Figures 5a, 6c) 50–60 μm long, 55–78 μm wide, with 15 teeth: five central teeth approximately with the same size or the central one slightly longer, plus five pairs of lateral teeth. Prementum: M appendage connected with apicolateral paramedian lamellae, the outermost pairs palmate.

Body

First three segments with thin and long setae; the rest of the segments with very thin and shorter setae. Procercus dark brown, 71–90 μm long; L/W 1.3–1.8. Two thin setae are respectively placed at 0.40–0.50 and 0.83–0.90 from the base of the procercus. Seven strong apical dark setae (Figure 5c,d) are present in the procercus: on each specimen, six of the apical setae are of similar sizes, 150–190 μm long, while one is shorter and 110–130 μm long.

Posterior parapods 160–215 μm ; lobe placed dorsally of the base of the posterior parapods, 60–70 μm long. Claws of two types, an apical row of long (100–140 μm) and a subapical row of short (10–20 μm) claws. Small setae in the parapodal lobe bifid. Anal tubules 52–65 μm long.

Diagnosis. The larvae of *P. albinervis* differ from those of other known *Podonomus* species by the combination of the following characters: presence of a few thin setae in the larval body – somewhat stronger and longer in the first three segments; length of antennal segments (μm): 50–54, 32, 8–12, 4; antenna 0.39–0.42 as long as the total head length; A_3 L/W ratio higher than 3; AR 1.05–1.10; blade on first antennal segment



Figure 5. Photographs of *Podonomus albinervis* Edwards, 1931, from Brundin's collection in the Swedish Museum of Natural History (SMNH). (a) Mentum, prementum, mandibles; (b) head, ventral view; (c) posterior abdominal parapods, procercus and abdominal tubules; (d) procercus; (e) pupa, dorsal view.

approximately the same size as the second segment; stylus 6 µm, inserted in subapical portion of second segment; mandible with seven teeth, preapical slightly longer; mentum 55–78 wide, with 15 teeth, five central teeth approximately with the same size or the central one slightly longer, plus five pairs of lateral teeth; six apical setae on procercus with similar sizes 150–190 µm long, plus one shorter seta 110–130 µm long; small setae in the parapodal lobe bifid.

Material examined

SMNH collection Slide number **BRD 344**, labeled 'Pod. albinervis CHILE: Villarica BRUNDIN SA 11 with larval heads (Figure 7). Slide number **BRD 345**, labeled

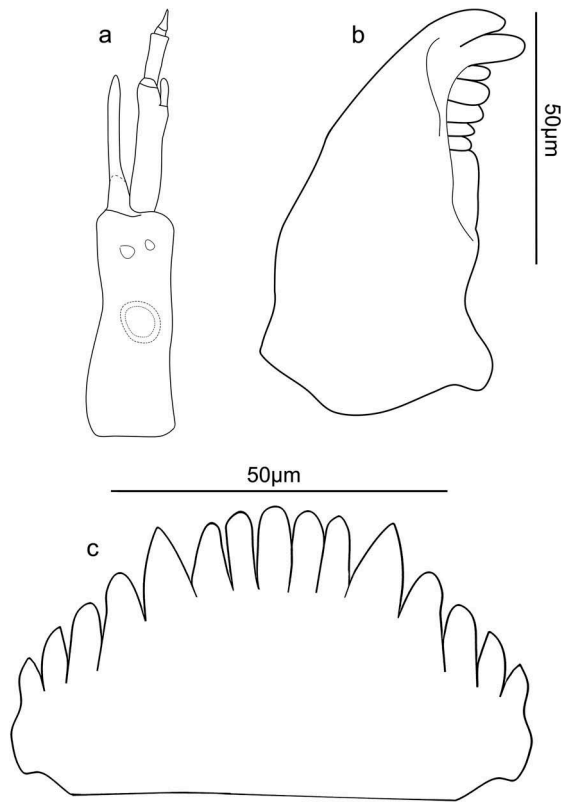


Figure 6. *Podonomus albinervis* Edwards, 1931. (a) Antenna; (b) mandible; (c) mentum.

'*Podonomus albinervis* EDW. CHILE: Villarica 3/11 1953 BRUNDIN SA11.' with five larvae without heads, apparently, the heads were mounted on slide BRD 344 (Figure 7).

Additional material examined: Slide number **BRD 380**, labeled 'Podonomus albinervis EDW. CHILE: Villarica 3/11 1953 BRUNDIN SA11.' with several pupae (Figure 5e) and pupal exuviae. Slide number **BRD 381**, labeled 'Podonomus albinervis EDW. CHILE: Villarica 3/11 1953 BRUNDIN SA2a.' with males and females (Figure 7).

Material Examined from ILPLA collection. Three larvae, ARGENTINA: Buenos Aires Province, Torquinst, 'E. Torquinst' Provincial Park, Toro stream, 38.021944 N, 62.025916 W, 672 m asl, 22 May 2011, D-net, Donato-Siri-Spaccesi cols; two larvae with same data as previous, except for date 4 November 2011.

Discussion

The *Podonomus* larval stage has been historically overlooked, possibly due to (1) the difficulty of collecting larvae (Shimabukuro et al. 2017), (2) issues related to associating larvae with pupal and adult stages, due to the difficulty of rearing them at laboratory, and (3) the difficulty of finding good diagnostic characters to distinguish *Podonomus* larvae.

A scarce knowledge of the larva is not restricted to the *Podonomus* genus, as it is observed across other genera in the Podonominae subfamily. Because *Podonomus* larvae can be quite similar, molecular tools have been used to associate life stages (e.g.

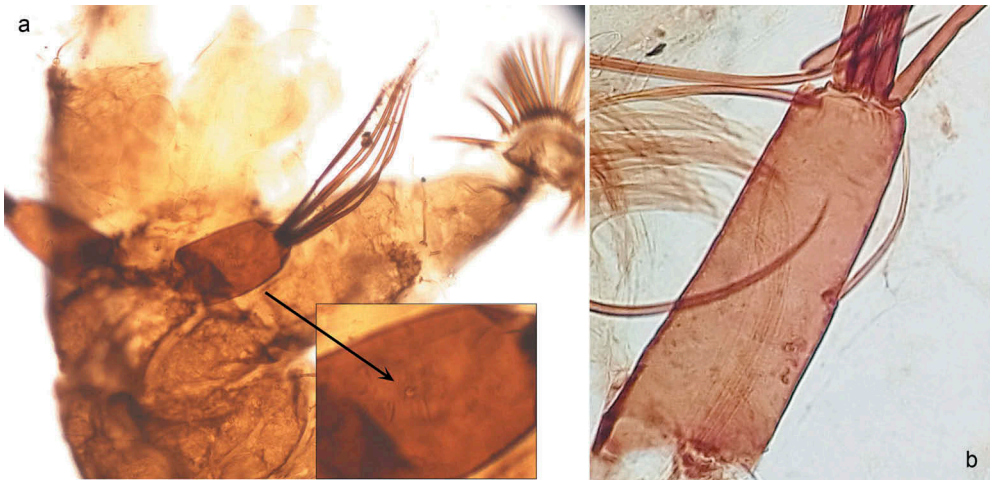


Figure 8. (a) Procercus of *Podonomus pepinellii* Roque and Trivinho Strixino, 2004, with median seta in detail; (b) procercus of *Podonomus fastigiatus* Brundin, 1966, showing strong and bifid median seta.

Brundin based on pupal and adult morphology (Brundin 1966). The validity of these groups has been already questioned, because previous studies have shown that the placement of some species diverges among development stages within a species (Trivinho-Strixino et al. 2012; Shimabukuro et al. 2017). Thus, the description of larval stages and also the association with imagines represent an important step to elucidate phylogenetic relationships of *Podonomus* species.

Based on the restricted number of specimens, we provide a preliminary identification key for known *Podonomus* larvae.

Key to known larvae of *Podonomus* species from Neotropical region

- 1. Mentum with 11 teeth; A_2/A_3 ratio = 2 (Pinho and Shimabukuro 2018, fig. 4F,G)..... *amarali*
- 1' Mentum with 15 or 17 teeth; A_2/A_3 ratio higher than 2.5..... 2
- 2. AR low (near 1.0); A_3 L/W ratio higher than 3; body without long setae (Figures 6a, 5c, respectively)..... *albinervis*
- 2' AR usually higher than 1.3; A_3 L/W ratio lesser than 3; body with or without long setae..... 3
- 3. Mentum wide, with 17 teeth (Figures 1c, 2c)..... *apolobambae*
- 3' Mentum not as wide, with 15 teeth..... 4
- 4. Preapical tooth of mandible as long as or slightly smaller than the apical (Figures 3a, 4b)..... *setosus*
- 4' Preapical tooth of mandible clearly longer than the apical..... 5

5. Apical setae on procercus with different sizes (in a ratio of 2:2:2:1) (Siri and Donato 2012, fig. 20)..... *tehuelche*
- 5' Apical setae on procercus with more or less similar size, except 2 which are usually shorter..... 6
6. Procercus long, L/W about 3.5 × antennal blade bifurcate (Roback 1970, figs 43, 45) *quito*
- 6' Procercus not as long, L/W ratio lesser than 3.0; antennal blade not bifurcate..... 7
7. Median seta of procercus very small and thin (Figure 8a)..... *pepinellii*
- 7' Median seta of procercus strong (Figure 8b)..... *fastigians*

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

- Brundin L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagylia. Kungliga Svenska Vetenskapakademiens Handlingar. 11(1):1–474.
- Hennig W. 1966. Phylogenetic systematics. Urbana: Univ. Illinois Press.
- Pinho LC, Shimabukuro EM. 2018. *Podonomus amarali* n. sp., a new species of the *albinervis* group (Diptera: Chironomidae: Podonominae) from Atlantic Forest, southern Brazil. Zootaxa. 4402(3):542–550. doi:10.11646/zootaxa.4402.3.
- Prat N, Añón-Suárez D, Rieradevall M. 2004. First record of Podonominae larvae living phoretically on the shells of the water snail *Chilina dombeyana* (Diptera: Chironomidae/Gastropoda: Lymnaeidae). Aquat Insects. 26:147–152. doi:10.1080/01650420412331327222.

- Roback SS. 1970. Podonominae from Ecuador, with notes on the sense organs and pupal respiratory organs (Diptera: Chironomidae). *J New York Entomol Soc.* 78(3):148–169.
- Roback SS, Coffman WP. 1983. Results of the Catherwood Bolivian- Peruvian Altiplano expedition part II. Aquatic diptera including Montane Diamesinae and Orthocladiinae (Chironomidae) from Venezuela. *Proc Acad Nat Sci Philad.* 135:9–79.
- Roque FO, Trivinho-Strixino S. 2004. *Podonomus pepinellii* n. sp., first record of the genus and subfamily from Brazil (Diptera: Chironomidae: Podonominae). *Zootaxa.* 689:1–7. doi:[10.11646/zootaxa.689.1.1](https://doi.org/10.11646/zootaxa.689.1.1).
- Sæther OA. 1980. Glossary of chironomid morphology terminology (Diptera: Chironomidae). *Entomol Scand.* 14:1–51.
- Shimabukuro EM, Pepinelli M, Perbiche-Neves G, Trivinho-Strixino S. 2017. A new trap for collecting aquatic and semi-aquatic insects from macicolous habitats. *Insect Conserv Divers.* 8(6):578–583. doi:[10.1111/icad.12135](https://doi.org/10.1111/icad.12135).
- Shimabukuro EM, Pepinelli M, Trivinho-Strixino S. 2017. Two new species of *Podonomus* Philippi (Diptera: Chironomidae: Podonominae) from mountains of southeastern Brazil. *Zootaxa.* 4290(1):155–166. doi:[10.11646/zootaxa.4290.1.9](https://doi.org/10.11646/zootaxa.4290.1.9).
- Siri A, Donato M. 2012. Two new species of *Podonomus* (Diptera: Chironomidae: Podonominae) of the Brundin's *decarthrus* group from Ventania system, Argentina. *Zootaxa.* 3548:39–54.
- Siri A, Paggi A, Donato M. 2009. *Podonomus fastigians* (Chironomidae: Podonominae): redescription of the adult male and female, the pupa, and description of the larva. *Entomol News.* 120:522–529. doi:[10.3157/021.120.0509](https://doi.org/10.3157/021.120.0509).
- Trivinho-Strixino S, Pepinelli M, Siqueira T, Roque FO. 2012. DNA barcoding of *Podonomus* (Chironomidae, Podonominae) enables stage association of a named species and reveals hidden diversity in Brazilian inselbergs. *Ann Limnol.* 48:411–423. doi:[10.1051/limn/2012032](https://doi.org/10.1051/limn/2012032).
- Wegener A. 1922. *Die Entstehung der Kontinente und Ozeane* [On the origin of continents and oceans]. English translation of 3rd edition by J. G. A. Skerl (1924). London: Methuen; 212 p.