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Revision of *Prodontocharax* and revalidation of *Amblystilbe* (Teleostei: Characidae: Cheirodontinae), with description of a new species

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Prodontocharax species are revised and the genus *Amblystilbe* is revalidated based on analysis of type-material and additional specimens. Both genera are diagnosed based on unique synapomorphies among members of the Cheirodontinae related to shape, size, number and arrangement of teeth in the jaw bones. *Prodontocharax melanotus*, from the upper rio Madeira basin, Brazil and Bolivia, is redescribed, and a new species is described from the rio Huallaga basin, Peru. The genus *Amblystilbe* and its type-species, *A. howesi*, are redescribed from the Amazonas River basin, Bolivia, Brazil, and Peru, and *Prodontocharax alleni* is considered a junior synonym of *A. howesi*. The two species of *Prodontocharax* are distinguished by the color pattern, number of lamellae of the olfactory rosette in male and female and number of gill rakers, and differ from *A. howesi* by the number and shape of teeth, color pattern and number of branched anal-fin rays. According to recent studies, the species of *Prodontocharax* and *A. howesi* cluster into two distinct clades among the cheirodontines.

Keywords: Amazon basin, Characiformes, Cheirodontini, Neotropical, Taxonomy.

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As espécies de *Prodontocharax* são revisadas e o gênero *Amblystilbe* é revalidado com base na análise do material-tipo e exemplares adicionais. Ambos os gêneros são diagnosticados com base em sinapomorfias únicas entre os membros de Cheirodontinae, relacionadas à forma, tamanho, número e disposição dos dentes das maxilas. *Prodontocharax melanotus* é redescrita para a bacia do alto rio Madeira, Brasil e Bolívia, e uma espécie nova é descrita para a bacia do rio Huallaga, Peru. O gênero *Amblystilbe* e sua espécie-tipo, *A. howesi*, são redescritos para a bacia do rio Amazonas, Bolívia, Brasil e Peru e *Prodontocharax alleni* considerado sinônimo júnior de *A. howesi.* As espécies de *Prodontocharax* se diferenciam pelo padrão de colorido, número de lamelas da roseta olfativa em machos e fêmeas e número de rastros branquiais, e diferem de *A. howesi* pelo número e forma dos dentes, padrão de colorido e número de raios ramificados da nadadeira anal. De acordo com estudos recentes, as espécies de *Prodontocharax* e *A. howesi* formam dois clados distintos dentre os queirodontíneos.

Palavras-chave: Bacia Amazônica, Characiformes, Cheirodontini, Neotropical, Taxonomia.

INTRODUCTION

The genus *Prodontocharax* Eigenmann & Pearson, 1924 and its type-species, *P. melanotus* Pearson, 1924 were described from Tumupasa, Bolivia, and diagnosed mostly based on modifications of jaws related to the unusual ventral position of the mouth, the "teeth mostly tridentate", and the short anal fin (Pearson, 1924). The genus *Amblystilbe* Fowler, 1940 and its type-species *Amblystilbe howesi* Fowler, 1940 were latter described from the Río Chimoré, Cochabamba, Bolivia, and likewise *Prodontocharax* diagnosed by modifications of jaws related to the unusual ventral position of the mouth and very minute "tridentate" teeth (Fowler, 1940). The genus *Amblystilbe* is presently considered a junior synonym of *Prodontocharax* (Géry, 1977:590; Böhlke, 1984:48; Malabarba, 2003:218).

Böhlke (1953) reviewed *Prodontocharax* and provided an extended description, considering its species "superficially appearing much like certain species of the genus *Odontostilbe* Cope". According to Böhlke, the genus occupies an isolated position among cheirodontine characids, being distinguished on the basis of its distinctly inferior mouth, and associated changes in jaw-bones and teeth. In the same paper, Böhlke (1953) described a new species from the rio Ucayali, Peru (*Prodontocharax alleni* Böhlke, 1953), considered as a distinct species, but possibly related to *A. howesi* based on a comparison to Fowler (1940:86, fig. 48) description and figures. Böhlke (1953) further redescribed and designated a lectotype and paralectotypes to *P. melanotus*.

Géry (1977) listed *Prodontocharax* in his *Aphyodite*-group in Cheirodontinae, comprising *Aphyodite* and 14 genera of "puzzling" characids [sic]. Most of these genera were later removed from Cheirodontinae by Malabarba (1998), except for *Prodontocharax*, *Amblystilbe* (listed in key by Géry, 1977:590 as a junior synonym of *Prodontocharax*), and *Macropsobrycon* that were maintained in that subfamily. Géry (1977:590) recognized

two species of *Prodontocharax*, *P. melanotus* and *P. alleni*, considering in footnote that "*A. howesi*, the type of *Amblistilbe* [sic], may be a distinct species".

The initial phylogenetic analyses dealing with the Cheirodontinae genera included only the type-species of *Prodontocharax*, *P. melanotus*, and did not include the type-species of the monotypic genus *Amblystilbe*, leaving the synonym of the two genera unchanged. In the first comprehensive cheirodontine phylogeny, Malabarba (1998) found *P. melanotus* (MZUSP 26068) diagnosable by three autapomorphies related to jaw and teeth morphology and one related to the color pattern. The genus then appeared in a basal polytomy in the subfamily along with the genera *Odontostilbe* Cope, 1870, *Aphyocheirodon* Eigenmann, 1915, *Pseudocheirodon* Meek & Hildebrand, 1916, and *Cheirodontops* Schultz, 1944. Mirande (2010) further recovered *P. melanotus* as sister group to remaining cheirodontines analyzed therein (*Odontostilbe*, *Serrapinnus* Malabarba, 1998, and *Cheirodon* Girard, 1855) and described nine autapomorphies for the type-species of the genus, but none exclusive to *Prodontocharax.*

The hypothesis of relationships of *Prodontocharax melanotus* to the cheirodontine was further supported in molecular analyzes. Calcagnotto *et al*. (2005) and Javonillo *et al*. (2010) found *Prodontocharax* sp. (AMNH 233236, examined and identified herein as *P. melanotus*) as sister group to clades containing the remaining Cheirodontinae analyzed in each paper (*Aphyocheirodon* and *Cheirodon* in Calcagnotto *et al*., 2005, and *Serrapinnus*, *Odontostilbe*, *Compsura* Eigenmann, 1915, *Macropsobrycon*, and *Cheirodon* in Javonillo *et al*., 2010). Oliveira *et al*. (2011) found *P. melanotus* (AMNH 233264) belonging to Cheirodontinae and as sister group to *Saccoderma* Schultz, 1944, and this clade as sister group to all other east Andean cheirodontines analyzed in that paper. Finally, in a hypothesis based on molecular data set of mitochondrial and nuclear DNA sequences of the subfamily Cheirodontinae, Mariguela *et al*. (2013) found *P. melanotus* (listed in that paper as *Prodontocharax* sp., STRI uncat., from Río Amazona, Peru) and *P. melanotus* (tissue collection catalog number AMNH 102082, corresponding to AMNH 233264 voucher from Calcagnotto *et al*., 2005, Javonillo *et al*., 2010, and Oliveira *et al*., 2011) form a clade in Cheirodontinae.

Bührnheim (2006) and Jerep (2011), in two unpublished theses, added a second species of the genus in their analyzes and found *Prodontocharax melanotus* and *P. alleni* forming sister species, supported by eleven morphological synapomorphies. Each of these monotypic clades were further supported by several autapomorphies in both analyzes. In the most recent hypothesis incorporating the morphological matrices of Bührnheim (2006) and Jerep (2011), and six molecular markers, *P. melanotus* and *P. alleni* were found to form separate and not closely related clades in Cheirodontinae (Chuctaya, 2022). This work deals with a revision of the diversity of *Prodontocharax*, including the type-species of its junior synonym, *Amblystilbe*, so far absent in systematic reviews in this group.

MATERIAL AND METHODS

Counts were taken as described by Fink, Weitzman (1974), except for the number of scale rows below lateral line counted from the scale row ventral to lateral line to the scale row nearest the first pelvic-fin ray. Counts of vertebrae, supraneurals, gill rakers on the first arch, and procurrent caudal-fin rays were taken from cleared and stained specimens (c&s) prepared according to Taylor, Van Dyke (1985). Tooth counts were taken on c&s specimens, except in *A. howesi*, which counts were also taken from alcohol preserved specimens of the type series. The gill raker at the junction of the ceratobranchial and the epibranchial is included in the counting of gill rakers of lower limb. Lamellae of the olfactory organ were counted with the head immersed in 70% alcohol; the tissue that joins the two nostrils (anterior and posterior nostril) was removed to have a complete view of the lamellae. Vertebral counts include the four vertebrae of the Weberian apparatus, and the terminal centrum was counted as a single element. Lower and upper jaws of c&s specimens were prepared for SEM (scanning electronic microscopy) by drying in acetone followed by gold metalization. The x-rays of lectotype of *P. melanotus* and holotype of *P. alleni* were analyzed. Counts indicated by an asterisk belong to the holotype or lectotype. Measurements were taken point to point with a caliper on the left side of specimens. Measurements are expressed as percentages of standard length (SL) except for subunits of the head, which are recorded as percentages of head length (HL). The listing of non-type-material of the new species of *Prodontocharax* aims to provide complementary information on the distributional records of the new species that currently has a large number of cataloged lots in the MUSM fish collection. The combined measurement data were examined with Principal Components Analysis (PCA) calculated in Past 4.13 version 2023 (Hammer *et al*., 2001) to determine if distinct groups were identified.

Specimens examined belong to the following institutions: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; INHS, Illinois Natural History Survey, Illinois; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; LIRP, Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MHNG, Muséum d'Histoire Naturelle, Genève; MNRJ, Museu Nacional, Rio de Janeiro; MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima; MZUSP, Museu de Zoologia de São Paulo, São Paulo; UFRGS, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre; UMMZ, University of Michigan Museum of Zoology, Michigan; UNT, Laboratório de Ictiologia Sistemática, Universidade Nacional do Tocantins, Porto Nacional; USNM, National Museum of Natural History, Washington D.C. Other abbreviations: STRI, Smithsonian Tropical Research Institute, Balboa.

RESULTS

The revision of the specimens of *Prodontocharax* and *Amblystilbe* allowed the recognition of three species arranged in two morphologically distinct groups. The first group is referred to as *Prodontocharax*, and contains the type-species of the genus, *P. melanotus*, and one undescribed species. The second group is referred to the genus *Amblystilbe*, herein removed from the synonym of *Prodontocharax*, and includes the type-species of *Amblystilbe*, *A. howesi. Prodontocharax alleni* does not differ from *A. howesi* and is herein proposed as its junior synonym. These two groups correspond to the two clades recovered by Chuctaya (2022). The species of both genera have the mouth slit located at the horizontal through the lower margin of the eye, that distinguishes them from all other cheirodontines. We provide a morphological diagnosis of each group.

Prodontocharax Eigenmann & Pearson, 1924

Prodontocharax Eigenmann & Pearson in Pearson, 1924:35 (Type-species: *Prodontocharax melanotus* Pearson, 1924. Type by monotypy. Gender: masculine). —Géry, 1977:590 (listed in identification key). —Böhlke, 1984:48 (listed). —Almirón *et al*., 2001:38 (compared to *Hypobrycon*). —Malabarba, 2003:221 (listed). —Mirande 2009:08 (phylogenetic relationships). —Mirande 2010:531 (phylogenetic relationships). —Oliveira *et al*., 2011:15 (phylogenetic relationships).

Diagnosis. The inferior mouth, with mouth slit located at horizontal through inferior margin of eye diagnoses *Prodontocharax* from other cheirodontine genera (except *Amblystilbe*). The premaxilla with 4 to 6 teeth (*vs.* 8 to 10); the central cusp larger than lateral ones *vs*. similarly sized cusp on all teeth; the posterior edentulous lamina of the maxilla medially curved in relation to the anterior toothed portion (*vs.* posterior edentulous lamina of the maxilla flat and plane); the anteriormost portion of dentary at the symphyseal joint corresponding to nearly three times the height of the middle length portion of dentary (*vs.* the anteriormost portion of dentary at the symphyseal joint very narrow in lateral view, at least seven times narrower than the height of the middle length portion of dentary); the dentary teeth decreasing in size and tooth cusp number posteriorly, forming an anterior series of large and tricuspidate teeth followed by a second and not aligned series of small conical teeth (*vs.* dentary teeth nearly equal in size, shape and cusp number, forming a continuous series along the dentary); anal fin with 15 or less branched rays (*vs.* anal fin with 19 or more branched rays) diagnoses *Prodontocharax* from *Amblystilbe*.

Prodontocharax aquilaepinnae, new species

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(Figs. 1–3; Tab. 1)

Holotype. MUSM 38647, 1, 49.9 mm SL, male, Peru, Junín, Satipo, Río Tambo, Cubitiali stream, Río Huallaga basin, upper Río Amazonas basin, 11°20'19"S 73°31'25"W, 31 Jan 2010, J. Espino, E. Ríos, F. Cristobal & M. Pishirovanti.

Paratypes. Peru, Cusco: MUSM 69931, 10, 29.1–33.5 mm SL, Megantoni, Lote 58, Río Urubamba basin, Río Pagoreni, 11°44'04"S 73°13'09"W, 22 Sep 2021, F. Cari. **Huánuco:** ANSP 116450, 20 of 50 (2 c&s), 31.3–51.9 mm SL, cueva de Pavos near Puente Perez, about 0.25 mi above Río Huallaga, vicinity Tingo Maria, 09°22'16"S 75°58'32"W, 30 Sep 1955, C. G. Chaplin & M. Hohn. ANSP 166928, 10, 33.0–44.9 mm SL, Tingo Maria, 09°18'04"S 76°00'23"W, 1951, Servicio de Pesqueria. MUSM 14855, 18, 41.6–62.0 mm SL, Tingo Maria, Río Huallaga, Las Pavas stream, 09°22'14"S 75°58'31"W, 12 Jul 1998, F. Chang & M. Velasquez. **Junín:** MUSM 38591, 3, 33.6–51.9 mm SL, Satipo, Río Tambo, Río Mayapo, 11°15'31"S 73°33'46"W, 26 Jan 2010, J. Espino, E. Ríos, F. Cristobal & M. Pishirovanti. **San Martín:** MUSM 32661, 7, 38.3–46.9 mm SL, M. Caceres, Huicungo, Río Abiseo, Pepe stream, 07°24'05"S 76°52'03"W, 21 May 2008, H. Ortega. MUSM 54518, 7, 57.8–60.6 mm SL, Tocache, Uchiza, Huallaga, Río Huaynabez, Chuallaga, 08°19'48"S 76°16'19"W, 23 Nov 2006, F. Cari.

Non-type specimens. Peru, Cusco: MUSM 11979, 77, 32.9–49.1 mm SL, La Convención, Urubamba, Parotori stream, 11°59'48"S 73°07'39"W, 19 May 1997, F. Chang. MUSM 18862, 19, 16.1–40.1 mm SL, La Convención, Echarate, Río Urubamba, 11°53'46"S 72°56'27"W, 2 May 2001, E. Castro. MUSM 23063, 2, 38.5–44.8 mm SL, Quebrada Katchungari, Camana, alto Urubamba, 11°59'01"S 73°08'11"W, 26 Sep 2004, H. Ortega *et al*. MUSM 30708, 11, 35.8–47.9 mm SL, Echarate, La Convención, Bajo Urubamba, Picha, katshigari stream, 11°59'00"S 73°08'13"W, 22 Jun 2004, H. Ortega *et al*. MUSM 31168, 4, 30.5–42.2 mm SL, La Convención, Echarate, Bajo Urubamba, Picha, CN Camaná, Río Paratori, 11°59'16"S 73°08'09"W, 20 Jan 2005, B. Rengijo *et al*. MUSM 31467, 1, 42.8 mm SL, La Convención, Echarate, Bajo Urubamba, Picha, CN Camaná, Katchingari, 11°59'09"S 73°07'53"W, 20 Jan 2005, H. Ortega *et al*. MUSM 31838, 1, 32.4 mm SL, La Convención, Echarate, Bajo Urubamba, Picha, Alto Camisea, 11°49'49"S 72°34'25"W, 9 Oct 2007, H. Ortega *et al*. MUSM 31892, 26, 31.8–33.7 mm SL, La convención, Echerate, Timpia, Río Timpia, 12°04'13"S 72°49'11"W, 15 Jan 2005, H. Ortega. MUSM 34331, 31, 29.3–43.7 mm SL, La Convencion, Echarate, CN Camana, Alto Urubamba, Canchingari stream, 11°59'01"S 73°08'11"W, 29 Sep 2008, I. Corahua *et al*. MUSM 36444, 36, 37.5–54.6 mm SL, La convención, Echarate, RC Matziguenga, 12°08'43"S 73°02'22"W, 12 Dec 2010, J. Arana. MUSM 40092, 4, 36.2–46.9 mm SL, La Convención, Echarate, CN Nuevo Mundo, Bajo Urubamba, Río Huitiricaya, 11°30'07"S 73°15'13"W, 5 Jul 2010, I. Sipión. MUSM 41576, 1, 28.5 mm SL, La Convención, Echerate, Río Camisea, 11°49'19"S 72°47'30"W, 27 Aug 2011, I. Sipión. MUSM 45386, 3, 41.8–45.4 mm SL, La Convención, Megantoni, Porotobango, Kitepampanis, rio Urubamba, Huitiricaya stream, 11°27'38"S 73°18'44"W, 19 Jun 2017, Sipion. MUSM 45409, 2, 44.3–44.5 mm SL, La Convención, Megantoni, Porotobango, Kitepampanis, Río Urubamba, Huitiricaya stream, 11°27'45"S 73°18'25"W, 21 Jun 2017, I. Sipión. MUSM 45440, 16, 38.1–47.2 mm SL, La Convención, Megantoni, Porotobango, Nuevo Mundo, Urubamba, Río Huitiricaya, 11°30'04"S 73°15'15"W, 16 Jun 2017, I. Sipión. MUSM 45567, 29, 31.3–47.6 mm SL, La Convención, Megantoni, Porotobango–Kitepampani, Urubamba, Río Huitiricaya, 11°27'42"S 73°18'51"W, 26 Sep 2017, I. Sipión. MUSM 48043, 1, 55.5 mm SL, La Convención, Echerate, Cashiari, Tornillo stream, Río Urubamba, 11°51'47"S 72°43'27"W, 28 Jun 2013, L. Santamaria. MUSM 48090, 2, 36.8–47.7 mm SL, La Convención, Echerate, Mipaya, Pitonari stream,

rio Urubamba, 11°34'35"S 73°09'52"W, 25 Jun 2013, L. Santamaria. MUSM 48161, 2, 45.5–46.7 mm SL, La Convención, Echerate, Mipaya, Pitonari stream, 11°34'19"S 73°10'10"W, 2 Jun 2013, L. Santamaria. MUSM 49348, 1, 48.3 mm SL, La convención, Echarate, Sagari, Río Urubamba, Huitiricaya stream, 11°25'49"S 73°21'44"W, 9 Mar 2014, V. Meza. MUSM 60459, 17, 27.6–48.7 mm SL, La Conveción, Megantoni, Urubamba, Río Pagoreni, 11°45'42"S 73°18'34"W, 8 Sep 2017, R. Mejia. MUSM 63951, 2, 31.3–41.8 mm SL, La convención, Megantoni, Urubamba, Río Sensa, Porotobango, 11°24'27"S 73°21'42"W, 26 Mar 2018, I. Sipion. MUSM 63997, 4, 32.0–43.8 mm SL, La Convención, Megantoni, Urubamba, 11°27'36"S 73°18'58"W, 22 Mar 2018, I. Sipión. MUSM 69015, 1, 44.2 mm SL, La Convención, Megantoni, Serjali, Río Serjali, unnamed stream, 11°45'19"S 72°29'47"W, 21 Oct 2019, A. Mendoza. MUSM 66332, 2, 41.5–42.4 mm SL, La Convención, Megantoni, Cashiriari, rio Urubamba, 11°52'00"S 72°49'33"W, 21 May 2018, I. Sipión. MUSM 67879, 2, 48.9–49.3 mm SL, La Convención, Megantoni, Río Urubamba, Las Pavas stream, 11°52'53"S 72°52'08"W, 20 May 2019, L. Valenzuela *et al*. MUSM 69825, 11, 29.0–35.6 mm SL, La Convención, Echarate, lote 88, Tsonkiri stream, Camisea, Urubamba, 11°47'42"S 72°50'17"W, 25 Sep 2021, I. Sipion. MUSM 69864, 1, 46.2 mm SL, La convención, Echarate, lote 88, Tsonkiri stream, Camisea, Urubamba, 11°46'47"S 72°42'39"W, 20 Sep 2021, I. Sipión. **Junín:** MUSM 37777, 4, 32.0–49.9 mm SL, Satipo, Río Tambo basin, Mayapo stream, 11°22'27"S 73°29'58"W, 31 Jan 2005, G. Trevejo & P. Zuñiga. MUSM 45728, 4, 45.9–51.5 mm SL, Satipo, Río Tambo, Soroja, Río Mayapo, 11°22'13"S 73°29'58"W, 21 Sep 2017, I. Sipión. MUSM 51100, 6, 32.7–49.6 mm SL, Satipo, Río Tambo, CN Mayapo,

FIGURE 1 | *Prodontocharax aquilaepinnae*, Peru, Junín, Satipo, Tambo River, Huallaga River basin, upper Amazonas River basin; **A.** MUSM 38647, holotype, male, 49.9 mm SL, Cubitiali stream; **B.** MUSM 38591, paratype, female, 51.9 mm SL, Mayapo River. Photos: Dario F. Fuster and Junior Chuctaya.

Ucayali, Mayapo stream, 11°22'27"S 73°29'58"W, 28 Jan 2010, R. Olivera. MUSM 51182, 27, 32.5–52.1 mm SL, Junín, Satipo, Río Tambo, CCNN Mayapo, cuenca Río Ucayali, Mayapo stream, 11°22'10"S 73°30'00"W, 8 Jan 2010, R. Olivera. MUSM 70320, 1, 42.6 mm SL, Satipo, Tambo, Santonano stream, 11°09'09"S 74°01'09"W, 16 Dec 2021, D. Faustino. **Huánuco:** ANSP 168629, 20, 27.8–32.3 mm SL, Peru, Departamento de Huanuco, vicinity of Tingo Maria, back-water near Puerto Nuevo, flowing into Río Tullamayo, *ca*. 09°18'S 75°59'W, 649 m, 27 Sep 1955, Catherwood Foundation Peruvian Amazon Expedition. MHNG 2725.025, 1 of 2, 46.2 mm SL, Cueva de las Pasava, affluent of Río Huallaga, Tingo Maria, Leoncio Prado, 08°17'37"S 76°21'05"W, 14 Sep 2008, S. Fisch-Muller, R. Covain, P. de Rham, V. Mesa Vargas, D. Ordonez & A. Minaya. MUSM 14898, 64, 27.0–40.0 mm SL, Tingo María, Huallaga, 09°18'00"S 76°00'00"W, 11 Jul 1998, F. Chang & M. Velasquez. MUSM 28279, 2, 26.6–28.4 mm SL, Pto Inca, Río Pachitea, Río Sungaruyacu, 09°28'17"S 75°14'41"W, 11 Jul 2005, V. Palacios & M. Rojas. MUSM 39311, 3, 41.7–45.2 mm SL, Leoncio Prado, Tingo Maria, Huallaga, Las pavas stream, 09°21'50"S 75°58'31"W, 19 Sep 2008, H. Ortega *et al*. **Loreto:** MUSM 15886, 3, 41.7–44.9 mm SL, Ucayali, Rashaya, Vibra Caño, 07°58'04"S 75°24'00"W, 17 May 1997, M. Hidalgo. MUSM 15907, 5, 36.5–42.3 mm SL, Río Ucayali, Rashaya, Norte stream, 07°58'04"S 75°24'00"W, 16 May 1997, M. Hidalgo. **San Martín:** MHNG 2725.024, 4 of 9, 50.8–60.6 mm SL, Río Cachiyacu, affluent of Río Huallaga, versant Chapaja, Chapaja, Tocache, 08°17'37"S 76°21'05"W, 14 Nov 2008, S. Fisch-Muller & A. Minaya. MUSM 15642, 3, 46.9–55.4 mm SL, Tarapoto, Morales, San Antonio, Río Cumbaza, 06°32'08"S 76°21'54"W, 18 Sep 1998, Guerra *et al*. MUSM 67361, 10, 27.4–34.7 mm SL, Mariscal Cáceres, Pajarillo, Amazonas, Huallaga, 07°10'55"S 76°41'46"W, 23 Jun 2019, R. Quispe *et al*. **Ucayali:** MUSM 35790, 2, 43.3–46.3 mm SL, Padre Abad, Aguaytia, Ucayali, Río Aguaytia, Río Shambo, Tigre stream, 08°54'49"S 75°38'24"W, 12 Aug 2009, R. Oliveira & G. Quezada. MUSM 47702, 1, 40.9 mm SL, Atalaya, Reymondi, quebrada Coconal, affluent of Río Urubamba, 10°41'02"S 73°07'31"W, 21 Mar 2013, R. Olivera. MUSM 59300, 4, 44.8–49.3 mm SL, Padre Abad, Aguaytia, Ucayali, Río Aguaytia, 09°02'24"S 75°30'10"W, 17 Oct 2016, F. Peñaloza.

Diagnosis. *Prodontocharax aquilaepinnae* is distinguished from *P. melanotus* by the anal fin pigmented along the base to median portion of second to seventh branched rays (*vs.* not pigmented); by the number of olfactory organ lamellae, with 32 in males and 24 in females (*vs*. 40–42 in males and 30–32 in females), and by the number of gill-rakers on upper limb (10–11 *vs*. 13).

Description. Morphometric data summarized in Tab. 1. Largest male 49.9 mm SL, largest female 51.9 mm SL. Body elongated and compressed, with greatest body depth near dorsal-fin origin. Dorsal body profile slightly convex from nostril to dorsal-fin origin, slightly or strongly concave at supraoccipital; posteroventrally slanted at dorsal-fin base; nearly straight from last dorsal-fin ray to caudal peduncle. Ventral head profile nearly straight. Ventral body profile deeply convex from pectoral-fin origin to pelvic-fin origin, and nearly straight to anal-fin origin. Anal-fin base nearly straight. Caudal peduncle very elongate, nearly straight to slightly concave in the dorsal and ventral margins.

Head relatively small. Snout rounded from margin of upper lip to vertical through anterior nostrils. Mouth distinctly inferior, mouth slit at horizontal through inferior border of eye. Maxilla very short. Obliquely positioned maxilla ending at vertical near or at anterior border of eye and at horizontal on inferior eye border. Premaxilla with 5 teeth tricuspid, central cusp longer and broader than lateral cusps; distal margin of teeth arched (n = 2). Maxilla with 4 to 5 teeth tricuspid, rarely conical (n = 2). Dentary with 6 to 8 teeth; anterior 6 teeth large and tricuspid, followed posteriorly by 2 teeth conical and small (n = 2). Anterior 5 to 6 dentary teeth inserted at the anterior and anterolateral border of bone and radially projected to anterior and lateral borders of the mouth; dentary teeth main axis positioned horizontally (n = 2). All cusp tips slightly curved inside the mouth (Fig. 2). Olfactory rosette slightly oval with 24(2) lamellae in females, and 32(2) lamellae in males around of central median raphe (Fig. 3).

Dorsal-fin rays ii,9* (n = 27); first unbranched ray approximately half length of second ray. Dorsal-fin origin slightly behind to vertical line projected through pelvic-fin origin. Adipose-fin located just posterior to vertical through posteriormost anal-fin ray insertion. Anal fin rays ii–iv,12–14 (iv,15*, mean = 13, n = 27). First unbranched ray normally only apparent in c&s specimens. Anal-fin origin posterior to vertical line projected through base of last dorsal-fin rays. Pectoral-fin rays i,10–11* (n = 27). Pectoral fin not reaching pelvic-fin origin in both sexes. Pelvic-fin rays i,6,i* (n = 27). Pelvic-fin origin anterior to a vertical line projected through dorsal-fin origin. Caudal fin forked, with 19* principal rays (n = 27); lobes similar in size. Dorsal procurrent rays 11–12, and ventral procurrent rays 9–11 (n = 2).

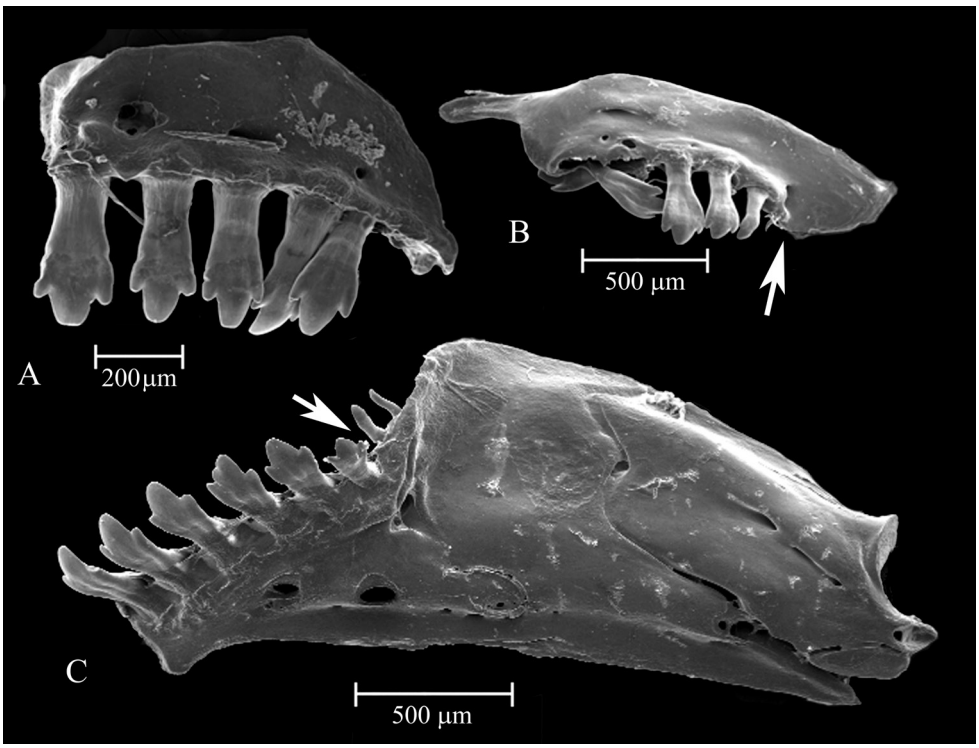

FIGURE 2 | *Prodontocharax aquilaepinnae*, ANSP 116450, 47.6 mm SL, paratype. Scanning electronic microscopy (SEM) image of left side upper and lower jaws teeth. **A.** Premaxilla. **B.** Maxilla; arrow indicates the twisted posterior edentulous portion of the maxilla. **C.** Dentary; arrow indicates the separation of an anterior large tooth series angled and discontinuous with the posterior small tooth series.

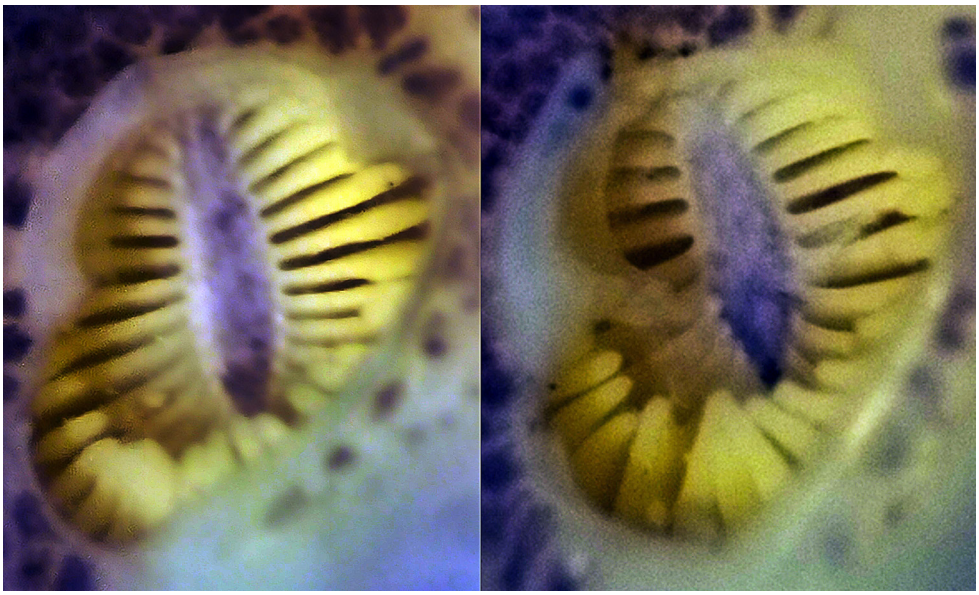

FIGURE 3 | Lamellae of central median raphe of olfactory rosette of *Prodontocharax aquilaepinnae*, MUSM 14855, paratypes, male, 43.8 mm SL (left), female, 52.1 mm SL (right), Peru, Huánuco, Tingo Maria, Huallaga River, Las Pavas stream. Photos: Junior Chuctaya.

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 35–37 (36*, mean = 35.4, n = 18). Scale rows between dorsal-fin origin and lateral line 5–6* (mean = 5.4, n = 20); scale rows between lateral line and pelvic-fin origin 4* (n = 20). Predorsal scales 10–12* arranged in regular series (mean = 11, n = 18). Scales rows around caudal peduncle 14* (n = 20). No modified scales on caudal-fin. Scale sheath along anal-fin base formed of 4–5 scales in single series, extending to base of fourth to fifth branched rays.

Precaudal vertebrae 17; caudal vertebrae 17–18; total vertebrae 34–35. Supraneurals 5 (n = 2). Gill-rakers of first gill arch 10–11 on upper limb and 17 (n = 2) on lower limb.

Coloration in alcohol. General ground body color brownish or yellowish. Scales near dorsal midline clearly delineated with dark chromatophores. Scales on lateral surface of body weakly pigmented, if at all. Dark unpigmented triangular area at pseudotympanum. Narrow midlateral body stripe extending from vertical line through near dorsal-fin origin to caudal-fin base, weakly pigmented at base of median caudal-fin rays, forming small black spot. Dorsal fin with densely pigmented dark spot between median portion of third to seventh branched rays. Anal fin pigmented along base to median portion of second to seventh branched rays. Adipose fin not pigmented (Fig. 1).

Sexual dimorphism. Males of *Prodontocharax aquilaepinnae* are easily recognized by the presence of bony hooks on anal and pelvic-fin rays and by anal-fin profile, nearly straight in males, and smoothly concave in females. Branched anal-fin ray length decreasing gradually from first to last rays in males, and length of branched anal-fin ray decreasing rapidly from first to fourth or fifth rays and gradually decreasing in remaining rays in females. Anal-fin rays of males bearing one pair of retrorse bony

hooks per segment of lepidotrichia along posterolateral border. Hooks usually in last unbranched ray and along anterior nine branched rays, rarely through tenth ray, more numerous along second through fourth rays. Hooks located along posteriormost branch of branched ray, and two thirds to half distal length of ray. Tip of pelvic fin reaching urogenital opening in females, and reaching or close to anal-fin origin in males. Pelvic fin of males bearing usually one, rarely two, retrorse and short bony hooks per segment of lepidotrichia, along posteriormost branch of all branched rays, rarely found in anteriormost branches. Hooks distributed along ventromedial border and usually more than 2/3 of distal length of each ray. Males and females also slightly differ in the relative pelvic-fin length (larger in males than females, Tab. 1). The number of lamellae in olfactory rosette is greater in males than in females (32 and 24–26, respectively). Non-histological examination of the first gill arch of a male (ANSP 116450, 46.7 mm SL) shows the anterior five filaments of the lower branch of the first gill arch apparently fused in a gill organ.

Geographical distribution. *Prodontocharax aquilaepinnae* is known from the Huallaga, Ucayali, and Urubamba river basins, upper Amazonas River basin, Peru (Fig. 4).

TABLE 1 | Morphometric data of *Prodontocharax melanotus*, lectotype (L, CAS 59793), paralectotypes (CAS 117471) from Beni River basin, and non-types (AMNH 39738, ANSP 143527, 143528, 143530, 143531, 143534, 143536, 143537, MZUSP 27807, USNM 303023, 303147, 303149, 325193, 325196, 325221, 326908, 356443) from upper Madeira River basin (Madre de Dios, Beni, and Guaporé rivers), and *P. aquilaepinnae*, holotype, male (H, MUSM 38647), and paratypes (ANSP 116450) from Huallaga River basin.

	P. melanotus							*P. aquilaepinnae*			
	L	Paralectotypes				Non-types		H		Paratypes	
		N	Range	Mean	N	Range	Mean		N	Range	Mean
Standard length (mm)	45.1	5	33.9–44.4	38.8	93	17.0–48.4	29.8	49.9	28	31.3–51.9	41.0
Percents of standard length											
Preanal distance	66.1	5	62.7–67.7	65.4	93	62.7–70.6	66.8	67.6	28	64.3–69.2	66.5
Predorsal distance	48.7	5	48.5–51.9	50.2	92	47.4–55.8	50.4	48.6	28	46.7–51.8	49.6
Prepelvic distance	46.3	5	44.8–47.5	46.6	93	44.6–51.0	47.3	47.8	28	42.4–48.9	46.2
Dorsal-fin base	12.4	5	12.3–13.7	13.0	93	11.9–16.8	13.8	14.3	28	11.7–14.3	13.1
Anal-fin base	17.3	5	15.4–18.8	18.0	93	14.4–20.5	17.7	19.4	28	15.9–19.4	17.6
Caudal peduncle length	19.3	5	17.1–19.2	18.1	93	14.4–22.0	18.2	17.7	28	16.6–21.4	18.7
Caudal peduncle depth	12.9	5	12.1–13.4	12.8	93	10.1–13.8	12.2	12.8	28	11.3–13.4	12.4
Body depth	28.8	5	28.2–33.2	30.5	93	27.1–36.7	30.4	27.9	28	27.4–35.7	32.1
Dorsal-fin length	23.9	5	22.1–27.5	25.5	90	22.1–31.3	26.7	28.3	26	23.7–28.3	25.7
Pelvic-fin length (m)	–	2	17.9–18.3	18.1	15	16.3–22.2	18.1	20.9	12	17.0–23.5	19.2
Pelvic-fin length (f)	15.1	3	15.1–16.4	15.5	77	14.9–20.3	17.0	–	14	16.3–19.3	17.4
Pectoral-fin length (m)	–	2	20.8–21.8	21.3	15	19.4–22.9	21.2	21.7	13	19.4–22.7	20.6
Pectoral-fin length (f)	20.6	3	20.0–21.4	20.6	78	18.8–23.7	20.8	–	13	18.0–21.8	19.5
Head length	22.4	5	20.8–23.8	22.5	93	20.6–28.0	23.3	22.9	27	19.6–22.9	21.4
Percents of head length											
Snout length	25.8	5	25.7–28.7	27.5	92	21.8–29.9	25.9	28.9	27	22.8–28.9	25.7
Upper jaw length	26.9	5	26.9–30.1	28.7	93	25.4–36.1	29.7	26.5	27	26.5–32.0	29.6
Orbital diameter	28.7	5	28.1–31.3	29.1	93	28.1–42.1	35.9	34.4	27	30.0–35.4	32.3
Interorbital width	34.9	5	34.9–39.7	36.7	93	32.8–42.6	37.0	40.7	27	33.7–40.7	36.2

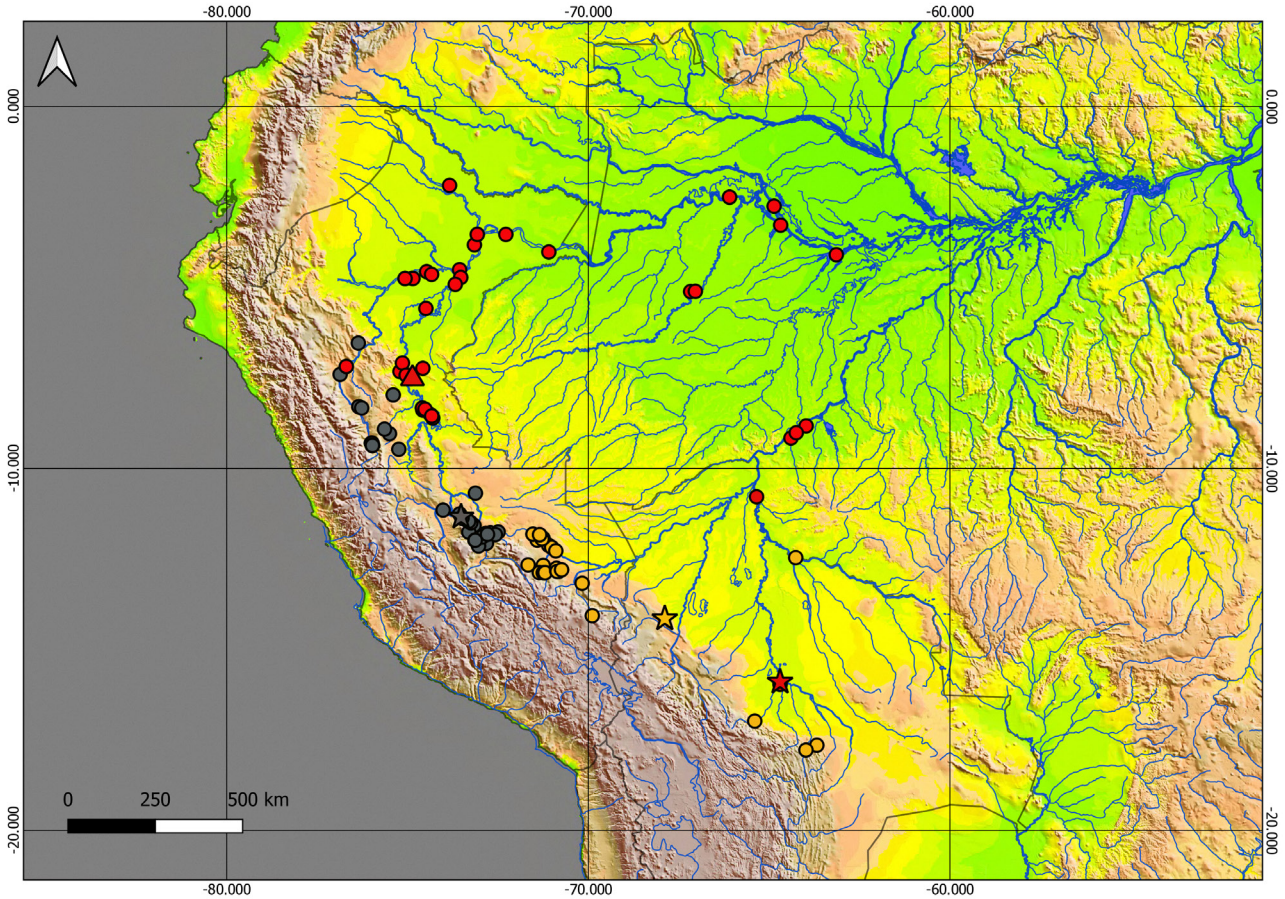

FIGURE 4 | Map of central and northern South America showing the distribution of *Amblystilbe howesi* (red dots), *Prodontocharax melanotus* (yellow dots) and *P. aquilaepinnae* (gray dots). Some symbols represent more than one lot or locality. Stars represent the type localities. Red triangle represents the type-locality of *P. alleni*.

Ecological notes. The holotype of *Prodontocharax aquilaepinnae* was collected in the Cubiriali stream, Tambo River basin. This stream is 6 m wide and 1 m deep. It presents moderate water velocity, clear water with greenish coloration. The bottom substrate characterized by stones and gravel and with the margins covered by vegetation (Fig. 5).

Etymology. The name *aquilaepinnae* is from the Latin, *aquiluus*, blackish or dark-colored, and *pinnae*, fins, referring to the pigmented dorsal and anal fins. A noun in adjective.

Conservation status. No significant threats were identified for the *Prodontocharax aquilaepinnae*, which is suggested to be categorized as Least Concern (LC), according to IUCN criteria (IUCN, 2022).

FIGURE 5 | Type-locality of *Prodontocharax aquilaepinnae*, Cubiriali stream, Tambo River basin, Huallaga River basin, Junín, Peru. Photo: Jessica Espino.

Prodontocharax melanotus Pearson, 1924

(Figs. 6–9; Tab. 1)

Prodontocharax melanotus Pearson, 1924:36, pl. 12, fig. 1 (type-locality: Tumupasa, 30 miles northwest of Rurrenabaque, about 1000 feet, Bolivia). —Böhlke, 1953:660 (lectotype designation). —Mirande, 2010:411, fig. 45 (suspensorium; phylogenetic relationships). —Jerep, Malabarba, 2011:309 (comparison to Cheirodontinae with spots on dorsal fin). —Oliveira *et al*., 2011:15 (phylogenetic relationships). —Oliveira *et al*., 2012:353–56, figs. 2, 4 (description and illustration of the gill organ). —Lima *et al*., 2013:340–41 (photo; short description). —Mariguela *et al*., 2013:26–31 (phylogenetic relationships). —Sarmiento *et al*., 2014:185 (listed to Bolivia). —Netto-Ferreira, Vari, 2017:373, fig. 5 (photo of the holotype). —Meza-Vargas *et al*., 2021:19 (listed to Loreto, Peru).

Prodontocharax sp. —Calcagnotto *et al*., 2005:09 (phylogenetic relationships). —Mariguela *et al*., 2013:26–31 (phylogenetic relationships).

Diagnosis. *Prodontocharax melanotus* is distinguished from *P. aquilaepinnae* by the absence of pigment along the base to middle length of branched rays *vs.* anal-fin pigmented along the base to middle length of second to seventh branched rays; by the number of olfactory organ lamellae, with 40–42 in males and 30–32 in females (*vs.* 30 in males and 24 in females), and by the number of gill-rakers on upper limb (13 *vs.* 10–11).

Description. Morphometric data summarized in Tab. 1. Largest male 48.5 mm SL, largest female 45.8 mm SL. Body elongated and compressed; greatest body depth near at dorsal-fin origin. Dorsal body profile slightly convex from nostril to dorsal-fin origin, slightly concave at supraoccipital; posteroventrally slanted at dorsal-fin base; nearly straight from last dorsal-fin ray to caudal peduncle. Ventral head profile nearly straight. Ventral body profile deeply convex from pectoral-fin origin to pelvic-fin origin, and nearly straight to anal-fin origin. Anal-fin base nearly straight. Caudal peduncle very elongate, nearly straight to slightly concave in the dorsal and ventral margins.

Head relatively small. Snout rounded from margin of upper lip to vertical through anterior nostrils. Mouth distinctly inferior, mouth slit at horizontal through inferior border of eye. Maxilla very short. Obliquely positioned maxilla ending at vertical near or at anterior border of eye and at horizontal on inferior eye border. Premaxillary teeth 4 to 5 (6 teeth only on lectotype) tricuspid; central cusp longer and broader than lateral cusps (n = 5). Maxilla with 5 to 7 teeth tricuspid, posterior teeth conical or asymmetric (n = 5). Dentary with 8 to 11 teeth; anterior 7 to 9 teeth large and tricuspid, followed by 2 small teeth conical or with 2 to 3 asymmetric cuspids (n = 5). Anterior 8 to 9 dentary

FIGURE 6 | *Prodontocharax melanotus*. **A.** CAS 59793, Lectotype (Copyright The California Academy of Sciences, Ichthyology Section). **B.** CAS 117471, Paralectotype, 47.5 mm SL, Tumupasa, 30 mi NW of Rurrenabaque, La Paz, Bolivia. **C.** ANSP 143528, 36.5 mm SL, Shintuya, Alto Madre de Dios, Peru. Photos **B** and **C** by Luiz R. Malabarba.

FIGURE 7 | *Prodontocharax melanotus*. Live not preserved specimens. **A.** Colorado River, Rerserva Comunal Amarakaeri, Peru. **B.** Estación Biológica Villa Carmen, Piñi Piñi River, Peru. Photos: Julio Araujo.

teeth inserted at the anterior and anterolateral border of bone and radially projected to anterior and lateral borders of the mouth; dentary teeth main axis positioned horizontally (n = 5). All cusps tips slightly curved inside the mouth (Fig. 8). Olfactory rosette slightly oval with 30(1) and 32(1) lamellae in females, and 40(1) and 42(1) lamellae in males around the central median raphe (Fig. 9).

Dorsal-fin rays ii,9* (n = 71; one with ii,8 and ii,10); first unbranched ray approximately half length of second ray. Dorsal-fin origin slightly behind to vertical line projected through pelvic-fin origin. Adipose fin located just posterior to vertical through posteriormost anal-fin ray insertion. Anal-fin rays ii–iv,11–15 (ii,13*, mean =13.1, n = 99). First unbranched ray normally only apparent in c&s specimens. Longest branched rays reaching origin of last anal-fin ray when fin depressed. Anal-fin origin posterior to vertical line projected through base of last dorsal-fin rays. Pectoral-fin rays i,9–12, (i,10*, mean = 10.6, n = 71). Pelvic-fin rays i,6,i* (n = 71). Pelvic-fin origin anterior to vertical line projected through dorsal-fin origin. Caudal fin forked, with 19* principal rays (n = 70); lobes similar in size. Dorsal procurrent rays 10–11, and ventral procurrent rays 8–10 (n = 5).

Scales cycloid, moderately large. Lateral line complete; 34–37 perforated scales (36*, mean = 35.6, n = 70). Scale rows between dorsal-fin origin and lateral line 5–6* (mean = 5.8, n = 89); scale rows between lateral line and pelvic-fin origin 4*–5 (mean = 4.5, n = 89). Predorsal scales 9–12* arranged in regular series (mean = 11.2, n = 69). Scales rows

around caudal peduncle 14* (n = 67). No modified scales on caudal-fin. Scale sheath along anal-fin base with 3–5 scales in single series, extending to base of fourth or fifth branched rays.

Precaudal vertebrae 17; caudal vertebrae 17–18; total vertebrae 34–36 (n = 6). Supraneurals 4–6 (n = 5). Gill-rakers of first gill arch 13 on upper limb and 17–18 (n = 4) on lower limb.

Coloration in alcohol. General ground body color brownish or yellowish. Scales near dorsal midline clearly delineated with dark chromatophores. Scales on lateral and ventral surfaces of body weakly pigmented, if at all. Dark unpigmented triangular area at pseudotympanum. Narrow midlateral body stripe extending from vertical line through near dorsal-fin origin to caudal-fin base, weakly pigmented at base of median caudal-fin rays, forming small and sparse spot. Dorsal fin with densely pigmented black

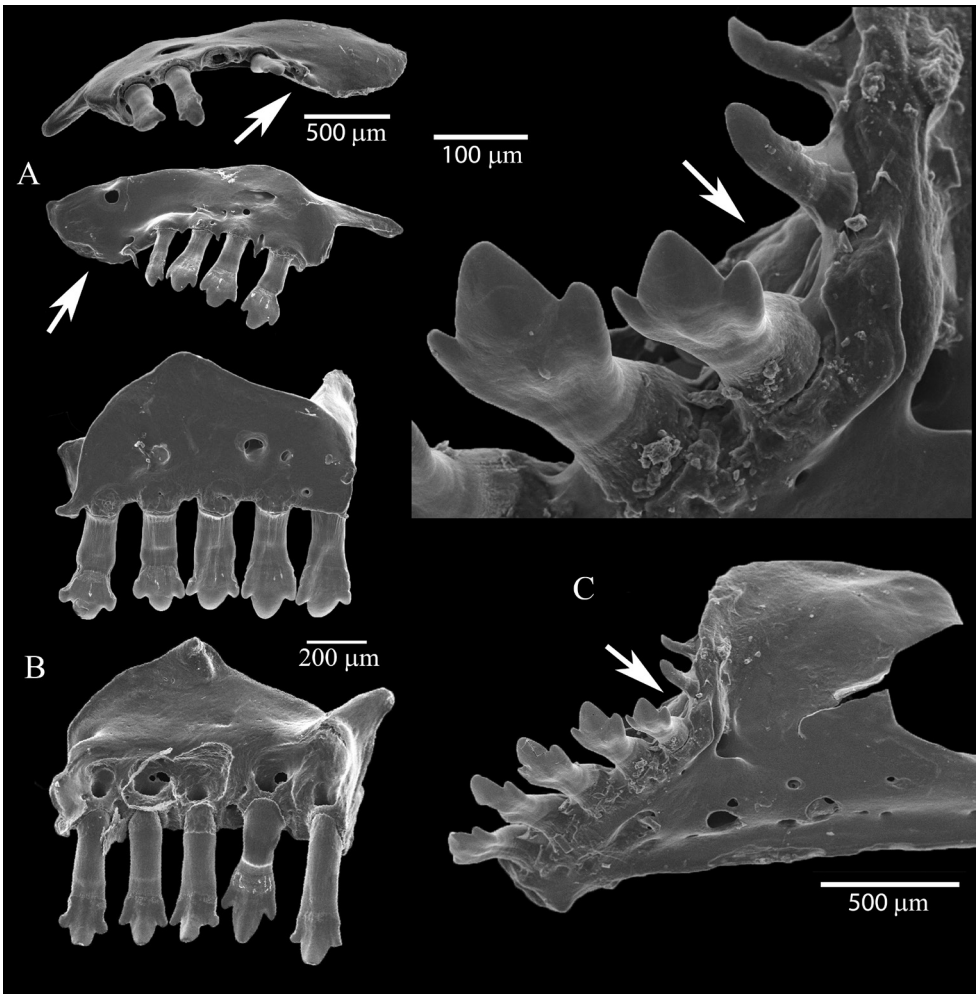

FIGURE 8 | *Prodontocharax melanotus*, ANSP 143528, 35.5 mm SL. Scanning electronic microscopy (SEM) image of left side upper and lower jaws teeth. **A.** Maxilla left above and right below; arrow indicates the twisted posterior edentulous portion of the maxilla. **B.** Premaxilla in frontal (top) and medial (bottom) views. **C.** Dentary; arrow indicates the separation of an anterior large tooth series angled and discontinuous with the posterior small tooth series (at the top in detail).

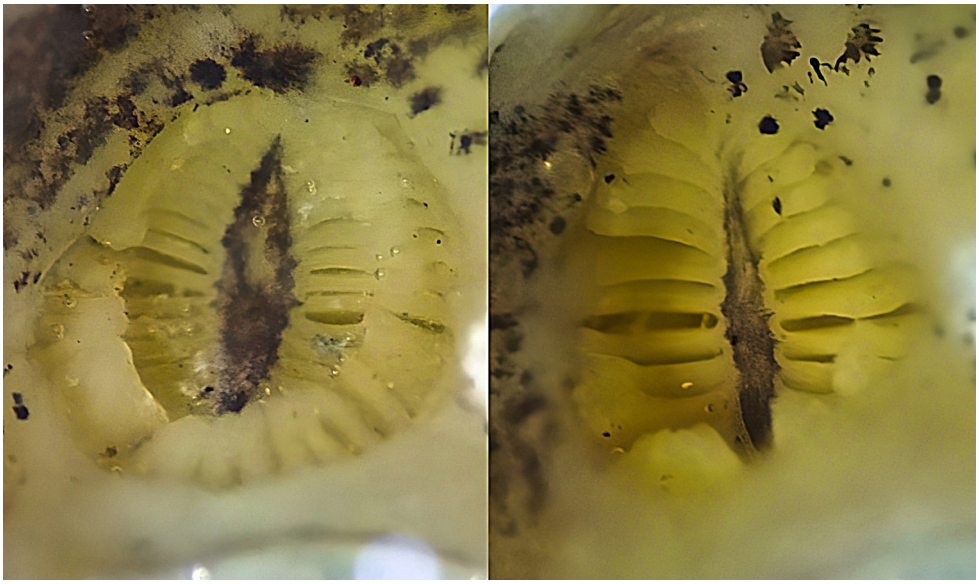

FIGURE 9 | Lamellae of central median raphe of olfactory rosette of *Prodontocharax melanotus*, MUSM 53623, male, 44.4 mm SL (left), female, 49.9 mm SL (right), Colorado River, Madre de Dios, Peru. Photos: Junior Chuctaya.

spot between median portions of first to sixth branched rays. Anal fin lightly pigmented along base of second to sixth branched rays or without pigments. Adipose fin not pigmented (Fig. 6).

Coloration in life. Overall body and head color pattern yellowish and silver. Upper portion of the eye and upper middle portion of the dorsal fin are reddish. Caudal-fin base pigmented at base of median caudal-fin rays. Other fins are slightly yellowish (Fig. 7).

Sexual dimorphism. Males of *Prodontocharax melanotus* are easily recognized by the presence of bony hooks on anal and pelvic-fin rays and by anal-fin profile, nearly straight in males and concave in females. Branched anal-fin rays length decreasing gradually from first to last rays in males, and length of branched anal-fin rays decreasing rapidly from first to fourth or fifth rays and gradually decreasing in remaining rays in females. Anal-fin rays of males bearing one pair of retrorse bony hooks per segment of lepidotrichia along their posterolateral borders. Hooks usually in last unbranched ray and along anterior 10 branched rays, rarely through eleventh ray and more numerous along third through fourth rays. Hooks located along posteriormost branch of each branched ray, and two thirds to half distal length of each ray. Hooks of posterior branched rays straight, nearly the size of the segment of lepidotrichia, and longer than those of unbranched ray and anterior branched rays. Pectoral fin almost reaching pelvic-fin origin in males and not reaching pelvic-fin origin in females. Pectoral fin almost reaching pelvic-fin origin in males and not reaching pelvic-fin origin in females. Tip of pelvic fin reaching urogenital opening in females, and reaching or close to anal-fin origin in males. Pelvic fin of males bearing usually one, rarely two, retrorse and elongate bony hooks per segment of lepidotrichia, along posteriormost branch of all branched

rays, rarely found in anteriormost branches. Hooks distributed along ventromedial border and usually more than 2/3 of distal length of each ray. Males and females also slightly differ in the relative pelvic-fin length (Tab. 1). The number of lamellae in olfactory rosette is greater in males than in females (40–42 and 28–32, respectively). Gill organs are present in males formed by the anterior four filaments of the lower branch of the first gill arch (Oliveira *et al*., 2012: figs. 2, 4).

Geographical distribution. *Prodontocharax melanotus* is known from Beni River, Bolivia, Itenez River, Bolivia/Brazil, and upper Madre de Dios River basin, upper Madeira River basin, Peru (Fig. 4).

Ecological notes. Based on field information from material cataloged in the fish collections of the MUSM, most specimens of *Prodontocharax melanotus* were collected in rivers and shallow streams, with a rocky bottom substrate, white water, and with the presence of moderate riparian vegetation (Fig. 10).

Conservation status. No significant threats were identified for the *Prodontocharax melanotus*, which is suggested to be categorized as Least Concern (LC), according to IUCN criteria (IUCN, 2022).

FIGURE 10 | Collection locality of *Prodontocharax melanotus*, near confluence between the Manu and Madre de Dios rivers, Alto Madre de Dios, Peru.

Material examined. Bolivia, La Paz. CAS 59793, 45.1 mm SL, female, lectotype of *Prodontocharax melanotus*, Tumupasa, 30 mi NW of Rurrenabaque, Dec 1921, 14°08'59"S 67°53'18"W, N. E. Pearson. CAS 117471, 6 (1 c&s), 33.9–44.4 mm SL, paralectotypes of *Prodontocharax melanotus*, collected with the lectotype. **Bolivia.** AMNH 39738, 1, 35.4 mm SL, Río Itenez 2 km SW of Costa Marques (Brazil), Beni, *ca*. 12°28'S 64°16'W, 2 Sep 1964, R. M. Bailey & R. Ramos. AMNH 233236, 1, 34.7 mm SL, Amboró National Park, aguas blancas river, la chonta camp, Ichilo, Santa Cruz, 17°39'02"S 63°40'55"W, 24 Oct 2001, D. Calcagnoto *et al*. AMNH 233260, 1, 44.6 mm SL, AMNH 233261, 45.8 mm SL, Amboró National Park, la Chonta river, la chonta camp, Ichilo, Santa Cruz, *ca*. 11°47'S 63°59'W, 24 Oct 2001, D. Calcagnotto *et al*. MZUSP 27807, 1, 44.9 mm SL, Río Chapare, Villa Tunari, *ca*. 16°59'S 65°24'W, 22 Jun 1983, Conv. Piscic. ORSTOM-UTB. **Peru, Madre de Dios.** ANSP 143527, 3, 17.0–18.7 mm SL, tributary on NE bank of Río Manu, bellow Boca Saurez, 12°07'37"S 71°05'56"W, 10 Aug 1977, R. Horwitz. ANSP 143528, 20 of 78 (2 c&s), 28.7–37.5 mm SL, at Shintuya, Alto Madre de Dios, 12°40'53"S 71°15'02"W, 1 Aug 1977, R. Horwitz. ANSP 143530, 12, 25.2–30.9 mm SL, 15 km upstream from Boca Manu, Alto Madre de Dios, *ca*. 12°40'S 71°04'W, 3 Aug 1977, R. Horwitz. ANSP 143531, 5, 21.2–26.7 mm SL, near Pakitsa, tributary entering SW bank of Río Manu at Cosha Sandoval, 11°59'S 71°25'W, 9 Aug 1977, R. Horwitz. ANSP 143534, 12 (2 c&s), 40.0–48.5 mm SL, mouth of Río Carbon, below Atalaya on N/S road, above and below ford, 12°52'51"S 71°21'30"W, 18 Jul 1977, R. Horwitz. ANSP 143536, 10, 23.7–30.4 mm SL, ANSP 143537, 7, 20.1–25.5 mm SL, Río Manu, beach bellow Boca Pinquen, 12°52'51"S 71°21'30"W, 10 Aug 1977, R. Horwitz. USNM 303022, 1, 27.8 mm SL, cocha off Río Alto Madre de Dios, 2 km below Erika, Manu, *ca*. 12°53'S 71°12'W, 5 Sep 1988, H. Ortega *et al*. USNM 303023, 3, 23.8–24.0 mm SL, USNM 325196, 2, 24.1–24.6 mm SL, Río Manu at Pakitza, Manu, *ca*. 12°55'S 71°15'W, 10 Sep 1988, H. Ortega *et al.* USNM 303142, 3, 27.7–30.4 mm SL, side stream to Río Alto Madre de Dios, about 1.5 km upstream from Erika, between Salvacion and Atalaya, Manu, *ca*. 12°53'S 71°12'W, 6 Sep 1988, H. Ortega *et al*. USNM 303147, 2, 22.1–24.8 mm SL, Río Manu, beach seining at Cocha Salvador, Manu, *ca*. 11°49'S 71°32'W, 14 Sep 1988, H. Ortega *et al.* USNM 303149, 3, 19.3–23.1 mm SL, Río Manu, quebrada Fortaleza, Manu, *ca*. 11°49'S 71°32'W, 19 Sep 1988, H. Ortega *et al.* USNM 303157, 21, 21.7–26.5 mm SL, quebrada Pachija, Río Manu basin, and above mouth, Manu, 11°55'48"S 71°15'18"W, 12 Sep 1988, H. Ortega *et al*. USNM 324117, 15, 20.9–25.3 mm SL, boca Panahua, where quebrada Panahua joins rio Manu, Manu, 12°16'46"S 70°54'08"W, 11 Sep 1988, H. Ortega *et al*. USNM 325193, 8, 20.9–26.2 mm SL, Río Manu at above mouth, Quebrada Pachija, Manu, *ca*. 11°57'S 71°17'W, 12 Sep 1988, H. Ortega *et al.* USNM 325221, 1, 23.8 mm SL, rio Manu, about 3 hours upriver from Romero, Manu, *ca*. 11°49'S 71°32'W, 8 Sep 1988, H. Ortega *et al.* USNM 326908, 1, 35.6 mm SL, quebrada Picaflor, Paktiza, Manu National Park, Manu, *ca*. 11°50'S 71°21'W, 29 Sep 1991, H. Ortega & F. Zambrano. USNM 326941, 1, 37.6 mm SL, Paktiza radial 3 trail, estaca 22, quebrada Picaflor, Manu National Park, Manu, *ca*. 11°50'S 71°21'W, 24 Feb 1992, H. Ortega & M. Guevara. USNM 356443, 1, 37.6 mm SL, quebrada Picaflor, Paktiza, Manu National Park, Manu, *ca*. 11°50'S 71°21'W, 24 Feb 1992, H. Ortega & M. E. Guevara. MUSM 54240, 8, 33.6–41.2 mm SL, Manu, MDD, Río Colorado, Pinkiri, 12°50'23"S 70°48'56"W, 15 Jun 2014, J. Espino. MUSM 53415, 9, 33.2–43.6 mm SL, Manu, Río Colorado, Río Silaba, 12°50'14"S 70°52'37"W,

13 Aug 2015, J. Espino. MUSM 59262, 5, 33.9–46.2 mm SL, Huepetue, Río Pinkiri, 12°50'21"S 70°51'54"W, 23 Apr 2014, J. Espino. MUSM 53693, 3, 36.0–48.6 mm SL, Madre de Dios, Río Colorado, Río Silaba, 12°50'23"S 70°48'56"W, 14 May 2015, J. Espino. MUSM 53351, 3, 31.7–35.6 mm SL, Manu, Río Colorado, Río Silaba, 12°50'23"S 70°48'56"W, 11 Dec 2014, J. Espino. MUSM 54216, 4, 28.2–37.8 mm SL, Manu, Río Colorado, Río Mabues, 12°45'33"S 70°52'57"W, 27 Sep 2014, J. Espino. MUSM 54391, 3, 38.9–39.1 mm SL, Manu, Río Colorado, Río Silaba, 12°50'49"S 70°51'56"W, 4 Dec 2014, J. Espino. MUSM 53882, 7, 28.4–46.3 mm SL, Manu, Río Colorado, Río Silaba, 12°48'06"S 70°44'35"W, 12 Aug 2015, J. Espino. MUSM 36923, 18, 17.9–20.8 mm SL, Tambopata, Las Piedras, Cachuela, 14°04'10"S 69°53'37"W, 2 Jun 2011, Albert *et al*. MUSM 53623, 54, 38.8–48.4 mm SL, Río Colorado, Río Silaba, 12°48'06"S 70°44'35"W, 20 Jul 2015, J. Espino. **Puno.** MUSM 11445, 7, 43.6–49.6 mm SL, Carabaya, Río Inambari, Cuesta Blanca, 13°10'31"S 70°10'24"W, 18 Apr 1997, F. Chang & W. Umpire.

Amblystilbe Fowler, 1940

Amblystilbe Fowler, 1940:85 (type-species: *Amblystilbe howesi* Fowler, 1940 by original designation; gender feminine). —Géry, 1977:590 (synonym of *Prodontocharax* Eigenmann & Pearson, 1924). —Böhlke, 1984:48 (synonym of *Prodontocharax* Eigenmann & Pearson, 1924). —Malabarba, 2003:218 (synonym of *Prodontocharax* Eigenmann & Pearson, 1924).

Diagnosis. The inferior mouth, with mouth slit located at horizontal through inferior margin of eye, diagnoses *Amblystilbe* from other cheirodontine genera (except *Prodontocharax*). The premaxilla with 8 to 10 teeth (*vs.* 4 to 6); the central cusp is larger than lateral ones *vs*. similarly sized cusp on all teeth; the posterior edentulous lamina of the maxilla flat and plane (*vs.* posterior edentulous lamina of the maxilla medially curved in relation to the anterior toothed portion); the anteriormost portion of dentary at the symphyseal joint very narrow in lateral view, at least seven times narrower than the height of the middle length portion of dentary (*vs.* the anteriormost portion of dentary at the symphyseal joint corresponding to nearly three times the height of the middle length portion of dentary); the dentary teeth nearly equal in size, shape and cusp number, forming a continuous series along the dentary (*vs.* dentary teeth decreasing in size and tooth cusp number posteriorly, forming an anterior series of large and tricuspidate teeth followed by a second and not aligned series of small conical teeth); the longer anal fin with 19 to 25 branched rays (*vs.* short anal fin with 11 to 15 branched rays) diagnoses *Amblystilbe* from *Prodontocharax*.

Amblystilbe howesi, Fowler, 1940

(Figs. 11–13; Tab. 2)

Amblystilbe howesi Fowler, 1940:85, fig. 47 (type-locality: Boca Chapare, Río Chimore, Cochabamba, Amazon system, Bolivia).

Prodontocharax alleni Böhlke, 1953:661 (type-locality: Cashiboya, Peru, Río Ucayali). —Ortega, Vari, 1986:09 (catalog). —Vari, Howe, 1991:35 (catalog). —Malabarba, 2003:218 (listed). —Barriga Salazar, 2014:109 (listed to Ecuador). —Sarmiento *et al*., 2014:185 (listed to Bolivia). —Meza-Vargas *et al*., 2021:19 (listed to Loreto, Peru). —Chuctaya *et al*., 2022:24 (listed to Ucayali basin, Peru).

Prodontocharax howesi. —Malabarba, 2003:218 (valid species). —Sarmiento *et al*., 2014:185 (listed to Bolivia).

Diagnosis. The same for the genus.

Description. Morphometric data summarized in Tab. 2. Largest specimen 44.4 mm SL. Body elongate and compressed, with greatest body depth at or slightly anterior to dorsal-fin origin. Dorsal body profile convex from nostril to dorsal-fin origin, slightly convex at supraoccipital; nearly straight or slightly concave from first dorsal-fin ray to caudal peduncle. Ventral head profile nearly straight. Ventral body profile convex from pectoral-fin origin to pelvic-fin origin, and straight to anal-fin origin. Anal-fin base straight. Caudal peduncle elongate, slightly concave in the dorsal and ventral margins.

Head relatively small. Snout pronounced, nearly pointed anteriorly. Mouth distinctly ventral, mouth slit at horizontal through inferior border of eye. Maxilla very short. Obliquely positioned maxilla ending at vertical near or at anterior border of eye and at horizontal on inferior eye border. Premaxilla with 8 or 10 tricuspid teeth, central cusp slightly longer and broader than lateral cusps; distal margin of teeth arched (n = 28). Maxilla with 4 to 5 tricuspid teeth, rarely conical (n = 28). Dentary with 11 to 13 teeth; anterior 10 large teeth, tricuspid, followed posteriorly by 1 to 3 small, conical teeth (n = 28). Anterior 7 to 8 dentary teeth inserted at anterior border of bone and anteriorly projected (n = 28); dentary teeth main axis positioned horizontally. All cusps tips slightly curved inside the mouth (Fig. 12).

FIGURE 11 | *Amblystilbe howesi*. **A.** Holotype, ANSP 69070, 41.8 mm SL, Boca Chapare, Chimore River, Cochabamba, Bolivia. **B.** MCP 39868, 41.1 mm SL, Mamoré River at Cristo Rei district, Madeira River basin, Guajará-Mirim, Rondônia, Brazil. Photos: Luiz R. Malabarba.

TABLE 2 | Morphometric data of *Amblystilbe howesi*, holotype (H, ANSP 69070), paratypes (ANSP 69071, n = 10) from Boca Chapare, Chimore River basin, and non-types from the Amazonas River basin (ANSP 149926, MCP 39868, MZUSP 12405, 12406, 12407, 25943, USNM 356381, 280541, n = 99), and *Prodontocharax alleni*, holotype (H, CAS 117472) and paratypes (CAS 117473, 119050, USNM 157366, n = 20), from the Ucayali River basin.

	A. howesi					*P. alleni*		
		Paratypes		Non-types			Paratypes	
	H	Range	Mean	Range	Mean	H	Range	Mean
Standard length (mm)	41.8	38.5–41.7	40.3	24.7–44.4	37.4	33.6	24.7–37.1	32.3
Percents of standard length								
Preanal distance	68.7	64.9–69.5	67.3	63.3–71.6	65.7	65.8	65.0–69.4	67.1
Predorsal distance	48.9	49.0–52.5	50.6	45.4–52.0	48.4	46.8	47.0–51.3	49.0
Prepelvic distance	46.2	45.2–48.8	46.8	42.5–49.5	45.2	–	43.9–48.1	46.3
Dorsal-fin base	13.4	11.8–13.3	12.8	10.4–14.6	13.3	13.4	11.6–14.6	13.2
Anal-fin base	29.4	27.4–31.4	28.7	22.2–29.4	26.9	21.4	22.2–29.7	24.8
Caudal peduncle length	8.0	7.7–10.8	9.5	8.0–13.3	11.8	10.7	9.2–13.3	11.1
Caudal peduncle depth	11.3	10.8–12.1	11.3	9.7–12.2	11.1	10.4	9.7–11.6	10.8
Body depth	31.2	30.6–33.3	31.9	25.7–31.8	28.5	27.7	26.1–30.0	28.1
Dorsal-fin length	28.8	26.4–30.6	28.9	24.0–29.9	27.6	–	24.6–28.2	26.9
Pelvic-fin length	15.9	15.8–17.7	16.5	14.7–18.3	16.1	14.0	15.2–17.2	16.3
Pectoral-fin length	18.6	18.7–20.2	19.4	18.0–18.8	18.5	16.7	18.0–21.3	19.3
Head length	22.8	22.5–23.6	23.0	20.9–25.4	22.0	23.8	22.2–25.4	23.9
Percents of head length								
Snout length	23.9	22.8–25.8	23.9	21.0–29.5	25.4	25.0	21.0–25.3	23.7
Upper jaw length	26.3	24.0–27.2	25.7	24.0–33.6	28.9	32.5	25.4–33.0	30.4
Orbital diameter	30.8	31.0–34.2	31.9	28.9–40.2	31.7	31.2	30.9–37.9	33.7
Interorbital width	34.1	33.7–36.3	34.4	30.7–40.6	33.7	33.7	32.4–36.9	34.6

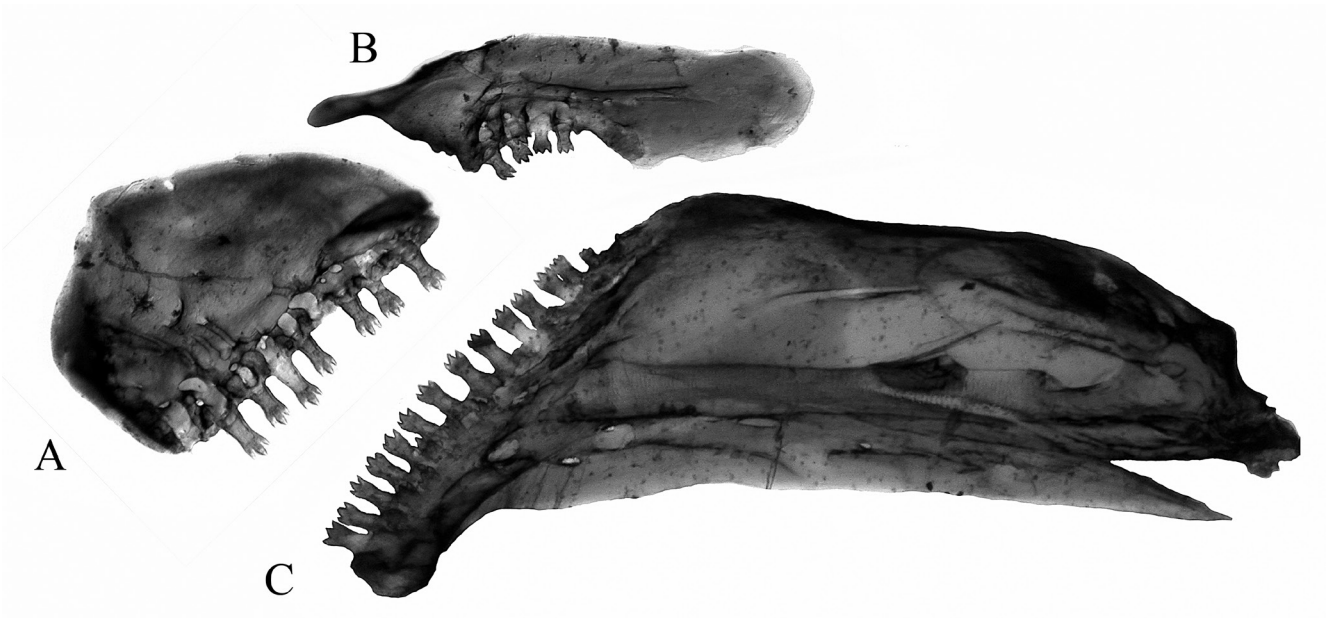

FIGURE 12 | *Amblystilbe howesi*, MCP 39868, 38.7 mm SL. SEM image of left side upper and lower jaws teeth. **A.** Premaxilla (with at least two missing teeth). **B.** Maxilla. **C.** Dentary.

Dorsal-fin rays ii,9* (n = 114); first unbranched ray approximately half length of second ray. Dorsal-fin origin slightly behind to vertical line projected through pelvic-fin origin. Adipose fin located approximately in vertical through fourth and fifth last anal-fin rays insertion, counted from posteriormost branched ray. Anal-fin rays ii–iv,19–25 (iii,24*, mean = 22.4, n = 134). First unbranched ray normally only apparent in cleared and stained specimens. Anal-fin profile smoothly concave. Branched anal-fin ray decreasing rapidly from first to fifth or sixth rays and gradually decreasing in remaining rays. Anal-fin origin posteriormost to vertical line projected through base of last dorsal-fin rays. Pectoral-fin rays i,11–13 (i,12*, mean = 11.7, n = 113). Pectoral fin not reaching pelvic-fin origin in both sexes. Pelvic-fin rays i,7* (rarely i,8; n = 115). Pelvic-fin origin anterior to a vertical line projected through dorsal-fin origin. Caudal fin forked, with 19* principal rays (n = 112); lobes similar in size. Dorsal procurrent rays 9–12, and ventral procurrent rays 9 (n = 6).

Scales cycloid, moderately large. Lateral line complete. Scales in longitudinal series 35–39 (37*, mean = 36.3, n = 101). Scale rows between dorsal-fin origin and lateral line 6*–7 (mean = 6.0, n = 109); scale rows between lateral line and pelvic-fin origin 4*–5 (mean = 4, n = 109). Predorsal scales 9–13 arranged in regular series (10*, mean = 10.5, n = 88). Scales rows around caudal peduncle 14* (n = 111). No modified scales on caudal-fin. Scale sheath along anal-fin base formed of 4–11 scales in single series, extending to base of fifth to tenth branched rays.

Precaudal vertebrae 17–18; caudal vertebrae 18–20; total vertebrae 35–37. Supraneurals 4–5 (n = 11). Gill-rakers of first gill arch 11–14 on upper limb and 19–20 (n = 6) on lower limb.

Coloration in alcohol. General ground body color brownish or pale yellow. Dark dorsum pigmentation from head to caudal peduncle. Dark unpigmented triangular area at pseudotympanum. Scales of body without dark chromatophores. Broad and conspicuous silvery midlateral body stripe extending from head to caudal peduncle. All fins without pigments. Some specimens that have lost some guanine pigments appear to have midlateral dark stripe (Fig. 11).

Coloration in life. Overall body and head color pattern yellowish and silver. Upper portion of the eye is slightly yellowish. Dorsal, pelvic and anal fins yellowish, caudal fin reddish and pectoral fin hyaline (Figs. 13A, B). A specimen photographed in life, and/or recently fixed, presents the dorsal, pectoral, pelvic, and anal fins yellowish and the caudal fin reddish (Lima *et al*., 2013:340).

Sexual dimorphism. In mature specimens, males differ from females by the presence of bony hooks on the anal and pelvic-fin rays. The anal-fin hooks are located along the posterior margin of the last unbranched ray, and the first to seventh branched ray (MUSM 259, 2294, and 40534). Little knobs were found on the first unbranched ray of the anal fin resembling initial stages of development of bony hook in a single male specimen (MZUSP 12406). The pelvic-fin hooks are located along the posterior margin of the first and seventh branched ray. Additionally, sexual dimorphism is observed in relation to the number of lamellae in the olfactory lobe (MUSM 40534), with 44 lamellae in total in males and 30 lamellae in total in females.

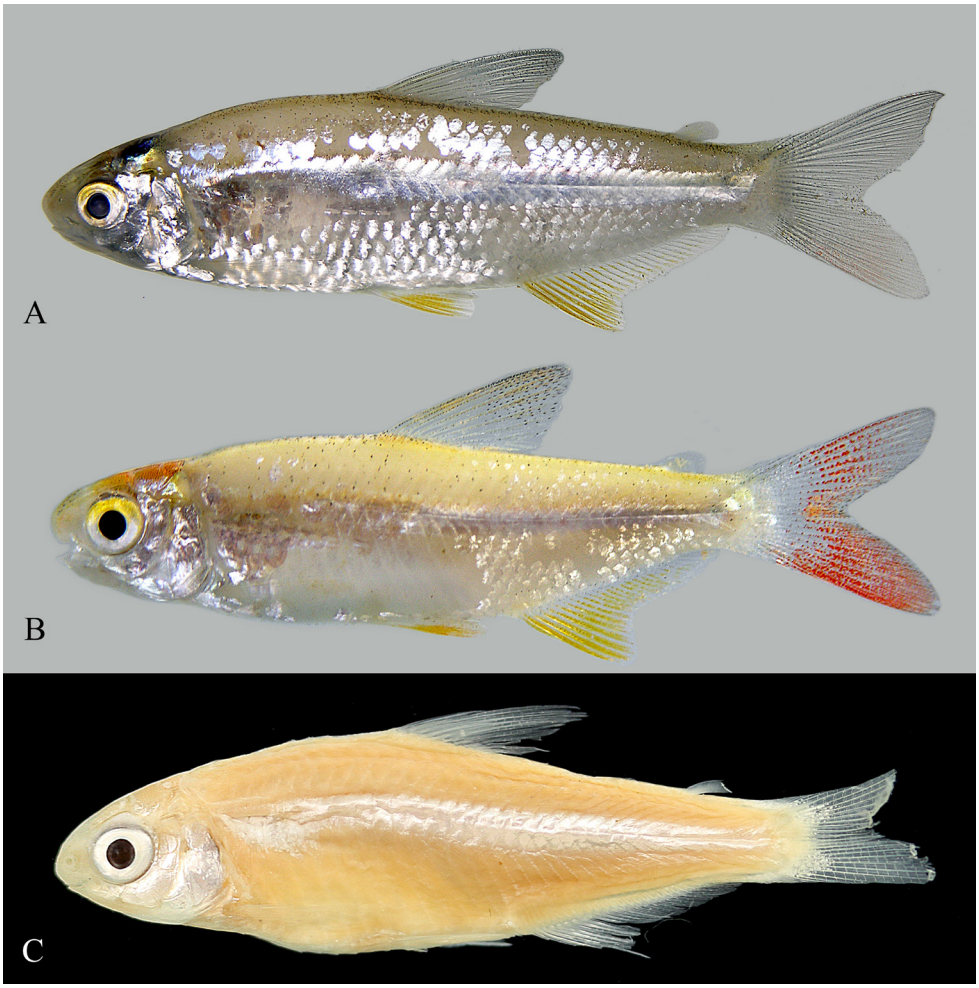

FIGURE 13 | *Amblystilbe howesi*. **A.** UFRGS 21765, 40.0 mm SL, **B.** UFRGS 21754, 33.0 mm SL, Juruá River, 2 km above mouth of Juburi, Carauari, Amazonas, Brazil. **C.** CAS 119050, paratype of *Prodontocharax alleni*, 28.1 mm SL, Ucayali River, Cashiboya, Ucayali, Peru. Photos: Luiz R. Malabarba.

Geographical distribution. *Amblystilbe howesi* is known from Amazonas River basin, Bolivia, Brazil and Peru (Fig. 4).

Ecological notes. Based on field information from material cataloged in the fish collections of the MCP, MUSM, and UFRGS. All specimens of *A. howesi* were collected on shallow beaches near the riverbanks (up to 1.5 m deep), in dark and moderately flowing water, sandy bottom and a small amount of aquatic and riparian vegetation (Fig. 14). Some specimens (MCP 39868) also were captured in a nocturnal collection using a beach seine net in the rio Mamoré.

Conservation status. No significant threats were identified for the *Amblystilbe howesi*, which is suggested to be categorized as Least Concern (LC), according to IUCN criteria (IUCN, 2022).

FIGURE 14 | Collection locality of *Amblystilbe howesi*, near Contamana, Ucayali River basin, Ucayali, Peru.

Material examined. *Amblystilbe howesi*: **Bolivia, Cochabamba.** ANSP 69070, 41.8 mm SL, holotype of *Amblystilbe howesi*, Boca Chapare, Río Chimore, 28 Aug 1937, M. A. Carriker & G. Howes. ANSP 69071, 10 of 20, 38.5–41.7 mm SL, paratypes of *Amblystilbe howesi*, collected with the holotype. *Prodontocharax alleni*: **Peru, Ucayali.** CAS 117472, 33.6 mm SL, holotype of *Prodontocharax alleni* lake of Río Ucayali, Cashiboya, *ca*. 07°31'S 74°55'W, 3–4 Aug 1920, W. R. Allen. CAS 117473, 16 (1 c&s), 28.3–37.1 mm SL, CAS 119050, 8, 24.7–31.0 mm SL, USNM 157366, 1, 35.6 mm SL, paratypes of *Prodontocharax alleni*, collected with the holotype. **Bolivia, Santa Cruz.** AMNH 77544, 1, 39.2 mm SL, rio Mamoré, about 2 km N of mouth of Río Chapare, 31 Jul 1965, M. P. Maclean. **Brazil, Amazonas.** MCP 14928, 15 (3 c&s), 26.7–43.5 mm SL, rio Solimões, across Jacaré, near Fonte Boa, 7 Oct 1968, EPA (Expedição Permanente da Amazônia). MCP 17088, 2 c&s, 40.0–41.6 mm SL, rio Solimões, Fonte Boa, 6 Oct 1968, EPA. MCP 31917, 1, 44.2 mm SL, rio Solimões, ilha do Içé, Alvarães, 03°16'36"S 64°41'01"W, 1 Jan 2001, W. Crampton. MZUSP 12405, 15, 26.1–35.1 mm SL, rio Solimões, ilha Sorubim, Coari, 04°05'38"S 63°08'39"W, 29 Nov 1968, EPA. MZUSP 12406, 5, 33.2–38.0 mm SL, rio Japurá, Manacabi, 02°45'07"S 64°51'54"W, 30 Oct 1968, EPA. MZUSP 12407, 42 (6 c&s), 38.1–44.4 mm SL, rio Solimões, Fonte Boa, 02°30'09"S 66°05'47"W, 6 Oct 1968, EPA. UFRGS 12877, 1, 26.3 mm SL, UFRGS 21754, 1, 30.9 mm SL, rio Juruá near Furo do Pupunha, Carauari, 05°06'44"S 67°10'26"W, 14 Jun 2008, L. R. Malabarba, V. A. Bertaco, F. C. Jerep, T. P. Carvalho & C. M. Bührnheim. UFRGS 21765, 3, 24.7–28.7 mm SL, rio Juruá, 2 km above mouth of Juburi, Carauari, 05°10'15"S 67°13'27"W, 15 Jun 2008, L. R. Malabarba, V. A. Bertaco, F. C. Jerep, T. P. Carvalho & C. M. Bührnheim. UFRGS 21803, 2, 21.1–21.4 mm SL, sand beach of rio Juruá, Carauari,

05°06'20"S 67°02'33"W, 17 Jun 2008, L. R. Malabarba, V. A. Bertaco, F. C. Jerep, T. P. Carvalho & C. M. Bührnheim. USNM 356381, 17 of 19, 29.1–42.0 mm SL, rio Amazonas, Manaus, *ca*. 03°14'S 59°59'W, 8 Nov 1977, P. Bayley. **Rondônia.** MCP 39868, 50 (2 c&s), 22.8–40.6 mm SL, rio Mamoré at Cristo Rei district, rio Madeira basin, Guajará-Mirim, 10°47'03"S 65°20'58"W, 25 Jul 2004, R. E. Reis, P. A. Buckup, P. Lehmann, V. A. Bertaco & F. Langeani. UFRGS 23293, 2, 40.3–44.9 mm SL, mouth of rio Jaci-Paraná into rio Madeira, Porto Velho, 09°09'41"S 64°23'55"W, 30 Nov 2014, M. Granai, L. F. M. Neto & R. R. Luna. UFRGS 25775, 22, 22.5–35.8 mm SL, rio Madeira, UHE Jirau, Porto Velho, 08°49'32"S 63°58'43"W, 1 Jul 2016, M. Granai, L. F. M. Neto & R. R. Luna. UFRGS 26693, 1, 30.4 mm SL, UHE Santo Antônio, above Cachoeira de Morrinhos, São Carlos, 09°00'46"S 64°15'05"W, 28 Jun 2015, M. Granai, L. F. M. Neto & R. R. Luna. **Peru, Loreto.** ANSP 149926, 12, 36.0–41.9 mm SL, Río Amazonas (Maranon) Isla Iquitos, 03°31'56"S 73°04'28"W, 16 Oct 1955, M. Hohn. INHS 39883, 14, 24.1–39.8 mm SL, Río Amazonas across from Puebla Gallito, 7.68 mi SE Iquitos, 03°49'15"S 73°09'43"W, 21 Aug 1996, M. H. Sabaj *et al*. INHS 40242, 2, 31.2–35.7 mm SL, Río Amazonas, about 10 and 40 min upstream from mouth caño Zapatilla, near town of Yanashi, *ca*. 03°32'S 72°17'W, 14 Aug 1996, M. H. Sabaj *et al*. MUSM 258, 11, 37.5–38.7 mm SL, Río Amazonas, Brinet., 04°01'04"S 71°05'43"W, 27 Sep 1982, H. Ortega. MUSM 10769, 3, 33.5–40.3 mm SL, Amazonas, Santa Elena, 02°10'43"S 73°50'26"W, 25 Sep 1973, W. Medina. MUSM 18088, 1, 42.6 mm SL, Parinari, Río Marañón, Frente a Berlin, 04°33'45"S 74°28'25"W, 8 Mar 2001, H. Ortega. MUSM 18103, 1, 48.2 mm SL, Nauta, Río Marañón, Gran Punta, 04°30'30"S 73°33'47"W, 10 Mar 2001, H. Ortega. MUSM 40534, 104, 28.2–48.8 mm SL, Parinari, Río Marañón, Santa Rita de Castilla, 04°38'20"S 74°20'16.9"W, 30 May 2011, J. Chuctaya. MUSM 40676, 57, 16.1–46.7 mm SL, Río Marañón, Trompeteros, 04°45'14"S 75°04'27"W, 29 May 2011, M. Rojas. MUSM 42219, 9, 38.2–42.7 mm SL, Río Marañón, aguas arriba de la CCNN San Pedro, 04°44'53"S 74°52'27"W, 15 Nov 2011, J. Chuctaya. MUSM 42243, 9, 37.9–41.8 mm SL, Trompeteros, Río Marañon, 04°45'02"S 74°51'10"W, 14 Nov 2011, J. Chuctaya. MUSM 48489, 11, 39.7–42.7 mm SL, Urarinas, Río Marañón, San Pedro, 04°45'03"S 75°04'18"W, 25 Nov 2013, D. Faustino. MUSM 50027, 1, 32.1 mm SL, Urarinas, Río Marañón, San Pedro, 04°45'03"S 75°04'18"W, 25 Jun 2014, D. Faustino. USNM 280635, 1, 19.7 mm SL, Río Amazonas about 30 km downriver of Iquitos, 03°31'56"S 73°04'28"W, 21 Aug 1986, R. P. Vari, H. Ortega & A. G. Gerberich. **San Martín.** MUSM 67360, 1, 30.6 mm SL, Mariscal Caceres, Pajarillo, Amazonas, Río Huallaga, 07°10'55"S 76°41'46"W, 23 Jun 2019, R. Quispe. **Ucayali.** MUSM 257, 4, 21.41–32.07 mm SL, Pucallpa, Río Ucayali, Bahuanisho, 08°32'26"S 74°20'20"W, 20 Apr 1983, H. Ortega. MUSM 259, 22, 37.6–40.6 mm SL, Ucayali, Pucallpa, Río Ucayali, Bagazan, 04°43'21"S 73°31'55"W, H. Ortega. MUSM 582, 15, 24.3–40.6 mm SL, Masisea, Río Ucayali, 08°33'03"S 74°20'03"W, 6 Oct 1975, H. Ortega. MUSM 1875, 64, 17.5–28.1 mm SL, Pucallpa, Río Ucayali, Bahuanisho, 08°32'26"S 74°20'20"W, 21 May 1974, H. Ortega. MUSM 2102, 1, 41.1 mm SL, Pucallpa, Bagazan, 04°43'21"S 73°31'55"W, 22 Dec 1986, H. Ortega. MUSM 2294, 5, 41.4–44.8 mm SL, Ucayali, Pucallpa, Río Ucayali, 08°19'51"S 74°35'30"W, 22 Dec 1986, H. Ortega-A. MUSM 3143, 3, 42.3–44.6 mm SL, Requena, Genaro Herrera, Ucayali, 04°54'44"S 73°40'59"W, 28 Feb 1992, P. de Rham & F. Chang. MUSM 9800, 2, 39.9–42.3 mm SL, Pucallpa, Río Ucayali, 08°19'51"S 74°35'30"W, 30 Oct 1982, C. Villanueva. MUSM 15053, 3, 34.0–37.5 mm

SL, Coronel Portillo, Pucallpa, Ucayali, Pto La Hoyada, 08°21'45"S 74°31'10"W, 20 Aug 1984, H. Ortega. MZUSP 25943, 1, 38.3 mm SL, Río Ucayali, Masisea, 08°36'28"S 74°18'19"W, 6 Nov 1975, H. Ortega. MZUSP 26149, 1, 39.0 mm SL, Río Ucayali, Bagazan, Cel. Portillo, 08°23'17"S 74°34'50"W, 25 Nov 1979, H. Ortega. UFRGS 27444, 9, 40.4–44.8 mm SL, Playa San José, Río Ucayali, near Contamana, 07°13'58"S 74°34'48"W, Sep 2018, J. Chuctaya. UFRGS 27445, 3, 40.5–43.1 mm SL, Río Ucayali at Capironal, near Contamana, 07°19'19"S 75°12'44"W, Sep 2018, J. Chuctaya. UFRGS 27446, 4, 32.8–42.3 mm SL, Río Ucayali at Cushibatay, near mouth of Río Cushibatay, 07°05'14"S 75°08'40"W, Sep 2018, J. Chuctaya. UFRGS 27447, 3, 40.4–47.3 mm SL, Río Ucayali, 05°34'42"S 74°29'42"W, Sep 2018, J. Chuctaya. UFRGS 27448, 1, 42.8 mm SL, Río Ucayali, near Galilea, 07°25'23"S 75°02'29"W, Sep 2018, J. Chuctaya. USNM 280541, 15 (3 c&s), 30.1–41.5 mm SL, Río Ucayali, 08°31'S 74°22'W, R. P. Vari, H. Ortega & A. G. Gerberich & J. A. Louton. **Madre de Dios.** MUSM 28147, 9, 39.6–43.0 mm SL, Tambopata, Cantera Cachuela Huesembre, 12°33'23"S 69°10'04"W, 5 Sep 2006, S. Martinez.

DISCUSSION

Prodontocharax and *Amblystilbe* are the only cheirodontines whose mouths are located below the horizontal through the lower edge of the eye, and share some similarities associated with changes in jaw bones and teeth. These include the tricuspidate and elongated teeth, the teeth regularly spaced not contacting each other at their bases or at their tips contrary to that usually observed in other genera of the subfamily, and the premaxilla lacking a medial ascending process.

Regardless of these similarities, some morphological differences in teeth and jaw bones support their recognition as separate genera. The teeth of the species of the two genera clearly differ in shape, size, number, and arrangement (Figs. 2, 8, 12). *Amblystilbe* teeth differs from other Cheirodontinae by the large number (8–10) of teeth in the premaxilla, nearly twice as observed in other genera (4–6); and by the regular size of dentary teeth along nearly all length of dentary instead of large teeth anteriorly followed by smaller teeth, as observed other Cheirodontinae. By comparison, these are putative autapomorphies that diagnose *Amblystilbe*.

In *Prodontocharax* the posterior edentulous lamina of the maxilla is helical, medially curved in relation to the anterior toothed portion (Figs. 2A, 8B) and not flat and parallel to the anterior toothed portion, as observed in other Cheirodontinae or characids; the dentary teeth form an anterior series of large and tricuspidate teeth followed by a second and angled series of small conical teeth in an arrangement that we have not seen in any other examined cheirodontines and characids. These are putative synapomorphies that support close relationships between the two species of *Prodontocharax* and that have not been observed in other genera of the subfamily. We herein refrain to further elaborate a discussion on the relationships of these two clades to other cheirodontines, that will be deeply discussed in a paper on the morphological and molecular phylogeny of the subfamily (J. Chuctaya and collaborators, work in progress).

A revision of specimens referred to *Prodontocharax melanotus* proved they constitute two different species: *P. melanotus* from Beni and Itenez rivers, Bolivia/Brazil, and upper Madre de Dios and upper Madeira rivers, Peru; and *P. aquilaepinnae* is from the Huallaga, Ucayali, and Urubamba rivers, upper Amazonas, Peru. The two species are distinguished by the color pattern, by the number of lamellae of the olfactory rosette in male and female, and by the number of gill rakers.

We have compared populations of *Amblistylbe howesi* from Chapare River, Bolivia, and Mamoré River, upper Madeira River basin, Brazil, with those identified as *P. alleni* from Ucayali (type-locality) and Madre de Dios rivers, Peru, and Amazonas River, Brazil, and found no consistent differences to support the presence of two species. Specimens from Chapare and Mamoré rivers compared to other Amazon drainages, showed small differences in the number of lateral line scales (35–38, mean = 36.0 *vs.* 37–39, mean = 37.5) and anal-fin rays (ii–iv,19–23, mean = 21.2 *vs.* iii–iv,22–25, mean = 23.6), that largely overlap. A morphometric comparison through Principal Components Analysis (PCA) of the type specimens of *A. howesi* and *P. alleni* also did not allow the recognition of separate morphological groups (Fig. 15). Böhlke (1953) noted in the original description of *P. alleni* that his new species was possibly related to *Amblystilbe howesi*. Herein, we synonymize *P. alleni* with *A. howesi*, because no significant morphological differences were found between the analyzed populations referred to these species.

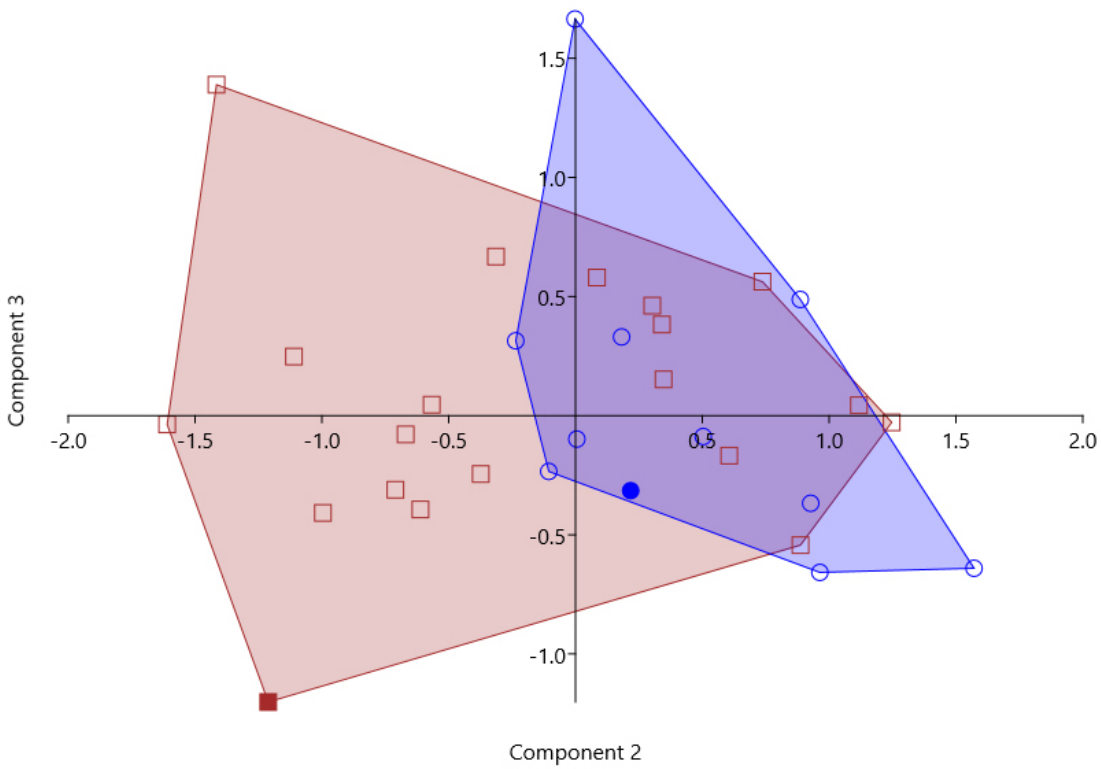

FIGURE 15 | Principal Components Analysis (PCA) comparing raw data between the type specimens of *Amblystilbe howesi* (blue circles, n = 10) and *Prodontocharax alleni* (red squares, n = 19). PC1 was not considered to avoid influence of size variable. Full symbols are from the holotypes.

Comparative material examined. Brazil. *Acinocheirodon melanogramma* Malabarba & Weitzman, 1999: MCP 19238, 1 male c&s. ANSP 176238, 7 paratypes. *Aphyocheirodon hemigrammus* Eigenmann, 1915: MNRJ 19470, 1 c&s of 9. *Cheirodon ibicuhiensis* Eigenmann, 1915: MCP 11910, 2 c&s. *Cheirodon interruptus* Eigenmann, 1915: MCP 6971, 4 c&s. *Cheirodon parahybae* Eigenmann, 1915: MNRJ 18009, 2 c&s of 94. *Cheirodon stenodon* Eigenmann, 1915: MZUSP 37175, 4 c&s of 19. MZUSP 35346, 6. *Ctenocheirodon pristis* Malabarba & Jerep, 2012: MZUSP 40535, 7 c&s. *Heterocheirodon jacuiensis* Malabarba & Bertaco, 1999: MCP 21672, 2 c&s of 190. *Heterocheirodon yatai* (Casciotta, Miquelarena & Protogino, 1992): MCP 11287, 4 c&s of 15. *Kolpotocheirodon figueiredoi* Malabarba, Lima & Weitzman, 2004: MZUSP 55219, 3 c&s of 26. *Kolpotocheirodon theloura* Malabarba & Weitzman, 2000: MCP 11161, paratype, 1 c&s. *Macropsobrycon uruguayanae* Eigenmann, 1915: MCP 11937, 4 c&s of 208. *Odontostilbe avanhandava* Chuctaya, Bührnheim & Malabarba, 2018: LIRP 3239, 48.7 mm SL. *Odontostilbe pacaasnovos* Chuctaya, Ohara & Malabarba, 2020: UFRGS 28509, 27.8 mm SL. *Odontostilbe paraguayensis* Eigenmann & Kennedy, 1903: MCP 35618, 2 c&s. *Odontostilbe parecis* Bührnheim & Malabarba, 2006: MCP 37319, 2 c&s of 80 paratypes. *Odontostilbe pequira* (Steindachner, 1882): MCP 33240, 1 c&s of 61. *Odontostilbe weitzmani* Chuctaya, Bührnheim & Malabarba, 2018: MZUSP 16851, 1. *Protocheirodon pi* (Vari, 1978): INPA 28491, 1 c&s of 8. *Serrapinnus aster* Malabarba & Jerep, 2014: MZUSP 40359, 2 c&s of 12. *Serrapinnus calliurus* (Boulenger, 1900): MCP 12537, 4 c&s of 21. *Serrapinnus heterodon* (Eigenmann, 1915): MCP 26896, 4 c&s of 16. *Serrapinnus lucindai* Jerep & Malabarba, 2014: UFRJ 1260, 4 c&s of 62. *Serrapinnus microdon* (Eigenmann, 1915): MCP 15077, 5 c&s of 30. *Serrapinnus micropterus* (Eigenmann, 1907): MCP 37316, 3 c&s of 10. *Serrapinnus notomelas* (Eigenmann, 1915): MCP 14873, 2 c&s of 126. *Serrapinnus piaba* (Lütken, 1875): MCP 14007, 4 c&s of 25. *Serrapinnus potiguar* Jerep & Malabarba, 2014: UFRGS 9216, 5 c&s of 13. *Serrapinnus tocantinensis* Malabarba & Jerep, 2014: MZUSP 40362, 4 c&s of 31. *Serrapinnus sterbai* Zarske, 2012: UNT 7227, 4 c&s of 54. **Bolivia.** *Odontostilbe dierythrura* Fowler, 1940: MCP 38624, 2 c&s of 7. *Odontostilbe microcephala* Eigenmann, 1907: USNM 319279, 4 c&s of 200. *Odontostilbe nareuda* Bührnheim & Malabarba, 2006: FMNH 106433, paratypes, 1 c&s of 30. **Chile.** *Cheirodon australe* Eigenmann, 1928: UMMZ 215046, 3 c&s of 17. USNM 084317, 12 paratypes. *Cheirodon galusdae* Eigenmann, 1928: UMMZ 212703, 3 c&s of 23. USNM 084319, 10 paratypes. *Cheirodon kiliani* Campos, 1982: UMMZ 219454, 2 c&s of 7. USNM 227310, 1 paratype. *Cheirodon pisciculus* Girard, 1855: MCP 11987, 2 c&s. *Compsura heterura* Eigenmann, 1915: MCP 17093, 3 c&s of 185. FMNH 57825, holotype. **Colombia.** *Odontostilbe splendida* Bührnheim & Malabarba, 2007: MCP 38862, 1 male c&s of 27 paratypes. *Saccoderma hastata*: FMNH 56383, holotype. **Costa Rica.** *Pseudocheirodon terrabae* Bussing, 1967: UMMZ 194214, 4 c&s of 33. **Ecuador.** *Odontostilbe ecuadorensis* Bührnheim & Malabarba, 2006: KU 13524, paratypes, 1 c&s of 32. **Panama.** *Compsura gorgonae* (Eigenmann & Goldsborough, 1909): USNM 64094, holotype. USNM 64095, 4 paratypes. USNM 127086 3 paratypes. *Odontostilbe dialeptura* (Fink & Weitzman, 1974): USNM 208524, holotype. USNM 208523, 132 paratypes. *Odontostilbe mitoptera* (Fink & Weitzman, 1974): USNM 208539, holotype. USNM 208513, 8 paratypes. *Pseudocheirodon arnoldi* (Boulenger, 1909): MCP 16134, 2 c&s. **Paraguay**. *Serrapinnus kriegi*: MCP 12043, 5 c&s. **Peru.** *Odontostilbe euspilurus* (Fowler, 1945): ANSP 143702, 2 c&s of 8. *Odontostilbe fugitiva* Cope, 1870: ANSP 178908, 2 c&s of 12. **Trinidad.** *Odontostilbe pulchra* (Gill, 1858): INHS 40101, 2 c&s of 20. **Venezuela.** *Cheirodontops geayi* Schultz, 1944: CAS 64344, 1 c&s of 66. USNM 121507, holotype. *Nanocheirodon insignis* (Steindachner, 1880): USNM 121511, 6 c&s of 352. *Odontostilbe pao* Bührnheim & Malabarba, 2007: MCP 40976, 1 c&s of 2 paratypes.

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Not applicable.

COMPETING INTERESTS

The author declares no competing interests.

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