

DISTRIBUTIONAL PATTERNS OF THE SOUTH AMERICAN SPECIES OF *BOECKELLA* (COPEPODA: CENTROPAGIDAE): A TRACK ANALYSIS

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A B S T R A C T

South American species of the freshwater copepod genus *Boeckella* are distributed in the Andean region, which corresponds to southwestern South America below 30° south latitude, also extending along the Andean highlands north of this latitude, and comprises the Subantarctic, Central Chilean, Patagonian, and Paramo-Puna subregions. Based on a track analysis, five generalized tracks were found: Subantarctic (involving some Subantarctic islands, the Falklands, Tierra del Fuego, and the southern portion of continental Chile and Argentina): *B. brevicaudata*, *B. poppei*, *B. valentini*, and *B. michaelseni*; Patagonian (in the southern Patagonia plateau): *B. brasiliensis*, *B. silvestrii*, and *B. longicauda*; Mid-southern Andes: *B. gibbosa* and *B. diamantina*; Paramo-Punan (in the central and northern Andes, from northwestern Argentina to western Colombia): *B. calcaris*, *B. palustris*, and *B. occidentalis*; and Neotropical (mainly in the Neotropical region, but reaching also Patagonia and the Puna): *B. meteoris* and *B. bergi*. Two nodes have been determined: one in southern Chile and Argentina, where the Subantarctic, Patagonian, and Neotropical tracks intersect, and the other in the central Andes, where the Paramo-Punan and Neotropical tracks intersect.

The freshwater copepod genus *Boeckella* de Guerne and Richard, 1889, comprises 38 species, distributed in Australia, New Zealand, South America, Antarctica, and the Subantarctic. Some South American species were originally described in the genus *Pseudoboeckella* Mrázek, 1901, a closely related taxon. Although assignment of species to *Boeckella* and *Pseudoboeckella* has not been generally disputed, a clear separation of both genera has been problematical (Ekman, 1905b; Marsh, 1925; Brehm, 1936a; Ringuelet, 1958), and recently Bayly (1992) treated these generic names as synonyms. Apparently species assigned to *Boeckella* and *Pseudoboeckella* represent extremes of a morphological and size gradient, from large and stout forms (*Pseudoboeckella*) (Figs. 1, 3) to small and gracile forms (*Boeckella*) (Figs. 2, 4). A convenient solution would be to maintain both names as subgenera until a cladistic analysis is performed to elucidate their status.

South American species of *Boeckella* have attracted authors from a biogeographical viewpoint (Brehm, 1936b, 1956a; Löffler, 1955; Ringuelet, 1958; Morrone, 1992; Katinas *et al.*, in press; Menu-Marque and Locascio de Mitrovich, 1998). Their distribution

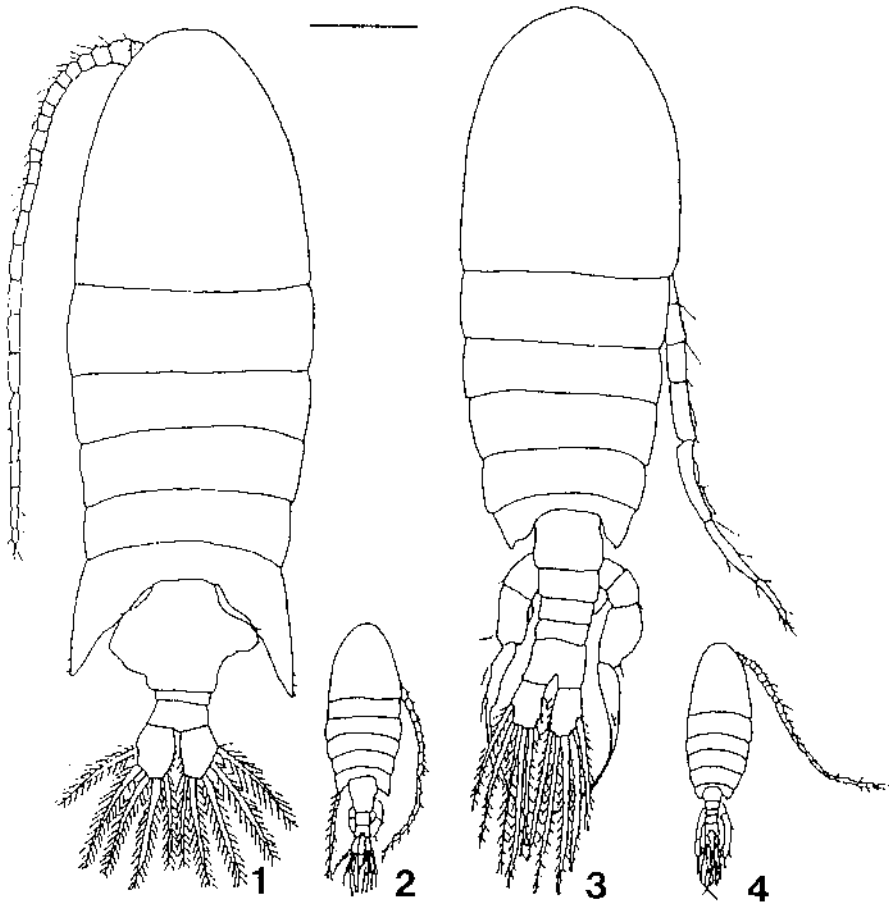
basically corresponds to the Andean region of the Austral kingdom (Morrone, 1999), with some species extending to the east into the Neotropical region (Menu-Marque and Locascio de Mitrovich, 1998).

In this paper, we analyze the geographical distribution of the South American species of *Boeckella* applying a track analysis, which has been successfully applied to other Crustacean taxa (Morrone and Lopretto, 1994; Grosso and Peralta, 1997; Lopretto and Morrone, 1998). Our main objective is to determine individual and generalized tracks for these species, in order to contribute to the knowledge of their spatial evolution.

MATERIALS AND METHODS

Data

Distributional data for this study were obtained from the literature (Lubbock, 1855; Brady, 1875; Poppe and Mrázek, 1895; Richard, 1897; Mrázek, 1901; Daday, 1902; Ekman, 1905a; Marsh, 1906; Tollinger, 1911; Rùhe, 1914; Scott, 1914; Brehm, 1926, 1935a–d, 1936a, b, 1937a, b, 1953, 1954, 1956a, b; Pesta, 1927; Delachaux, 1928; Kiefer, 1928, 1944, 1959; Harding, 1941, 1955; Olivier, 1952, 1955; Löffler, 1955, 1958, 1961, 1963; Ringuelet, 1958; Thomasson, 1959, 1963; Daciuk, 1968; Pezzani-Hernández, 1973; Heywood, 1977; Weller, 1977; Zúñiga and Domínguez, 1977, 1978; Paggi, 1980, 1983; Araya and Zúñiga, 1985; José de Paggi and Paggi, 1985;



Figs. 1–4. Habitus. 1, female *Boeckella* (*Pseudoboeckella*) *calcaris*; 2, female *B. (B.) gracilipes*; 3, male *B. (P.) calcaris*; 4, male *B. (B.) gracilipes*.

Locascio de Mitrovich, 1986, 1990; Mariazzi *et al.*, 1987; Janiec, 1988; Zúñiga, 1988; Andrew *et al.*, 1989; Clarke *et al.*, 1989; Gaviria, 1989; Balseiro and Modenutti, 1990; Balseiro, 1991; Modenutti and Balseiro, 1991, 1994; Reid, 1991; Soto and Zúñiga, 1991; Villalobos and Zúñiga, 1991; Bayly, 1992, 1995; Puig, 1992, 1994; Modenutti, 1993; Gloeden, 1994; Locascio de Mitrovich and Menu-Marque, 1994; Marinone, 1994; Menu-Marque and Zúñiga, 1994; Menu-Marque, 1996; Pilati, 1997a, b; Zagarese *et al.*, 1997; Menu-Marque and Locascio de Mitrovich, in press; Vega, in press). See Appendix for a complete detail of the localities. Coordinates of localities were obtained either from the literature or calculated on maps and rounded to minutes. Within each country localities are roughly ordered in a south-north direction. Authors citing Argentinean localities have been omitted to save space; they are listed in Menu-Marque and Locascio de Mitrovich (in press).

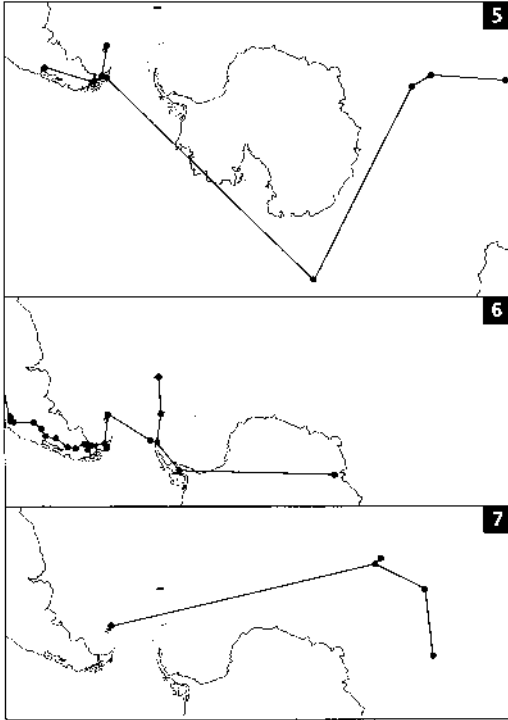
Methods

The panbiogeographic approach basically consists of plotting distributions of different taxa on maps, connecting their separate localities together with lines called in-

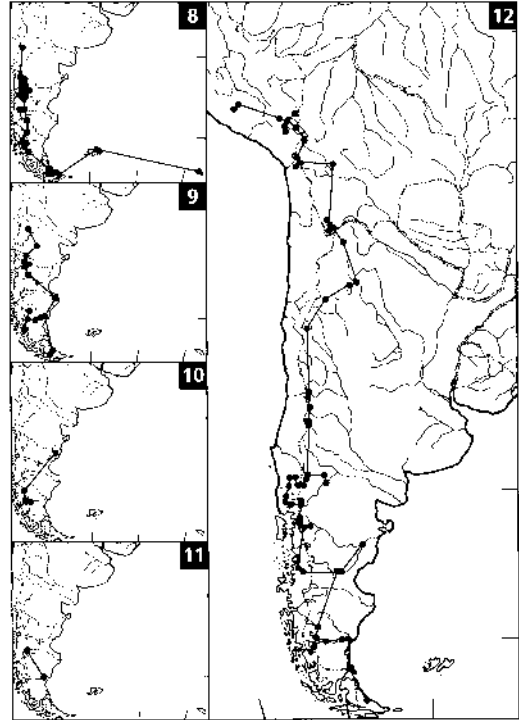
dividual tracks. These tracks represent the geographical coordinates of species or higher taxa, and operationally are lines drawn on a map of their localities, which are connected according to their geographical proximity. When different individual tracks are superimposed, the resulting summary lines are considered generalized tracks. Generalized tracks were interpreted as indicating the pre-existence of ancestral biotas, which subsequently become fragmented by tectonic and/or climatic change. If two or more generalized tracks intersect in a given area, they determine a node, which indicates that different ancestral biotic and geological fragments interrelate in space and time, as a consequence of terrain collision, docking or suturing, thus constituting a composite area. For details of the panbiogeographic methodology see Morrone and Crisci (1995) and Morrone and Lopretto (1994). In the maps, we follow the graphical conventions proposed by Fortino and Morrone (1997).

RESULTS

Boeckella brevicaudata (Brady) (Fig. 5) has a widespread distribution in the Circum-



Figs. 5–7. Individual tracks. 5, *Boeckella brevicaudata*; 6, *B. poppei*; 7, *B. vallentini*.



Figs. 8–12. Individual tracks. 8, *Boeckella michaelsoni*; 9, *B. brasiliensis*; 10, *B. silvestrii*; 11, *B. longicauda*; 12, *B. gracilipes*.

antarctic islands of eastern longitude, Falkland Islands, Tierra del Fuego, and a few localities in Patagonia, around 41°S.

Boeckella poppei (Mrázek) (Fig. 6) is the only species found on the Antarctic continent; it is distributed in Circumantarctic islands of western longitude, Tierra del Fuego, the Patagonian plateau, advancing northward along some Andean lakes, with its northernmost record at about 31°S, on a plateau containing relict Patagonian biota (Cei, 1972).

Boeckella vallentini (Scott) (Fig. 7) is distributed only in Circumantarctic islands from Kerguelen to the Falklands.

Boeckella michaelsoni (Mrázek) (Fig. 8) is distributed in South Georgia Islands, Falkland Islands, Tierra del Fuego, and along the Patagonian Andes up to about 40°S.

Boeckella brasiliensis (Lubbock) (Fig. 9) is widespread in Tierra del Fuego and the Patagonian Plateau to 39°S.

Boeckella silvestrii (Daday) (Fig. 10) has a restricted distribution from 44° to 50°S on the Patagonian Plateau.

The presence of *B. longicauda* Daday (Fig.

11) has been confirmed from only two localities of southern Patagonia.

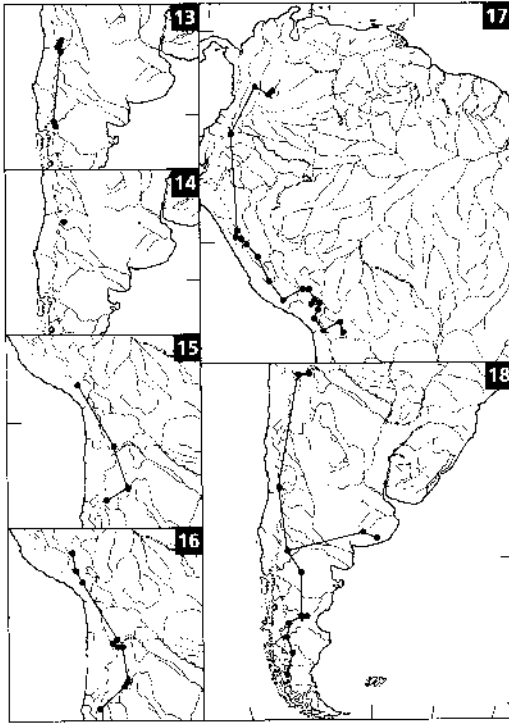
The distribution of *B. gracilipes* Daday (Fig. 12) is widespread in Patagonia and southern Chile, extending northward along some high mountain lakes of Argentina, Chile, Bolivia, and Peru, where it appears until 14°S.

Boeckella gibbosa (Brehm) (Fig. 13) is restricted to high mountain lakes of the Chile-Argentina border from 32° to 42°S, whereas its close relative, *B. diamantina* Menu-Marque and Zúñiga (Fig. 14), is found in the same region in a single lake about 34°S.

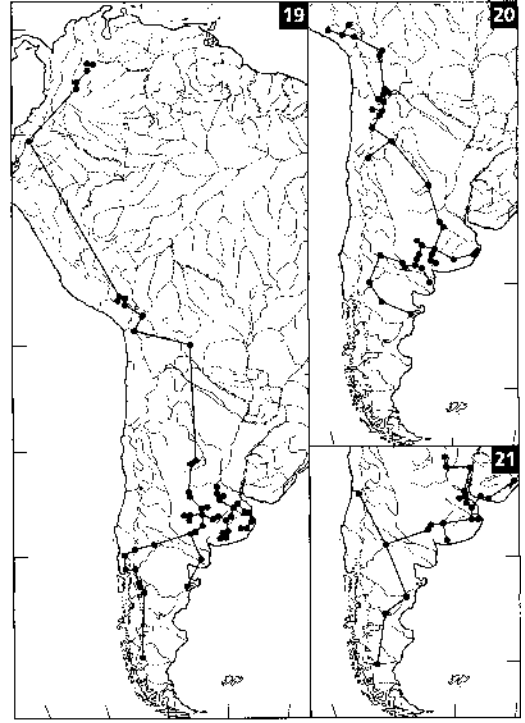
In the high mountain lakes and ponds of northern Argentina, western Bolivia and southern Peru, two closely related species share similar distributions: *B. calcaris* (Harding) (Fig. 15) and *B. palustris* (Harding) (Fig. 16).

Boeckella occidentalis Marsh (Fig. 17) appears in high elevation lakes of northern Chile, Bolivia, Peru, Ecuador and Colombia.

Boeckella meteoris Kiefer (Fig. 18) is distributed in lakes of the Patagonian Plateau,



Figs. 13–18. Individual tracks. 13, *Boeckella gibbosa*; 14, *B. diamantina*; 15, *B. calcaris*; 16, *B. palustris*; 17, *B. occidentalis*; 18, *B. meteoris*.



Figs. 19–21. Individual tracks. 19, *Boeckella gracilis*; 20, *B. pooipoensis*; 21, *B. bergi*.

branching eastward to the Pampean plain and northward reaching the border between Argentina and Bolivia.

Boeckella gracilis Daday (Fig. 19) is the most widely distributed species in South America, extending from southern Patagonia and the Chilean Lake District, advancing eastward in the Pampean plain where it is extremely well represented, and northward in central Argentina, Bolivia, then along the Andes across Peru, Ecuador, and reaching in Colombia the northernmost latitude for any species of the genus on this continent (6°13'N).

Boeckella pooipoensis Marsh (Fig. 20) is distributed from the north of the Patagonian Plateau to the Pampean plain, reaching almost the Atlantic coast, and branching northward along saline lakes of Argentina, Chile, Bolivia, and southern Peru, appearing exclusively in high conductivity environments from 43° to 15°S.

Boeckella bergi Richard (Fig. 21) is distributed from the Patagonian Plateau, extending to the north-east along the shallow

lakes and streams of the province of Buenos Aires, advancing northward along the Paraná and Uruguay rivers and eastward across Uruguay, reaching in southeastern Brazil the easternmost locality known for the genus in South America. This is the only species that has successfully colonized rivers, being found also in the freshwater section of the Río de la Plata estuary.

Our data reveal the existence of at least five generalized tracks (Fig. 22):

(1) Subantarctic track. It involves some Subantarctic islands, Tierra del Fuego and the southern portion of continental Chile and Argentina, having one portion linking the Subantarctic islands, the Falklands, Tierra del Fuego, and southern Chile (1a), and the other that goes northward in southern Chile and Argentina (1b). Species assigned to this track are *B. brevicaudata*, *B. poppei*, *B. vallentini*, and *B. michaelsoni*.

(2) Patagonian track. In the southern Patagonia plateau. Species assigned to this track are *B. brasiliensis*, *B. silvestrii*, and *B. longicauda*.

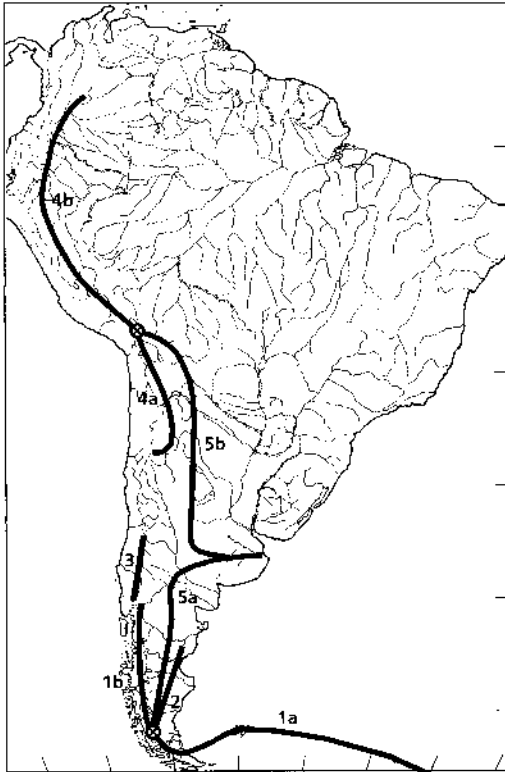


Fig. 22. Generalized tracks and nodes of the South American species of *Boeckella*.

(3) Mid-southern Andes track. *B. gibbosa* and *B. diamantina*.

(4) Paramo-Punan track. In the central and northern Andes. The southern portion (4a) goes from northwestern Argentina to southern Peru, whereas the northern portion (4b) extends northward to western Colombia. Species assigned to it are *B. calcaris*, *B. palustris*, and *B. occidentalis*.

(5) Neotropical track. Mainly in the Neotropical region, but reaching also Patagonia and the Puna. It has a southern portion (5a) with a southward direction, and a northern portion (5b) that extends to southern Peru. Species of this track are *B. meteoris* and *B. bergi*.

Three species are wide ranging, involving two or more of these tracks: *B. gracilipes* (Subantarctic, Patagonian, Mid-southern Andes and Paramo-Punan), *B. gracilis* (Subantarctic, Neotropical and Paramo-Punan), and *B. poopuensis* (Neotropical and Paramo-Punan).

Two panbiogeographic nodes have been determined: one in southern Chile and Argentina, where the Subantarctic, Patagonian, and Neotropical tracks intersect, and another in the central Andes, where the Paramo-Punan and Neotropical tracks intersect.

DISCUSSION

The Patagonian, mid-southern Andes, and Paramo-Punan tracks are delimited by the exclusive presence of species formerly included in the genus *Pseudoboeckella* (although the position of *B. occidentalis* has been a matter of much debate (Bayly, 1992), we are inclined, following Ringuelet (1958), to assign it to this taxon), whereas the Neotropical track includes only two species which were always considered to belong to *Boeckella*. This is also the case for *B. gracilipes*, *B. gracilis*, and *B. poopuensis*, whose ranges are so wide that they involve two or more of these tracks. There is a single track (Subantarctic) that involves one species of *Boeckella* (*B. michaelsoni*) and three of *Pseudoboeckella*, which renders it the only one of the five generalized tracks including members of the two above mentioned taxa. The separate biogeographic histories of *Boeckella* and *Pseudoboeckella* could reflect the existence of two separate taxa, whatever their taxonomic rank.

The biogeographic patterns exhibited by the species of *Boeckella*, which are also distributed in Australia and New Zealand, reflect the existence of an ancient Austral biota, with Gondwanaland events likely playing a major role in its evolution, and with species extending to the Neotropics probably linked to a more recent history. *Boeckella gracilis*, *B. poopuensis*, and *B. bergi* have the widest eastward distributions almost certainly involving dispersal.

These patterns confirm the complex origin of the Andean biota, evidenced in previous studies (Crisci *et al.*, 1991; Posadas *et al.*, 1997; Katinas *et al.*, in press). The Paramo-Puna, Patagonian, and Subantarctic subregions appear as panbiogeographic nodes, because of the numerous tracks that cross them, probably due to complex geological events. It is possible that the patterns analyzed are the consequence not only of vicariant events promoted by tectonic phenomena, but also of dispersal and/or extinctions that have concealed these events.

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Appendix. Localities of the South American species of *Boeckella*. Abbreviations: Ao. = arroyo (stream), E. = embalse (reservoir), Ea. = estancia (ranch), L. = lago (lake), La. = laguna (shallow or small lake), R. = río (river).

Boeckella (*B.*) *bergi* Richard, 1897. **ARGENTINA:** Pool near R. Santa Cruz (50°12'S, 71°38'W); L. Musters (45°22'S, 69°12'W); E. Ameghino (43°50'S, 66°29'W); L. Pellegrini (38°41'S, 67°00'W); Ao. Sauce Grande (38°37'S, 61°14'W); Puan (37°33'S, 62°48'W); Guaminí upon La. Del Monte (37°01'S, 62°22'W); Ao. Mapis (36°47'S, 61°15'W); Ao. El Carnero (36°40'S, 59°47'W); General Conesa (36°32'S, 57°18'W); La. Chascomús (35°36'S, 58°02'W), Atucha (35°32'S, 59°21'W); La. de Monte (35°27'S, 58°49'W), Cnel. Brandsen (35°17'S, 58°15'W); Melchor Romero (34°57'S, 58°03'W); Plátanos (34°48'S, 58°13'W); Adrogué (34°48'S, 58°23'W); E. Cascallares (34°41'S, 58°52'W); Ao. El Salado (34°36'S, 58°34'W); pool in Buenos Aires city (34°34'S, 56°26'W); Paraná River Delta near Tigre (34°20'S, 58°35'W); lagunas Middle Paraná foodplain (about 31°40'S, 60°33'W); Ao. Ayuí (31°17'S, 57°59'W); Gobernador Crespo (30°21'S, 60°24'W). **BRASIL:** Lagoa Mirim (32°20'S, 52°47'W) (Gloeden, 1994). **CHILE:** La. de Aculeo (33°50'S, 70°56'W) (Brehm, 1936a). **URUGUAY:** Atlántida (34°47'S, 55°46'W) (Brehm, 1937b); pools at Barra de Santa Lucía (34°48'S, 56°27'W); pool on the coast of Río de la Plata, close to Ao. Pajas Blancas; pool near Santiago Vázquez (34°45'S, 56°20'W) (Brehm, 1935d).

Boeckella (P.) brasiliensis (Lubbock, 1855) (= *B. setosa* Daday, 1901). **ARGENTINA:** Pool at Ushuaia Peninsula (54°50'S, 68°19'W); L. Fagnano (54°34'S, 68°00'W); L. Yehuin (54°22'S, 67°44'W); La. San Luis (53°55'S, 67°37'W); pool with basalt bottom (50°15'S, 70°08'W); pools at 50°12'S, 71°38'W and 50°08'S, 69°15'W; swamp at Amenkelt (50°03'S, 69°01'W); pool at Misioneros (49°59'S, 68°33'W); L. Cardiel (48°57'S, 71°14'W); Puerto Deseado (47°45'S, 65°54'W); La. Estrella (44°56'S, 71°13'W); Leleque (44°24'S, 71°04'W); L. Pico I (44°15'S, 71°30'W); La. Cronómetro (43°15'S, 71°02'W); La. Zeta (42°53'S, 71°42'W); La. Esquel (42°52'S, 71°04'W); shallow lake W of La. Carrillaufquen Grande (41°15'S, 69°32'W); La. Blanca (39°03'S, 70°23'W). **CHILE:** L. Jovito, La. Redonda, La. Larga, and pond in Torres del Paine National Park (all around 51°03'S, 72°53'W) (Bayly, 1992).

Boeckella (P.) brevicaudata (Brady, 1875) (= *B. vexillifera* Ekman, 1905, *P. remotissima* Brehm, 1953). **CIRCUMANTARCTIC ISLANDS:** Macquarie Is. (54°38'S, 158°53'E); Heard Is. (53°07'S, 73°20'E) (Bayly, 1992); Falkland Is.: pond W of Port Stanley (51°38'S, 57°52'W) (Ekman, 1905a); Kerguelen Is. (49°30'S, 69°30'E) (Brady, 1875); New Amsterdam Is. (37°52'S, 77°52'E) (Rühe, 1914). **ARGENTINA:** Pool at Ushuaia Peninsula (54°50'S, 68°19'W); moor at Rancho Hambre (54°47'S, 67°43'W); quarry W of San Sebastián (53°18'S, 68°38'W); La. Fantasma (41°07'S, 71°27'W); La. Los Juncos (41°04'S, 71°00'W). **CHILE:** La. de los Patos Bravos (Punta Arenas) (approx. 53°09'S, 70°57'W) (Mrázek, 1901).

Boeckella (P.) calcaris (Harding, 1955). **ARGENTINA:** La. Negra (27°34'S, 68°39'W); lagunas de Huaca Huasi at Cumbres Calchaquies (26°40'S, 65°44'W); Ranas, Circular, Grande, Muerta, Nostra, Vega Matadero. **BOLIVIA:** "Conchostraca" pool (22°18'S, 67°14'W) (Bayly, 1992). **PERU:** Tarn at San Antonio de Esquilache (16°06'S, 70°18'W) (Harding, 1955).

Boeckella (P.) diamantina Menu-Marque and Zúñiga, 1994. **ARGENTINA:** La. del Diamante (34°10'S, 69°42'W).

Boeckella (P.) gibbosa (Brehm, 1935). **ARGENTINA:** La. Schmoll and La. Toncek (41°13'S, 71°29'W); La. Jakob (41°12'S, 71°32'W); L. Frías (41°03'S, 71°47'W); L. Los Cántaros (40°59'S, 71°49'W); La. de los Horcones (32°40'S, 69°51'W). **CHILE:** Lake near L. Todos los Santos (approx. 41°03'S, 71°56'W) (Brehm, 1935c); La. Negra (33°36'S, 70°07'W) (Araya and Zúñiga, 1985); La. de los Indios and La. Lo Encañado (33°40'S, 70°08'W) (Brehm, 1936a); R. Manzanillo near Santiago (Brehm, 1935c).

Boeckella (B.) gracilipes Daday, 1901 (= *B. titicacae* Harding, 1955). **ARGENTINA:** La. San Luis (53°55'S, 67°37'W); reservoir SE of Río Gallegos (51°50'S, 69°01'W); Calafate (50°20'S, 72°18'W); pools at 50°08'S, 69°15'W and 50°05'S, 69°29'W; marsh at Amenkelt (50°03'S, 69°01'W); pool at Misioneros (49°59'S, 68°33'W); Horquetas (49°16'S, 68°00'W); L. Cardiel (48°57'S, 71°14'W); L. Colhue Huapi (45°30'S, 68°46'W); L. Musters (45°24'S, 69°12'W); Leleque (44°24'S, 71°04'W); E. Ameghino (43°50'S, 66°29'W); La. Cronómetro (43°15'S, 71°02'W); La. Nahuel Pan (42°58'S, 71°30'W); La. Zeta (42°53'S, 71°42'W); La. Esquel (42°52'S, 71°04'W); La. Chultas (42°10'S, 71°44'W); L. Puelo (42°10'S, 71°39'W); L. Steffen (41°31'S, 71°39'W); L. Guillermo (41°23'S, 71°29'W); L. Mascardi (41°18'S, 71°34'W); L. Escondido (41°02'S,

71°04'W); L. Los Cántaros (40°59'S, 71°49'W); L. Fonck (41°20'S, 71°37'W); L. Moreno Este (41°06'S, 71°29'W); L. Moreno Oeste (41°05'S, 71°33'W); L. Morenito (41°04'S, 71°31'W); L. Frías (41°03'S, 71°47'W); La. Trébol and La. Ezquerria (41°03'S, 71°31'W); La. Escondida; L. Nahuel Huapi (40°41'S, 71°30'W); L. Correntoso (40°41'S, 71°39'W); L. Espejo (40°36'S, 71°46'W); L. Lácar (40°10'S, 71°30'W); L. Quillén (39°25'S, 71°20'W); E. Ramos Mexía (39°25'S, 69°00'W); L. Ñorquinco (39°09'S, 71°17'W); La. Blanca (39°03'S, 70°23'W); La. Pozo de las Animas (35°11'S, 70°07'W); La. Valle Hermoso (35°10'S, 70°16'W); La. del Sosneado (34°51'S, 69°55'W); La. del Diamante (34°10'S, 69°42'W); La. de los Horcones (32°40'S, 69°51'W); La. de Hualca (reserva de San Guillermo) (28°10'S, 69°20'W); La. Negra (27°34'S, 68°39'W); Cañadón Tafí del Valle (26°52'S, 65°41'W); Lagunas de Huaca Huasi at Cumbres Calchaquies (26°40'S, 65°44'W): Circular, La Manga, Nostra, Ranas, Grande, Muerta, Partida, del Lobo, Verde, Cerritos; E. La Angostura (26°55'S, 65°41'W); pond at Espinazo del Diablo (Mina Aguilar) (23°12'S, 65°42'W). **BOLIVIA:** Campo Grande (22°33'S, 67°12'W), Totoral (22°32'S, 67°17'W), Penitas Blancas (22°25'S, 67°15'W), "Conchostraca" pool (22°18'S, 67°14'W), pools near Loromayu (22°18'S, 67°13'W), pool near Mama Khumu (22°16'S, 67°05'W), pool near Colorada (22°10'S, 67°47'W), Huancaroma (17°40'S, 67°30'W) (Bayly, 1992); R. Desaguadero (16°44'S, 69°00'W) (Harding, 1955); L. Titicaca (15°48'S, 69°26'W) (Marsh, 1906). **CHILE:** L. Sarmiento (51°04'S, 72°47'W) (Soto and Zúñiga, 1991); L. Morro, L. Cisnes, La. Tehuelches Este, La. Redonda, La. Larga, all in Torres del Paine National Park (around 51°03'S, 72°53'W) (Bayly 1992); L. La Paloma (45°56'S, 72°11'W), L. Elizalde (45°46'S, 72°20'W) (Araya and Zúñiga, 1985); L. Llanquihue (41°08'S, 72°49'W), L. Todos los Santos (41°06'S, 72°18'W), L. Rupanco (40°50'S, 72°31'W), L. Puyehue (40°39'S, 72°28'W), L. Rancho (40°15'S, 72°25'W), L. Pellaifa (39°36'S, 71°58'W), L. Calafquén (39°31'S, 72°13'W), L. Villarrica (39°15'S, 72°06'W) (Löffler, 1961); L. Trafún (Kiefer, 1959); L. Chapo (41°39'S, 72°31'W), L. Icalma (38°49'S, 71°17'W), L. Galletué (38°41'S, 71°16'W) (Soto and Zúñiga, 1991); L. Pichilafquen (39°13'S, 72°14'W) (Thomasson, 1963); L. Pirehueico (39°56'S, 71°49'W), L. Cabo Negro, L. Nelutume (39°47'S, 71°58'W), L. Panguipulli (39°43'S, 72°15'W), E. del Yeso (33°39'S, 70°05'W), La. Negra (33°36'S, 70°07'W) (Araya and Zúñiga, 1985); L. Riñihue (39°49'S, 72°19'W) (Zúñiga and Domínguez, 1977); L. Caburgua (39°07'S, 71°46'W) (Zúñiga, 1988); La. del Inca (32°48'S, 70°08'W) (Löffler, 1958); L. Parinacota (17°12'S, 69°34'W) (Villalobos and Zúñiga, 1991), L. Cotacotani (18°14'S, 69°13'W) (Bayly, 1992); L. Chungará (18°15'S, 69°10'W) (Araya and Zúñiga, 1985). **PERU:** Viscacha (16°53'S, 70°14'W), Loricopongo (16°50'S, 70°05'W), Colorada II (15°22'S, 70°21'W) (Bayly, 1992); Chulpa (15°06'S, 70°00'W), Rincunada, Seitokocho and Sillacunca (all in Puno Dpt. around 14°43'S, 69°25'W), Yauriviri (14°38'S, 73°57'W), 55 km W of Puquico (14°36'S, 73°43'W) (Löffler, 1955); L. Lagunillas (15°45'S, 70°44'W), tarns near Lagunillas, ponds A, C and J in Capachica Peninsula, near Camjata (15°37'S, 69°50'W), L. Langui (14°30'S, 71°16'W) (Harding, 1955).

Boeckella (B.) gracilis (Daday, 1902) (= *B. schwabei* Brehm, 1937, *B. camjatae* Harding, 1955, *B. bilobata* Brehm, 1958). **ARGENTINA:** Ea. "La Primera" N of

L. Viedma (49°35'S, 72°31'W); pool beside Route 40, 34 km S of Tecka (43°44'S, 70°51'W); Tecka (43°29'S, 70°45'W); ditch beside road NE of Trevelin (43°04'S, 71°28'W); vegetated pool beside Route 40 close to R. Percey (42°59'30"S, 71°29'W); pool near La. Terraplén (42°59'S, 71°30'W); Esquel (42°55'S, 71°20'W); Puerto Madryn (42°45'S, 65°02'W); L. Guillelmo (41°23'S, 71°29'W); L. Gutiérrez (41°12'S, 71°27'W); inundation pool between L. Gutiérrez and L. Mascardi; Conesa (40°05'S, 64°23'W); Plottier (38°58'S, 68°14'W); L. Aluminé (38°55'S, 71°09'W); Albardón Defferrari (38°17'S, 59°22'W); La. de los Padres (37°57'S, 57°44'W); La. La Brava (37°53'S, 57°58'W); La. San Antonio (37°37'S, 59°52'W); pond in Ea. "Los Tajamares" (37°32'S, 65°09'W); La. Quillalauquen (37°29'S, 60°30'W); La. Quetré Huitrú (37°22'S, 64°34'W); La. La Peluda (37°22'S, 64°37'W); La. Chimalauquen (37°17'S, 60°54'W); La. La Providencia (37°00'S, 60°11'W); La. El Tronco (36°57'S, 65°58'W); La. Cochicó (36°55'S, 62°18'W); La. Salada Grande (36°55'S, 56°58'W); La. Alsina (36°51'S, 62°06'W); La. La Fortuna (36°47'S, 65°37'W); La. Don Tomás (36°37'S, 64°19'W); La. Blanca Grande (36°29'S, 60°54'W); La. La Espuma (36°25'S, 65°41'W); La. Plaza Montero (36°11'S, 59°10'W); La. del Burro (35°42'S, 57°55'W); pond 3 km E of Gral. Pico Park (35°40'S, 63°43'W); La. La Limpia (35°37'S, 57°48'W); La. Chascomús (35°36'S, 58°02'W); La. Vitel (35°32'S, 58°07'W); pond in Ea. "El Ceibo" (35°32'S, 64°13'W); 10 more unnamed localities along roads of the province of La Pampa; La. de Monte (35°27'S, 58°49'W); La. de Gómez (34°37'S, 61°07'W); La. El Carpincho (34°35'S, 60°54'W); La. Mar Chiquita (Junín) (34°27'S, 61°11'W); La. La Andrea; La. Sarco, La. Encadenada, La. Tres Lagunas (all between 34°05'S and 34°37'S; 65°08'W and 65°38'W); La. Nassau (33°57'S, 65°22'W); La. Melincué (33°43'S, 61°28'W); R. Ceballos (31°12'S, 64°28'W); La. Santo Domingo (31°10'S, 64°20'W). **BOLIVIA:** Pond at Serranía de San José (17°58'S, 60°48'W) (Bayly, 1992). **CHILE:** L. Mause (Puerto Montt) (41°27'S, 72°58'W) (Brehm, 1937a); L. Calbuco (41°16'S, 72°32'W) (Löffler, 1961); L. Riñihue (39°49'S, 72°19'W) (Zúñiga and Domínguez, 1978); L. Chungará (18°15'S, 69°10'W) (Andrew *et al.*, 1989). **COLOMBIA:** Pool at Páramo Chisacá (4°21'N, 74°12'W), L. Tota (5°33'N, 72°58'W), La. Negra Superior (6°01'N, 73°00'W), La. Colorada (6°10'N, 72°30'W), La. Alto de las Cruces (6°13'N, 72°53'W) (Gaviria, 1989). **ECUADOR:** Lake near Papallacta (0°22'S, 78°07'W) (Löffler, 1963). **PERU:** Tarns at San Antonio de Esquilache (16°06'S, 70°18'W) and surroundings of Lagunillas (15°45'S, 70°44'W), pools A, B, C, D, E, H, and J at Capachica Peninsula, near Camjata (15°37'S, 69°50'W) (Harding, 1955); pool W of Puno (15°51'S, 70°03'W), L. Umayo (15°45'S, 70°10'W), pools near Juliaca (15°28'S, 70°09'W), L. Sillacunca (approx. 14°43'S, 69°25'W) (Löffler, 1955).

Boeckella (P.) longicauda Daday, 1901. **ARGENTINA:** Marsh at Amenkelt (50°03'S, 69°01'W); L. Ghio (47°19'S, 71°33'W).

Boeckella (B.) meteoris Kiefer, 1928 (= *B. dentifera* Brehm, 1935). **ARGENTINA:** L. Cardiel (48°57'S, 71°14'W); L. Ghio (47°19'S, 71°33'W); L. Blanco (45°54'S, 71°13'W); L. Colhue Huapi (45°30'S, 68°46'W); L. Musters (45°24'S, 69°12'W); La. Quichaura (43°33'S, 70°38'W); La. Ñe-Luan (41°29'S, 68°46'W); La. Blanca (39°03'S, 70°23'W); La. Salada (at La Dulce) (38°16'S, 59°09'W); La. El Paraíso (37°34'S, 60°47'W);

La. de Pozuelos (22°20'S, 66°00'W). **BOLIVIA:** La. Pelada (22°45'S, 67°10'W) (Bayly, 1992). **CHILE:** L. Cisnes and pond at Torres del Paine National Park (around 51°03'S, 72°53'W) (Bayly, 1992); Cajón de Plomo (33°07'S, 70°08'W) (Brehm, 1935b).

Boeckella (B.) michaelsoni (Mrázek, 1901) (= *B. pygmaea* Daday, 1901, *B. anderssonorum* Ekman, 1905). **CIRCUMANTARCTIC ISLANDS:** South Georgia Is. (54°16'S, 36°31'W); Falkland Is.: Port Stanley (51°38'S, 57°52'W), Port Louis (51°31'S, 58°08'W) (Ekman, 1905a). **ARGENTINA:** Ponds at Ushuaia Peninsula (54°50'S, 68°19'W); L. Roca (54°48'S, 68°36'W); La. Asher (53°47'S, 68°30'W); La. Luz (54°42'S, 65°40'W); L. San Ricardo (54°40'S, 67°43'W); L. Escondido (54°39'S, 67°49'W); L. Santa Laura (54°38'S, 67°40'W); La. Verde (54°36'S, 67°35'W); La. Los Renos; L. Fagnano (54°34'S, 68°00'W); La. Pescado (54°27'S, 67°02'W); L. Chepelmuth (54°24'S, 67°34'W); La. Antuk (54°24'S, 67°20'W); L. Yehuín (54°22'S, 67°44'W); La. Esperanza (54°20'S, 67°43'W); L. Roca (50°32'S, 72°50'W); L. Argentino (50°15'S, 72°33'W); pond near L. San Martín (approx. 49°00'S, 72°30'W); pond near L. Cardiel (approx. 48°59'S, 71°30'W); L. Posadas (47°30'S, 71°51'W); L. Fontana (44°56'S, 71°29'W); L. La Plata (44°52'S, 71°50'W); L. Pico 1 (44°15'S, 71°31'W); L. Pico 3 (44°15'S, 71°36'W); L. Pico 4 (44°12'S, 71°37'W); La. Los Niños (44°01'S, 71°29'W); L. Rosario (43°15'S, 71°22'W); La. Brecham (43°04'S, 71°29'W); E. Amutui Quimei (43°03'S, 71°45'W); La. Terraplén (42°59'S, 71°31'W); La. El Martillo (42°55'S, 71°32'W); L. Largo (42°54'S, 71°33'W); La. Willimanco (42°53'S, 71°16'W); L. Krugger (42°53'S, 71°45'W); L. Futalaufquen (42°50'S, 71°41'W); L. Verde (42°43'S, 71°44'W); L. Menéndez (42°43'S, 71°50'W); L. Rivadavia (42°34'S, 71°40'W); L. Cholila (42°28'S, 71°42'W); L. Lezama (42°27'S, 71°30'W); L. Epuyén (42°10'S, 71°39'W); L. Huechulafquen (39°46'S, 71°25'W). **CHILE:** L. Toro (51°12'S, 72°45'W), L. Pehoe (51°07'S, 73°04'W), L. Nordenskjöld (51°03'S, 72°58'W) (Soto and Zúñiga, 1991); L. Jovito, La. Redonda in Torres del Paine National Park (both around 51°03'S, 72°53'W) (Bayly, 1992); L. Lynch (48°33'S, 75°34'W), L. General Carrera (= L. Buenos Aires) (46°30'S, 72°00'W), L. Chiguay (45°56'S, 71°50'W), L. Pólux (45°43'S, 71°53'W) (Araya and Zúñiga, 1985).

Boeckella (P.) occidentalis Marsh, 1906 (= *B. godeti* Delachaux, 1928). **BOLIVIA:** L. Poopó (18°48'S, 67°06'W) (Marsh, 1906); Huancaroma (17°40'S, 67°30'S) (Bayly, 1992). **CHILE:** L. Chungará (18°15'S, 69°10'W) (Araya and Zúñiga, 1985); L. Cotacotani (18°14'S, 69°13'W) (Bayly, 1992). **COLOMBIA:** La. Corazón Partido (3°56'N, 74°10'W), La. La Guitarra (3°57'N, 74°13'W), La. El Sorbedero (3°57'N, 74°12'W), La. El Nevado (3°57'N, 74°11'W), La. La Primavera (3°59'N, 74°13'W), La. Bocagrande (4°19'N, 74°08'W) and pool in Páramo Curubital, La. del Otún (4°42'N, 75°28'W) (Gaviria, 1989). **ECUADOR:** Close to Cayambe Volcano (00°01'N, 77°54'W) (Löffler, 1963). **PERU:** L. Suches (16°56'S, 70°24'W), L. Saracocha (15°47'S, 70°38'W), Colorada II (15°22'S, 70°21'W), Pampamarca (14°08'S, 71°29'W) (Bayly, 1992); L. Titicaca (15°48'S, 69°26'W) (Marsh, 1906); L. Arapa (15°09'S, 70°01'W), L. Lagunillas (15°45'S, 70°44'W), L. Umayo (15°45'S, 70°10'W), R. Ramis, R. Desaguadero (16°44'S, 69°00'W), pool at Unduavi Pass, pond K at Capachica Peninsula near Camjata (15°37'S, 69°50'W) (Harding 1955); lake in Cordillera Apolobamba

(14°42'S, 69°20'W), Yauviviri (14°38'S, 73°57'W), Tun-gasuka close to Sicuani (14°10'S, 71°14'W), La. Junín (11°00'S, 76°08'W), lakes in Cordillera Huayhuash (approx. 10°19'S, 76°50'W), Cordillera Negra (approx. 94°7'S, 77°40'W) and Cordillera Blanca (approx. 8°55'S, 77°36'W) (Löffler, 1955); L. Naticocha (11°0'S, 76°25'W) (Delachaux, 1928).

Boeckella (P.) palustris (Harding, 1955) (= *P. peruviensis* Löffler, 1955). **ARGENTINA:** Vegas de la Gloria (reserva de San Guillermo) (28°10'S, 69°20'W); La. Los Cóndores in Nevados del Aconquija (27°15'S, 65°08'W); El Pozo in Nevado de las Animas (26°50'S, 65°55'W); Lagunas de Huaca Huasi in Cumbres Calchaquíes (26°40'S, 65°44'W); Vega Verde, Vega Laguna Azul, Vega del Pucará, Vega de la Ciénaga Grande, Vega Laguna del Lobo, pool beside Vega Matadero, Circular, Blanca, Neblina, Ranas, Grande, Muerta, Chica, Rosada, Gris; La. Pululos (22°35'S, 66°44'W). **BOLIVIA:** Pool near Chojllas (22°21'S, 67°06'W), "Conchostraca" pool (22°18'S, 67°14'W), pool near Mama Khumu (22°16'S, 67°05'W) (Bayly, 1992). **PERU:** L. Loripongo (16°50'S, 70°05'W) (Bayly, 1992); pond near Lagunillas (15°45'S, 70°45'W) (Harding, 1955); pool on the road Puno-Arequipa (14°09'S, 71°01'W) (Löffler, 1955).

Boeckella (B.) poopensis Marsh, 1906 (= *B. rahmi* Brehm, 1935, *B. birabenti* Brehm, 1954). **ARGENTINA:** Trelew (43°17'S, 65°06'W); La. Carrilauquen Grande (41°10'S, 69°29'W); La. Negra (39°30'S, 70°20'W); La. El Colegio (39°04'S, 62°45'W); R. Salado at Puelches (38°09'S, 65°54'W); pond beside Route 1 (La Pampa) (37°57'S, 63°36'W); La. La Isla (37°55'S, 62°31'W); La. San Antonio (37°37'S, 59°52'W); Puan (37°33'S, 62°48'W); La. El Carancho (37°27'S, 65°04'W); Balneario Utracán (37°17'S, 64°37'W); pond at Ea. "Los Manantiales" (37°12'S, 64°18'W); La. Los Carrizales (37°04'S, 67°52'W); La. Dulce (37°02'S, 62°38'W); La. Guaminí (37°01'S, 62°22'W); La. Los Horcones (37°00'S, 56°56'W); La. Salada Grande (36°55'S, 56°58'W); La. Cochicó (36°55'S, 62°18'W); La. del Monte (36°55'S, 62°28'W); La. Parque Luro (36°55'S, 64°17'W); ditch 2 km N of Naicó (36°55'S, 64°24'W); La. Alsina (36°51'S, 62°04'W); La. Chadilauquen (35°25'S, 64°19'W); 11 more localities along roads of the province of La Pampa; La. de Gómez (34°38'S, 61°07'W); La. Mar Chiquita (Junín) (34°27'S, 61°11'W); La. Melincué (33°43'S, 61°28'W); La. Mar Chiquita (30°42'S, 62°37'W); Salar del Hombre Muerto (25°30'S, 66°51'W). **BOLIVIA:** La. Verde (22°48'S, 67°48'W), Herrera (22°35'S, 67°33'W), Guacha (22°33'S, 67°31'W), Polques (22°32'S, 67°37'W), Catalcito (22°31'S, 67°15'W), Este (22°31'S, 67°29'W), Puripica Chico (22°31'S, 67°30'W), Chojllas (22°22'S, 67°06'W), Ramaditas (21°38'S, 68°05'W), R. Puntas Negras (22°23'S, 67°04'W), Khara (21°54'S, 67°52'W), Chulluncani (21°32'S, 67°52'W), Soledad (17°44'S, 67°22'W) (Bayly, 1992); L. Poopó (18°48'S, 67°06'W) (Marsh, 1906); pond near Pazña (18°39'S, 66°49'W)

(Harding, 1955). **CHILE:** Santa Rosa (27°05'S, 69°10'W), Calientes III (25°00'S, 68°38'W), Calientes II (23°31'S, 67°34'W), Calientes I (23°08'S, 67°25'W) (Bayly, 1992); salt lake close to Chiu-Chiu (22°20'S, 68°40'W) (Brehm, 1935a). **PERU:** L. Loriscota (16°52'S, 70°02'W), L. Parinacochas (15°17'S, 73°42'W), L. Collpacocho (15°15'S, 70°03'W) (Bayly, 1992).

Boeckella (P.) poppei (Mrázek, 1901) (= *B. entzi* Daday, 1901, *B. dubia* Daday, 1901, *B. klutei* Brehm, 1926, *B. erubescens* Brehm, 1935). **ANTARCTICA AND CIRCUMANTARCTIC ISLANDS:** Epishelf lakes: Beaver Lake (Amery Ice Shelf) (70°48'S, 68°15'E) (Bayly and Burton, 1993); Ablation Lake (70°49'S, 68°25'W) (Heywood, 1977). Graham's Land: L. Boeckella close to Esperanza (63°26'S, 57°01'W), (Ekman 1905); Horseshoe Bay (Harding, 1941). South Orkney Is.: Sombre Lake (Weller, 1977) and Heywood Lake (Clarke *et al.*, 1989) on Signy Is. (60°43'S, 45°38'W). South Shetland Is.: Livingston Is. (63°00'S, 60°00'W), Rey Jorge Is. (or 25 de Mayo) (62°01'S, 58°04'W) (Pezzani-Hernández, 1973); Potter Peninsula (62°14'S, 58°38'W) (Paggi, 1983); Decepción Is. (62°58'S, 60°59'W) (Ringuet, 1958); Petrel Lake on Penguin Is. (62°06'S, 57°56'W) (Janiec, 1988). South Georgia Is. (54°16'S, 36°31'W) (Poppe and Mrázek, 1895). Falkland Is.: pond W of Port Stanley (51°38'S, 57°52'W) (Ekman, 1905). **ARGENTINA:** Moor at Rancho Hambre (54°47'S, 67°43'W); La. Pescado (54°27'S, 67°02'W); La. San Luis (53°55'S, 67°37'W); Monte Observación (50°23'S, 68°55'W); El Zurdo (51°59'S, 71°13'W); Los Pozos at Gallegos Norte (51°35'S, 68°59'W); pond 35 km N of Coyle (50°38'S, 69°17'W); pool at 50°05'S, 69°29'W; marsh at Amenkelt (50°03'S, 69°01'W); pool at Misioneros (49°59'S, 68°33'W); Las Horquetas (49°16'S, 68°00'W); pond near L. Cardiel; La. Súnica (43°03'S, 71°04'W); Bariloche (41°09'S, 71°18'W); El Junco (40°28'S, 70°39'W); La. Blanca (39°03'S, 70°23'W); E. Los Barriales (38°34'S, 67°49'W); La. Pozo de las Animas (35°11'S, 70°07'W); La. La Niña Encantada (35°10'S, 69°52'W); La. del Sosneado (34°51'S, 69°55'W); tributary of R. La Hornilla (Pampa de Achala) (31°37'S, 64°53'W). **CHILE:** La. Tehuelches Este, La. Redonda, La. Larga, ponds at Torres del Paine National Park (all around 51°03'S, 72°53'W) (Bayly, 1992); E. del Yeso (33°39'S, 70°08'W); La. del Parrillar (Araya and Zúñiga, 1985); La. Piuquenes (approx. 33°35'S, 69°56'W) (Brehm, 1935c).

Boeckella (P.) silvestrii (Daday, 1901). **ARGENTINA:** Pool near R. Santa Cruz (50°12'S, 71°38'W); close to L. Viedma; L. San Martín (48°52'S, 72°40'W); La. de Garayalde (44°38'S, 66°44'W).

Boeckella (P.) vallengini (Scott, 1914) (= *B. volucris* Kiefer, 1944). **CIRCUMANTARCTIC ISLANDS:** Marion Is. (46°55'S, 37°45'E) (Kiefer, 1944), Prince Edward Is. (46°38'S, 37°55'E); Crozet Is. (46°27'S, 52°00'E); Kerguelen Is. (49°30'S, 69°30'E) (Bayly, 1992); Falkland Is. (51°38'S, 57°52'W) (Scott, 1914).