

# Distributional patterns of the South American species of *Hyaella* (Amphipoda: Hyaellidae)

## Patrones de distribución de especies sudamericanas de *Hyaella* (Amphipoda: Hyaellidae)

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### ABSTRACT

Distributional patterns of the South American species of the freshwater amphipod genus *Hyaella* were analysed using a panbiogeographic approach. Five generalized tracks were found: (1) northern Andes to Lake Titicaca (*H. dielaii*, *H. meinerti*, *H. dybowskii*, *H. jelskii*, *H. lubominsky*, and *H. pauperocavae*); (2) lake Titicaca (*H. armata*, *H. cuprea*, *H. latinamus*, *H. lucifugax*, *H. montforti*, *H. neveulemairei*, *H. robusta*, *H. tiwanaku*, *H. simplex simplex*, and *H. solida*); (3) central Andes (*H. fossamancinii* and *H. kochi*); (4) Pampas (*H. bonariensis*, *H. caeca*, *H. castroi*, *H. longispina*, *H. montenegrinae*, *H. pampeana*, *H. pernix*, *H. pseudoazteca*, and *H. warmingii*); and (5) Subantarctic (*H. patagonica*, *H. costera*, *H. curvispina*, *H. chilensis*, *H. falklandensis*, *H. franciscae*, *H. neonoma*, *H. patagonica*, and *H. simplex*). One node was found at lake Titicaca (intersection of generalized tracks 1, 2, and 3).

**KEYWORDS:** Chile, *Hyaella* South America, biogeography

### RESUMEN

Se estudió el patrón de distribución de especies Sudamericanas del género de anfípodo de agua dulce *Hyaella* mediante una aproximación panbiogeográfica. Se encontraron cinco trazos (1) Norte de los Andes al Lago Titicaca (*H. dielaii*, *H. meinerti*, *H. dybowskii*, *H. jelskii*, *H. lubominsky*, y *H. pauperocavae*); (2) Lago Titicaca (*H. armata*, *H. cuprea*, *H. latinamus*, *H. lucifugax*, *H. montforti*, *H. neveulemairei*, *H. robusta*, *H. tiwanaku*, *H. simplex simplex*, y *H. solida*); (3) Andes centrales (*H. fossamancinii* y *H. kochi*); (4) Pampas (*H. bonariensis*, *H. caeca*, *H. castroi*, *H. longispina*, *H. montenegrinae*, *H. pampeana*, *H. pernix*, *H. pseudoazteca*, y *H. warmingii*); y b (5) Subantártico (*H. araucana*, *H. costera*, *H. curvispina*, *H. chilensis*, *H. falklandensis*, *H. franciscae*, *H. neonoma*, *H. patagonica*, y *H. simplex*). Se encontró un nodo en el lago Titicaca que correspondió a la intersección de los trazos 1; 2 y 3.

**PALABRAS CLAVE:** Chile, *Hyaella* Sudamérica, biogeografía

### INTRODUCTION

Freshwater amphipods inhabit superficial and underground waters. They have different trophic roles: herbivores, carnivores, detritivores or omnivores (Witt and Hebert 2000; Väinöla *et al.* 2008). In South America, amphipods are represented by species inhabiting subterranean (Bogidellidae) and superficial (Hyaellidae) waters (Väinöla *et al.* 2008). Hyaellidae are represented in the Americas by the genus *Hyaella*, which has been recently studied from

a taxonomic perspective (Witt and Hebert 2000; Witt *et al.* 2003; González and Wattling 2002a-c, 2003a-c; González 2003; González *et al.* 2006), and is possibly found in New Zealand (Pugh *et al.* 2002).

Recent studies on Chilean species of *Hyaella* indicate that they inhabit subsaline inland waters, such as streams and shallow ponds in northern Chile (González 2003; De los Ríos *et al.* 2010), coastal inland waters (González 2003), and oligotrophic inland waters of Patagonia between 38-

51° S (González 2003; De los Ríos *et al.* 2007; De los Ríos and Roa 2010). Similar studies have investigated Central Argentina and Patagonia (Lopretto 1982, 1983a, b; Miserendino 2001; Jergentz *et al.* 2004; Miserendino *et al.* 2008; Zilli *et al.* 2008).

Integrative biogeographic studies of the species of *Hyaella* have not yet been conducted. Here we undertake a preliminary track analysis of the South American species of this genus to improve current understanding of their patterns of geographical distribution.

## MATERIAL AND METHODS

Distributional data for this study were obtained from the literature (Lopretto 1982, 1983a, b; Pereira, 1985, 1989, 2004 Pereira *et al.* 1985, 1989; Stock and Plavoet 1991; Bond-Buckup and Araujo 1998; Casset *et al.* 2001; González and Coleman 2002; González and Watling 2002a-c, 2003a-d; Carrera and Günkel 2003; González 2003; Jergentz *et al.* 2004; Pereira 2004; Coleman & González, 2006; Galan & Herrera, 2006; González *et al.* 2006; Da Silva and Bond-Buckup 2008; Dos Santos *et al.* 2008; Dutra *et al.* 2008; Zilli *et al.* 2008; Rauque and Semenas 2009; Spaccesi & Rodríguez. 2009; De los Ríos *et al.* 2007, 2010; De los Ríos and Roa 2010; Cardoso *et al.*, 2011; Bastos-Pereira & De Padua-Bueno, 2012). It was not considered the species names *H. curvispina cangallensis*, *H. aff. curvispina*, *H. thomsoni*, *H. sapropelica* and *H. lalage* (Brehm-Lunz, 1928, 1935; Gonzalez & Watling, 2003c; González *et al.*, 2006)

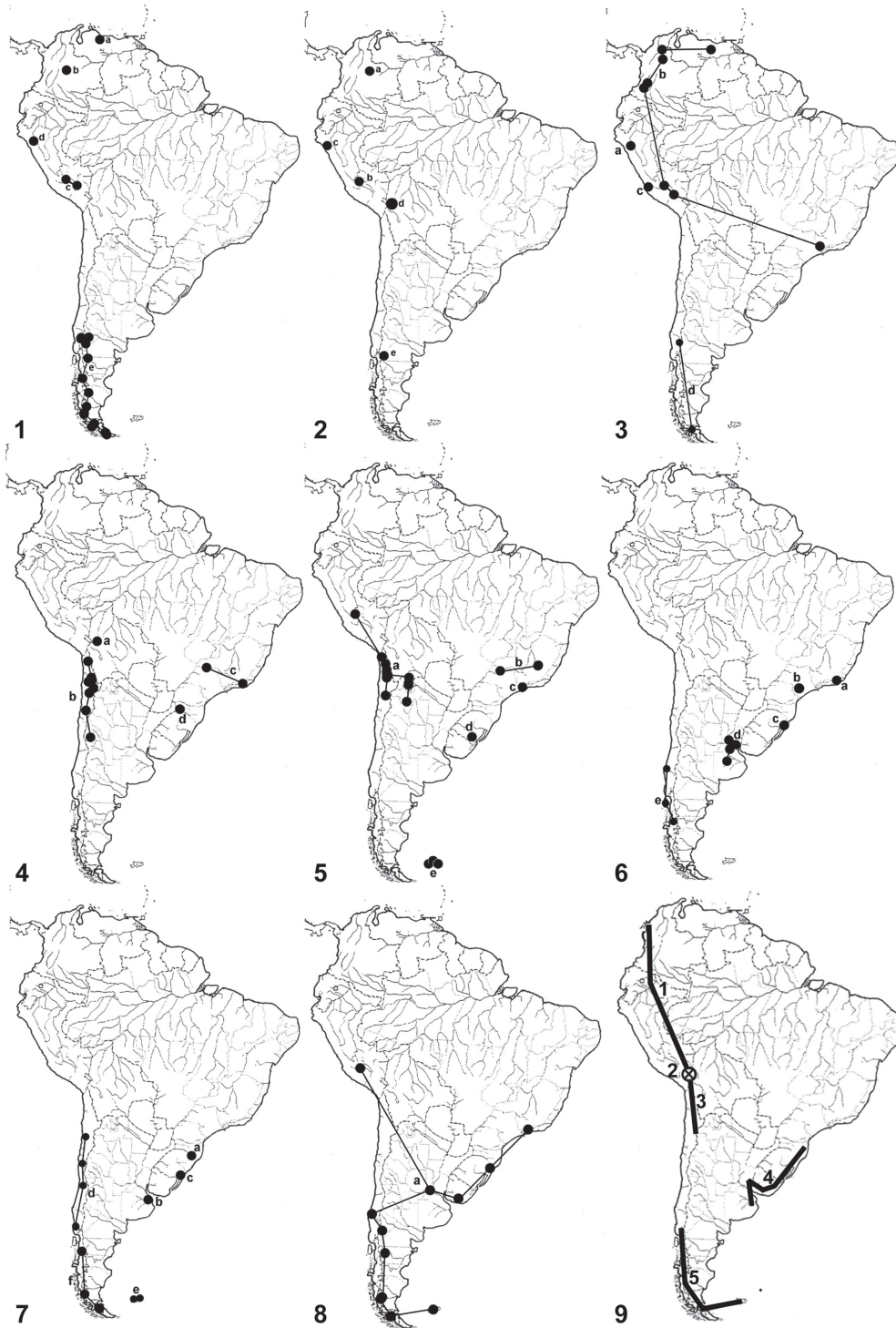
Coordinates of localities were obtained from the literature or calculated on maps and rounded to minutes. Within each country, localities are ordered roughly in a south-north direction. For details on the localities of each species see Appendix.

The panbiogeographic approach involves plotting distributions of different taxa on maps and joining their separate localities with lines called individual tracks. These tracks represent the geographical coordinates of species or higher taxa. Operationally, they consist of lines drawn on a map connecting the localities at which the taxa occur according to their geographical proximity. When different individual tracks are superimposed, the resulting summary lines are considered generalized tracks, which are interpreted as indicating the pre-existence of ancestral biotas that subsequently became 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. This node thus constitutes a

composite area. For further details about panbiogeographic methods, see Morrone (2004, 2006, 2009).

## RESULTS

Individual tracks and localities of the species analyzed are represented in figures 1-9. In northern South America, *H. anophthalma*, *H. azteca* and *H. inermis* has been reported from Venezuela (Fig. 1a) and *H. paramoensis* from northern Colombia (Fig. 1b). *Hyaella quindioensis* has been reported in inland mountain waters of the Colombian Andes (Fig. 2a). In the northern Andean inland waters, *H. simplex cangallensis* (Fig. 1c), *H. pauperocavae* (Fig. 2b), *H. lubomirskii* (Fig. 3a), *H. dybowskii* (Fig. 2c), and *H. meinerti* (Fig. 3b) have been reported. In coastal zones of Lake Titicaca (Peru and Bolivia), 17 species have been reported: *H. echinus*, *H. crawfordi*, *H. gauthieri*, *H. longipalma*, *H. neveulemairei*, *H. cuprea*, *H. nefrens*, *H. armata*, *H. lucifugax*, *H. montforti*, *H. tiwanaku*, *H. longipes*, *H. latimanus*, *H. robusta*, *H. longispina*, *H. solida*, and *H. jelskii* (Fig. 4a). *Hyaella fossamancinii* has been reported from inland waters of the Andes Argentina and northern Chile (Fig. 4b). *Hyaella kochi* occurs in Argentinean and Chilean mountain inland waters (Fig. 5a). Several species have been reported near the Atlantic coast: *H. gracilicornis* (Fig. 4c), *H. warmingi* (Fig. 5b), *H. pernix* (Fig. 5c), *H. spelaea*, *H. longistila* (Fig. 6a), *H. caeca* (Fig. 6b), and *H. dielaiiii* (Fig. 4d). The following species have been reported from southern Brazil: *H. carstica* (Fig. 2e), *H. longistila* (Fig. 2f), *H. pseudoazteca* (Fig. 5d), *H. montenegrinae* (Fig. 6c), *H. castroi* (Fig. 7a), and *H. pleoacuta* (Fig. 7c). Two species are restricted to streams from Buenos Aires province, Argentina: *H. bonariensis* (Fig. 6d) and *H. pampeana* (Fig. 7b). The species *H. costera* has been reported from coastal wetlands, streams, and shallow ponds from northern Chilean Patagonia to northern Chile, in the Antofagasta region (Fig. 7d). *Hyaella chiloensis* has been reported from Central Patagonia, coastal lakes in Chiloé Island, and Concepción in central Chile (Fig. 6e). *Hyaella falklandensis* (Fig. 7e) and *H. neonoma* (Fig. 5e) have been reported from the Falkland Islands (Islas Malvinas). In Patagonia, including nearby islands, *H. patagonica* has been reported (Fig. 1e). In Argentina, *H. curvispina* has been reported from southern, central and northern Argentinean Patagonia in large and deep lakes and in Buenos Aires province; it has also been reported from the Falkland Islands, Uruguay, southern Brazil specifically in coastal inland waters, and from Peru (Fig. 8a). *Hyaella rionegrina* has been reported from one locality in Chubut province, in Argentinean Patagonia (Fig. 2d). A species restricted to Chile is *H. simplex*, is known from southern Chilean Patagonia, specifically from coastal inland waters of the Strait of Magellan strait and from a high-mountain shallow lake in northern Chilean Patagonia



FIGURAS 1-8. Individual tracks: 1, *Hyaella anophtala*, *H. azteca*, *H. inermis* (a), *H. paramoensis* (b), *H. simplex cangallensis* (c), *Hyaella patagonica* (d); 2, *H. quindioensis* (a), *H. pauperocavae* (b), *H. dybowskii* (c), *H. rionegrina* (d); 3, *H. lubomirskii* (a), *H. meinerti* (b), *H. jelskii* (c), *H. simplex* (d); 4, *H. longipalma*, *H. neveulemairi*, *Hyaella cuprea*, *H. nefrens*, *H. armata*, *H. lucifugax*, *H. montforti*, *H. tiwanaku*, *H. longipes*, *H. latimanus*, *H. robusta*, *H. longispina*, and *H. solida* (a), *H. fossamanchini* (b), *H. gracilicornis* (c), *H. dielaiii* (d); *H. carstica* (e); 5, *H. kochi* (a), *H. warmingi* (b), *H. pernix* (c), *H. pseudoazteca* (d), *H. neonoma* (e); *H. longistila* (6); 6, *H. longistila* (a), *H. caeca* (b), *H. montenegrinae* (c), *H. bonariensis* (d), *H. chiloensis* (e); 7, *H. castroi* (a), *H. pampeana* (b), *H. pleoacuta* (c), *H. costera* (d), *H. falklandensis* (e), *H. franciscaae* (f); 8, *H. curvispina* (a). Fig. 9. Generalized tracks and nodes; 1, northern Andes generalized track; 2, lake Titicaca generalized track and node; 3, central Andes generalized track; 4, Pampas generalized track; 5, Subantarctic generalized track.

(Fig. 3d). *Hyaella franciscaae* has been reported from lakes of Torres del Paine National Park, in the Magellan region (Fig. 7f).

Based on the overlap of the different individual tracks, we identified five generalized tracks (Fig. 9):

(1) Northern Andes. Inland waters of Venezuela and Peru between 10° N-15° S. The species assigned to this track are *H. anophtalma*, *H. inermis*, *H. quindioensis*, *H. paramoensis*, *H. meinerti*, *H. dybowski*, *H. jelskii*, *H. lubominsky*, and *H. pauperocavae*.

(2) Lake Titicaca. The species assigned to this track are *H. armata*, *H. crawfordi*, *H. cuprea*, *H. echinus*, *H. gauthieri*, *H. latinamus*, *H. lucifugax*, *H. montforti*, *H. neveulemailei*, *H. robusta*, *H. tiwanaku*, *H. simplex simplex* and *H. solida*.

(3) Central Andes. Inland waters from central Argentina (31° S) to northern Chile (18-26° S). The species assigned to this track are *H. fossamancinii* and *H. kochi*.

(4) Pampas. Inland waters close to the Atlantic coast from Buenos Aires province (35° S) in central Argentina to Uruguay and southern Brazil (19° S). The species assigned to this track are *H. bonaerensis*, *H. caeca*, *H. carstica*, *H. castroi*, *H. dielaii*, *H. longistila*, *H. montenegrinae*, *H. pampeana*, *H. pernix*, *H. pseudoazteca*, and *H. warmingii*.

(5) Subantarctic. Andean inland waters of Argentina and Chile between 39-51° S, southern Patagonian plains between 51-53° S, Tierra del Fuego, and the Falkland Islands. Species assigned to this track are *H. curvispina*, *H. chilensis*, *H. falklandensis*, *H. franciscaae*, *H. neonoma*, *H. patagonica*, and *H. simplex*.

One node (Fig. 9) was found where generalized tracks 1, 2, and 3 intersect, at lake Titicaca.

## DISCUSSION

The generalized tracks identified are similar to those described by Menu-Marque *et al.* (2000), who applied this procedure to the copepod genus *Boeckella*. That study identified a generalized track in southern Patagonia, the Atlantic coast of Argentina, the Andean mountains of northern Argentina and Chile, and the Andean regions of Bolivia, Colombia and Ecuador. Nevertheless, the nodes reported in the present study differ from those identified by Menu-Marque *et al.* (2000). Species of *Hyaella* are also known from Mexico and Central America, Bousfield (1996) supported it, and suggested the presence of *Austrohyaella* and *Mesohyaella* genus in South America. Nevertheless,

the recent literature mentioned the presence of *Hyaella* genus for all American continent (Vainöla *et al.*, 2008; Witt & Hebert 2000; Witt *et al.*, 2006)

The absence of nodes in southern Patagonia agrees with analyses for Subantarctic islands (Pugh *et al.* 2002) and southern South America (Dos Santos *et al.* 2008), about similarities between continental Subantarctic species. Our results contrast with those from calanoid copepods (Menu-Marque *et al.* 2000) and fishes of the genus *Galaxias* (Cussac *et al.* 2004), that are known from southern Patagonia, New Zealand and adjacent islands, a different situation was reported for species of *Hyaella* that are widespread in South North America (Witt & Hebert, 2000; Witt *et al.* 2003). The results of geographical distribution of *Hyaella* genus are similar in comparison to freshwater crabs of *Aegla* genus that is located in central and southern Argentina and Chile, and east South America, specifically Brazil and Uruguay (Pérez-Lozada *et al.*, 2002, 2004, 2009). Nevertheless, species reports for practically all South American inland waters are rather scarce, so future analyses may modify these results, specifically between 18-8° N, the Titicaca basin, and eastern South America.

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APPENDIX

- H. anophthalma* (Ruffo, 1957). VENEZUELA: Cuevas de Hueque (Galán & Herrera, 2006).
- H. armata* (Faxon 1876). BOLIVIA: Achacache (16° 00' S; 68° 42' W). PERU: Coata bay (15° 30' S; 69° 54' W), Taquili/Amantane (15° 42' S; 69° 42' W), Chuquito (15° 53' S; 69° 52' W), Juli (16° 12' S; 69° 29' W), Isla Suana (16° 20' S; 68° 51' W), Golfo Desaguadero (16° 33' S; 69° 02' W) (González & Coleman 2002).
- H. bonariensis* Bond-Buckup *et al.* 2008. ARGENTINA: Salto, Buenos Aires province (34° 18' S; 60° 20' W), Pergamino river (35° 56' S; 60° 28' W), Cañada Honda, San Antonio de Areco (34° 04' S; 59° 30' W), Arroyo Manantiales (33° 42' S; 60° 20' W) (Dos Santos *et al.* 2008).
- H. brasiliensis* Bousfield 1996. BRAZIL: stream close to Prudentópolis (25° 12' S; 50° 57' W).
- H. caeca* Pereira & Goulart 1989. BRAZIL: Gruta Tobias de Baixo, Município de Ipiranga (around 23° 26' S; 47° 25' W) (Pereira 1989).
- Hyalella carstica* (Bastos-Pereira & Bueno, 2012). BRAZIL: High Sao Francisco River (20°19'59,6" S; 45°36'25.3"W) (Bastos-Pereira & Bueno, 2012).
- H. castroi* González *et al.* 2006. BRAZIL: Vale das Trutas (28° 47' S; 49° 51' W) (González *et al.* 2006).
- H. chiloensis* González & Watling 2001. CHILE: Notuco, Chiloé (42° 39' S; 73° 49' W), Laguna Redonda, Concepción (36° 48' S; 73° 04' W), río Ñirepan, Coihaique (around 45° 34' S; 72° 03' W) (González 2003).
- H. costera* González & Watling 2001. CHILE: Quebrada Paposo, Antofagasta (25° 01' S, 70° 28' W), Limache (32° 59' S; 71° 15' W), El Molle (29° 58' S; 70° 56' W), isla Teja, Valdivia (39° 48' S; 73° 12' W) (González 2003).
- H. crawfordi* (Coleman & González, 2006). Perú: Molinopampa lake Titicaca (6°11' S; 77°37'W); Catachaca, Bay of Puno (15°50' S; 71°08' W) (Coleman & González, 2006).
- H. cuprea* (Faxon 1876). BOLIVIA: Santa Rosa, lake Titicaca (16° 18' S; 60° 00' W), Lake Titicaca, unknown site (15° 50' S; 69° 25' W) (González & Watling 2003d).
- H. curvispina* Shoemaker 1942. ARGENTINA: Falkland Islands (51° 49' S; 59° 22' W), Argentinean lake (50° 15' S; 72° 33' W), Puerto Bandera (50° 18' S; 72° 47' W); laguna larga, Futalaufquen (42° 50' S; 71° 41' W); Lacar lake (40° 10' S; 71° 22' W); Horqueta stream, city of Arrefices, Buenos Aires province (34° 04' S; 60° 06' W) (Jergentz *et al.* 2004); Lujan river (34° 28' S; 59° 00' W); Samborombón river, Brandsen (35° 07' S; 60° 30' W), Samborombón river, Chascomús (35° 34' S; 58° 02' W), Samborombón Bay (35° 50' S; 57° 23' W). CHILE: Punta Arenas (53° 11' S; 70° 56' W). PERU: Pampa of Cangallo (13° 25' S; 74° 20' W). URUGUAY: Carrasco creek, Montevideo (around 34° 53' S; 56° 03' W) (Grosso & Peralta 1999; Casset *et al.* 2001; Dos Santos *et al.* 2008; Dutra *et al.* 2008; Spaccesi & Rodrigues 2009).
- H. dielaii* Pereira 2004. BRAZIL: Alto da Serra, São Paulo (around 27° 01' S; 52° 47' W) (Pereira 2004).
- H. dybowskii* (Wrzesniewski 1879). PERU: Paucal, Montaña Nacho (07° 00' S; 79° 08' W) (González & Watling 2002b).
- H. echinus* (Coleman & González, 2006). PERU: Siripata, Uruñi bay, lake Titicaca (15°50' S; 71°08' W) (Coleman & González, 2006).
- H. falklandensis* Bousfield 1996. ARGENTINA: West Falkland, 4 sites (around 51° 39' S; 59° 58' W); East Falkland, 4 sites (around 51° 49' S; 58° 52' W) (Stock & Plavoet 1991; Dos Santos *et al.* 2008).
- H. fossamanchini* Cavalieri 1959. ARGENTINA: San Juan province (31° 30' S; 68° 32' W). CHILE: Santa Bárbara (21° 58' S; 68° 36' W), Conchi (22° 00' S; 68° 36' W), Salado (20° 20' S; 68° 39' W), Salvador (22° 23' S; 69° 31' W); Toconao (23° 11' S; 68° 00' W), Miscanti (23° 44' S; 67° 47' W), Miniques (23° 45' S; 67° 47' W); Río La Ola, Copiapó (around 27° 21' S; 70° 18' W), Surire, Arica (18° 50' S; 69° 02' W), Putana river (22° 34' S; 67° 52' W), El Tatío (22° 21' S; 68° 00' W), Salar de Punta Negra (24° 35' S; 68° 58' W) (González 2003; Dos Santos *et al.* 2008; De los Ríos *et al.* 2010; De los Ríos-Escalante 2011).
- H. franciscae* González & Watling 2003. CHILE: Laguna El Paso, Torres del Paine (50° 29' S; 72° 58' W), Lago Risopatrón (44° 15' S; 72° 31' W), Laguna Melliza (51° 00' S; 73° 00' W), Laguna Redonda (51° 00' S; 73° 00' W), Laguna Larga (53° 20' S; 69° 00' W), Lago Sarmiento (51° 04' S; 72° 45' W); Laguna Melliza (51° 03' S; 72° 55' W); Tres Puentes wetland (53° 06' S; 70° 52' W), Porvenir pond (53° 17' S; 70° 19' W) (González 2003; González & Watling 2003a).
- Hyalella gauthieri* (Coleman & González, 2006). Perú: Oruñi Bay, Taquili island (15°46' S; 69°41' S) (Coleman & González, 2006).
- H. gracilicornis* (Faxon 1876). BRAZIL: Campos, Rio de Janeiro (21° 28' S; 41° 13' W), Represa Belvedere, Campus da UFV, Minas Gerais State (18° 55' S; 48° 01' W) (González & Watling 2003c).
- H. inermis* Smith 1875. ECUADOR: Río Itambi (07° 11' S; 78° 12' W). VENEZUELA: Lake Valencia (10° 11' N; 68° 00' W) (Carrera & Gunkel 2003; González & Watling 2003b).
- H. jelskii* (Wrzesniewski 1879). PERU: Cordillera de Punamarca (14° 02' S; 76° 16' W) (González & Watling 2002b).
- H. kochi* González & Watling 2001. ARGENTINA: Jujuy province, Yavi Chico River (22° 05' S; 65° 25' W), reservoir near Escuela Agrotécnica in Huamahuaca (23° 11' S; 65° 20' W), Tilcara, lake north of Tilcara, near Río Grande (23° 33' S; 65° 23' W), Tucumán province, streamlet tributary of Río de Los Sojas, route 307 in the direction of Tucumán with Tafi del Valle (26° 56' S; 65° 39' W). CHILE: Guallatire, Arica (18° 29' S; 70° 16' W), Bofedal de Arabilla, Arica (19° 14' S; 68° 51' W), El Tatío (22° 21' S; 68° 00' W), Salar de Punta Negra (24° 35' S; 68° 58' W), Loa river, Antofagasta (22° 14' S; 68° 36' W); Santa Bárbara (21° 58' S; 68° 36' W), Conchi (22° 00' S; 68° 36' W), Salado (20° 20' S; 68° 39' W). PERU (12° 03' S; 75° 07' W) (González 2003; González & Watling 2002b; Dos Santos *et al.* 2008; De los Ríos *et al.* 2010).
- H. latimanus* (Faxon 1876). BOLIVIA: Llampopata, lake Titicaca (16° 00' S; 69° 15' W), Isla Coati, lake Titicaca (16° 15' S; 68° 40' W), Huatajata, lake Titicaca (16° 15' S; 68° 45' W) (González & Watling 2003d).
- H. longipalma* (Faxon 1876). BOLIVIA: lake Titicaca (16° 25' S; 68° 45' W) (González & Watling 2003d).

- H. longipes* (Faxon 1876). BOLIVIA: Achacache, lake Titicaca (16° 06' S; 68° 26' W) (González & Watling 2003d).
- H. longispina* González & Coleman 2002. BOLIVIA: Paton (15° 38' S; 69° 15' W), Ancoraimes (15° 54' S; 68° 42' W), Siripata Bay (16° 05' S; 69° 03' W). PERU: Molinopampa (around 16° 13' S; 69° 22' W), lake Titicaca, Chococoyo Bay (15° 24' S; 69° 30' W), Capachica (15° 39' S; 69° 47' W), Tamar (15° 37' S; 69° 52' W) (González & Coleman 2002).
- H. longistila* (Faxon 1876). BRAZIL: swamp 3 miles from Campos, Rio de Janeiro (21° 28' S; 41° 13' W) (González & Watling 2003c). Ijaci, Minas Gerais State (21°10'24" S; 44°56'24.2" W), Lagoa Feia, Rio do Janeiro State (21°05' 53.8" S; 41°20' 22.4" W)(Bastos-Pereira & Bueno, 2012).
- H. lubomirskii* (Wrzesniowski 1879). PERU: Pacasmayo (07° 25' S; 79° 34' W) (González & Watling 2002b).
- H. lucifugax* (Faxon 1876). BOLIVIA: Juli, lake Titicaca (16° 10' S; 69° 30' W) (González & Watling 2003d).
- H. meinerti* Stebbing 1899. BRAZIL: Sao Paulo (23° 20' S; 46° 22' W). COLOMBIA: Río Meléndez (08° 16' N; 73° 36' W), Río Cali (07° 10' N; 73° 28' W), Río Piendamó (03° 00' N; 76° 00' W), Laguna de San Rafael (02° 50' N; 76° 15' W). PERU: Apurimac river, NE Ayacucho (15° 00' S; 72° 00' W). VENEZUELA: Laguna de Espino (08° 23' S; 66° 06' W). ECUADOR: Camar province (03° 20' S; 46° 22' W) (González & Watling 2002b, 2003b).
- H. montenegrinae* Bond-Buckup & Araujo 1998. BRAZIL: Rio Grande do Sul, municipio de Sao José dos Ausentes (29° 29' S; 50° 15' W) (Bond-Buckup & Araujo 1998).
- H. montforti* Chevreux 1907. BOLIVIA: Bay of Challa (16°30' S; 68°50' W; Isla del Sol (16°00' S; 69° 15' W); Achacache Bay (15° 58' S; 68° 50' W), Río Suchez, lake Titicaca (15° 37' S; 69° 05' W). PERU: small lake in Isle of Ampura (15°40' S; 69° 52' W) (González & Watling 2003d).
- H. nefrens* González & Watling 2003. BOLIVIA: Santa Rosa, lake Titicaca (16° 18' S; 60° 00' W) (González & Watling 2003d).
- H. neonoma* Stock & Platvoet 1991. ARGENTINA: West Falkland: Pebble Island (51° 19' S; 59° 34' W); New Island (51° 42' S; 61° 16' W); Big Pond, Pebble Island (51° 19' S; 59° 34' W); East Falkland: small pond at Bertha's Beach (51° 53' S; 58° 22' W); unnamed creek on Wireless Ridge near Stanley (around 51° 40' S; 57° 55' W); Murrell River, around Stanley (around 51° 42' S; 57° 50' W); Mullet Creek stream, Fitzroy river, unnamed stream at the crossing with Mount Pleasant (all around 51° 49' S; 58° 26' W) (Stock & Platvoet 1991; Dos Santos *et al.* 2008).
- H. neveulemairei* Chevreux 1904. BOLIVIA: Bay of Challa (16° 30' S; 68° 50' W), Isla del Sol (16° 00' S; 69° 15' W), Bay of Achacache (15° 58' S; 68° 50' W); near archipiélago de Campanario, lago Grande (15° 40' S; 69° 20' W), Escoma, lake Titicaca (15° 35' S; 69° 10' W). PERU: Small lake in Isle of Ampura (Yapura) (15° 40' S; 69° 52' W) (González & Watling 2003d).
- H. pampeana* Cavalieri 1968. ARGENTINA: Arroyo Vitel, Chascomús lagoon (35° 33' S; 58° 03' W); Laguna de Cardiel (Lopretto 1983a; Dos Santos *et al.* 2008).
- H. patagonica* (Cunningham 1871) (= *H. araucana* Grosso & Peralta 1999, see Morrone 2001). ARGENTINA: Peninsula near Ushuaia, streamlet Gente Grande (54° 43' S; 68° 01' W), Fagnano lake (54° 34' S, 68° 00' W), Santa Cruz, Fossiles river (50° 20' 21" S; 72° 15' 22" W), Puelo lake (42° 10' S, 71° 39' W), Lacar lake (40° 10' S; 71° 22' W); Verde lagoon, Chapelco (40° 07' S; 71° 13' W); Blanca lagoon, Neuquén (39° 02' S; 70° 21' W); Santa Cruz province, arroyo Calafate (50° 20' S; 72° 15' W), lake Escondido, Ushuaia (54° 39' S; 67° 49' W), stream near Lake Escondido (54° 43' S; 68° 01' W); Olmie river, Santa Cruz (47° 45' S; 71° 30' W) (Santos *et al.* 2008); lake Mascardi (41° 17' S; 71° 38' W). CHILE: river of los Dervos (Ciervos), Magallanes (around 53° 10' S; 70° 56' W); Peninsula Brunswick (53° 30' S; 71° 25' W); Deseado lake (54° 22' S; 68° 40' W), Azopardo river (54° 28' S; 68° 58' W); De las Minas river, Pta. Arenas (53° 09' S; 70° 54' W), Puerto Natales (51° 55' S; 72° 27' W); Pólux lake (45° 43' S; 71° 53' W), Chorrillo de la Piedra (52° 12' S; 74° 46' W); Seco river (53° 05' S; 70° 52' W); Lago de los Ciervos, Punta Arenas (53° 11' S; 70° 56' W); Lago Sarmiento (51° 04' S; 72° 45' W); Negra lagoon (39° 15' S; 71° 42' W); Tinquilco lake (39° 10' S; 71° 43' W), Toro lake (39° 08' S; 71° 42' W), Chico lake (39° 08' S; 71° 42' W), Verde II lake (39° 08' S; 71° 42' W), Los Patos lagoon (39° 10' S; 71° 42' W); Conguillío lagoon (38° 38'; 71° 37' W), Verde I lagoon (38° 41' S; 71° 46' W), Arcoiris lagoon (38° 40' S; 71° 37' W), Captren lagoon (38° 38' S; 71° 42' W); Tres Puentes wetland (53° 07' S; 70° 52' W); Isla Picton (55° 03' S; 66° 55' W) (Schallenberg 1931; González 2003; De los Ríos *et al.* 2007; Santos *et al.* 2008; De los Ríos & Romero-Mieres 2009; Rauque & Semenas 2009; De los Ríos & Roa, 2010).
- H. paramoensis* Andres 1988. COLOMBIA: Laguna Negra, Paramo de Chisaca (04° 20' N; 74° 12' W) (González & Watling 2003b).
- H. pauperocavae* González & Watling 2002. PERU: trout culture station "El Ingenio", Huancayo (12° 03' S; 75° 07' W) (González & Watling 2002b).
- H. pernix* (Moreira 1903). BRAZIL: Lagoa Esgotada, Itatiaia, Rio de Janeiro (around 22° 30' S; 44° 37' W) (Pereira 1985).
- H. pleoacuta* González *et al.* 2006. BRAZIL: Rio Grande Do Sul, Sao José Dos Ausentes, Vale das Trutas (28° 47' S; 49° 50' W) (González *et al.* 2006; Da Silva & Bond-Buckup 2008).
- H. pseudoazteca* González & Watling 2003. BRAZIL: Reserva Ecológica de Taim, Rio Grande do Sul State (32° 27' S; 52° 38' W) (González & Watling 2003c).
- H. quindioensis* González & Watling 2003. COLOMBIA: Quindio (06° 14' N; 73° 26' W) (González & Watling 2003b).
- H. rionegrina* Grosso & Peralta 1999. ARGENTINA: Prov. Río Negro: El Bolsón (around 41° 58' S; 71° 30' W) (Dos Santos *et al.* 2008).
- H. robusta* Chevreux 1907. BOLIVIA: Bay of Achacache (16° 06' S; 68° 26' W) (González & Watling 2003d).
- H. simplex* Schellenberg 1943. CHILE: Punta Arenas (53° 10' S; 70° 54' W), Punta Delgada, Magallanes (52° 15' S; 69° 45' W), Lago Quillehue (39° 34' S; 71° 32' W); Redonda lagoon (51° 01' S; 72° 52' W); Larga lagoon (51° 01' S ; 72° 52' W); Monserrat lagoon (51°07' S; 72° 57' W); Puerto Natales ponds (51° 42' S; 72° 47' W); Río Seco ponds (53° 06' S; 70° 53' W); Tres Puentes wetland (53° 06' S; 70° 52' W); Porvenir pond (53° 17' S; 70° 19' W) (González 2003; González & Watling 2003a).
- H. simplex cangallensis* Schellenberg 1943. PERU: Pampa de Cangallo (13° 25' S; 74° 20' W), Laguna Urcos, Cuzco (13° 41' S; 71° 37' W) (González & Watling 2002b).



*H. solida* (Chevreux 1907). PERU: Small lake in isle of Ampura (Yapura) (15° 40' S; 69° 52' W) (González & Watling 2003d).

*H. tiwanaku* González & Watling 2003d. BOLIVIA: Tiquina, lake Titicaca (16° 10' S; 68° 45' W), Moro, lake Titicaca (16° 00' S; 69° 15' W), Majal, lake Titicaca (16° 00' S; 69° 15' W), Puerto Pérez, lake Titicaca (16° 20' S; 68° 35' W), Chua, lake Titicaca (16° 10' S; 68° 45' W), Lago Mullini (17° 04' S; 66° 37' W) (González & Watling 2003d).

*H. warmingi* (Stebbing 1899). BRAZIL: Lagoa Santa, Minas Gerais State (19° 38' S; 43° 53' W), Gruta Mirasol, Sao Paulo State (20° 00' S; 49° 00' W) (González & Watling 2003c).

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