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FIRST CONFIRMED REPORT OF A PRIMARY FRESHWATER CRAB (BRACHYURA: PSEUDOTHELPHUSIDAE) ASSOCIATED WITH BROMELIADS IN THE NEOTROPICS

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ABSTRACT

Bromeliads can hold water in their axils, which can harbor an astonishing diversity of macro invertebrates, including decapod crustaceans. Except of a casual report from Trinidad, true freshwater crabs in these phytotelmata have been found exclusively in the Old World, and observations in the New World of crabs associated with bromeliads have been limited to sesarmid crabs, non-primary freshwater crabs that generally do not breed in freshwater. Here we report the presence of a true, or primary, freshwater crab in water-filled axils of a bromeliad in the Neotropics. Immature specimens of the pseudothelphusid crab provisionally identified as *Epilobocera* cf. *gilmanii* (Smith, 1870) were collected from inside the bromeliad *Hohenbergia penduliflora* (A. Richard) Mez. in western Cuba. Pseudothelphusid crabs have developed additional respiratory structures, which make them suitable candidates for a life in phytotelmic microhabitats. It is still uncertain whether in Cuba these crabs actually breed in phytotelmata or only use this microhabitat during their early life stages.

KEY WORDS: Cuba, *Epilobocera*, *Hohenbergia*, phytotelmata

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INTRODUCTION

Phytotelmata are semi-permanent bodies of water found in living or dead terrestrial plants. These freshwater microhabitats are quite common, especially in the tropics, but due to their small size and their concealment in inaccessible places they have often been overlooked by scientists (Mogi, 2004; Jocquet et al., 2013). The fauna living in the phytotelmata is diverse and is dominated by insects and other macro invertebrates (Maguire, 1971; Greeney, 2001; Mogi, 2004). A more recent study on the Pacific coast of Colombia (Aguilera Arango et al., 2011) revealed the presence of 42 genera of arthropods associated with bromeliads in mangrove forests, including the sesarmid crab *Sesarma sulcatum* Smith, 1870. Other grapsid crabs found in the water tanks of bromeliads have been mentioned by von Hagen (1977) in his study of tree-climbing crabs from Trinidad.

The decapod crustacean fauna of phytotelmata comprises mainly sesarmids (Cumberlidge et al., 2005; Jocquet et al., 2013) and falls into two groups: 1) tree-climbing crabs that use the trees for protection, concealment and as a food source, but their offspring do not need to develop in phytotelmic water reservoirs (Cumberlidge et al., 2005), and 2) crabs that breed in phytotelmata, the so-called primary freshwater crabs (Diesel, 1989; Diesel and Schubart, 2007). Primary, or true, freshwater crabs are brachyurans that have adopted freshwater, semi-terrestrial, or terrestrial modes of life, and that reproduce by direct development, never having free-living larval stages (Yeo et al., 2008; Cumberlidge and Ng, 2009).

An increasing number of primary freshwater crabs have been reported from phytotelmata in the Old World, including rainforests in Africa, mangroves in Asia, and rainforest canopies in Madagascar (Cumberlidge et al., 2005). The vast majority of these primarily freshwater species inhabit tree holes. According to Cumberlidge et al. (2005), reports of phytotelmic freshwater crabs (Potamonautidae and Gecarcinucidae) have all been from the Old World, and phytotelmy has not been reported among New World freshwater crabs (Trichodactylidae and Pseudothelphusidae). An often-missed note (Anonymous, 1983), however, briefly reported the presence of a pseudothelphusid crab in a bromeliad in Trinidad.

All primary freshwater crab species from Cuba belong to *Epilobocera* Stimpson, 1860 (Pseudothelphusidae), but the exact number of species is difficult to establish because to their confusing and unstable taxonomy (Rodríguez and Magalhães, 2005). Chace and Hobbs (1969), Pretzmann (1972), and Rodriguez (1982) recognized four species and subspecies. Pretzmann (2000), Capolongo and Pretzmann (2002), and Capolongo (2003, 2005) recognized these species but also introduced several new taxa at subgeneric, specific, and subspecific levels in addition to some varieties as *nomina nuda*, or invalid names. The most recent species

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lists include 9 (Ng et al., 2008) or 14 (Villalobos and Álvarez, 2008) species and subspecies from Cuba. We report here the first authenticated instance of a primary freshwater crab (Pseudothelphusidae) living in the water-filled axils of a bromeliad from the Neotropics (New World).

Material and Methods

Specimens were collected at the *mogote* Dos Hermanas (22°35′25″N, 83°40′49″W), an isolated, steep-sided and dome-like limestone hill, or karst, located in Valle de Viñales, Municipio Viñales, Pinar del Río, western Cuba (Fig. 1). There are no natural bodies of water in the immediate vicinity of the sampling site. The nearest permanent stream is located roughly 5 km southwest of the collection site. Temporary creeks are dry most of the year (between November to April), as during collection, and are located about 1 km southeast and 2 km northeast of the collection site. Both bodies of water are separated from the collection site by cultivated lowlands and abrupt elevations of several hundred meters height.

Crabs were collected from water-filled leaf axils of a bromeliad, *Hohenbergia penduliflora* (A. Rich.) Mez (Fig. 2), found growing attached to the walls of the *mogote* at a height of 12 m. All bromeliads with crabs were of a similar size, and the volume of the water reservoir ranged between 125 and 480 ml (Table 1). Each plant contained a single crab, typically located close to the water pool at the bottom of the plant. Bromeliads with crabs were placed on a white tray, leaves were carefully detached, and crabs were transferred into labeled vials containing 80% alcohol. A total of seven crabs were collected, but another four or five specimens jumped to the ground and rapidly disappeared.

Specimens are deposited in Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA), Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José (UCR-MZ), and in the collection of the Grupo de Aguas Interiores, División de Ecología Funcional, Instituto de Ecología y Sistemática, La Habana, Cuba (IES). Crabs were identified according to the descriptions and/or keys provided by Rathbun (1905), Chace and Hobbs (1969), Rodriguez (1982), and Capolongo (2003) as well as by comparisons with voucher material of species of *Epilobocera* from Cuba deposited in INPA. The following abbreviations are used: carapace width (cw), measured across the carapace at its widest point; carapace length (cl), measured along the midline, from the frontal to the posterior margin; and male first gonopod (G1). Illustrations were made using a Leica M8 stereomicroscope equipped with a camera lucida. Measurements are in millimeters.

Fig. 2. Bromeliads (*Hohenbergia penduliflora*) at the collection site, the *mogote* Dos Hermanas in Valle de Viñales, Municipio Viñales, Pinar del Río, western Cuba. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x.

Systematics

Infraorder Brachyura Latreille, 1802
Family Pseudothelphusidae Ortmann, 1893
Epilobocera Stimpson, 1860
Epilobocera cf. *gilmanii* (Smith, 1870)
(Figs. 3, 4)

Material Examined.—1 immature male (cw 25.0, cl 14.9), INPA 2013, Cuba, Pinar del Río Province, Viñales, Dec.

Fig. 1. General view of the collection site, the *mogote* "Dos Hermanas" in Valle de Viñales, Municipio Viñales, Pinar del Río, western Cuba. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x.

Table 1. General characteristics of the seven plants of the bromeliad *Hohenbergia penduliflora* where crabs were collected in western Cuba.

	Plant no.						
	1	2	3	4	5	6	7
Water content (ml)	165	125	240	190	390	480	435
Number of leaves	12	10	14	13	12	15	15
Diameter (m)	1.84	2.20	1.80	1.59	1.57	2.15	2.0
Leave width (cm)	10.2	10.2	9.4	8.3	6.8	10.0	9.7

2012, Orestes Carlos Bello-González leg.; 2 immature individuals (cw 27.0, cl 17.5; cw 23.0, cw 15.5), IES, Cuba, Pinar del Río Province, Viñales, Dec. 2012, Orestes Carlos Bello-González leg.; 1 immature female (cw 24.3, cl 14.5), UCR-MZ 3229-01 (Fig. 3), same collection site; 3 juvenile males (cw 18.0, cl 10.7; cw 14.2, cl 8.7; 1 specimen with damaged carapace), UCR-MZ 3230-01, same collection site, Feb. 2013, Orestes Carlos Bello-González leg.

Additional Material Examined.—*Epilobocera* cf. *cubensis* Stimpson, 1860: 1 male, INPA 1455, Guantánamo Province, Baracoa, cueva del Humo, Aug. 2001, unkown collector;

Fig. 3. Dorsal and ventral view of an immature male of *Epilobocera* cf. *gilmanii* (UCR-MZ 3229-01) collected from a bromeliad (*Hohenbergia penduliflora*) at the *mogote* Dos Hermanas in Valle de Viñales, Municipio Viñales, Pinar del Río, western Cuba. Scale bars = 1 cm. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1937240x.

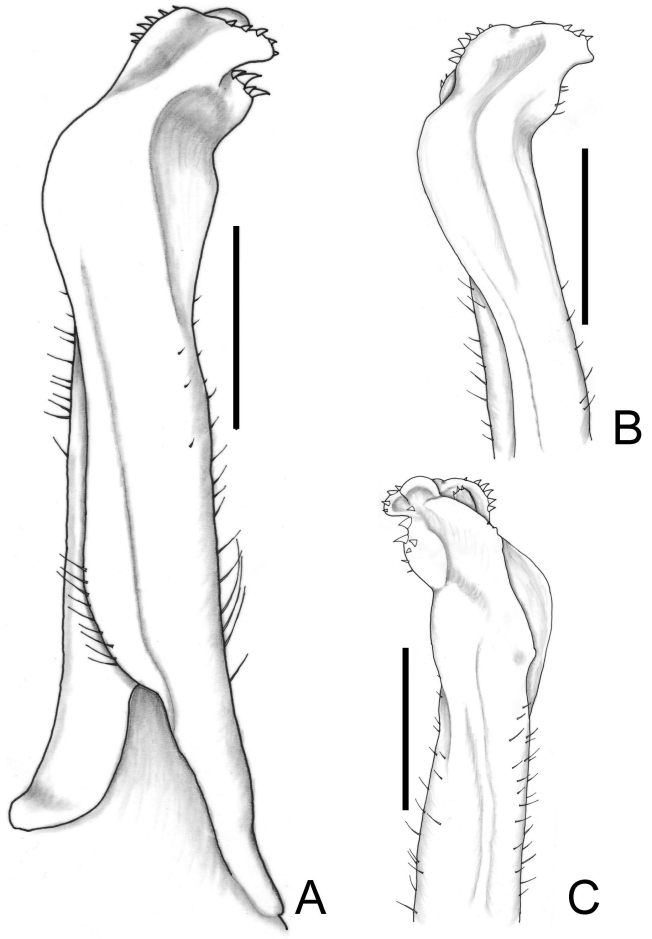

Fig. 4. First gonopod of *Epilobocera* cf. *gilmanii* (INPA 2013), immature male collected in a bromeliad (*Hohenbergia penduliflora*) from Cuba: A, entire gonopod, caudomesial view; B, distal part, mesial view; C, distal part, laterocephalic view. Scale bars = 1 mm.

1 male, INPA 1457, Camagüey Province, Najasa, 24 Oct. 1949, unkown collector). *Epilobocera* cf. *gilmanii* (Smith, 1870): 1 male, INPA 1459, Matanzas Province, Unión de Reyes, Río Negro, 27 Oct. 2004, unknown collector; 1 male, INPA 1460, Isla de Pinos (= Isla de la Juventud), 10 March 2002, unknown collector; 1 male, INPA 1461, Cuba, La Habana Province, 2 April 2003, unknown collector.

Gonopods.—The male specimen is a subadult and its gonopods and chelipeds are therefore not fully developed. The specimen nevertheless exhibits the characters diagnostic to the genus (Fig. 4).

The first gonopd long, slender, with distinct rounded mesial bulge directed cephalically with marginal suture clearly twisted from caudomesial side to cephalic side in distal third. Apical portion with subterminal lateral bulge armed with 4 teeth, few setae, mesial process comb-like with row of 6 teeth directed cephalically. Caudal margin of apex nearly straight, projected caudally into developing finger-like caudal process with row of 5 teeth; cephalic margin irregular, with few minute proximal papillae, distinct rounded plate projected apically in median position. Both margins enclosed laterally by intermediate narrow plate with 3 small denticles on apical margin.

Discussion

The specific identity of the crab is provisional because of the somewhat confusing taxonomic status of the Cuban pseudothelphusids (Capolongo, 2003, 2014; Rodríguez and Magalhães, 2005) as well as the subadult condition of the specimens on hand. Capolongo (2003) recognized four species from Cuba; of these, *E. cubensis* is found in eastern-central Cuba, and *E. gilmanii* in western-central Cuba and the Isla de la Juventud (= Isla de Pinos), the type locality. Capolongo (2003) considered that the crab populations from this island as different subspecies. The present specimens possess morphological characters (such as the front gradually curving downwards, aperture of the efferent branchial channel with a slim spine, and third maxilliped with the distal border of the merus slightly concave) that have been used to characterize *E. gilmanii* by several authors (Rathbun, 1905; Chace and Hobbs, 1969; Rodriguez, 1982; Capolongo, 2003). The features of the G1 (Fig. 3) are similar to those of its congeners (see Chace and Hobbs, 1969; Rodríguez and Williams, 1995). Although the specimens came from western Cuba (Viñales), which is near the type locality of *E. gilmanii synoecia* Capolongo and Pretzmann, 2002 (Cuevas de Santo Tomás), it is preferable not to assign a subspecific category to our specimens since their subadult condition with not fully developed gonopods precludes a conclusive identification. A comprehensive morphological and genetic study is needed to resolve the taxonomic issues related to the Cuban pseudothelphusids.

Considering that the specimens of the Cuban species of *Epilobocera* are large animals, with individuals reaching carapace widths of over 80 mm (Rodriguez, 1982), the subadult and juvenile specimens on hand might be using the bromeliad axils as a temporary habitat, probably for shelter or eventually for foraging. Moreover, species of *Hohenbergia* are considered as relatively small bromeliads, which in Jamaica seldom harbor crabs, and if they do the crabs are typically found as single and not fully-grown individuals (Diesel and Schubart, 2007). Diesel and Schubart (2007) hypothesized that there was a relationship between the size of bromeliads and the presence and size of the crabs found in the plant's water reservoir. It is therefore possible that larger Cuban bromeliads might contain adult and perhaps even breeding specimens of *Epilobocera* cf. *gilmanii*.

Primary freshwater crabs that are phytotelmic have direct development (like all freshwater crabs), but not all freshwater crabs habitually breathe air, so the ability of pseudothelphusids to do this makes it possible for these crabs to exploit these unusual microhabitats (see Cumberlidge et al., 2005). There is no direct evidence that *Epilobocera* cf. *gilmanii* completes its entire life cycle in bromeliads, and additional observations are necessary to better understand the association between the different life stages of the crab and the phytotelmata of different species of bromeliads.

Only 8 out of more than 1300 species of primary freshwater crabs are so far known to live in phytotelmic microhabitats, and all of these are from different localities in the Old World (Cumberlidge et al., 2005; Cumberlidge and Ng, 2009). Phytotelmic primary freshwater crabs are phylogenetically diverse and include species of Potamonauti-

Table 2. Primary, or true, freshwater crabs known to live in phytotelmic microhabitats (modified from Cumberlidge et al., 2005).

Species	Family	Geographic region	Microhabitat	References
Old World				
Globonautes macropus (Rathbun, 1898b)	Potamonautidae (Deckeniinae)	West Africa	Tree holes	Cumberlidge (1991, 1996 a, b); Cumberlidge and Sachs (1991, 2000)
Malagasya goodmani (Cumberlidge, Boyko and Harvey, 2002)	Potamonautidae (Deckeniinae)	Madagascar	*Pandanus* tree axils	Cumberlidge et al. (2002)
Malagasya antongilensis (Rathbun, 1905)	Potamonautidae (Deckeniinae)	Madagascar	Rainforest, tree holes, *Ravenala* leaf axils	Cumberlidge et al. (2005)
Potamonautes raybouldi Cumberlidge and Vannini, 2004	Potamonautidae (Potamonautinae)	East Africa	Tree holes	Cumberlidge and Vannini (2004)
Ceylonthelphusa scansor Ng, 1995	Gecarcinucidae	Sri Lanka	Tree holes	Ng (1995)
Archipelothelphusa sp. Ng, 1991	Gecarcinucidae	Philippines	Tree holes	Ng (1991a)
Arachnothelphusa sp. Ng, 1991	Gecarcinucidae	Borneo	Tree holes	Ng (1991b)
Arachnothelphusa merarapensis Grinang, Min and Ng, 2015	Gecarcinucidae	Borneo	Tree holes	Grinang et al. (2015)
New World				
Epilobocera cf. *gilmanii* (Smith, 1870)	Pseudothelphusidae	Cuba	Bromeliad axils	Present study
Unidentified species	Pseudothelphusidae	Trinidad	Bromeliad axils	Anonymous (1983)

dae (4) and Gecarcinucidae (4) (Cumberlidge et al., 2005; families according to the current system proposed by Cumberlidge and Ng, 2009). The present finding is the first well-documented record of a species of primary freshwater crabs from a bromeliad in the New World, and adds another species of Pseudothelphusidae to this list (Table 2). There is actually a previous report that is the first observation of a primary freshwater crab in phytothelma from the Neotropics, based on a specimen of pseudothelphusid found in a bromeliad from Trinidad (Anonymous, 1983). The specimen, however, could not be accurately identified. Robert Gore examined the specimen and speculated that it could be *Potamocarcinus* cf. *dentatus* (currently *Guinotia dentata* (Latreille, 1825)). *Guinotia dentata*, however, does not occur in Trinidad (Rodriguez, 1982). The pseudothelphusid fauna of Trinidad consists of only two species: *Rodriguezus garmani* (Rathbun, 1898a) and *Microthelphusa odaelke* (Bott, 1970) (see Rodriguez, 1982). The first is a large-sized (adults can reach up to 110 mm cw), amphibious, burrowing species (Maitland et al., 2002) whose adults are often found using natural boulder or crevice refuges, but smaller specimens have been collected from burrows, hidden beneath boulders or in rock crevices around clear, fast-flowing streams (Maitland, 2003). No ecological information is available for the second species. The photo in Anonymous (1983) does not offer any clues that would allow an accurate identification of the species, except perhaps for an impression that it is of a small specimen. Taking into account the behavior and microhabitat preferences of *R. garmani* and the small size of the species of *Microthelphusa* (Rodriguez, 1982), one might suspect that the Trinidad specimen could represent either *M. odaelke* or an undescribed species.

Pseudothelphusids are well adapted to live outside the water, and numerous representatives of this family are found far away from bodies of water living under rocks in dried-up river basins or in the holes of dry, rotten logs in forests where it does not rain for several months of the year (Holthuis, 1959; C.M. and I.S.W., pers. obs.). The extraordinary capacity of these crabs to survive outside of water is related to their ability for aerial respiration. Díaz and Rodríguez (1977) reported that the branchial chambers of terrestrial crabs and of pseudothelphusids have an accessory breathing organ known as "pseudolung" in addition to retaining functional gills for aquatic respiration. This adaptation has enabled these crabs to explore habitats outside permanent water bodies, including phytotelmic microhabitats.

It is not clear why freshwater crabs have not been reported more often from phytotelmata in the Neotropics other than the traditionally low level of exploration combined with the inaccessible nature of phytotelmic microhabitats. Cumberlidge et al. (2005) noted that it is relatively rare to find crabs in phytotelmic habitats. Except for a casual finding (Anonymous, 1983), extensive explorations of phytotelmata in the cloud forests of Panama (Myers, 1969) and South America (C. W. Myers, pers. comm. to CM, 26 February 2013) aimed at surveying amphibians have not yielded a single published record of a primary freshwater crab from a bromeliad. Several studies have nevertheless reported the presence of grapsids in bromeliads in Brazil (Sattler and Sattler, 1965; Abele,

1972; Teixeira and Santos Sá, 1998) and Jamaica (Diesel, 1989; Schubart et al., 1998, 2010; Diesel et al., 2000), with *Metopaulias depressus* Rathbun, 1896 from Jamaica representing one of the most described relationships between a grapsid and its bromeliad habitat (Diesel and Schubart, 2007).

Bromeliad grapsids from Jamaica live in the axil water reservoirs of ground-dwelling bromeliads found on steep karst hills as well as in plants living up to 20 m above the ground (Diesel, 1989) This habitat is similar to our sampling site in Cuba, which could suggest that bromeliads on limestone hills are promising locations to encounter associated crabs. This microhabitat has been occupied by grapsid crabs in Jamaica and this evolutionary trend seems to favor the complete absence of primary freshwater crabs on this island (Rodriguez, 1982). In contrast, primary freshwater crabs might have successfully occupied this ecological niche in Cuban bromeliads and it is possible that grapsid crabs only rarely live in bromeliads water reservoirs in Cuba. It nevertheless remains to be clarified whether these crabs actually breed in phytotelmata or use this microhabitat only for protection, concealment, and feeding (see Cumberlidge et al., 2005).

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