

Recent advances in the biology of the Neotropical freshwater crab family Pseudothelphusidae (Crustacea, Decapoda, Brachyura)

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ABSTRACT. Pseudothelphusidae is a well diversified group of Neotropical freshwater crabs currently comprising 40 genera and at least 255 species and subspecies. The biology of these crabs has been an active field of research in the last 20 years. The aim of the present contribution is to discuss the significance of the new knowledge on the biology of these freshwater crabs after September 1992, to stress the interconnection of the diverse lines of research and at the same time to suggest promising new lines of investigation. All taxa described from September 1992 to October 2004 are listed, including one genus, one subgenus, 62 species and five subspecies. The implications of this new knowledge on the taxonomy, systematic and biogeography of the family are commented.

KEY WORDS. Biodiversity, biogeography, Neotropical region, taxonomy.

RESUMO. Avanços recentes no estudo da biologia dos caranguejos de água doce neotropicais da família Pseudothelphusidae (Crustacea, Decapoda, Brachyura). Pseudothelphusidae é um grupo bem diversificado de caranguejos de água doce neotropicais que compreende atualmente 40 gêneros e pelo menos 255 espécies e subespécies. A biologia desses caranguejos vem sendo um ativo campo de pesquisa nos últimos 20 anos. O objetivo desta contribuição é discutir o significado do conhecimento adquirido sobre a biologia desses caranguejos dulcícolas após setembro de 1992, enfatizar a relação das diversas linhas de pesquisa e, ao mesmo tempo, sugerir novas linhas promissoras de investigação. São relacionados todos os táxons descritos de setembro de 1992 a outubro de 2004, compreendendo um gênero, um subgênero, 62 espécies e cinco subespécies. São comentadas as implicações desse novo conhecimento na taxonomia, sistemática e biogeografia da família.

PALAVRAS CHAVE. Biodiversidade, biogeografia, região Neotropical, taxonomia.

The pseudothelphusids are a group of freshwater crabs of significance in several fields of biology, and in particular in tropical medicine due to the role of many of its species as secondary hosts for several species of lung flukes of the genus *Paragonimus* Braun, 1899 (Trematoda, Troglotrematidae). These crabs are a food staple in many rural communities in the Neotropics, particularly in Indian communities, passing the helminths not only to man, but also to pigs, dogs, felids and mustelids. From these organisms they pass to the primary hosts that are snails of several genera, to complete their cycles in the crabs (ACHA & SZYFRES 2001).

The biology of these crabs has been an active field of research in the last 20 years, including their taxonomy, biogeography and phylogenetic. The monograph by RODRÍGUEZ (1982) on the family Pseudothelphusidae listed all taxa published to that date, together with the respective bibliographic references. Later this list and bibliography was updated to 1992 by the same author (RODRÍGUEZ 1992). The aim of the present contribution is

to discuss the significance of the new knowledge on the biology of these freshwater crabs after September 1992, to stress the interconnection of the diverse lines of research and at the same time to suggest promising new lines of investigation.

New taxa, faunistic lists and taxonomic modifications described after September 1992

Since September 1992, 62 new species and five new subspecies have been described, and one genus and one subgenus have been erected (Tab. I). A review of the literature about the family showed that it currently has 40 genera and at least 255 valid species and subspecies, of which the largest number is found in Colombia (Tab. II).

Mexico. The Mexican species have been dealt with in a series of contributions by ÁLVAREZ & VILLALOBOS (1994, 1996, 1997, 1998) and VILLALOBOS & ÁLVAREZ (2003). Two new species of the genus *Phrygiopilus* Smalley, 1970, three new *Odontothelphusa* Rodríguez, 1982, one new *Potamocarcinus* H. Milne-Edwards,

Table I. New taxa of the Neotropical freshwater crab family Pseudothelphusidae described after September 1992, with their respective authority and countries of occurrence.

Taxon	Authority	Country
Epilobocerinae		
<i>Epilobocera</i>		
<i>E. capolongoi</i>	Stimpson, 1860	
<i>E. cubensis cubensis Natio baracoensis</i>	Pretzmann, 2000 ¹	Cuba
<i>E. cubensis cubensis Natio guisensis</i>	Capolongo & pretzmann, 2002	Cuba
<i>E. cubensis najasensis</i>	Capolongo & pretzmann, 2002	Cuba
<i>E. cubensis najasensis</i>	Capolongo & pretzmann, 2002	Cuba
<i>E. gilmani cuevanensis, nomen nudum</i>	Capolongo & Pretzmann, 2002	Cuba
<i>E. gilmani placensis</i>	Capolongo & Pretzmann, 2002	Cuba
<i>E. gilmani synoecia</i>	Capolongo & Pretzmann, 2002	Cuba
<i>E. wetherbeeii</i>	Rodríguez & Williams, 1995	Hispaniola
<i>E. (Neopilobocera)</i> type: <i>E. (N.) gertraudae</i> Pretzmann, 1965	Capolongo & Pretzmann, 2002	Cuba ²
Pseudothelphusinae: Hypolobocerini		
<i>Chaceus</i>		
<i>C. curumanensis</i>	Pretzmann, 1965	
<i>C. ibiricensis</i>	Campos & Valencia, 2004	Colombia
<i>C. ibiricensis</i>	Campos & Valencia, 2004	Colombia
<i>Hypolobocera</i>		
<i>H. barbacensis</i>	Ortmann, 1897	
<i>H. bouvieri rotundilobata</i> ³	Campos, Magalhães & Rodríguez, 2002	Colombia
<i>H. dantae</i>	Rodríguez, 1994	Colombia
<i>H. emberarum</i>	Rodríguez & Suárez, 2004	Peru
<i>H. esmeraldensis</i>	Campos & Rodríguez, 1995	Colombia
<i>H. kamsarum</i>	Rodríguez & Sternberg, 1998	Ecuador
<i>H. konstanzae</i>	Campos & Rodríguez, 1995	Colombia
<i>H. mindonensis</i>	Rodríguez & Sternberg, 1998	Ecuador
<i>H. muisnensis</i>	Rodríguez & Sternberg, 1998	Ecuador
<i>H. murindensis</i>	Campos 2003a	Colombia
<i>H. noanamensis</i>	Rodríguez Campos & López, 2002	Colombia
<i>H. ucayalensis</i>	Rodríguez & Suárez, 2004	Peru
<i>H. velezi</i>	Campos, 2003a	Colombia
<i>Lindacatalina</i>		
<i>L. sinuensis</i>	Pretzmann, 1977	
<i>L. sumacensis</i>	Rodríguez, Campos & López, 2002	Colombia
<i>L. sumacensis</i>	Rodríguez & Sternberg, 1998 ⁴	Ecuador
<i>Moritschus</i>		
<i>M. altaquerensis</i>	Pretzmann, 1965	
<i>M. caucasensis</i>	Rodríguez, Campos & López, 2002	Colombia
<i>M. caucasensis</i>	Campos, Magalhães & Rodríguez, 2002	Colombia
<i>Neostrengeria</i>		
<i>N. aspera</i>	Pretzmann, 1965	
<i>N. binderi</i>	Campos, 1992	Colombia
<i>N. gilberti</i>	Campos, 2000	Colombia
<i>N. libradensis appressa</i>	Campos, 1992	Colombia
<i>N. lobulata</i>	Campos, 1992	Colombia
<i>N. macaranae</i>	Campos, 1992	Colombia
<i>N. perijaensis</i>	Campos & Lemaitre, 1998	Colombia
<i>N. tencalanensis</i>	Campos, 1992	Colombia
<i>N. tonensis</i>	Campos, 1992	Colombia
Pseudothelphusinae: Kingsleyini		
<i>Achagua</i>		
<i>A. casanarensis</i>	Campos, 2001	
<i>A. casanarensis</i>	Campos, 2001	Colombia

Continued

Table I. Continued.

Taxon	Authority	Country
<i>Fredius</i>	Pretzmann, 1967	
<i>F. granulatus</i>	Rodríguez & Campos, 1998	Colombia
<i>F. stenolobus</i>	Rodríguez & Suárez, 1994 ⁵	Venezuela
<i>Kingsleya</i>	Ortmann, 1897	
<i>K. junki</i>	Magalhães, 2003	Brazil
<i>Microthelphusa</i>	Pretzmann, 1968	
<i>M. sucrensis</i>	Rodríguez & Campos, 2000	Venezuela
<i>Odonthelphusa</i>	Rodríguez, 1982	
<i>O. lacandona</i>	Álvarez & Villalobos, 1998	Mexico
<i>O. lacanjaensis</i>	Álvarez & Villalobos, 1998	México
<i>O. palanquensis</i>	Álvarez & Villalobos, 1998	Mexico
<i>O. toninae</i>	Álvarez & Villalobos, 1998	Mexico
Pseudothelphusinae: Potamocarcinini		
<i>Potamocarcinus</i>	H. Milne-Edwards, 1853	
<i>P. chajulensis</i>	Álvarez & Villalobos, 1998	Mexico
<i>P. lobulatus</i>	Campos & Lemaitre, 2002	Panamá
<i>P. pinzoni</i>	Campos, 2003b	Colombia
<i>P. roatensis</i>	Rodríguez & López, 2003	Honduras
<i>P. vulcanensis</i>	Rodríguez, 2001	El Salvador
<i>Phrygiopilus</i>	Smalley, 1970	
<i>P. montebelloensis</i>	Álvarez & Villalobos, 1998 ⁶	México
<i>P. yoshibensis</i>	Álvarez & Villalobos, 1998 ⁶	México
<i>Ptychophallus</i>	Smalley, 1964	
<i>P. barbillaensis</i>	Rodríguez & Hedström, 2000	Costa Rica
<i>P. kuna</i>	Campos & Lemaitre, 1999	Panama
<i>P. micracanthus</i>	Rodríguez, 1994	Costa Rica
<i>P. uncinatus</i>	Campos & Lemaitre, 1999	Panama
<i>Villalobosus</i> , substitute for <i>Stygothelphusa lopezformenti</i> (Álvarez & Villalobos, 1991); type: <i>S. lopezformenti</i> (Álvarez & Villalobos, 1991)	Ng & Álvarez, 2000	México
<i>Pseudothelphusa</i>	De Saussure, 1857	
<i>P. ayutlaensis</i>	Álvarez & Villalobos, 1997	Mexico
<i>P. hoffmannae</i>	Álvarez & Villalobos, 1996	Mexico
<i>P. nayaritae</i>	Álvarez & Villalobos, 1994	Mexico
<i>Tehuana</i>	Rodríguez & Samalley, 1969	
<i>T. chontalpaensis</i>	Villalobos & Álvarez, 2003	Mexico
<i>T. jacatepecensis</i>	Villalobos & Álvarez, 2003	Mexico
<i>T. lamothei</i>	Álvarez & Villalobos, 1994	Mexico
Pseudothelphusinae: Strengerianini		
<i>Chaceus</i>	Pretzmann, 1965	
<i>C. turikensis</i>	Rodríguez & Herrera, 1994	Venezuela
<i>Phallangothelphusa</i>	Pretzmann, 1965	
<i>P. magdalenensis</i>	Campos, 1998	Colombia
<i>Strengeriana</i>	Pretzmann, 1971	
<i>S. cajaensis</i>	Campos & Rodríguez, 1993	Colombia
<i>S. casallasi</i>	Campos, 1999	Colombia
<i>S. flagellata</i>	Campos & Rodríguez, 1993	Colombia
<i>S. florenciae</i>	Campos, 1995	Colombia
<i>S. maniformis</i>	Campos & Rodríguez, 1993	Colombia

¹ See also CAPOLONGO & PRETZMANN (2002); ² See also CAPOLONGO & PRETZMANN (2002); ³ See also CAMPOS (2003a); ⁴ See also RODRÍGUEZ *et al.* (2002); ⁵ See also RODRÍGUEZ & CAMPOS (1998); ⁶ See also RODRÍGUEZ (2001).

1853, and one new *Tehuana* Rodríguez & Smalley, 1969, were described from the state of Chiapas. In the genus *Pseudothelphusa* de Saussure, 1857 one species was described from the state of Nayarit and two from the state of Guerrero. With these additions the pseudothelphusid fauna of Mexico consists at present of 13 genera and 48 species (Tab. II), but there are many areas unexplored in southern Mexico, in the state of Chiapas, that may contain undescribed species (ÁLVAREZ & VILLALOBOS 1998). Of the additions made during this period one of the most interesting concerns the genus *Phrygiopilus*, previously restricted to Guatemala. With the two new species reported from Mexico the geographic range of the genus extends northward 335 km.

Table II. Total number of genera and species of Pseudothelphusidae in several areas of the Neotropics up to 2004.

Geographical areas	Genera	Species
México	13	48
Central America	13	43
Antillas	2	12
Venezuela	10	32
Atlantic Guianas	3	5
Colombia	13	82
Ecuador	3	19
Peru	4	7
Brazil	5	12

Central America. Eight new species have been added to those known from Central America (CAMPOS & LEMAITRE 1999, 2002, RODRÍGUEZ 2001, RODRÍGUEZ & HEDSTRÖM 2000, RODRÍGUEZ & LÓPEZ 2003), including three new species of *Potamocarcinus* from Panamá, El Salvador, and the Roatan Island off Honduras, and five new species of the endemic Central American genus *Ptychophallus* Smalley, 1964, from Panamá and Costa Rica. CAMPOS & LEMAITRE (1999) reviewed the taxonomic status of other species and theorizations about the role of the morphology and evolution of the structure of the first gonopod in different species were made by RODRÍGUEZ & HEDSTRÖM (2000).

Antilles. RODRÍGUEZ & WILLIAMS (1995) described a new species of the West Indian genus *Epilobocera* Stimpson, 1860, *E. wheterbeei*, from Hispaniola characterized by its very small size. At the same time they presented SEM illustrations of the gonopods of three other of then known species.

The papers by PRETZMANN (2000) and CAPOLONGO & PRETZMANN (2000, 2002) deserve special attention, because they made considerable alterations to the taxonomy of the genus *Epilobocera*, and their results were reported in a publication of very restricted diffusion, *AGEMUS Nachrichten*, the "organ of internal information of the working group on Evolution, Human Destiny and Meaningfulness ("Arbeits-Gemeinschaft Evolution Menschheitszukunft und Sinnfragen")".

Former authors distinguished four species in Cuba: (a) *Epilobocera armata* Smith, 1870, with the upper border of the front forming a strong tuberculated crest (RATHBUN 1905, BOTT 1968, CHACE & HOBBS 1969, RODRÍGUEZ 1982). According to available records, the species is restricted to the eastern end of the island. The type locality is probably Baracoa, Provincia de Oriente, and other records are from the vicinities of this city (RATHBUN 1905, CHACE & HOBBS 1969, RODRÍGUEZ 1982), with the exception of a record from Guantánamo, 80 km SE of Baracoa (RATHBUN 1905). (b) *Epilobocera cubensis* Stimpson, 1860, with the front curving downwards very gradually (RATHBUN 1905, CHACE & HOBBS 1969, RODRÍGUEZ 1982). The type locality is Rio Yateras, near Guantánamo, Provincia de Oriente, a basin continuous to the area of *E. armata*. The species has been recorded westward, up to the neighborhood of Havana (RATHBUN 1905, RODRÍGUEZ 1982), and Provincia Pinar del Rio (San Diego de los Baños) (RATHBUN 1905). (c) *Epilobocera gilmani* (Smith, 1870), with the front curving downwards very gradually as in *E. cubensis*, but distinguished from this last by the shape of the third maxilliped (RODRÍGUEZ 1982). BOTT (1968) gave this form a subspecific rank as *Epilobocera cubensis gilmani*. The type locality is in the Isla de Pinos (Isla de la Juventud) and according to the authors mentioned above, it is restricted to this island. (d) *Epilobocera gertraudae* Pretzmann, 1965, a species clearly differentiated from the other Cuban species by its pronounced stygobiont traits and only previously known from its type locality, Los Baños, Provincia Pinar del Rio [Cueva El Toro].

We have examined the material of *Epilobocera gertraudae* in the reference collection of the Instituto Venezolano de Investigaciones Científicas (IVIC), as follows: Cueva superior Majagua, Sierra de San Carlos, Provincia Pinar del Rio, Cuba, 2.VIII.1977, leg. O. Gómez, 1 male, carapace length 31.5 mm, carapace breath 49.3 mm.

According to the taxonomic arrangement proposed by PRETZMANN (2000) and CAPOLONGO & PRETZMANN (2000, 2002), the distribution of the species of *Epilobocera* in the Island of Cuba would be as follows:

a) *Epilobocera cubensis cubensis*. CAPOLONGO & PRETZMANN (2002) included under this species *Epilobocera armata* Smith, 1870, as a junior synonym. In the diagnosis, the front of the species is stated as acute, clearly advanced ("Stirn scharf, deutlich vorspringend"), and in the description the upper border is said to be weakly granulated, a little dentate ("Stirnrand ist schwach granuliert, wening eingedellt"). Finally, in the discussion of the distribution of species, the authors stated that all populations of *E. cubensis* are characterized by an acute advanced upper margin of front ("Alle diese Tiere sind durch eine scharfen vorspringenden oberen Stirnrand gekennzeichnet"). CAPOLONGO & PRETZMANN (2002) reported the typical *Epilobocera cubensis cubensis* from La Maya [25 km NE of Santiago, approximately], and *Epilobocera cubensis najasensis*, a subspecies of this (by inference), from the type locality Najasa [Sierra de Najasa, S of Cama-

guez, Provincia de Camaguey]. The typical form is fragmented into *Epilobocera cubensis cubensis* Natio *baracoensis* [type locality: Baracoa, Provincia de Oriente] and additional paratypes from Paso de Cuba [10 km SSE of Baracoa]; *Epilobocera cubensis cubensis* Natio *guisensis*, type locality Río Guisa [draining into Cauto river, approximately 15 km NE of Bayamo, Provincia de Oriente].

- b) *Epilobocera gilmani* is said to comprise the typical form and two more subspecies. *Epilobocera gilmani gilmani*, in addition to the type locality in Isla de Pinos, is recorded from Cotorro [12 km W of Havana, Provincia de la Havana] and R. Jaimanitas [a locality not identified]. *Epilobocera gilmani placensis*, type locality Placetas [32 km ENE of Santa Clara, Provincia de Villa Clara], and *Epilobocera gilmani synoecia*, type locality Cueva S. Tomas [Cueva San Tomás, Provincia de Pinar del Río], also inhabited by *E. gertraudae*. In their discussion of the distribution of species, CAPOLONGO & PRETZMANN (2002: 4) used the name *Epilobocera gilmani cuevanensis* (*nomina nuda*) for a subspecies from Cueva S. Tomas. This is possibly a lapse for *Epilobocera gilmani synoecia*.
- c) *Epilobocera capolongoi* a new species, whose type locality is Topo de Collantes, central Cuba [Topes de Collantes, at foot of Sierra de Trinidad, 50 km S of Santa Clara, Provincia de Villa Clara]. This species has the upper border of front finely dentate and well marked, bent forward; the merus of the third maxilliped is rounded; the very wide exognath of third maxilliped (width/length = 0.5 according to figure 1 of PRETZMANN 2000), distinguish this species from all other in the island.
- d) *Epilobocera* (*Neopilobocera*) *gertraudae*, restricted to the type locality (see above).

The classification postulated by CAPOLONGO & PRETZMANN (2002) poses the following difficulties:

1) The synonymization of *Epilobocera cubensis* and *E. armata* is problematic. The illustrations of the first male gonopod of both species in CHACE & HOBBS (1969, figs 39a, b) shows substantial differences in the shape of the finger-like caudal process; furthermore, the number of strong spines on the bulging lateral process is 13 in *E. armata* and 8 in *E. cubensis* (for the significance of this last character, see RODRÍGUEZ & WILLIAMS 1995).

2) Regarding the extension of the range of *Epilobocera gilmani* from Isla de Pinos to cover the western half of Cuba, it must be remarked that this species differs from *E. cubensis* only by a minor detail of the third maxilliped. Thus the descriptions given by CHACE & HOBBS (1969) of both species are identical, except for the statements that in *E. cubensis* the "third maxilliped [has the]... distal margin [of merus] slightly concave", and in *E. gilmani* the "third maxilliped [has the]... distal margin [of merus] slightly regularly convex".

The diagnosis of this species by CAPOLONGO & PRETZMANN (2002) is based mostly on negative characters and does not provide a firm ground for the separation of the species: Exognath of third maxilliped not expanded [to discriminate from *Epilobocera capolongoi*, but similar to the rest of species of

the genus], legs not particularly slender [to discriminate from *E. gertraudae*, but similar to the rest of species of the genus], upper margin of front smooth, not projected [similar to *E. cubensis*]. RODRÍGUEZ (1982) has suggested that the two forms probably could be unified and *E. gilmani* considered a junior synonym of *E. cubensis*. However, before this action is taken, a careful examination of the first male gonopod of specimens from Isla de Pinos is advisable.

3) The extension of the geographical area and the division of a species of doubtful status, such as *Epilobocera gilmani*, into subspecies is inadvisable. A similar argument can be made for the split of *Epilobocera cubensis*, whose status regarding *E. armata* is insecure. The meaning of tetranomials such as *Epilobocera cubensis cubensis* Natio *guisensis* is not clear. Does 'Natio' refer to genetically differentiated populations or demes, or to the locality where the specimens were found? Due to the conflicting views regarding the status of the various populations in the islands of Cuba and Pinos, with the consequent nomenclatural confusion, it is possible that the only way to resolve this incertitude would be through a molecular genetics study.

Venezuela. Three new species have been added to the Venezuelan fauna during this period (RODRÍGUEZ & HERRERA 1994, RODRÍGUEZ & SUÁREZ 1994, RODRÍGUEZ & CAMPOS 2000). *Fredius stenolobus* Rodríguez & Suárez, 1994 was described from the basin of the Río Caura, a tributary of the Río Orinoco. *Chaceus turikensis* Rodríguez & Herrera, 1994 is a stygophile from a complex of caves in Mesa Turik, western Venezuela. *Microthelphusa sucrensis* Rodríguez & Campos, 2000 presents an interesting case of teratology (RODRÍGUEZ & CAMPOS 2000). It was collected for the first time in 1930 in an inaccessible area at 1730 m altitude in eastern Venezuela, state of Sucre, and could not be identified due to the malformation of the first gonopod. A second collection in the same area at 1900 m altitude, in 1993, also produced male specimens with malformations in the first gonopod. Since malformations of the sexual appendages of Neotropical freshwater crabs are very rare, a genetical factor cannot be discarded.

With the addition of the taxa mentioned above, the total number of species and subspecies known from Venezuela increases to 32 (Table II). However, the morphology of the gonopod and the extension of the endognath of the third maxilliped in *Eudaniela pestai* (Pretzmann, 1965) led CAMPOS (2001) to transfer it to her newly-erected genus *Achagua*. By this action the number of genera in Venezuela was elevated to ten.

Colombia. The intense faunistic work in Colombia by CAMPOS (1995, 1998, 1999, 2000, 2001, 2003a, b), CAMPOS & LEMAITRE (1998), CAMPOS & RODRÍGUEZ (1993, 1995), CAMPOS & VALENCIA (2004), CAMPOS *et al.* (2002), RODRÍGUEZ *et al.* (2002), and RODRÍGUEZ & CAMPOS (1998) has resulted in an important increase in the number of known species of pseudoscorpionids in that country. According to M. Campos (personal communication) there are at present 82 species and subspecies (Table II). However there are still unexplored areas such as the isolated sierras to the east of the Andes, Serranía de San Lucas, Sierra de

la Macarena, and Sierra de Chiribiquete. This last is geologically related to the Precambrian Guiana Shield and its geomorphology consists of tabletop mountains, similar to those of the Guianas (SÁNCHEZ PÁEZ *et al.* 1990). It may be guessed that the pseudothelphusid fauna of these sierras may consist either of Andean, Amazonian or Guianan species.

Brazil and the Atlantic Guianas. MAGALHÃES & RODRÍGUEZ (2002) discussed the taxonomic and biogeographical status of *Fredius reflexifrons* (Ortmann, 1897) and *Fredius fittkaui* (Bott, 1967) and confirmed the validity of the former taxon. MAGALHÃES (2003), in his revision of the freshwater crabs of the Rio Xingú in the Amazon region, described the new species *Kingsleya junki*. The morphology of the first male gonopod in this species widely diverges from that of other four known species of the genus by the shape of the apical plate, with a rudimentary proximal lobe and an enlarged and serrated distal lobe. Another new species of this genus is being described from Rio Tocantins, in the southeastern Amazon basin (MAGALHÃES in press). *Kingsleya* sp. and *K. siolii* Bott, 1967 were considered as possible sister species that probably originated in the Tertiary period. With the addition of these species, 12 species divided among at least five genera, *Brasiliothelphusa* Magalhães & Türkay, 1986, *Fredius* Pretzmann, 1967, *Kingsleya* Ortmann, 1897, *Microthelphusa* Pretzmann, 1968 and *Prionoithelphusa* Rodríguez, 1980 are recognized from the Amazon region of Brazil.

No new taxa has been added to the three genera and 5 species known from Atlantic Guianas.

Ecuador. A revision of the known species in Ecuador, including the description of five new species, *Hypolobocera esmeraldensis*, *H. konstanzae*, *H. muisnensis*, *H. mindonensis* and *Lindacatalina sumacensis*, were provided by RODRÍGUEZ & STERNBERG (1998). The validity of pentanomial names proposed in the literature for some Ecuadorian species was revised, the genera *Hypolobocera* Ortmann, 1897, *Moritschus* Pretzmann, 1965 and *Lindacatalina* Pretzmann, 1977 were redefined, and several species were reasigned among these genera. As it stands at present, the number of species known to occur within the Ecuadorian territory is 19 (Tab. II), divided among the three genera already mentioned.

Peru. RODRÍGUEZ & SUÁREZ (2004) reviewed six species of pseudothelphusid crabs from Peru. Among these, two new species of the genus *Hypolobocera* were described, bringing the number of pseudothelphusid species known to the country to seven.

Species vectors for paragonimiasis

Twenty two species of the more than 200 species of Pseudothelphusidae known has been cited as secondary hosts for *Paragonimus* (Tab. III). All these records were made before 1993, except those by LAMOTHE-ARGUMEDO (1995) and VELEZ *et al.* (2003).

The species of *Paragonimus* involved are *P. amazonicum* Miyazaki, Grados & Uyema, 1973, *P. caliensis* Little 1968, *P. inca* Miyazaki, Mazabel, Grados & Uyema, 1975 and *P. mexicanus* Miyazaki & Ishii, 1968. The records of *Paragonimus westermani* (Kerbert, 1878) from the Americas are incorrect and due to misidentifications owing to the assumption that this was the

sole species of lung fluke (BLAIR *et al.* 1999). Areas of endemisms have been reported from Mexico, Central America, Colombia, Ecuador and Peru. The occurrence in Venezuela was mentioned by TONONI (2004) based on reports of paragonimiasis cases from the state of Sucre. The parasites have not yet been reported in crabs from Brazil, although they are used as food by Indian populations in the country (C. Magalhães, unpublished data). Such a possibility still remains to be verified.

An interesting fact that can be derived from the knowledge available is that all the species of crabs involved are large (carapace breadth 5-10 cm) and inhabit areas below 300 m altitude. This fact can correlate with the location of human populations at these altitudes or the unedibility of the smaller crabs, rather than immunity of the crabs to the parasites. Research along these lines could be of great practical interest.

Cavernicolous species

Four species were recorded associated with caves since 1992, as follows: *Epilobocera gilmani synoecia* from Cueva San Tomas, Cuba, do not display adaptations to cave life in the eyes, color (which is described as darker than the typical subspecies), or other characters of carapace; only the legs are described as more slender particularly those of the fifth pair (CAPOLONGO & PRETZMANN 2002). *Chaceus turikensis* from Cueva de Las Lianas, Venezuela, display as only obvious stygobiontic character the slenderness of the pereopods, including the cheliped. The species is epigeous in localities where the daylight is considerably reduced (RODRÍGUEZ & HERRERA 1994). *Phrygiopilus montebelloensis* Álvarez & Villalobos, 1998 from Gruta del Arco, and *Phrygiopilus yoshibensis* Álvarez & Villalobos, 1998 from Sumidero Yoshib, both in the state of Chiapas, Mexico, come from subterranean waters, but ÁLVAREZ & VILLALOBOS (1998) stated that their presence there is accidental, since they have no trogllobious adaptations. Effectively, RODRÍGUEZ (2001) recorded the first species from Laguna de Tizcaco, near the type locality, and the second in a stream 80 km from the type locality.

Probably only *Chaceus turikensis* could be considered as truly troglophile. If the other three species mentioned above are excluded, the number of cave pseudothelphusids would be 20. However the difficulties mentioned in RODRÍGUEZ (1992) regarding the discrimination of species from subterranean waters as stygobiont, stygophyle, or stygoxene must be taken into account.

Anatomical adaptations

The first male gonopods of Pseudothelphusidae display on their terminal portion a complex structure which usually consists of several processes. Each species possesses a distinctive morphology in these intromittant organs which differs from that of any other species within the family. PRETZMANN (1973) showed that there are also species-associated differences in the openings of the females. A plausible hypothesis is that the corresponding differences in both male and female organs act as a mechanism of lock and key to prevent copulation between different species.

Table III. Species of Pseudothelphusidae crabs reported as hosts for lung flukes of the genus *Paragonimus* (Trematoda, Troglotremitidae)¹.

Host species	Country	Parasite
<i>Eudaniela garmani</i>	Venezuela	<i>P. mexicanus</i>
<i>Hypolobocera aequatorialis</i>	Ecuador	<i>P. mexicanus</i>
<i>H. gracilignatha</i>	Peru	<i>P. inca</i>
<i>H. bouvieri monticola</i> ²	Colombia	<i>Paragonimus</i> spp.
<i>H. chilensis</i>	Peru	<i>P. caliensis</i> , <i>P. amazonicum</i> , <i>P. mexicanus</i>
<i>H. emberarum</i>	Colombia	<i>Paragonimus</i> spp.
<i>Odontotelphusa maxillipes</i>	México	<i>P. mexicanus</i>
<i>Potamocarcinus magnus</i>	Costa Rica	<i>P. caliensis</i> , <i>P. mexicanus</i>
<i>Pseudothelphusa belliana</i>	México	<i>P. mexicanus</i>
<i>P. dilatata</i>	México, Costa Rica	<i>P. mexicanus</i>
<i>P. nayaritae</i> ³	México	<i>P. mexicanus</i>
<i>P. propinqua</i>	Guatemala	<i>P. mexicanus</i>
<i>P. terrestris</i> ³	México	<i>P. mexicanus</i>
<i>Ptychopthalmus coclensis</i>	Panamá	<i>P. mexicanus</i>
<i>P. costaricensis</i>	Costa Rica	<i>P. mexicanus</i>
<i>P. exilipes</i>	Panamá	<i>P. caliensis</i>
<i>P. richmondi</i>	Panamá, Costa Rica	<i>P. mexicanus</i>
<i>P. tristani</i>	Costa Rica	<i>P. caliensis</i> , <i>P. mexicanus</i>
<i>P. tumimanus</i>	Costa Rica	<i>P. mexicanus</i>
<i>Raddaus bocourti</i>	Guatemala	<i>P. mexicanus</i>
<i>R. tuberculatus</i>	México	<i>P. mexicanus</i>
<i>Strengeria</i> sp.	Colombia	<i>P. caliensis</i>

¹ For references to records before 1993 see BLAIR *et al.* (1999); ² VELEZ *et al.* (2003); ³ LAMOTHE-ARGUMEDO (1995).

Although presumably there is a weak selection pressure acting on the male organs (STERNBERG *et al.* 1999a), it has been observed that the progressive transformation of one type of gonopod into a slightly different one, forming the various species a continuous chorological series (RODRÍGUEZ 1986). RODRÍGUEZ & HEADSTÖM (2000) observed this type of morphocline in the species of the genus *Ptychopthalmus* consisting in the progressive reaccommodation of the lateral lobe and the various components of the apex of the gonopod, to form a structure that possibly serves to receive and keep the spermatophore once it is extruded. This is fully developed in *Ptychopthalmus goldmanni* Pretzmann, 1965, but the other species can be arranged in a morphocline comprising several stages of development of this structure. If the hypothesis advanced above is correct, there must be a corresponding rearrangement of the female opening, in a sort of monospecific "coevolution", but RODRÍGUEZ & HEADSTÖM (2000) did not touch upon this aspect of the problem.

Ecology

Ecological studies about pseudothelphusid crabs are too few and sporadic. TERAN *et al.* (1995), studying the food habits of river turtles in the Rio Guaporé, state of Rondonia, Brazil, showed that *Podocnemis unifilis* (Trochel, 1848) consumed pseudothel-

phusid crabs, which occurred in 10.8% of the sampled stomachs. MAITLAND *et al.* (2002) reported the practical use of radio transmitters to track the amphibious freshwater land crab, *Eudaniela garmani* (Rathbun, 1898), in the rainforests of the Caribbean island of Tobago. In this same island, MAITLAND (2003) also reported a very interesting case of predation on snakes by crabs of this species. In the southeastern part of the Brazilian Amazon, PORT-CARVALHO *et al.* (2004) recorded the predation of unidentified pseudothelphusid crabs by a population of the tufted capuchin monkey, *Cebus apella* (Linnaeus, 1758). More biological and ecological studies on representatives of this family are needed to better understand their role in the ecosystem.

Biogeography

Answering an argument by BĂNĂRESCU (1990), who asserted that freshwater crabs are not a useful tool in biogeography, NG & RODRÍGUEZ (1995) put forward several arguments in favor of the use of these organisms to falsify biogeographical hypotheses. In support of his assertion BĂNĂRESCU (1990) maintained that freshwater crabs are able to cross salt-water barriers, or are derivatives of not too distant marine ancestors. Bănărescu's belief is based partially on the occurrence of pseudothelphusids in the Antilles and the mainland. Regarding this point, NG &

RODRÍGUEZ (1995) have pointed out that an alternative vicariant hypothesis has more factual support. A recent survey of insular species by RODRÍGUEZ & LÓPEZ (2003) examined the case of the three species of the family found in Roatan Island (Honduras), Gorgona Island (Colombia), and the multiple distribution of the same species, *Eudaniela garmani*, in mainland Venezuela, Margarita Island and Trinidad, and *Microthelphusa odaelkae* (Bott, 1970) in Trinidad and Venezuela. In the case of the new species found in Roatan Island, *Potamocarcinus roatensis* Rodríguez & López, 2003, a cladistic analysis shows that the sister species is *Potamocarcinus magnus* (Rathbun, 1896), a widespread species found throughout Central America. The vicariant disjunction of the two species is supported by paleographic data. A similar case occurs with *Eudaniela garmani*, but the geographical connection of the three disjunct areas up to late Quaternary possibly explain the lack of a vicariant speciation. The distribution of *Microthelphusa odaelkae* probably reflects an older connection with the continent. In the case of *Hypobocera gorgonensis* von Prael, 1983, found in mainland Ecuador and in Gorgona Island, the most probable explanation is rafting along the Humboldt Current.

BANÁRESCU'S (1990) contention that freshwater crabs are derivatives of not too distant marine ancestors belong to a school of thought that assumes that freshwater crabs are a para- or polyphyletic assemblage, with each family (or even genera) originating from a nearby marine ancestor. A more recent hypothesis proposes the monophyly of all freshwater crab families, with sister group relationships for the Pseudothelphusidae + Gecarcinucoidea and the Potamoidea + Trichodactylidae (see NG & RODRÍGUEZ 1995). These two schools of thought have been termed as the polyphyletic school and the archaic population school, respectively, by STERNBERG *et al.* (1999a). These authors, based on a cladistic analysis, proposes a third alternative hypothesis which states that "a widespread, predominantly littoral, marine urthoracotreme clade emerged during the Cretaceous", with a pancoastal distribution along the southern Thethys sea. This clade would have been monophyletic on the basis of 13 shared synapomorphies. This monophyletic group underwent an independent diversification in the freshwater or estuarine environments, whereas others diverged after entering freshwater.

Another result of STERNBERG *et al.* (1999a) cladistic study is that the Pseudothelphusidae appears as a basal group, with the rest of the thelphusids forming a sister clade, implying a more ancient differentiation of the family in relation to other freshwater crabs.

Two recent studies tend to elucidate the origin of the Kingsleyini. A cladistic analysis by STERNBERG *et al.* (1999b) has shown that the genus *Eudaniela* Pretzmann, 1971 is a paraphyletic group. *Eudaniela pestai* is positioned as the most basal taxon, not only in relation to *Eudaniela*, but within all kingsleyinian species compared in the analysis. This primitive condition is sustained by its underived first gonopod and longest third maxilliped exopod within the Kingsleyini. Additionally,

the discovery in the llanos of Colombia by CAMPOS (2001) of a new species, *Achagua casanarensis*, closely related to *Eudaniela pestai* by these primitive traits, considerably extends the distribution of this basal group. However, being *E. pestai* (Pretzmann, 1965) the type species of the genus *Eudaniela* Pretzmann, 1971, the action of transferring *E. pestai* to the new genus *Achagua*, as proposed by CAMPOS (2001), implied that *Eudaniela* and *Achagua* are synonyms, with *Eudaniela* taking priority over *Achagua*. A correcting action is in preparation (M.R. Campos, personal communication).

The prototypical Strengerianini-like gonopod and the partially enclosed efferent channel relates the basal group *Achagua casanarensis/A. pestai* to the Strengerianini. Data by G. Rodríguez & H. Suárez (as yet unpublished) show that some undescribed species of the genus *Microthelphusa* from flattop mountains (tepuyes) in the Venezuela Guiana, display a gonopodal topology homologous to that of *Achagua casanarensis*. This anatomical confluence and the presence of small isolated tepuyes in the Colombian llanos point to the existence of an ancestral pre-*Achagua* population, derived from the ancient Strengerianini and widely distributed from the Colombian llanos, to the eastern Venezuelan and to the Venezuelan Guiana. A survey of the still unknown Colombian tepuyan pseudothelphusid fauna could be valuable to falsify this hypothesis.

Another interesting result of STERNBERG *et al.* (1999b) is the positioning of *Eudaniela garmani* as basal taxon for *Eudaniela* sibling complex. Following the fragmentation of *E. garmani* range during Quaternary times (RODRÍGUEZ & LÓPEZ 2003), cladogenetic events would have proceeded in a westward direction along the Venezuelan coastal range. Combining the results of STERNBERG *et al.* (1999b) with those of RODRÍGUEZ & LÓPEZ (2003) it is apparent that the several vicariant events that led to the allopatric speciation of the *Eudaniela* sibling complex took place in quite recent geological time.

Several taxonomic studies have shed light on the areal distributions of the Pseudothelphusidae. Research by ÁLVAREZ & VILLALOBOS (1998) has evidenced a high diversification of pseudothelphusids in the Mexican state of Chiapas. Seven genera and thirteen species, representing three of the five tribes that compose the subfamily Pseudothelphusinae are found in Chiapas, and these authors anticipate that more new species will be found, since vast areas still remain unexplored. This number of taxa represents 27% of all the species found in the Mexican territory. This high biodiversity is in line with RODRÍGUEZ' (1986) assertion that the neighboring areas east of the Isthmus of Tehuantepec are an area of maximum concentration of genera and species, where three distinct phyletic lines converge. The high speciation in this area is explained by this author by the marine transgressions that occurred during the Cenozoic that, although were not complete and did not produce disruptions of the land areas, conditions of aridity may have acted as temporary barriers and promoted repeated allopatric speciations.

Another area of high diversity is found in Colombia (RODRÍGUEZ 1986) where the variety of topographical relief determines a multiplicity of environments favorable for allopatric speciation. However, this rich pseudothelphusid fauna is not biogeographically homogeneous. CAMPOS *et al.* (2002) have found that the southern Andean pseudothelphusids of Colombia have affinities with the pseudothelphusid fauna of Ecuador, and points to a taxonomic compact of southern taxa that extends into southeastern Colombia and the Amazonian and Pacific slopes of Ecuador. This southern compact is separated by the water divides of the San Juan, Cauca and Magdalena basins from the northern species found at a short distance north of these divides.

The southern set of species mentioned comprises three distinct phyletic lines: (a) The species of the genus *Hypolobocera* with a lanceolate apex; (b) the genus *Lindacatalina*; and (c) the genus *Moritschus*. These three phyletic lines constitute the pseudothelphusid fauna of Ecuador (RODRÍGUEZ & STERNBERG 1998), and continues southward to Peru distributed in two distinct geographical areas, separated by the water divides of the Andean Cordillera. After a peak of biodiversity in the Ecuadorian Andes, a sharp decrease is observed in a southward direction (RODRÍGUEZ & SUÁREZ 2004). These authors quantified this decline computing the total number of species and the number of species that appeared for the first time at each degree of latitude from 6°N to 12°S. In the southern Colombian Andes (6°N to 2°N) the diversity of species is high, but it increases even further in Ecuador (1°N to 5°S); there is a sharp decline in the Peruvian Andes and after 11°S no new species appear. Thus it is an impoverished pseudothelphusid fauna that reaches the southern limits of the family, and beyond 13°S, no species of pseudothelphusid is found.

Three taxonomic groups of freshwater crabs are clearly delimited in the Amazon basin: (a) the Kingsleyini, restricted to the lower planes of the Amazon basin; (b) the Hypolobocerini, that do not descend beyond 400 m altitude; and (c) the species of the family Trychodactylidae which share a common territory throughout the basin with the Kingsleyini (RODRÍGUEZ & SUÁREZ 2004). Each kingsleyinian species seems to have a territorial delimitation, as exemplified by the separation of *Fredius reflexifrons* and *F. fittkaui* which occupy discrete areas along the main axis of the Amazon River and in the upper Rio Negro basin, respectively, with a short overlap only in the Atlantic Guianas (MAGALHÃES & RODRÍGUEZ 2002). The water divides of Ucayali River form the southwestern Amazonian limit of the pseudothelphusids and no species are found in the neighboring southern basins (RODRÍGUEZ & SUÁREZ 2004). This group, however, extended its eastern limits beyond the Amazon basin, as *Fredius reflexifrons* was recently recorded in the Serra da Ibiapada region, in the state of Ceará, Northeastern Brazil (MAGALHÃES *et al.* 2005). The kingsleyinian fauna of southern tributaries of the eastern Amazon Basin is still poorly known, but recent findings from Rio Xingu, Rio Tocantins and Rio Tapajós basins (MAGALHÃES

2003, in press, and unpublished data) indicate that this group may have had a quite complex evolutionary history within the Amazonian portion of the Brazilian Shield.

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