

## Taxonomic and Biogeographical Status of Three Species of the Spider Crabs of the Genus *Acanthonyx* Latreille, 1828 (Majoidea: Epialtidae) as Determined by DNA Barcoding and Morphological Analyses Along the Western Atlantic

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**Ana Francisca Tamburus and Fernando Luis Mantelatto (2016)** The genus *Acanthonyx* Latreille, 1828 contains 17 valid species, including *A. dissimulatus* Coelho, 1993, *A. petiverii* H. Milne Edwards, 1834 and *A. scutiformis* (Dana, 1851), which occur along the Brazilian coast. The high degree of intraspecific variation in the angle of hepatic region, size of the tubercles of the carapace and length of setae on the carapace and pereopods has resulted in difficulties with the taxonomy of this genus. Analysis of more consistent morphological and molecular characters are required to clarify the status of the three species that occurs in Brazil. For the molecular data, we used the barcode region of the mitochondrial gene COI as a marker, and we correlated this with morphological characters of adults and juveniles. The three species of *Acanthonyx* were morphologically similar and the matrix of genetic distances and maximum likelihood trees showed that *A. dissimulatus* and *A. scutiformis* belonged to the same group with *A. petiverii*. They could not be separated using the diagnosing characters proposed in the original description or genetically (present study), thus indicating that the taxonomic status of the first two species is questionable. The division into two distinct groups corresponding to A (Caribbean, Brazil, Venezuela) and B (USA, Mexico) was well supported and indicated that there are genetic differences between these populations. Present study suggests the existence of a single species in Brazil and Caribbean, assigned to *A. petiverii* (type locality in Antilles). The existence of a new species restricted to North America confirms the cryptic diversity within *Acanthonyx*.

**Key words:** Brachyura, Cryptic diversity, Species complex, Molecular taxonomy, Morphological variability.

### BACKGROUND

The superfamily Majoidea Samouelle, 1819 are the commonly termed spider crabs. These brachyuran crabs live in marine and coastal systems and are important in the intertidal areas of rocks and reefs (Hendrickx 1999). They are found among submerged plants and algae, where they often decorate themselves putting pieces of marine organisms, algae or grains of sand among the hooked setae of the exoskeleton and use these items to camouflage with the environment to avoid

predators (Wilson 1987; Coelho and Torres 1993; Wicksten 1993).

According to Ng et al. (2008) and Windsor and Felder (2014), Majoidea includes seven families; among them, Epialtidae MacLeay, 1838 with 76 genera, with *Acanthonyx* Latreille, 1828 containing 17 valid species (Emparanza et al. 2007; Ng et al. 2008). The genus is widely distributed in Atlantic, Pacific and Indian oceans, Mediterranean and Red Sea (Rathbun 1925; Griffin and Tranter 1986; Emparanza et al. 2007).

Three species occur along the Brazilian coast,

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*Acanthonyx dissimulatus* Coelho, 1993, *A. petiverii* H. Milne Edwards, 1834 and *A. scutiformis* (Dana, 1851). They are found in coastal regions in shallow water on hard substrates, sandy bottoms, or reefs (Coelho and Torres 1993; Melo 1996; Hendrickx 1999; Felder et al. 2009). Along the American coast, *A. dissimulatus* (type-locality Paraíba State, Brazil) (Coelho and Torres 1993) is found from Maranhão to São Paulo, Brazil (Coelho and Torres 1993; Melo 1996; Dall'Occo et al. 2004; Coelho et al. 2008) and Mexico (Tamburus and Mantelatto 2012); *A. scutiformis* (type-locality Rio de Janeiro, Brazil) (Dana 1851) is endemic to Brazil, occurring from Espírito Santo to São Paulo (Coelho and Torres 1993; Dall'Occo et al. 2004; Melo 2008). *Acanthonyx petiverii* (type-locality Antilles) (H. Milne Edwards 1834) has been recorded in the eastern Pacific, from Magdalena Bay, Baja California (Mexico) to Valparaíso (Chile), including Marías, Revillagigedo and the Galapagos Islands (Garth 1958; Retamal 1981; Hernández-Aguilera et al. 1997) as well as in the western Atlantic from the USA (Florida) to Brazil (Rio Grande do Norte, Paraíba, Pernambuco, Bahia, Rio de Janeiro, São Paulo), the Bahamas and Antilles (Rathbun 1925; Garth 1958; Fausto-Filho 1966; Hendrickx 1999; Marcano and Bolaños 2001; Cruz-Castaño and Campos 2003; Felder et al. 2009).

About thirty years ago, Griffin and Tranter (1986) suggested a complete revision of the genus *Acanthonyx*, since several taxonomic problems were identified (e.g. number of abdominal segment; if the sutures between these segments are indistinct or clearly fused). Currently, there is a lack of diagnosing morphological character to identify the species belonging to this genus. Considering morphology of the three co-occurring species in Brazil, they are remarkably similar, and only adult specimens can be distinguished using the angle of the hepatic region, the size of the tubercles of the carapace and the length of the setae distributed in the carapace and pereopods (Coelho and Torres 1993; Melo 1996).

The objective of this study was to reexamine the taxonomical status of the three co-occurring species of the genus *Acanthonyx* in Brazil, considering the morphology as well as the molecular data (DNA barcode).

## MATERIALS AND METHODS

### Sample collection

Specimens of *Acanthonyx dissimulatus*, *A. petiverii* and *A. scutiformis* were obtained by manual collection and SCUBA diving at different localities along the Brazilian coast during the years 2002-2012. They were fixed and stored in EtOH 80%.

Those specimens were deposited in the Crustacean Collection of the Department of Biology (CCDB), Faculty of Philosophy, Sciences and Letters at Ribeirão Preto (FFCLRP), University of São Paulo (USP), Ribeirão Preto, São Paulo State, Brazil. Additional material was loaned from the following crustacean collections: Universidade Federal de Pernambuco (DOUFPE - Recife, Pernambuco State, Brazil), Museu Nacional do Rio de Janeiro (MNRJ - Rio de Janeiro, Rio de Janeiro State, Brazil), Museu de Zoologia da Universidade de São Paulo (MZUSP - São Paulo, São Paulo State, Brazil), University of Louisiana-Lafayette, Zoological Collections (ULLZ - Lafayette, Louisiana, USA), Universidad Nacional Autónoma de México (UNAM - Mexico City, Coyoacán, Mexico), and Museo de Zoología de la Universidad de Costa Rica (UCR - San Pedro, San José, Costa Rica). All specimens were measured (i.e., carapace length, CL: from the posterior to the anterior margin, including the rostrum) using vernier calipers to the nearest 0.1 mm.

### Morphological analysis

We obtained and analyzed 25 specimens of *Acanthonyx dissimulatus* (11 males, 4 females, 7 ovigerous females and 3 juveniles), 71 samples of *A. petiverii* (31 males, 26 females, 1 ovigerous female and 13 juveniles) and two samples of *A. scutiformis* (1 male and 1 ovigerous female). The morphological analysis (Table 1) considered characters widely used by previous authors for the genus (Coelho and Torres 1993; Emparanza et al. 2007), as well as for the family (Rathbun 1925, 1933; Garth 1958; Melo 1996), and we added four characters for both sexes and across a size range.

We analyzed the structure of the male first pleopod since it has been used as a comparative character within the genus (Manning and Holthuis 1981; Griffin and Tranter 1986; Emparanza et al. 2007) and in other studies on majoids (Garth 1958; Windsor and Felder 2009; Tavares and Santana 2011; Wicksten and Stachowicz 2013).

## Molecular analysis

The partial fragment of the barcode region of the mitochondrial gene cytochrome oxidase subunit I (COI) was chosen as an efficient molecular marker in other studies of decapods crustaceans

(Hultgren and Stacowicz 2008; Mantelatto et al. 2007; Negri et al. 2012). We obtained sequences from 12 specimens, 2 specimens of *Acanthonyx dissimulatus*, 9 specimens of *A. petiverii*, and 1 specimen of *A. scutiformis*. We use other 2 sequences of *A. petiverii* and 2 of *A. lunulatus* from

**Table 1.** Morphological characters used to compare the species *Acanthonyx dissimulatus*, *A. petiverii* and *A. scutiformis*

Characters	Results
Carapace	shape; distribution and type of setae and tubercles Carapace elongate, subpentagonal; presence/absence of tufts of hair and tubercles; size and thickness of setae variable
Rostrum	shape; type of setae Short, deflexed and bifid; setae size and thickness variable
Orbits*	angle in relation to the rostrum Lateral angles obtuse; preorbital lobes not pointed
Eyes	presence or absence of setae Dorsal surface with short setae, sometimes absent
Preorbital tooth	presence or absence; type of setae Teeth elevated, not pointed; size and thickness of setae variable
Postorbital tooth	presence or absence Absent
Hepatic Region	shape; angles indorsal view; presence or absence of setae With almost rectangular angles, lateral lobes curved forwards and upwards; rectangular angle in specimens identified as <i>A. dissimulatus</i> ; inclined forward in specimens identified as <i>A. scutiformis</i>
Gastric, cardiac and intestinal regions	presence or absence of setae and tubercles; distribution and type of setae Gastric region with 2 setiferous tubercles on the protogastric, 1 on mesogastric; slightly elevated in specimens identified as <i>A. dissimulatus</i> . Cardiac region not evident; absent or obsolete tubercle.
Brachial Region	presence or absence of teeth; type of setae 2 small teeth not pointed, with short and long setae; setae can be absent in specimens identified as <i>A. scutiformis</i>
Basal article of antenna	shape; articles position in relation to the rostrum; distribution and type of setae Base wider than the extremity; the following 2 articles subcylindrical; distal end of 2° article with long setae; 3° article with tufts of setae on the inner margin. Setae can be absent in all species.
Chelipeds	size; presence or absence of gap between fingers Short, considerably enlarged in males; less strong, short and smaller in females.
Ischium*; merus*; carpus*; propodus; dactylus	presence or absence of setae, tubercles, crest and teeth; type of setae Ischium: 1-5 thin setae; merus: 3 setiferous lobes at the distal end, 1-2 spines on the proximal dorsal surface; carpus: a setiferous external crest, 3 setiferous tubercles. Propodus of chelipeds gaping in adult male, dentate on outer surface; sometimes a bigger central tooth in large males identified as <i>A. dissimulatus</i> and <i>A. petiverii</i> .
Pereopods	size; distribution and type of setae Subchelate, more pronounced from the 4° to the 1° pair, posteriorly decreasing in size; setae sometimes absent.
Ischium*; merus; carpus; propodus; dactylus	shape; presence or absence of setae, lobe, tubercles, spines; distribution and type of setae Merus: 3 lobes in distal end of the 1° and 2° pereopods with or without setae; carpus: subtriangular in the last two pereopods; propodus: compressed and subtriangular; dactylus: ventral surface with 2 rows of minute spines
Thoracic sternum	shape; position; presence or absence of setae Smooth
Abdominal somites	degree of fusion; shape; presence or absence of setae 4-5 united in both genders, triangular abdomen in males, telson triangular in both genders
Male first pleopod	shape Extremity with a subtriangular lobe with minute spines

\*New character analyzed.

GenBank (Table 2). The methodology followed the protocols proposed by Mantelatto et al. (2007), adjusted according to the materials used.

Genomic DNA was extracted from eggs of ovigerous females and from the muscle tissue of walking legs of adults. DNA fragments were amplified by Polymerase Chain Reaction (PCR). Thermal cycling conditions with the primers COH6 (5'-TADACTTCDGGRTGDCCAAARAAYCA-3') and COL6b (5'-ACAAATCATAAAGATATYGG-3') (Schubart and Huber 2006) included an initial denaturation step of 94°C for 2 min, followed by 35 cycles of 94°C for 30/45 s, 42-50°C for 30/45 s and 1 min at 72°C, with a final extension at 72°C for

2 min. All products were visualized under ultraviolet light in 1% agarose gels stained with GelRed™ (Biotium, Inc.; 3159 Corporate Place, Hayward, California 94545, USA). A comigrating 1000-bp ladder was used as a molecular weight marker to confirm amplification of the correct fragments.

The PCR products were purified using Sure Clean® protocols and sequenced using the Big Dye® Terminator Mix (Applied Biosystems, 850 Lincoln Centre Drive, Foster City, California 94404, USA).

All sequences were confirmed by sequencing both strands. A consensus sequence for each of the two strands was obtained using the

**Table 2.** Molecular analysis of the barcoding gene COI. Specimens used for DNA sequences with respective dates and sites of collection, museum catalog numbers, and genetic database accession numbers (GenBank). (CCDB: Crustacean Collection of the Department of Biology, FFCLRP, University of São Paulo; CNCR: Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México)

Species	Date	Locality	Catalog Number	GenBank
<i>Acanthonyx scutiformis</i> (Dana, 1851)	2002	Grande Beach, Ubatuba, São Paulo, Brazil	CCDB 4479	KC695767
<i>Acanthonyx dissimulatus</i> Coelho, 1993	02/07/2002	Quintana Roo, La Mancha Rodes, Mexico	CCDB 2430	KC695765
	01/12/1995	Itaguá Beach, Ubatuba, São Paulo, Brazil	CCDB 103	KC695768
	Unknown	United States of America	Unknown*	EU682454
	Unknown	United States of America	Unknown*	EU682455
	26/08/2007	Veracruz de Ignacio de la Llave, San Andrés Tuxtla, Mexico	CNCR 24952	KC695766
<i>Acanthonyx petiverii</i> H. Milne Edwards, 1834	06/04/2007	Cahuita Beach, Costa Rica (Atlantic)	CCDB 3725	KC685776
	05/08/2011	Paunch Beach, Bocas del Toro, Panama (Atlantic)	CCDB 1063	KC695774
	25/08/2011	La Restinga, Venezuela	CCDB 3633	KC695775
	03/11/2010	Boca Chica, Isla Margarita, Venezuela	CCDB 2428	KC695771
	06/04/2012	Boa Viagem Beach, Recife, Pernambuco, Brazil	CCDB 3814	KC695773
	06/11/2010	Badusca Beach, Ilhéus, Bahia, Brazil	CCDB 2427	KC695769
	12/05/2010	Flamengo Bay, Ubatuba, São Paulo, Brazil	CCDB 2436	KC695770
01/10/2002	Grande Beach, Ubatuba, São Paulo, Brazil	CCDB 760	KC695772	
<i>Acanthonyx lunulatus</i> (Risso, 1816)	01/02/2008	Stretto di Sicilia, Sicily, Italy	Unknown**	JQ305884
	01/02/2008	Scala dei Turchi, Sicily, Italy	Unknown**	JQ305885
<i>Epiplatys bituberculatus</i> H. Milne Edwards, 1834	05/08/2011	Bocas del Toro, Panama (Atlantic)	CCDB 917	KC695784
<i>E. brasiliensis</i> Dana, 1852	12/05/2010	São Paulo, Brazil	CCDB 2441	KC695786
<i>Menaethius monoceros</i> (Latreille, 1825)	Unknown	Japan	Unknown*	EU682856
	Unknown	Japan	Unknown*	EU682857

\*Hultgren and Stachowicz 2008. \*\*Matzen da Silva et al. 2011.

computational program BioEdit 7.0.9.0 (Hall 1999). The sequences were aligned using the Clustal W program with the BioEdit interface using default parameters (Thompson et al. 1994).

Pairwise genetic distances were calculated in the Mega5 program (Tamura et al. 2011). The construction of the tree was performed using the maximum likelihood method (Huelsenbeck and Crandall 1997), which was executed in the RAxML program (Randomized Accelerated Maximum Likelihood; Stamatakis 2006) using the Cipres online platform (Cyberinfrastructure for Phylogenetic Research) (Miller et al. 2010). The nucleotide substitution model assumed was GTR+G+I. The consistency of tree topologies was evaluated by the bootstrap method (1000 replicates), and bootstrap confidence values  $\leq 50\%$  were not reported on the molecular tree.

For rooting the COI tree, two species of *Epialtus* (*Epialtus bituberculatus* H. Milne Edwards, 1834, *Epialtus brasiliensis* Dana, 1852) and one of *Menaethius monoceros* (Latreille, 1825) were used as an outgroup according to the phylogenies of the superfamily proposed by Marques and Pohle (2003) and Hultgren and Stacowicz (2008). In one of them *Menaethius* was sister to *Epialtus* + *Acanthonyx* (Marques and Pohle 2003); in the other one, *Menaethius* was sister-group of *Acanthonyx* (Hultgren and Stacowicz 2008). Based in the tree, we calculated the genetic distances between the groups (North American and Brazil plus Central America) in the Mega5 program (Tamura et al. 2011).

## RESULTS

The morphological analysis (Table 1) indicated that the studied species of *Acanthonyx* were very close and could not be separated using the diagnosing characters proposed in the original description (H. Milne Edwards 1834; Dana 1851; Coelho and Torres 1993). The main characters defined as diagnosing-angle of hepatic region of the carapace, the size of tubercles of the carapace and the length of the setae in the carapace and pereopods were variable (e.g. hepatic lobe with tuft of long setae or this tuft absent). The structure of the male first pleopod (Table 1), showed no variation in all specimens analyzed and therefore was uninformative. Considering the angle of the hepatic region, it is not always rectangular, and the curvature varies from acute to obtuse in specimens of the same place, e.g. Ubatuba/São Paulo/

Brazil. This angle and curvature of hepatic lobes, and setal length have been used to separate *A. scutiformis* and *A. dissimulatus* (Coelho and Torres 1993; Melo 1996), with the first species showing the hepatic lobe curved forwards and upwards, lateral margin with long setae and the second showing hepatic lobe acute smooth or with short setae. The combination of characters could not be used to differentiate the studied populations.

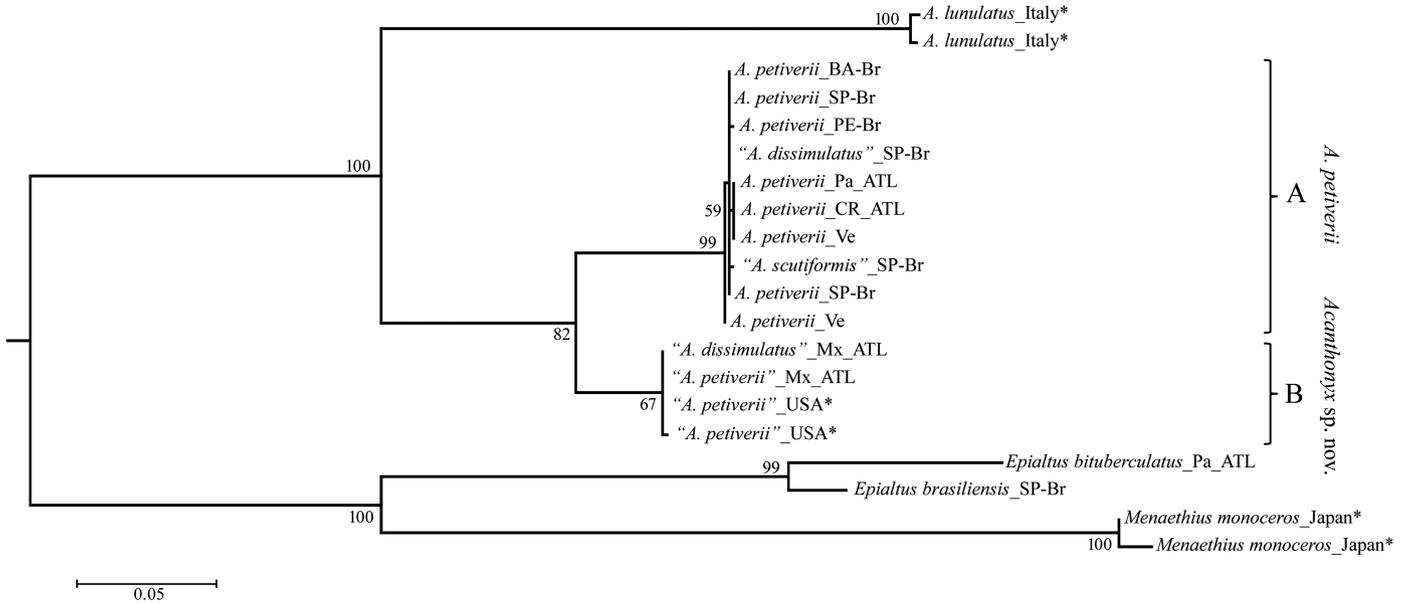
Chelipeds of *A. petiverii* have dactylus and fixed finger dentate along outer surface, inner surface with two tufts of simple setae. That character, which were regarded as diagnosing features (Garth 1958; Coelho and Torres 1993), does not allow the separation between that species and *A. dissimulatus*. In three males of *A. petiverii* from Rio de Janeiro (MNRJ 4470) and Paraíba (MNRJ 6487) fingers were predominantly smooth or had teeth only in the tips; in *A. dissimulatus*, they were smooth, with 1-3 bigger teeth or presented teeth in all outer surface. The presence of tubercles with or without setae in the carapace region is a variable character and different combinations were observed: gastric region with 3 evident tubercles, obsolete tubercle or absent, tubercles can be setiferous or not; cardiac region with one setiferous tubercle or absent. Additionally, the distribution, length and thickness of the setae along the body and in the articles also vary: body and legs completely smooth; tufts of long and short setae only in the regions of carapace; 1 or 2 setae only in the extremity of legs.

The obtained sequences of the barcoding gene COI contained 529-640 base pairs. The genetic divergence within the genus *Acanthonyx* ranged from 0 to 15.3% (Table 3). The interspecific distances between *A. dissimulatus* and *A. scutiformis* ranged from 0 to 6.3%; between *A. dissimulatus* and *A. petiverii*, the distances ranged from 0 to 6.1%; and among *A. scutiformis* and specimens of *A. petiverii*, the distances ranged from 0 to 6.3%. The intraspecific distances for *A. petiverii* ranged from 0 to 6.3% (Table 3).

The phylogram constructed using the maximum likelihood method for the barcoding gene COI suggested a clear separation between *A. lunulatus* and the three species focused on in this study. Specimens of *A. dissimulatus* and *A. scutiformis* were included within the group *A. petiverii* (Fig. 1), but two distinct groups were observed: group A, with specimens from Central and South America (now called *A. petiverii*), and group B, with specimens from North America (called *Acanthonyx* sp. nov. in this study) (Fig. 1). The genetic distance

between these two groups were 6.7%. The branch with groups A and B was well supported, with a bootstrap value of 82; groups A and B were well

supported, with bootstrap values of 99 and 67, respectively (Fig. 1).



**Fig. 1.** Genetic comparison between species of the genus *Acanthonyx* Latreille, 1828. Phylogram obtained from Maximum Likelihood analysis of barcoding COI sequences. The numbers are significance values for 1000 bootstraps; values  $\leq 50\%$  are not shown. The species names in inverted commas refer to the original identification (\*GenBank sequences: JQ305885; JQ305884, EU682455, EU682454, EU682857, EU682856; A: Central and South America; ATL: Atlantic coast; B: North America; BA: Bahia; Br: Brazil; CR: Costa Rica; Mx: Mexico; SP: São Paulo; Pa: Panama; PE: Pernambuco; USA: United States of America; Ve: Venezuela).

**Table 3.** Genetic divergence matrix. Comparison between partial sequences of the barcoding COI gene among the specimens of genus *Acanthonyx* [\*GenBank Sequences: (1) JQ305885, (2) JQ30588, (3) EU682854, and (4) EU682855. ATL: Atlantic coast; BA: Bahia; CR: Costa Rica; USA: United States of America; SP: São Paulo; PE: Pernambuco; RJ: Rio de Janeiro; Ve: Venezuela]. The species names in inverted commas refer to the original identification

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 <i>A. lunulatus_Italy*</i>	0.0															
2 <i>A. lunulatus_Italy*</i>	0.4	0.0														
3 "A. petiverii"_USA*	15.3	15.1	0.0													
4 "A. petiverii"_USA*	15.3	15.1	0.0	0.0												
5 "A. dissimulatus"_Mexico_ATL	15.3	15.1	0.0	0.0	0.0											
6 "A. dissimulatus"_SP-Br	14.0	14.1	6.1	6.1	6.1	0.0										
7 "A. scutiformis"_SP-Br	14.1	14.3	6.3	6.3	6.3	0.2	0.0									
8 "A. petiverii"_México_ATL	15.3	15.1	0.0	0.0	0.0	6.1	6.3	0.0								
9 <i>A. petiverii_CR_ATL</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0							
10 <i>A. petiverii_Pa_ATL</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0	0.0						
11 <i>A. petiverii_Ve</i>	14.0	14.1	6.1	6.1	6.1	0.2	0.4	6.1	0.2	0.2	0.0					
12 <i>A. petiverii_Ve</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0	0.0	0.2	0.0				
13 <i>A. petiverii_PE-Br</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0	0.0	0.2	0.0	0.0			
14 <i>A. petiverii_BA-Br</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0	0.0	0.2	0.0	0.0	0.0		
15 <i>A. petiverii_SP-Br</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	
16 <i>A. petiverii_SP-Br</i>	14.0	14.1	6.1	6.1	6.1	0.0	0.2	6.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0

***Acanthonyx petiverii* H. Milne Edwards, 1834**  
(Fig. 2)

*Cancer muricatus compressum* Petiver, 1712: plate 20: Fig. 8.

*Acanthonyx petiverii* H. Milne Edwards, 1834: 343, plate 15: Fig.s 6-8; Bell, 1841: 62; Moreira, 1901: 66; Rathbun, 1925: 142, Fig. 52, plate 44, plate 222: Figs. 1-6; Rathbun, 1933: 13, Fig. 11; Garth, 1946: 376, Fig. 4, plate 63; Garth, 1958: 223, plate 25: Fig. 2; Fausto-Filho, 1966: 33; Houvenaghel and Houvenaghel 1974: 143; Abele and Kim, 1986: 43, 495 (key); Hernández-Aguilera et al., 1997: 60, Fig. d, plate 3; Marcano and Bolaños, 2001: 74.

*Acanthonyx emarginatus* H. Milne Edwards & Lucas, 1843: 9.

*Acanthonyx debilis* Dana, 1851: 272.

*Peltinia scutiformis* Dana, 1851: 273.

*Acanthonyx simplex* Dana, 1852 - Empananza et al., 2007: 534 (Table 1), 535, Fig. 1.

*Acanthonyx concamerata* Kinahan, 1857: 334, plate 14: Fig. 1.

*Acanthonyx scutiformis* - Coelho and Torres, 1993: 228; Melo, 1996: 171; Melo, 1998: 455; Melo, 2008: 4; Teixeira et al., 2009: 89.

*Acanthonyx dissimulatus* Coelho, 1993: 231, Fig. 1; Melo, 1998: 455.

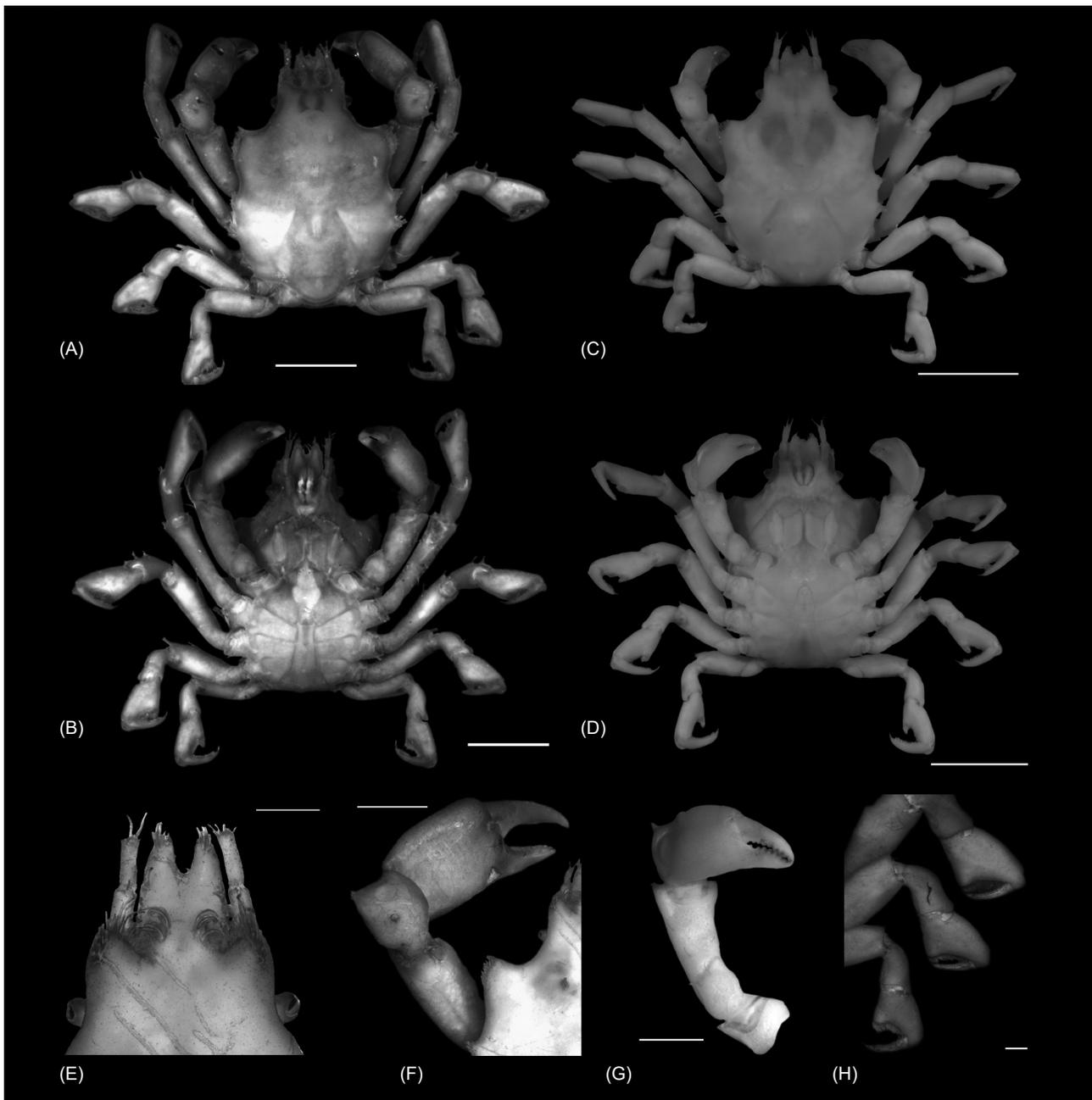
**Type locality:** The Antilles (H. Milne Edwards 1834; Rathbun 1925; Garth 1958), in the western Atlantic. The holotype of *A. petiverii* (male with 18 mm) is in the Muséum National d'Histoire Naturelle, Paris, France (Rathbun 1925; Garth 1958). Examined (see Discussion).

**Material examined:** UNITED STATES OF AMERICA, Florida, Miami: 1 male (CL 12.57 mm), 22/III/1965, J. Cabrera leg. (CNCR 1152); MEXICO, Compostela, Nayarit: 1 female (CL 7.7 mm), 11/III/1993, J.L. Villalobos, E. Cadena, M.E. Camacho, F. Álvarez and E. Lira leg. (CNCR 15302); San Andrés Tuxtla, Veracruz de Ignacio de la Llave: 1 male (CL 4.2 mm), 26/VIII/2007, coll. not available (CNCR 24952); Veracruz, El Moro: 1 male (CL 9.35 mm), 01/VI/1973, J.A. Rickner leg. (ULLZ 11303); Veracruz, Punta Delgada: 3 males (CL 4.8 - 5.8 mm), 1 female (CL 4.9 mm), 07/II/2002, D.L. Felder, R. Robles and T. Rodriguez leg. (ULLZ 6163); COSTA RICA, Isla Murciélago: 2 ovigerous females (CL 7.0 and 8.6 mm), 08/V/1999, coll. not available (UCR 2295-II); PANAMA, Bocas del Toro: 1 male (CL 5.2 mm), 09/VIII/2004, D.L. Felder leg. (ULLZ 10755); Bocas del Toro, Playa Paunch: 1 male (CL 13.5 mm), 1 ovigerous female (CL 11.4 mm), 05/VIII/2011, F.L. Mantelatto leg. (CCDB 1063); VENEZUELA, Isla Margarita, Boca Chica: 1 male (CL 8.4 mm), 1 female (CL 10.0 mm), 03/XI/2010, R. Lopez leg. (CCDB 2428); La Restinga: 1 male (CL 12.4 mm), 1 female (CL 16.4 mm), 25/VIII/2011, J. Bolaños leg. (CCDB 3633); BRAZIL, Ceará, Aracati, Retiro Grande Beach: 1 male (CL

14.7 mm), 1 ovigerous female (CL 13.8 mm), 17/I/1964, A.L. Castro leg. (MNRJ 4468); Ceará, Mucuripe: 1 female (CL 9.9 mm), 1 juvenile (CL 6.54 mm), 23/IV/1965, coll. not available (MNRJ 4462); Pernambuco, Recife, Piedade Beach: 2 males (CL 10.3 and 19.2 mm), 1 female (CL 8.52 mm), 1 ovigerous female (CL 15.06 mm), 24/VI/1986, A.L. Castro, P. Coelho and G. Melo leg. (MNRJ 4478); Pernambuco, Recife, Boa Viagem Beach: 4 males (CL 7.0 - 17.6 mm), 1 female (CL 9.7 mm), 1 juvenile (CL 5.5 mm), 06/IV/2012, F.L. Mantelatto leg. (CCDB 3814); Pernambuco, Ipojuca, Serrambi county, Serrambi Beach: 1 male (CL 8.3 mm), 1 juvenile (CL 5.3 mm), 25/XII/2012, F.L. Mantelatto and F.B. Mantelatto leg. (CCDB 4481); Paraíba, Jacunã, Tambaba Beach: 2 males (CL 6.9 and 17.8 mm), 1 female (CL 9.1 mm), 1 ovigerous female (CL 14.0 mm), 23/III/1995, P.S. Young and C.S. Serejo leg. (MNRJ 6487); Alagoas, Marechal Deodoro, Francês Beach: 1 ovigerous female (CL 18.7 mm), 16/II/1995, P.S. Young and C.S. Serejo leg. (MNRJ 6630); Alagoas, Marechal Deodoro, Torto Beach: 1 female (CL 10.7 mm), 16/II/1995, P.S. Young and C.S. Serejo leg. (MNRJ 6671); Bahia, Lauro de Freitas, Ipitanga Beach: 1 female (CL 13.2 mm), 22/XII/2011, F.L. Carvalho and E.A. Souza-Carvalho leg. (CCDB 3789); Bahia, Itacaré, Ribeira Beach: 3 males (CL 3.7 - 11.4 mm), 4 females (CL 4.6 - 7.8 mm), 9 juveniles (CL 2.3 - 3.7 mm), 22/III/1994, P.S. Young and M.M. Britto-Pereira leg. (MNRJ 4507); Bahia, Ilhéus, Morro de Pernambuco, Badusca Beach: 4 males (CL 4.2 - 6.0 mm), 6 females (CL 3.6 - 13.8 mm), 6/XI/2010, F.L. Mantelatto, F. Carvalho and L. Pileggi leg. (CCDB 2427); Bahia, Ilhéus, Morro de Pernambuco, Badusca Beach: 4 males (CL 7.4 - 11.5 mm), 3 females (CL 6.7 - 9.9 mm), 2 ovigerous females (CL 9.9 and 13.1 mm), 1 juvenile (CL 3.9 mm), 21/II/2011, F. Carvalho and E.A. Souza-Carvalho leg. (CCDB 3423); Espírito Santo, Guarapari, Castanheiros Beach: 1 ovigerous female (CL 10.1 mm), 30/X/1993, P.S. Young leg. (MNRJ 4547); Espírito Santo, Vitória, Boi Island: 1 male (CL 20.7 mm), 11/III/1987, Flávio and Iara leg. (MNRJ 4664); Espírito Santo, Vitória, Tubarão Harbor: 1 male (CL 18.5 mm), 1 ovigerous female (CL 16.6 mm), 10/XI/1987, coll. not available (MNRJ 4663); Rio de Janeiro, Cabo Frio, Però Beach: 1 male (CL 9.4 mm), 2 females (CL 6.3 and 7.9), 28/VII/1965, A.L. Castro leg. (MNRJ 4661); Rio de Janeiro, Niterói, Itaipú Beach: 1 male (CL 19.6 mm), IV/1963, J. Becker leg. (MNRJ 4471); Rio de Janeiro, Niterói, Itaipú Beach: 1 male (CL 14.4 mm), 1 female (CL 9.6 mm), 3/IV/1992, A.

Macedo leg. (MNRJ 4515); Rio de Janeiro, Rio de Janeiro, Barra de Guaratiba: 1 male (CL 13.1 mm), 30/IV/1953, N. Santos leg. (MNRJ 4467); Rio de Janeiro, Rio de Janeiro, Flamengo Bay: 1 male (CL 17.9 mm), 06/VIII/1982, R. Leite leg. (MNRJ 4470); São Paulo, Ubatuba, Grande Beach:

1 male (22.6 mm), 04/XI/1987, F.L. Mantelatto leg. (CCDB 0067); São Paulo, Ubatuba, Itaguá Beach: 2 males (CL 21.3 mm), 2 ovigerous females (15.7 and 16.1 mm), VI/1999, F.L. Mantelatto leg. (CCDB 0046); São Paulo, Ubatuba, Grande Beach: 1 male (CL 17.6 mm), 1 ovigerous female (CL 15.2 mm),



**Fig. 2.** Overview of samples of *Acanthonyx* Latreille, 1828 and some parts of their body. "*A. petiverii*" H. Milne Edwards, 1834, male CL 13.5 mm (CCDB 1063). (A) dorsal view, (B) ventral view; "*A. dissimulatus*" Coelho, 1993 male CL 12.2 mm (CCDB 1421) (C) dorsal view, (D) ventral view; (E) bifid rostrum, male CL 24.5 mm (CCDB 3949); (F) dorsal view of male left cheliped, CL 24.5 mm (CCDB 3949); (G) ventral view of female right cheliped, CL 8.3 mm (CCDB 3423); (H) subchela of the propodus of the last three ambulatory pereopods, male CL 24.5 mm (CCDB 3949). Scale bars: 5 mm (A, B, C, D, F); 2 mm (E, G); 0.6 mm (H). The species names in inverted commas refer to the original identification.

X/2002, F.L. Mantelatto leg. (CCDB 0760); São Paulo, Ubatuba, Ubatuba Bay: 1 female (CL 12.3 mm), 13/V/2010, F.L. Mantelatto leg. (CCDB 2436); São Paulo, Ubatuba, Grande Beach: 1 male (CL 24.8 mm), 08/XII/2012, I.C. Leone leg. (CCDB 3949).

Additional material initially identified as *A. dissimulatus*. MEXICO, Quintana Roo, La Mancha Rodes: 1 male (CL 15.9 mm), 1 ovigerous female (CL 8.2 mm), 02/VII/2002, coll. not available (CCDB 2430); BRAZIL, Rio Grande do Norte, Potiguar Basin: 1 ovigerous female (CL 9.9 mm), 23/XI/2003, coll. not available (DOUFPE 13837); Rio Grande do Norte, Potiguar Basin: 2 males (CL 7.1 and 10.7 mm), 23/XI/2003, coll. not available (DOUFPE 13906); Rio Grande do Norte, Potiguar Basin: 1 male (CL 15.4 mm), 21/XI/2003, coll. not available (DOUFPE 13920); Rio Grande do Norte, Potiguar Basin: 1 female (CL 8.6 mm), 2 ovigerous females (CL 10.5 and 13.5 mm), 21/XI/2003, coll. not available (DOUFPE 13927); Pernambuco, Santo Aleixo Island: 1 female (CL 8.2 mm), 06/II/2007, coll. not available (DOUFPE 13523); Pernambuco, Santo Aleixo Island: 1 ovigerous female (CL 11.5 mm), 2 juveniles (CL 2.9 and 3.6 mm), 06/II/2007, coll. not available (DOUFPE 13524); Bahia, Corumbau, Itacolomis: 3 males (CL 4.9 - 8.0 mm), 16/II/2000, P.C. Paiva leg. (MNRJ 16748); Rio de Janeiro, Arraial do Cabo, Anjos Beach: 1 male (CL 24.3 mm), 1 ovigerous female (CL 20.2 mm), 06/IX/2003, C.E.L. Ferreira leg. (MNRJ 19254); São Paulo, Ubatuba, Itaguá Beach: 2 males (CL 8.8 and 18.7 mm), 1 female (CL 8.5 mm), 2 ovigerous females (CL 17.2 and 18.5 mm), 1 juvenile (CL 9.3 mm), XII/1995, coll. not available (CCDB 103); São Paulo, Ubatuba, Grande Beach: 1 male (CL 11.7 mm), 04/V/2004, F.L. Mantelatto leg. (CCDB 1421).

Additional material initially identified as *A. scutiformis*. BRAZIL, Rio de Janeiro, Angra do Reis: 1 male (CL 13.1 mm), 22/V/1966, coll. not available (MZUSP 2781); 1 ovigerous female (CL 15.6 mm), 21/V/1966, coll. not available (MZUSP 2782).

**Diagnosis:** Rostrum short, deflexed, bifid; gastric region protuberant; hepatic region with lateral lobes curved forwards and upwards; propodus of chelipeds gaping in adult male; ambulatory pereopods subchelate.

**Description:** Carapace elongate (almost elliptical), subpentagonal, smooth; tubercles in gastric, sometimes absent; cardiac and intestinal region, with no apparent pattern; lateral margins nearly parallel or parallel, with 3 setiferous teeth,

1 on margin of hepatic region, 2 on branchial region, sometimes absent; antennae visible on either side of rostrum. Rostrum short, deflexed, bifid; extremity with minute spine and 1 tuft of setae, setae filling entire sinus of rostrum; long and fine setae distributed laterally on dorsal margin; row of hooked setae on each side of dorsal surface adjacent to preorbital tooth. Orbits absent; orbital region with lateral angles obtuse; preorbital lobes not pointed, elevated, curved forwards and inwards. Eyes visible from above carapace, small, mobile, with short and thick setae on dorsal surface, sometimes absent. Preorbital teeth elevated, not pointed, presence of setae with variable length and thickness along lateral margin. Postorbital teeth absent. Hepatic region usually with almost rectangular angles in dorsal view, lateral margins curved forwards and upwards, with setae of variable length and thickness along margins. Gastric region slightly elevated, with 3 small setiferous tubercles distributed in a triangle, 2 on protogastric and 1 on mesogastric region. Cardiac region not evident; obsolete tubercle, with tuft of setae of variable length and thickness. Branchial region with 2 small teeth not pointed, with short and long setae. Intestinal region smooth or 2 lateral obsolete tubercles, with 3 tufts of setae, a central and 2 lateral tufts. Basal article of antenna with base wider than extremity; following 2 articles subcylindrical, attaining end of rostrum; distal end of second article with long setae; third article with tufts of short and long setae on inner margin; flagellum slender, with setae, sometimes absent. Chelipeds less strong, short, smaller than first pair of ambulatory pereopods in females and males up to 8 mm of carapace length; chelipeds short, considerably enlarged in adult males (carapace length more than 12 mm). Distal end of ischium with 1-5 thin setae on ventral surface. Merus with 3 setiferous lobes at the distal end (1 central and 2 lateral lobes); 1-2 spines on the proximal dorsal surface; a row of 1-3 thin setae on ventral surface. Carpus with setiferous external crest, sometimes smooth; 3 setiferous tubercles (1 proximal, 1 distal, 1 central); row of 7 thin setae along inner margin. Propodus enlarged in lateral margins and compressed in upper margin, less enlarged and compressed in females; fingers gaping extremity in males, almost entirely closed in females; fixed finger smooth in larger males, dentate on outer surface and smooth on inner surface in other males and females, with tufts of setae near distal end. Dactylus dentate on outer surface and smooth on inner surface, with tufts of setae near distal

end. Ambulatory pereopods subchelate in larger specimens, not subchelate in smaller specimens; posteriorly decreasing in size. Merus with 3 lobes in distal end of first and second pereopods, 1 or 2 long and stout setae in the central lobe; 1 or 2 setae on dorsal surface and sometimes on ventral surface. Merus of third and fourth pairs with less pronounced distal lobes, with setae on extremity, sometimes smooth. Carpus of first, second and third pairs with a setae on distal inner margin, 1 or 2 on median of dorsal surface, 1 setae on distal outer margin; fourth pair smooth; subtriangular in last 2 ambulatory pereopods. Propodus of ambulatory pereopods compressed, subtriangular, with rounded end where dactylus articulates, forming structure with dactylus; distal margin lined with setae. Subchela more pronounced from fourth to first pair. Dactylus with 2 rows of minute spines intercalated with fine setae on ventral surface; end smooth, not pointed. Anterior thoracic sternum smooth. Fourth and fifth abdominal somites fused in both genders, triangular abdomen in males, almost elliptical in females, rounded in ovigerous females; telson triangular; extremity of male first pleopod with subtriangular lobe with minute spines.

**Description of juveniles:** Carapace transparent, lobes and spines less pronounced than adults; rostrum not deflexed, bifid and more divergent than in adults, forming an obtuse angle and a pronounced cavity; preorbital lobes not curved forwards and inwards, with long and thick setae between preorbital lobes and between preorbital and hepatic lobes; hepatic region smooth, without rectangular angles in dorsal view, lateral margins not curved forwards and upwards; gastric region without tubercles and setae. Chelipeds not strong, articles with setae distributed arbitrarily; carpus without external crest or less pronounced, without tubercles and sometimes only with setae (row with up to 6 thin setae on inner margin); propodus not enlarged and compressed, fingers entirely closed. Ambulatory pereopods subcylindrical, with setae distributed arbitrarily; propodus with almost rounded end where dactylus articulates, but not subchelate. Abdomen almost triangular, but not so marked and thin as in males.

**Coloration:** It is variable and depends entirely upon the color of the surrounding macroalgae (Coelho and Torres 1993). Co-ordinated with its body ornaments, its color allows the crab to be confused with algae and difficult to recognize (Teixeira et al. 2009). Crabs are typically brown or dark green, with bits of algae, grains of sand and/or debris attached to the body. Fresh specimens can

present a dark heart-shaped stain in the gastric region and two round spots in the protogastric region around the area of the tubercles. The tips of the cheliped fingers are white and red, and the hepatic region is orange. There are two darker bands in the region between the preorbital teeth.

**Remarks:** The species in Brazil cannot be effectively separated with the current accepted suite of morphological characters (H. Milne Edwards 1834; Dana 1852; Rathbun 1925, Coelho and Torres 1993; Melo 1996), and with the male first pleopods proving not to be useful. The male first pleopod of *Acanthonyx petiverii* (Garth 1958: plate O, Fig. 3) is similar to that of other species, such as *A. minor* (cf. Manning and Holthuis 1981: Fig. 64h), and clearly differs from *A. depressifrons* and *A. formosa* (cf. Manning and Holthuis 1981: Fig. 62f, Wu et al. 1999: Fig. 3d), which means that this character can be used to recognize some species within the genus but is not informative for the species here analyzed.

The original description of *A. petiverii* (H. Milne Edwards 1834) was short and general, addressing only features of three morphological characters (orbits, carapace and legs). We redescribed *A. petiverii* with more details and characters based on samples from distinct localities of its distribution. The specimens of *A. petiverii* studied herein agree with the original description (H. Milne Edwards 1834) in lateral margin with three teeth, the anterior one bigger than the others; they were similar to those described by Garth (1958) and Hendrickx (1999), except for the size variation (the smallest specimen had a CL of 2.9 mm, and the largest specimen had a CL of 24.8 mm) observed in the present study, which was less than that reported in the original description (approximately 20.0 mm) and greater than that reported by Garth (1958) (CL ranging from 4.5 to 34.6 mm) and Hendrickx (1999) (CL ranging from 3.6 to 11.8 mm).

Similar to the present study, Garth (1958) and Emparanza et al. (2007) observed considerable variation in the presence or absence of tufts of setae and tubercles on the carapace and in the angle of the hepatic lobe, whether acute or obtuse. Both variations in the carapace as well as its color appear to be related to the color of the host algae (e.g. green, brown, or red) in the region where the crabs live (Emparanza et al. 2007). The specimens analyzed here have their colors related to the color type of algae that they were taken from, brown specimens occurring on *Sargassum* sp. and *Hypnea* sp.; green specimens living on *Padina*

sp. and *Ulva* sp. Finally, carapace shape variation seems to be morphological not a consequence of the ornamentation.

Ambulatory legs of specimens analyzed herein were less cheliform in females and in young males compared with adult males, and this had already been noted as an age-related character (Rathbun 1925). Coelho and Torres (1993) described *A. dissimulatus* and reviewed *A. scutiformis*, but they noted that adults of *A. petiverii* were similar to juveniles and adults of *A. scutiformis* and *A. dissimulatus*.

The type locality of *A. petiverii* is the Antilles (H. Milne Edwards 1834; Rathbun 1925; Garth 1958) but we did not analyze material of this region. Then, we had observed specimens from Costa Rica, Panama and Venezuela aiming to cover some Central America regions, places that are close to the type locality. We examined a possible specimen that correspond to the holotype in the Muséum National d'Histoire Naturelle via recent photos made by the curator, but doubts raised about its origin due to lack of information available in the original label, which lead us uncomfortable and with uncertainties during our analysis. The type locality of *A. dissimulatus* is in Paraíba State (Brazil), and the holotype (male, MZUSP 6596) was supposedly deposited in Museu de Zoologia da Universidade de São Paulo (Coelho and Torres 1993). The type locality of *A. scutiformis* is Rio de Janeiro State (Brazil), and its holotype is noted in the literature as non-existent (Dana 1851; Moreira 1901; Coelho and Torres 1993; Melo 1996). At this stage, we analyzed the original description but not the specimens, although we analyzed material from this locality.

The genus *Acanthonyx* has a wide distribution with 17 valid species, but its systematics and taxonomy are little studied. *Acanthonyx petiverii*, *A. dissimulatus* and *A. scutiformis* are American species of this genus; however, we did not find a consistent morphological feature to differentiate these species from each other. Thus, we chose some available character and performed a morphological comparison based on species from distinct geographical distributions described and well supported in the literature (Table 4): *A. depressifrons* Manning and Holthuis, 1981 and *A. minor* Manning and Holthuis, 1981 from West Africa (Manning and Holthuis 1981); *A. limbatus* A. Milne-Edwards, 1862 and *A. euryseroche* Griffin and Tranter, 1986 from Indo-West Pacific (Griffin and Tranter 1986); and *A. formosa* from Taiwan (Wu et al. 1999).

We can infer that those combined character that fail to separate *A. petiverii*, *A. dissimulatus* and *A. scutiformis*, can be used to distinguish species from other geographic region, e.g. shape of the rostrum plus male first pleopod can distinguish *A. depressifrons* from *A. minor* (Manning and Holthuis 1981).

The variation observed in taxonomic relevant characters among specimens of *Acanthonyx* from Brazil, allow us to question their validity. However, our molecular results suggested a clear division in two groups. Therefore, for specimens from Caribbean and Brazil (clade A) we suggest the synonymization of *A. dissimulatus* and *A. scutiformis* with *A. petiverii*. We validate the name of the last one because its type locality is in the Antilles, and it is a senior subjective synonym of *A. dissimulatus* and *A. scutiformis*. Additionally, from North America (clade B), we suggest that there is a different species, here named as *Acanthonyx* sp. nov. because we cannot find any clear character to diagnose and chose an appropriate name.

## DISCUSSION

The three species of *Acanthonyx* that occur in Brazil show overlapping distributions. *Acanthonyx petiverii* has the widest distribution in the western Atlantic, from the USA to Brazil (Hendrickx 1999; Marcano and Bolaños 2001; Cruz-Castaño and Campos 2003; Felder et al. 2009). The distributions of *A. dissimulatus*, from Maranhão to São Paulo (Coelho and Torres 1993; Melo 1996; Dall'Occo et al. 2004; Coelho et al. 2008), and *A. scutiformis*, from Espírito Santo to São Paulo (Coelho and Torres 1993; Dall'Occo et al. 2004; Melo 2008), fit into this range. There is a gap, which includes Espírito Santo and Rio de Janeiro, where there is no record of *A. dissimulatus* (Coelho and Torres 1993; Almeida and Coelho 2008), and *A. scutiformis* has been found only in southeastern Brazil (Coelho and Torres 1993; Melo 2008).

The morphological similarities (e.g. carapace shape, rostrum, ambulatory legs, male first pleopod) observed herein indicate the unclear separation between the different species. The diagnosing features used in the literature for each of these species of *Acanthonyx* (Rathbun 1925; Garth 1958; Coelho and Torres 1993; Melo 1996) were determined to be variable, suggesting a single wide-range species with intraspecific variations, such as suggested in *Hippolyte obliquimanus* Dana, 1852 (Terossi and Mantelatto 2012).

**Table 4.** Morphological characters of some species of *Acanthonyx* Latreille, 1828. (CL: carapace length)

Species/Characters	CL Maximum size (mm)	Rostrum	Carapace shape	Preorbital teeth	Brachial Region
<i>A. petiverii</i>	> 25	"U"-shaped	elongate, subpentagonal, 2 lateral lobes, smooth or tubercles with no apparent pattern; lateral margins nearly parallel or parallel	curved forwards	2 small teeth, not pointed
<i>A. depressifrons</i> Manning and Holthuis, 1981	< 5	"V"-shaped; strongly depressed	3 lateral lobes, smooth,	blunt, rounded, much shorter than rostral teeth	-
<i>A. euryseroche</i> Griffin and Tranter, 1986	<18	spines weakly deflexed, basally broad, narrower in the apex, sometimes apically incurved	3 lateral lobes, broad, smooth, small tubercles	directed forward and slightly outward but hardly upward	3 evident teeth
<i>A. formosa</i> Wu, Yu and Ng, 1999	<28	"V"-shaped	longitudinally ovate; dorsal surface smooth, covered with very low, felt-like pubescence tubercles well marked	triangular, directed obliquely outwards	2 relatively large and triangular lobes
<i>A. limbatus</i> A. Milne-Edwards, 1862	-	-	-	directed obliquely upwards	3 evident teeth
<i>A. lunulatus</i> (Risso, 1816)	> 15	"U"-shaped	-	-	-
<i>A. minor</i> Manning and Holthuis, 1981	< 5	"V"-shaped, not markedly depressed	3 lateral lobes, smooth, tubercles not evident	short and blunt	-

Species/Characters	Fingers of chelipeds	Thoracic sternum	Abdominal somites	Male first pleopod	Reference
<i>A. petiverii</i>	gaps at the extremities, dentate or smooth	smooth without depressions	4+5 fused in both genders	extremity with a subtriangular lobe with minute spines	present study
<i>A. depressifrons</i> Manning and Holthuis, 1981	almost closed, dentate	-	as illustrated in Fig. 62e	as illustrated in Fig. 62f	Manning and Holthuis 1981
<i>A. euryseroche</i> Griffin and Tranter, 1986	cutting edges with numerous teeth along the entire length of both fingers	smooth, a pair of small submedial pits directly behind the anterior margin, a shallow central depression in front of the abdominal fossa	7 segments in males, 4-6 fused in females	straight, broad, slightly narrowed before broad apex; anterior margin recurved ventrally, medial angle rounded, lateral angle subacute; aperture subterminally on sternal surface	Griffin and Tranter 1986
<i>A. formosa</i> Wu, Yu and Ng, 1999	large males with smoother fingers; subadult males and females with numerous small teeth along the edges of the fingers	smooth, with pits on sternite 2, sternite 3 and sternite 4 with depressions	3-5 fused in males, 3-6 fused in females	distal one-third gently curving outwards; distal most part gently bent outwards, dorsal fold (inner-distal margin) low, tip relatively sharp	Wu et al. 1999
<i>A. limbatus</i> A. Milne-Edwards, 1862	almost close, a large tooth on dactylus	-	segments of the male abdomen are not as clearly separated; the junctions between both segments 4 and 5 and segments 5 and 6 are indistinct	the aperture on the sternal surface just before the anterior margin; a small, rounded lobe on the proximal edge of the aperture	Griffin and Tranter 1986
<i>A. lunulatus</i> (Risso, 1816)	-	-	4+5 fused	as illustrated in Fig. 154i, j (Zariquiey-Alvarez 1968)	Manning and Holthuis 1981; Griffin and Tranter 1986
<i>A. minor</i> Manning and Holthuis, 1981	almost close, dentate	-	as illustrated in Fig. 64g	as illustrated in Fig. 64h	Manning and Holthuis 1981

The DNA analysis do not support the separation of three *Acanthonyx* species from Brazil; the phylogram suggested the existence of two groups: clade A included specimens of all three species from Brazilian coast and Central American seashore, and clade B with North American specimens of *A. dissimulatus* and *A. petiverii*. Thus, both clades were nominate on geographic distribution, type locality and possible synonyms.

In the original description, H. Milne Edwards (1834: 343) named *A. petiverii* assigning it to the "Antilles", without any indication of the analyzed specimens, only citing the book "Pterigraphia Americana" by Petiver (1712). Thus, we assume that he named the species from the plate presented by Petiver (1712). The figure in question (Petiver 1712: plate 20) clearly shows an *Acanthonyx* shape-species mentioned by H. Milne Edwards (1834); these specimens came from Barbados, which is part of the Antilles and very close to Venezuela. Specimens of *A. petiverii* were examined and/or recorded in Lower California (USA), Peru, Chile, Galapagos Islands (Pacific coast) (Bell 1841; Moreira 1901; Rathbun 1925; Garth 1946; Garth 1958; Houvenaghel and Houvenaghel 1974) and in some localities in Atlantic coast (H. Milne Edwards 1834; Moreira 1901; Rathbun 1925; Garth 1958; Fausto-Filho 1966; Hernández-Aguilera et al. 1997; Marcano and Bolaños 2001); some of them from Caribbean Sea or close to it such as Bahamas, Cuba, Jamaica, Porto Rico and Panama (Rathbun 1925; 1933) or Venezuela (Rathbun 1925; Marcano and Bolaños 2001). We have some specimens grouped in a single branch that come from Venezuela, also from Panama and Costa Rica, which are part of the Caribbean Sea. In an attempt to solve this branch of the tree, we suggest to name these specimens as *A. petiverii*, with support from molecular results.

In the Pacific Ocean, besides *A. petiverii*, there are two known species, *A. simplex* and *A. formosa* Wu, Yu & Ng, 1999 (Dana 1852; Manning and Holthuis 1981; Griffin and Tranter 1986; Wu et al. 1999; Emparanza et al. 2007). In addition, from Pacific and Atlantic populations of *A. petiverii* there are no obvious characters that can be used to separate them and, as such, these must be treated as conspecifics (Garth 1958; Emparanza et al. 2007). The valid species *A. formosa* is thus far only known from Taiwan (Wu et al. 1999) and is clearly different from *A. petiverii*, e.g. rostrum shape, abdominal somites and male first pleopod (Table 4).

The four synonyms, *A. emarginatus* H. Milne

Edwards & Lucas, 1843, *A. debilis* Dana, 1851, *A. simplex* Dana, 1852 and *A. concamerata* Kinahan 1857, associated with *A. petiverii* (Rathbun 1925; Ng et al. 2008; Emparanza et al. 2007) are specimens from Pacific (Chile, Peru) that according to their description and figures (H. Milne Edwards & Lucas 1843; Dana 1851, 1852; Kinahan 1857; Emparanza et al. 2007) were similar to specimens analyzed herein.

The close resemblance between *A. simplex* and *A. petiverii* was notable, e.g. narrow rostrum and U-shaped, and carapace with 2 tubercles or absent, lateral margins parallel; thus, it was regarded as a synonym of *A. petiverii* (Emparanza et al. 2007). The species *A. emarginatus*, *A. debilis* and *A. concamerata* were consider synonym by Rathbun (1901, 1925). *Acanthonyx concamerata*, like *A. petiverii*, have carapace slightly convex, sides parallel; two setiferous tubercles in the median region and fourth and fifth somites fused in both genders (Kinahan 1857). *Acanthonyx debilis* differs from *A. petiverii* in the small hands of the males, teeth of the fingers, the cristate carpus, and the two obsolete tubercles on the stomach region (Dana 1852). *Acanthonyx emarginatus* is a closely allied species of *A. petiverii* and *A. dentatus*; it differs from the first one due to the expansion of propodus of ambulatory legs and the crest that adorns the top edge of the fifth pair of legs, and it is different from *A. dentatus* by the lack of a spiniform tooth that exists in external orbital angle (H. Milne Edwards & Lucas 1843). All these differences were considered morphological variation in the present study, thus, we agree with the four synonyms. Since they are specimens from Pacific we do not use any of their names to nominate the branch with specimens from North American; therefore, we named it as *Acanthonyx* sp. nov.

We suggest that morphological similarities among the three species or misidentification due to the use of variable characters arise doubts about previous records of *A. petiverii* in the Gulf of Mexico (Hernández-Aguilera et al. 1997; Felder et al. 2009), records of *A. dissimulatus* in Mexico (Tamburus and Mantelatto 2012) and the restricted occurrence in Southeast Brazil of *A. scutiformis* (Coelho and Torres 1993; Melo 1996; Dall'Occo et al. 2004; Melo 2008).

Phylogenetic tree showed all Brazilian and Caribbean specimens of *Acanthonyx* clustered in the same clade. This lack of genetic structure across distant geographic sites might be explained by the planktonic nature of the larval stages of *Acanthonyx* species, *A. petiverii* and *A. lunulatus*

have two zoeal stages and a megalopa, with approximately 15 days of zoea development (Hiyodo et al. 1994, Guerao and Abelló 1996). This period that the larvae remain in the water column (Bacardit 1986) increases the dispersion potential of the species, maintaining a high gene flow among populations (Mathews et al. 2002). Population genetic homogeneity, such as that observed herein, have been reported in other marine decapods that distribute along the western Atlantic, e.g., *Petrolisthes armatus* (Gibbes, 1850) (Mantelatto et al. 2011).

Genetic comparison based on COI sequences revealed two clades (North America and Brazil plus Caribbean) separated by a genetic distance enough to suggest two species. The same situation was observed in other groups, such as the lobster *Panulirus argus* (Latreille, 1804) (Sarver et al. 1998) and the hermit crab *Clibanarius vittatus* (Bosc, 1802) (Negri et al. 2012). However, we have no observed diagnosing characters that justify such separation. Therefore, we conclude that there is unique wide-ranging species across the Atlantic with intraspecific variation such as in *Petrolisthes armatus* (Mantelatto et al. 2011) and *Hippolyte obliquimanus* (Terossi and Mantelatto 2012); or alternatively, two species that have recently started to radiate, like in *Panulirus argus* (Sarver et al. 1998) and *Clibanarius vittatus* (Negri et al. 2012). Thus, to test these alternative hypotheses, we encourage future studies using a wider range of molecular markers and, increasing the number of *A. dissimulatus* and *A. scutiformis* specimens and populations, but finally including species from Pacific.

## CONCLUSIONS

For the species *Acanthonyx dissimulatus*, *A. petiverii* and *A. scutiformis*, the morphological characters did not allow the clear separation between them, calling into question the taxonomic position of *A. dissimulatus* and *A. scutiformis*. We suggest the existence of cryptic speciation and the need of a revision of the genus considering morphological as well as molecular data. The establishment of the two branches - Central and South America (clade A) and North America (clade B) - showed genetic differentiations between specimens separated geographically. However, we did not observe morphological characters to support this division. Thus, based on molecular data, we propose named clade A as *A. petiverii*

and clade B is assigned as *Acanthonyx* sp. nov. Finally, it would be important to add other genes with different evolution rates in future studies, in order to verify the hypothesis of a recent radiation of species or a population analysis with more specimens would be required to infer a concrete separation between populations.

## List of abbreviations

ATL: Atlantic coast  
 BA: Bahia  
 Br: Brazil  
 CCDB: Crustacean Collection of the Department of Biology  
 Cipres: Cyberinfrastructure for Phylogenetic Research  
 CL: carapace length  
 CNCR: Colección Nacional de Crustáceos, Universidad Nacional Autónoma de México  
 COI: Cytochrome Oxidase Subunit I  
 CR: Costa Rica  
 DOUFPE: Universidade Federal de Pernambuco  
 FFCLRP: Faculty of Philosophy, Sciences and Letters at Ribeirão Preto  
 MNRJ: Museu Nacional do Rio de Janeiro  
 MZUSP: Museu de Zoologia da Universidade de São Paulo  
 Mx: Mexico  
 Pa: Panama  
 PE: Pernambuco  
 PCR: Polymerase Chain Reaction  
 RAxML: Randomized Accelerated Maximum Likelihood  
 RJ: Rio de Janeiro  
 SP: São Paulo  
 UCR: Museum of Zoology of Universidad de Costa Rica  
 ULLZ: University of Louisiana-Lafayette, Zoological Collections  
 UNAM: Universidad Nacional Autónoma de México  
 USA: United States of America  
 USP: University of São Paulo  
 Ve: Venezuela

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