Memoirs of Museum Victoria 60(1): 79–85 (2003)

ISSN 1447-2546 (Print) 1447-2554 (On-line)
http://www.museum.vic.gov.au/memoirs

Geographic and depth distributional patterns of western Atlantic Porcellanidae (Crustacea: Decapoda: Anomura), with an updated list of species

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Abstract

Werding, B., Hiller, A., and Lemaitre, R. 2003. Geographic and distributional patterns of western Atlantic Porcellanidae (Crustacea: Decapoda: Anomura), with an updated list of species. In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 79–85.

Information on horizontal and vertical distributions of all known western Atlantic species of Porcellanidae is summarised, and an updated list of the 48 currently valid species is presented. The distributions and zoogeographic affinities of the group are discussed. In the western Atlantic, the Caribbean-West Indies region is the richest in number of species with 43, of which 40 species occur in the southern Caribbean. Species numbers decrease towards the peripheral regions of Florida, with 17 species, and Brazil, with 19 species (including two endemics). The Caribbean-West Indies porcellanid fauna shares 17 species with tropical Florida and 17 with tropical Brazil. There is a clear similarity in species composition between the tropical faunas of Florida and Brazil, sharing 11 species. Based on depth ranges, the species can be divided into "intertidal" (range $\leq$ 7 m) and "sublittoral" (range > 7 m) species. A relationship was observed between depth distributions and geographic ranges of western Atlantic porcellanids: "sublittoral' species have wide geographic ranges, presumably as result of greater dispersal potential and ability to colonise a variety of ecological habitats; "intertidal" species have narrow geographic ranges, presumably as result of lower dispersal ability and narrow ecological requirements. For western Atlantic porcellanids, the Amazon River delta and the Florida Current are dispersal barriers more effective for "intertidal" than for "sublittoral" species.

Keywords Crustacea, Anomura, Porcellanidae, western Atlantic, biogeography, distribution patterns, dispersal patterns

Introduction

Since Haig's (1956) compilation of the Porcellanidae from the western North Atlantic, a good deal of taxonomic work has been done on this family in the western Atlantic, particularly in Panama and other parts of the Caribbean (e.g. Gore, 1970, 1974, 1982; Gore and Abele, 1973, 1976; Werding, 1977, 1982, 1983, 1984, 1992, 1996; Scelzo, 1982; Hernández et al., 1999; Lemaitre and Campos, 2000; Werding et al., 2001; Werding and Hiller, 2001, Werding and Hiller, in press; Werding and Kraus, in press), the south-western Gulf of Mexico (e.g. Rickner, 1975), and Brazil (Veloso and Melo, 1993). Some areas, however, remain incompletely explored such as the Caribbean coast of Central America north of Panama, parts of the Greater Antilles and the Bahamas, and the Guyanas in north-eastern South America. Nevertheless, the relatively detailed records that already exist of porcellanids from the western Atlantic allow a reasonable assessment of their horizontal and vertical distributional patterns as well as zoogeographic affinities.

According to a list of valid species by Werding (1992) and updated herein, the total number of species for the entire western Atlantic is 48, although it is recognised that there are two widely distributed and morphologically highly variable taxa, *Petrolisthes armatus* (Gibbes, 1850) and *P. galathinus* (Bosc, 1902), believed to represent complexes of species. The western Atlantic porcellanid fauna is third in the world in richness after the Indo-West-Pacific, with some 110 species, and the eastern Pacific, with about 90 species. The region with the least number of species is the eastern Atlantic with only 15 species known so far. The porcellanid fauna of the western Atlantic has the strongest affinity with that of the eastern Pacific, sharing ten genera, whereas only five genera are shared with each of the eastern Atlantic, and Indo-West Pacific regions. The eastern Atlantic has eight genera in common with the Indo-West Pacific. The biogeography of the porcellanid fauna from the Pacific coast of the Americas was discussed by Carvacho (1980); however, that of the Atlantic porcellanids has never been discussed on a comprehensive basis. In this study, the geographic and depth distributions, zoogeographic affinities, and possible ecological factors that affect species dispersal of these anomuran crabs across the entire western Atlantic are discussed for the first time.

Distributional patterns and zoogeographic affinities

Geographic patterns. Based on the relatively detailed distributional records now available of porcellanids from the western Atlantic (see Table 1), the fauna of these crabs from this part of the world can be characterised as a homogeneous assemblage with a concentration of species in the southern Caribbean (40 species), and decreasing in number of species towards peripheral areas to the north (Florida) and south (Brazil). The porcellanid fauna of the Antilles, Bahamas and Bermuda, an area that comprises the tropical West Indian Province of Briggs (1974), is distinguished from that of the southern Caribbean by a lower species number (34 species). The almost complete lack of strictly temperate species in the western Atlantic implies that the family is represented in the northern Gulf of Mexico, and on the eastern coast of the United States by eurythermal, tropical species that can range northward to those northern regions. The only strictly warm temperate species found north of the tropical western Atlantic is *Euceramus praelongus* Stimpson, 1860, known from the north-eastern coast of the United States (Delaware Bay) to the northern Gulf of Mexico (Texas). South of the tropical western Atlantic, in tropical Brazil and temperate South America, the situation is somewhat similar. With the exception of *Pachycheles greeleyi* (Rathbun, 1900) from Brazil, all tropical species found there are also present in the southern Caribbean. Two species, *Pachycheles chubutensis* Boschi, 1963, and *P. laevidactylus* Ortmann, 1892, are temperate in distribution in South America, although the latter does extend far into the tropics of Brazil (Boschi, 1963; Harvey and De Santo, 1996). A very particular case is *P. robsonae* Glassell, 1945, an eastern Pacific species that has been found in the vicinity of the Atlantic opening of the Panamá Canal (Haig, 1960; Gore and Abele, 1976) where it has migrated repeatedly without becoming successfully established in the Caribbean.

The overwhelming majority of western Atlantic porcellanid species (43 out of 48) has a Caribbean-West Indian distribution (Fig. 1). The exceptional species richness of the southern Caribbean is accentuated by the presence of at least three endemic species: *Neopisosoma orientale* Werding, 1986, known from Trinidad, *Petrolisthes gertrudae* Werding, 1996, known from Guadeloupe and Bonaire, and *P. cristobalensis* Gore, 1970, known from a limited area around the Panamá Canal. Quite possibly three other species recently discovered in the Colombian Caribbean might also represent endemics, two from Islas del Rosario, *Petrolisthes sanmartini* Werding and Hiller, in press, and P. sp. (being named by Werding and Kraus, in press), and *Porcellana lillyae* Lemaitre and Campos, 2000, from the Gulf of Morrosquillo. Other species such as *Pachycheles chacei* Haig, 1956, *P. susanae* Gore and Abele, 1973, and probably *Petrolisthes magdalenensis* Werding, 1978, are restricted to limited areas of the South American Atlantic continental coast and adjacent islands. *Pachycheles greeleyi*, from Brazil, represents the only tropical endemic that occurs to the south of the Caribbean-West Indian region. *Pachycheles laevidactylus* does reach the tropics of Brazil, but its main distribution is on the temperate Atlantic coast of South America.

Patterns in number of species. A decrease in number of species can be observed from the Caribbean towards the north and south (Fig. 1). From a total of 43 species known from the Caribbean-West Indian region, 40 are present in the southern Caribbean and 34 in the Antilles. Only 17 species occur in tropical Florida, and 19 in tropical Brazil. All 17 Florida species are found also in the Caribbean-West Indian region. A similar situation can be observed in the Brazilian fauna where 17 of the 19 species that occur there are also found in the Caribbean-West-Indian region; only two are restricted in distribution, *Pachycheles greeleyi*, and *P. laevidactylus*, ranging from Brazil to Argentina. There is a noticeable similarity in species composition between the faunas of Florida and tropical Brazil, with 11 species in common. Only six of the 17 species that occur in Florida are not represented in tropical Brazil, and six of the Brazilian species that range into the Caribbean-West-Indian fauna are not present in Florida.

Patterns in depth and relative geographic ranges. A summary is presented (Table 2) of the depth (intertidal vs sublittoral) and relative geographic distributions of all tropical species from Florida, the Caribbean-West Indies, and Brazil, based on a critical review of the literature, and additional data (Werding, 1992; pers. obs.). Two strictly temperate species, *Euceramus praelongus* and *Pachycheles chubutensis*, and the eastern Pacific immigrant, *Petrolisthes robsonae*, are excluded as they are not part of the tropical western Atlantic porcellanid fauna.

The study of the geographic and depth distributions of porcellanids (Table 2) from the three regions shows that 22 species (20 in the Caribbean-West Indies, and 2 in Brazil) have a "limited" geographic range restricted to only one of the regions, whereas 23 species have a "wide" geographic range and are present in two or all three of the regions. Twenty-five species can be considered "intertidal", although some can be found down to 7 m in depth. Of those, 21 species are "limited" in range to either the Caribbean (19 species) or Brazil (2 species). Twenty species are found below 7 m in depth and are "sublittoral"; of these, all but *Porcellana lillyae* have a "wide" geographic range.

A comparison of the distributions of "intertidal" and "sublittoral" species from the three regions studied (Table 2, Fig. 2) shows that 14 or 70% of the "sublittoral" species of the Caribbean-West-Indian fauna occur in tropical Florida where they make up 82.4% of that fauna. Sixteen species or 80% from the Caribbean-West Indian fauna are shared with the Brazilian fauna where they make up 84.2% of that fauna. When the "intertidal" species are considered, only three species or 13% of the Caribbean-West Indian fauna occur in Florida, representing 17.6% of that fauna. Just one "intertidal" species or 4.3% of the Caribbean-West Indian fauna has been found in Brazil, making up only 5.3% of that fauna. Altogether, 11 or 55% of the Caribbean-West Indian "sublittoral" species are common to both Florida and Brazil, whereas no "intertidal" species are common to both of these peripheral regions.

Table 1. List of currently valid species of porcellanids from the western Atlantic, and their geographic distributions. (*Petrolisthes* sp. is an undescribed species being named by Werding and Kraus, in press).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Clastotoechus Haig, 1960													
C. nodosus (Streets, 1872)						•	•	•	•	•			
C. vanderhorsti (Schmitt, 1924)					•	•			•	•			
Euceramus Stimpson, 1860													
E. praelongus Stimpson,1860	•	•											
Megalobrachium Stimpson, 1858													
M. mortenseni Haig, 1962						•		•	•			•	•
M. poeyi (Guérin, 1855)			•		•	•	•	•	•	•			
M. roseum (Rathbun, 1900)						•		•	•	•		•	•
M. soriatum (Say, 1818)	•	•	•			•	•	•	•			•	•
Minyocerus Stimpson, 1858													
M. angustus (Dana, 1852)							•	•	•	•	•	•	•
Neopisosoma (Haig, 1960)													
N. angustifrons (Benedict, 1901)				•	•	•	•	•	•	•			
N. curacaoense (Schmitt, 1924)				•		•	•			•			
N. neglectum Werding, 1986									•				
N. orientale Werding, 1986						•							
Pachycheles Stimpson, 1858													
P. ackleianus A. Milne-Edwards, 1880			•		•	•	•	•	•	•	•	•	
P. chacei Haig, 1956							•	•	•				
P. chubutensis Boschi, 1963													•
P. cristobalensis Gore, 1970								•					
P. greeleyi (Rathbun, 1900)												•	
P. laevidactylus (Ortmann, 1892)												•	•
P. monilifer (Dana, 1852)	•		•			•	•		•	•		•	•
P. pilosus (H. Milne Edwards, 1837)	•		•	•	•	•	•		•	•			
P. riisei (Stimpson, 1859)			•		•	•	•		•	•		•	
P. rugimanus A. Milne-Edwards, 1880	•		•			•	•				•	•	
P. serratus (Benedict, 1901)					•	•		•	•	•			
P. susanae Gore and Abele, 1973						•		•	•				
Parapetrolisthes Haig, 1962													
P. tortugensis (Glassell, 1945)			•	•	•	•	•		•	•			
Petrolisthes Stimpson, 1858													
P. amoenus (Guérin, 1855)			•		•	•	•		•	•		•	
P. armatus (Gibbes, 1850)	•	•	•	•	•	•	•	•	•	•		•	•
P. caribensis Werding, 1983			•		•	•	•	•	•	•			
P. columbiensis Werding, 1983					•				•				
P. dissimulatus Gore, 1983					•	•			•	•			
P. galathinus (Bosc, 1802)	•	•	•		•	•	•	•	•	•	•	•	•
P. gertrudae Werding, 1996						•							
P. jugosus (Streets, 1872)			•		•	•	•	•	•	•			
P. magdalenensis Werding, 1978								•	•	•			
P. marginatus Stimpson, 1859						•	•	•	•	•		•	
P. politus (Gray, 1831)			•	•	•	•	•		•	•			
P. quadratus Benedict, 1901				•	•	•	•	•	•	•			
P. robsonae Glassell, 1945								•					
P. rosariensis Werding, 1978					•	•	•	•	•			•	
P. sanmartini Werding and Hiller, in press									•				
P. sp.									•				
P. tonsorius Haig, 1960					•	•			•	•			
P. tridentatus Stimpson, 1859				•	•	•	•	•	•	•			
Pisidia Leach, 1820													
P. brasiliensis Haig, 1968									•			•	
Polyonyx Stimpson, 1858													
P. gibbesi Haig, 1956	•	•	• ?		•			•		•		•	•
Porcellana Lamarck, 1801													
P. lillyae Lemaitre and Campos, 2000									•				
P. sayana (Leach, 1820)	•	•	•	•	•	•	•	•	•	•	•	•	•
P. sigsbeiana A. Milne-Edwards, 1880	•	•	•	•	•	•	•		•	•	•	•	
Total number of species	10	7	17	10	23	32	25	24	37	28	6	19	11

1. temperate North America; 2. northern Gulf of Mexico; 3. tropical Florida; 4. Bahamas; 5. Greater Antilles; 6. Lesser Antilles; 7. south-western Gulf of Mexico to Costa Rica; 8. Panama; 9. Colombia; 10. Venezuela; 11. Guyanas; 12. Tropical Brazil; 13. temperate Brazil.

Table 2. List of porcellanid species from the tropical western Atlantic with their general and relative geographic distributions, and arranged according to depth range. Abbreviations: Eu, eulittoral; C-WI, Caribbean-West Indies.

		Geographic range			Depth range	
Species	Depth (m)	Florida 1 C-WI 2 Brazil 3	Wide	Limited	Sublittoral (> 7 m)	Intertidal (≥ 7 m)
Clastotoechus nodosus	Eu	2		•		•
Neopisosoma curacaoense	Eu	2		•		•
Neopisosoma neglectum	Eu	2		•		•
Neopisosoma orientale	Eu	2		•		•
Petrolisthes quadratus	Eu	2		•		•
Petrolisthes tonsorius	Eu	2		•		•
Petrolisthes tridentatus	Eu	2		•		•
Neopisosoma angustifrons	Eu <1	2		•		•
Pachycheles cristobalensis	<1	2		•		•
Petrolisthes marginatus	<2	2,3	•			•
Clastotoechus vanderhorsti	Eu <3	2		•		•
Pachycheles susanae	<3	2		•		•
Petrolisthes magdalenensis	<3	2		•		•
Petrolisthes politus	<3	1,2	•			•
Petrolisthes sp.	<3	2		•		•
Pachycheles chacei	<4	2		•		•
Petrolisthes sanmartini	<4	2		•		•
Pachycheles greeleyi	<5	3		•		•
Pachycheles laevidactylus	<6	3		•		•
Pachycheles serratus	<6	2		•		•
Petrolisthes columbiensis	<6	2		•		•
Petrolisthes dissimulatus	<6	2		•		•
Petrolisthes gertrudae	<6	2		•		•
Petrolisthes jugosus	Eu<6	1,2	•			•
Pachycheles pilosus	Eu<7	1,2	•			•
Pachycheles riisei	<10	1,2,3	•		•	
Megalobrachium roseum	<14	2,3	•		•	
Petrolisthes caribensis	<22	1,2	•		•	
Petrolisthes rosariensis	<24	2,3	•		•	
Megalobrachium mortenseni	<30	2,3	•		•	
Petrolisthes armatus	<30	1,2,3	•		•	
Pisidia brasiliensis	<31	2,3	•		•	
Pachycheles monilifer	<33	1,2,3	•		•	
Petrolisthes amoenus	<37	1,2,3	•		•	
Parapetrolisthes tortugensis	<40	1,2	•		•	
Megalobrachium poeyi	<46	1,2	•		•	
Polyonyx gibbesi	<47	1,2,3	•		•	
Petrolisthes galathinus	<54	1,2,3	•		•	
Minyocerus angustus	<59	2,3	•		•	
Pachycheles ackleianus	<81	1,2,3	•		•	
Porcellana sayana	<92	1,2,3	•		•	
Porcellana lillyae	<100	2		•	•	
Megalobrachium soriatum	<111	1,2,3	•		•	
Pachycheles rugimanus	<145	1,2,3	•		•	
Porcellana sigsbeiana	<393	1,2,3	•		•	

Discussion

Origins of porcellanid fauna and general factors affecting distributions. The modern porcellanid fauna of tropical America (Table 1), like other faunas from this area, is derived from the tertiary Caribbean Province which included the tropical eastern Pacific until the closure of the Central American land bridge at the end of Pliocene (Woodring, 1974). The speciation events that took place after the final closure of the Panamanian isthmus approximately 3 million years ago (Ekman, 1953; Briggs, 1974; Marshall et al., 1979), combined with the southward displacement during the Pleistocene of tropical species from northern regions such as Florida, can be used to explain the concentration of porcellanid species seen in the modern Caribbean-West Indies and the southern Caribbean faunas. After displacement, most tropical species became extinct in

Figure 1. Comparison of the tropical porcellanid faunas from different regions of the western Atlantic. Large, simple circles indicate total number of species in Florida and Brazil regions; small, simple circles indicate species shared by regions; double circle indicates species in Caribbean-West Indian region; rectangle indicates species in southern Caribbean; oval indicates species in the Antilles.

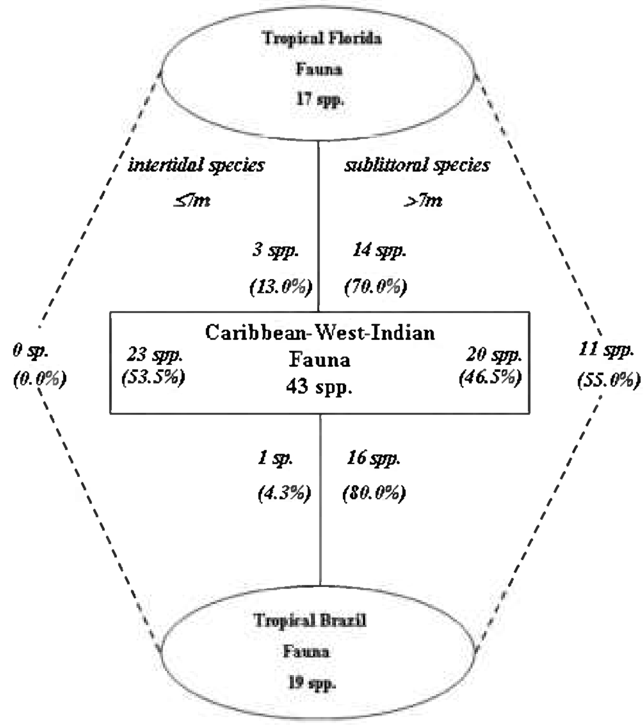

Figure 2. Comparison of intertidal and sublittoral porcellanid faunas of the Caribbean-West-Indies (rectangle) and peripheral (ovals) regions of tropical Florida and Brazil. Italics indicate intertidal (left) and sublittoral (right) species; numbers on dashed lines, and near solid lines connecting rectangle and ovals, are species in common between faunas.

Florida, and recolonisation aided by ocean currents likely occurred when climatic conditions became favourable again.

The colonisation success of porcellanids can be attributed primarily to dispersal and ecological potentials of the species. Species with broad ecological potentials and capable of competing with species already established in the region being colonised, can be expected to be more successful in conquering new areas than those species with narrow habitat requirements, and that seems to apply to the western Atlantic porcellanids. That ecological characteristics of species can affect their distributions has been documented for other marine organisms such as fishes and molluscs: fish species living on rocky shores are generally less widely distributed than those living on soft bottoms (Rosenblatt, 1963); intertidal gastropods are generally less well dispersed, and have more endemic species than deeper living gastropods (Vermeij, 1972); molluscs inhabiting rocky surfaces, in some cases, tend to have more endemics than those inhabiting neighbouring boulders (Vermeij and Porter, 1971); shallow-water infaunal bivalves living in depths of 1 m or less have wider geographical distributions than those in deeper waters because the former tolerate a wider range of environmental conditions than the latter (Jackson, 1974). Among crustaceans, stomatopod species living in shallow-water or having a broad depth range, tend to occupy a wider geographical area than those limited to greater depths (Reaka, 1980).

Dispersal factors. There is a remarkable similarity in species composition between the porcellanid faunas of tropical Florida and Brazil. Species that have become successfully established on distant, peripheral regions, and thus have wide distributional ranges, also have greater abilities to cross barriers and overcome suboptimal ecological conditions. The crab stages of porcellanids are incapable of long-range migrations, and thus any significant dispersal is primarily confined to the larvae. The larval development of porcellanids undergoes two zoeal stages which take no more than two weeks under tropical conditions, followed by a megalopa stage that settles quickly, and altogether lasts on average a maximum of about three weeks (see Gore, 1972; Werding and Müller, 1990; Hernández, 1999). Since dispersal ability of larvae can be considered similar in most species, their dispersal success will largely depend on the ability of adults to adapt to varying ecological conditions.

During this study it has been observed that in western Atlantic porcellanids, the extent of depth distribution often is indicative of ecological requirements. Many western Atlantic porcellanids (e.g. species of *Clastotoechus, Neopisosoma,* and *Petrolisthes quadratus*) are restricted to the intertidal where they live in narrowly defined habitats on hard substrates of the upper littoral (Werding, 1977, 1978). Such habitats are often isolated and separated by large distances of soft-bottom structures. Another, more ubiquitous assemblage of species has wider ranges of depth distribution, and are found in a variety of substrates and habitats. Among the deeper sublittoral species, only the presumably commensal species *Porcellana sigsbeiana* A. Milne Edwards, 1880, *P. lillyae* and *Pachycheles rugimanus* A. Milne Edwards, 1880, do not fit this pattern since they depend on the depth range of their host (Werding, 1983).

Geographic and depth ranges. The depth distributions of western Atlantic porcellanids show a clear relationship with geographic range (see Table 2). The majority of species found at greater depths are geographically the most widespread, and can be found in the peripheral regions (Florida, Brazil). As previously mentioned, the ability to live in a broad depth range provides additional possibilities for settling in a wide range of habitats. After the planktonic life of the zoeae, the megalopae need to find a suitable substrate or risk perishing. Thus, the probability of success increases proportionally to the variety of habitats acceptable to a given species. Some "intertidal" Caribbean species, like *Neopisosoma angustifrons* (Benedict, 1901), *N. neglectum* Werding, 1986 and *Clastotoechus nodosus* (Streets, 1872), must find a highly structured intertidal fouling community or otherwise they will not survive (Werding, 1978). Coastal areas with such characteristics are normally scattered, and separated by large distances of sandy beaches. Even islands with large, rich reef structures such as the Colombian Islas del Rosario (off mainland Colombia) or Isla Providencia (on the western Caribbean), do not provide adequate habitats for such ecologically narrow species (Werding, 1982, 1984). In contrast, for "sublittoral", wide-ranging species like those of the genus *Megalobrachium* Stimpson, 1858, the alternatives are by far more numerous since they are able to settle in boulder habitats, dead coral, hard substrates on seagrass meadows, or sponge communities in deeper waters.

Barrier effects. Two major barriers are usually considered in zoogeographic discussions of the western Atlantic fauna. To the south, the mouth of the Amazon River, and to the north, the Florida Current. The coastline between the mouths of the rivers Orinoco and Amazon, with numerous additional freshwater effluents in the Guyana region, covers a length of about 2,700 km. In regard to this southern barrier, an interesting case relevant to porcellanids is that reported for fishes by Collette and Rützler (1977). These authors documented a rich reef fish fauna associated with a diverse West-Indian sponge fauna below the massive freshwater influence of the Amazon River, in salinities ranging from 34.5 to 36.4‰, and depths of 48 to 73 m. They concluded that this river system functions as a barrier primarily for the dispersal of shallow-water reef organisms. Such conclusion is applicable as well to porcellanids, and is supported by the distributions of species; only one intertidal species, *Petrolisthes marginatus*, and sixteen sublittoral species, occur on both sides of this barrier.

The Florida Current is considered a distributional barrier between the Antilles and Florida (Briggs, 1974), and is of a completely different nature, although its effectiveness as an obstacle for the dispersal of decapod crustaceans has sometimes been questioned (e.g. Lemaitre, 1984). In the Straits of Florida, the distance between Cuba and southern Florida reaches only a maximum of some 200 km, and the Florida Current does seem to impede the easy passage of some planktonic larvae between the Greater Antilles and southern Florida. However, the crossing of larvae of many species is facilitated by the existence of numerous small islands and shoals bordering the margins of the Straits that serve as stepping stones for colonisation, and increase the successful establishment of populations. The data show that the Florida Current is a selective barrier for the intertidal species since only three of them (*Petrolisthes politus, P. jugosus* and *Pachycheles pilosus*) are present on both sides of that barrier whereas 14 sublittoral species fulfil that condition.

Concluding remarks. The distributional and ecological factors mentioned in this study do provide at least one explanation of the origins and patterns of relative richness and composition of porcellanids in the regions of Florida, Caribbean-West Indies, and Brazil. However, it is clear that much more information is needed on western Atlantic porcellanids in order to fully understand historical tracks of dispersal that have lead to the modern fauna of these crabs. It would be critical, for example, to conduct studies on phylogenetic biogeography and systematics of western Atlantic porcellanids using molecular evidence, such as the one now available for species of *Petrolisthes* and *Pachycheles* in the eastern Pacific (Stillman and Reeb, 2001). Further data on the geological and geophysical history of these regions, and ecology and ontogeny of the species, will also allow a clearer evaluation of any correspondence between distributional and ecological patterns in Porcellanidae from these regions.

Acknowledgements

Financial support for this study was provided by the German DAAD, and the Colombian INVEMAR-COLCIENCIAS project (code No. 210509-10401), and INVEMAR-FONADE administrative agreement (code No. 001065). We thank Christopher C. Tudge, Michael Türkay, Alan W. Harvey, and an anonymous reviewer, for useful comments on the manuscript.

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