

Species richness and distribution of hermit crabs of the family Diogenidae (Crustacea: Decapoda: Anomura) in the eastern Pacific

Manuel Ayón-Parente and Michel E. Hendrickx

(MAP) Postgraduate Program, Laboratorio de Invertebrados Bentónicos, Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, P.O. Box 811, Mazatlán, Sinaloa, 82000, Mexico.

(MEH) Laboratorio de Invertebrados Bentónicos, Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, P.O. Box 811, Mazatlán, Sinaloa 82000, Mexico.

Corresponding author: michel@ola.icmyl.unam.mx.

Abstract

Based on a thorough revision of the Diogenidae (Crustacea: Decapoda: Anomura) of the eastern Pacific, 55 species belonging to 11 genera are reported from the region. Species of *Paguristes* are by far the most abundant (22 species, 40%). As a group, they are found from the intertidal to the upper slope (460 m), in virtually all habitats, with a significant proportion of species (47%) found from the intertidal to 20 m depth. The vast majority of species (93%) shows a clear tropical-subtropical affinity. Only seven species occur in the northern temperate subregion and seven in the southern temperate subregion. The majority of species (51) is typical of the eastern tropical Pacific or has at least one record in this subregion. The degree of endemism is particularly high (36%) in the Cortés Province, but this figure is probably linked to a lack of comprehensive studies of the group in Central and South America. Nine species have been recorded from at least one oceanic island of the eastern Pacific, with a maximum of six in the Galapagos. *Calcinus explorator* is the most widely distributed species among the islands.

Key words: Anomura, Diogenidae, eastern Pacific, species richness, distribution, depth.

Introduction

The hermit crabs of the eastern Pacific have been subject to numerous studies and reviews. As a group, they range from Canada and northern USA to southern Chile. Tropical species include representatives of all four families occurring in the region (*i.e.*, Coenobitidae, Diogenidae, Paguridae, and Parapaguridae), with a clear dominance of Diogenidae, while the Paguridae dominate in the higher latitudes (*see* Holmes, 1900; Rathbun, 1904; Hendrickx and Harvey, 1999; Retamal and Jara, 2002). Despite their ecological importance as a group worldwide, their distribution patterns have been little studied (Lemaitre, 1999; Forest and McLay, 2001; Poupin and Lemaitre, 2003; Poupin *et al.*, 2003; Raz-Guzmán *et al.*, 2004).

Basic studies on hermit crabs of the eastern tropical Pacific are by Benedict (1892), Glassell (1937), Janet Haig and collaborators (*e.g.*, Ball and Haig, 1974; Haig, 1976, 1977; Haig *et al.*,

1970; Haig and Harvey, 1991), Snyder-Conn (1980), and Patsy McLaughlin and collaborators (McLaughlin 1981a, 1981b, 1982; Harvey and McLaughlin, 1991; McLaughlin and Haig, 1993). Many habitats adequate for small to medium-sized hermit crabs, however, have not been effectively sampled. Small species often look very similar and detailed morphological analyses are needed to properly identify the specimens to species level. Besides, large collections of hermit crabs available in museums have often been neglected due to lack of interest, lack of experts or both.

The geographic distribution of marine decapod crustaceans in the tropical eastern Pacific has not been fully elucidated (*see* Hendrickx, 1992, 1993; Wicksten, 1989; Boschi, 2000). This is partly due to lack of abundant samples from some areas or to difficulties in recognizing species that have remained unidentified in collection holdings for a long time.

An extensive study of the Diogenidae occurring in the tropical eastern Pacific has been undertaken by the Laboratorio de Invertebrados Bentónicos, ICML, UNAM, Mazatlán, Mexico, in recent years. Examination of large series of specimens collected in Mexico and Central-South America, available in museum collections, allowed the description of several new taxa and updating of their distribution ranges. Based on these new findings, a review of the distribution of the family Diogenidae along the west coast of America is presented here.

Material and Methods

Distribution data for each species of Diogenidae were gathered using previously published information, specimens available in museum collections, and recent, previously unidentified material collected in the area between 1990 and 2008. Collections of Crustacea revised during this study were: in Mexico, the Colección Regional de Invertebrados (EMU), Mazatlán; the Colección Nacional de Crustáceos, Instituto de Biología (EM), UNAM, México D.F.; the Colección of the Centro de Ecología de la Costa (CEC), Universidad de Guadalajara, Melaque, Jalisco; the Colección de Crustáceos del CICIMAR, La Paz, BCS; in the USA, the Crustacean Collection of the Los Angeles County Museum of Natural History, (LACM-CR), Los Angeles; the Crustacean Collection of the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C.; the Invertebrates Collection at the University of Arizona (UAZ), Museum of Natural History, Tucson; the Crustacean Collection of SCRIPPS (SIO-C), La Jolla. Additional material was loaned by the American Museum of Natural History New York (AMNH), the Invertebrates Collection of the Harvard University (MCZ), U.S.A., and by the Colección de Crustáceos, Museo de Zoología (MZUCR), Universidad de Costa Rica.

Based on available records and material examined, the geographic distribution of each species of Diogenidae occurring in the eastern Pacific was established considering their northernmost and southernmost limits. Because frequency and locations of sampling activities vary considerably in the region, sampling points between these two limits, if available, were not considered in the subsequent analysis (*see* Gibbons, 1997; Blackburn and Gaston, 1998).

Zoogeographic provinces in the eastern Pacific were defined based on Brusca and Wallerstein (1979) modified by Hendrickx (1992), Lancelotti and Vazquez (1999), and Espinosa-Pérez and Hendrickx (2006) (Fig. 1). In total, 10 provinces were considered, divided into the three subregions currently recognized in the area (northern cold-temperate, subtropical-tropical, and southern cold temperate) (Fig. 1).

The Bray-Curtis similarity index (Bray and Curtis, 1957; Southwood and Henderson, 2000) was used based on the presence/absence of species to compare their occurrence in each province. A Q-type dendrogram using the UPGMA method (unweighted pair-group method with arithmetic mean) was selected to visualize the grouping (Sneath and Sokal, 1973; Krebs, 1989). The Bray-Curtis index has been widely used to analyze composition of benthic communities at different scales (Magurran, 1988; Vázquez-Domínguez, 2003) and allows comparison of the specific composition in a pair of samples or areas (Southwood and Henderson, 2000). Its value varies from 1 for a maximum similarity (all species present in the pair of samples or areas) to 0 when no species are shared (Magurran, 1988). The dendrogram was obtained using the Primer 5.0 program.

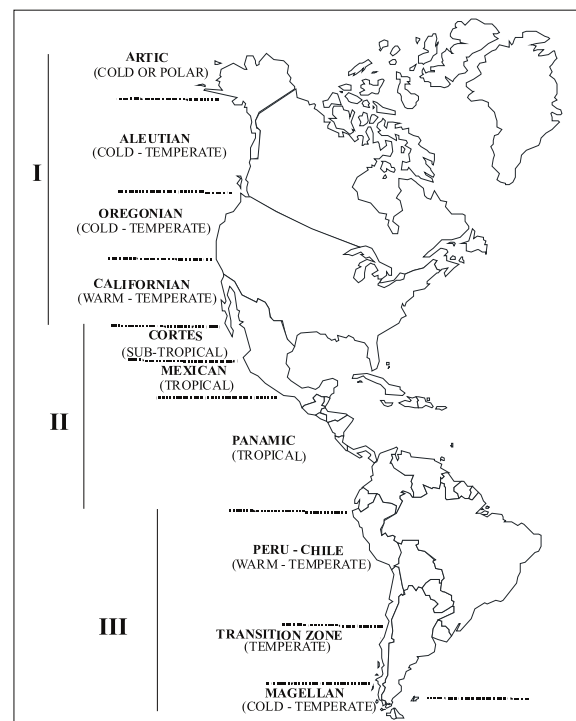


Figure 1. Subregions (I, II, III) and provinces considered for the eastern Pacific. I, Northern Temperate; II, eastern tropical Pacific; III, Southern Temperate.

Results

Species richness

A total of 55 species of hermit crabs of the family Diogenidae were recognized during this study for the entire eastern Pacific (from The Bering Sea to the Magellan Strait). This figure includes 14 undescribed species. These 55 species belong to 12 genera, one of which is undescribed (Table I; Fig. 2). The genus with the highest diversity is *Paguristes* (22 species, 40% of total), followed by *Areopaguristes* and *Dardanus* (7, 13% and 6, 11%, respectively). *Clibanarius* and *Calcinus* include five species (9% each) and *Isocheles* four (7%). *Allo-dardanus*, *Aniculus*, *Cancellus*, *Petrochirus*, *Trizopagurus* and the new, undescribed genus, are each represented by a single species.

Bathymetric distribution (Figs. 3, 4) and substrate (Table I)

About 47% of the species are found from the intertidal to ca 20 m depth. The rest feature a wider bathymetric range or are found only in deeper waters (Fig. 3). Virtually all major habitats are used by Diogenidae (Table II). The unique species of *Allo-dardanus* in the area, *A. rugosus*, is associated with sandy bottoms, in 73-84 m depth. *Aniculus elegans* is found from 3 to 24 m depth, on a variety of substrates. Species of *Calcinus* are common from the intertidal to the subtidal environment, generally in less than 5 m. *Calcinus mclaughlinae* is known from

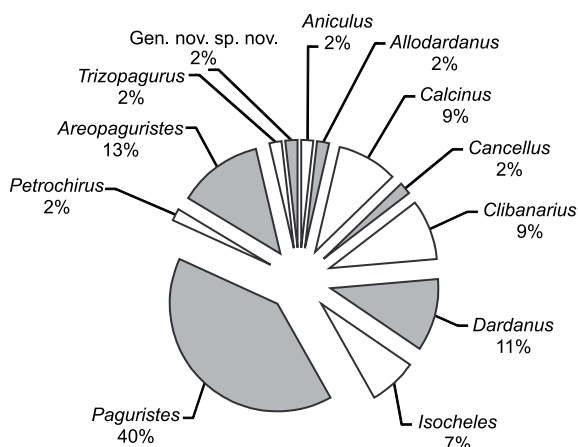


Figure 2. Proportion of species of Diogenidae in each genus recorded for the eastern Pacific.

0 to 22 m and two species are associated with *Pocillopora* coral. There are no data related to the habitat of *C. chilensis*, but it probably occurs in the rocky intertidal. *Cancellus tanneri* is found between 27 and 121 m, on sand, rocks and coral. Species of *Clibanarius* are commonly found in the intertidal, generally associated with coastal lagoons, except *Clibanarius janethaigae*, a marine species occurring on the shelf (7 to 90 m). They are found on many substrates. Species of *Dardanus* are found from shallow subtidal to 145 m (sandy and occasionally rocky substrates), with peak of abundance between 20-60 m. The species of *Isocheles* are typical of the intertidal in shallow bays and estuaries (sand and mud).

Of the 22 species of *Paguristes* recognized in the area, only eight are common in both the intertidal and the shallow subtidal. The other 14 species are typically associated with deeper water (90 to 150 m). *Paguristes turgidus* features the widest bathymetric range, from 5 to 465 m, but occurs mostly between 200 and 220 m. The species of *Paguristes* recorded in the area are usually found predominantly on sand and muddy-sand, but also occurs on rocks and among algae.

Petrochirus californiensis, the only species of this genus in the area, occurs from the intertidal to 120 m depth, on various substrates. Species of *Areopaguristes* are commonly found in the low intertidal, except for the shelf species *Areopaguristes praedator* (mostly found below 60 m). They also occur in a wide variety of substrates. *Trizopagurus magnificus* is another species found in the intertidal and to 9 m depth, almost always among rocks or coral. Finally, an undescribed species belonging to a new genus is typical of the shallow subtidal (1-2 m), on rocks or algae.

Considering all depth intervals available for the 55 species of Diogenidae, there is a regular decrease of species richness with increasing depth (Fig. 4). Strictly intertidal species, however, are few (10-14 species) (Fig. 3), but this figure is probably biased due to the fact that tidal range in the region vary from just above one meter to over six meters in the northern Gulf of California (Brusca, 1980).

Geographic distribution

The number of species of Diogenidae found in the northern temperate subregion is seven (in three genera), and there are four species (in three genera) in the southern temperate subregion.

Table I. Presence of the species of Diogenidae (total, 55) of the eastern Pacific in different types of substrates. Alg, algae; MS, muddy sand; Cor, coral; Spo, sponges; Gra, gravel; Man, mangrove.

Species	Alg	Sand	MS	Cor	Spo	Gra	Man	Rock
<i>Allodardanus rugosus</i>		x						
<i>Aniculus elegans</i>		x		x		x		x
<i>Calcinus californiensis</i>	x			x				x
<i>Calcinus explorator</i>				x				
<i>Calcinus chilensis</i>								x ?
<i>Calcinus mclaughlinae</i>				x				
<i>Calcinus obscurus</i>	x			x				x
<i>Cancellus tanneri</i>		x		x				x
<i>Clibanarius albidigitus</i>								x
<i>Clibanarius digueti</i>	x							x
<i>Clibanarius janethaigae</i>		x	x		x			
<i>Clibanarius panamensis</i>			x				x	x
<i>Dardanus janethaigae</i>		x	x					x
<i>Dardanus magdalenensis</i>		x	x	x				x
<i>Dardanus nudus</i>		x	x					x
<i>Dardanus pilosus</i>		x	x					
<i>Dardanus sinistripes</i>		x						x
<i>Dardanus stimpsoni</i>		x	x					x
<i>Isocheles aequimanus</i>		x						
<i>Isocheles pacificus</i>		x						
<i>Isocheles pilosus</i>		x	x					
<i>Isocheles</i> sp.		x	x					
<i>Paguristes anahuacus</i>		x						x
<i>Paguristes aztatlanensis</i>		x						x
<i>Paguristes bakeri</i>		x	x					
<i>Paguristes digueti</i>		x						
<i>Paguristes fecundus</i>								x
<i>Paguristes haigae</i>		x						
<i>Paguristes holmesi</i>		x						
<i>Paguristes occator</i>		x						
<i>Paguristes oculiviolaceus</i>		x						
<i>Paguristes parvus</i>	x							x
<i>Paguristes perrieri</i>								x
<i>Paguristes sanguinimanus</i>		x						x
<i>Paguristes tomentosus</i>			x					
<i>Paguristes turgidus</i>			x					x
<i>Paguristes ulreyi</i>	x	x						x
<i>Paguristes weddelli</i>								x
<i>Paguristes</i> sp.1		x						
<i>Paguristes</i> sp. 2			x			x		
<i>Paguristes</i> sp. 3		x						
<i>Paguristes</i> sp. 4		x						
<i>Paguristes</i> sp. 5								x
<i>Paguristes</i> sp. 6		x						
<i>Petrochirus californiensis</i>		x				x		x
<i>Areopaguristes mclaughlinae</i>		x						
<i>Areopaguristes praedator</i>		x	x					
<i>Areopaguristes</i> sp. 1		x	x					
<i>Areopaguristes</i> sp. 2		x						
<i>Areopaguristes</i> sp. 3								x
<i>Areopaguristes</i> sp. 4								x
<i>Areopaguristes</i> sp. 5				x				
<i>Trizopagurus magnificus</i>				x				x
Gen. nov., sp. nov.	x							x

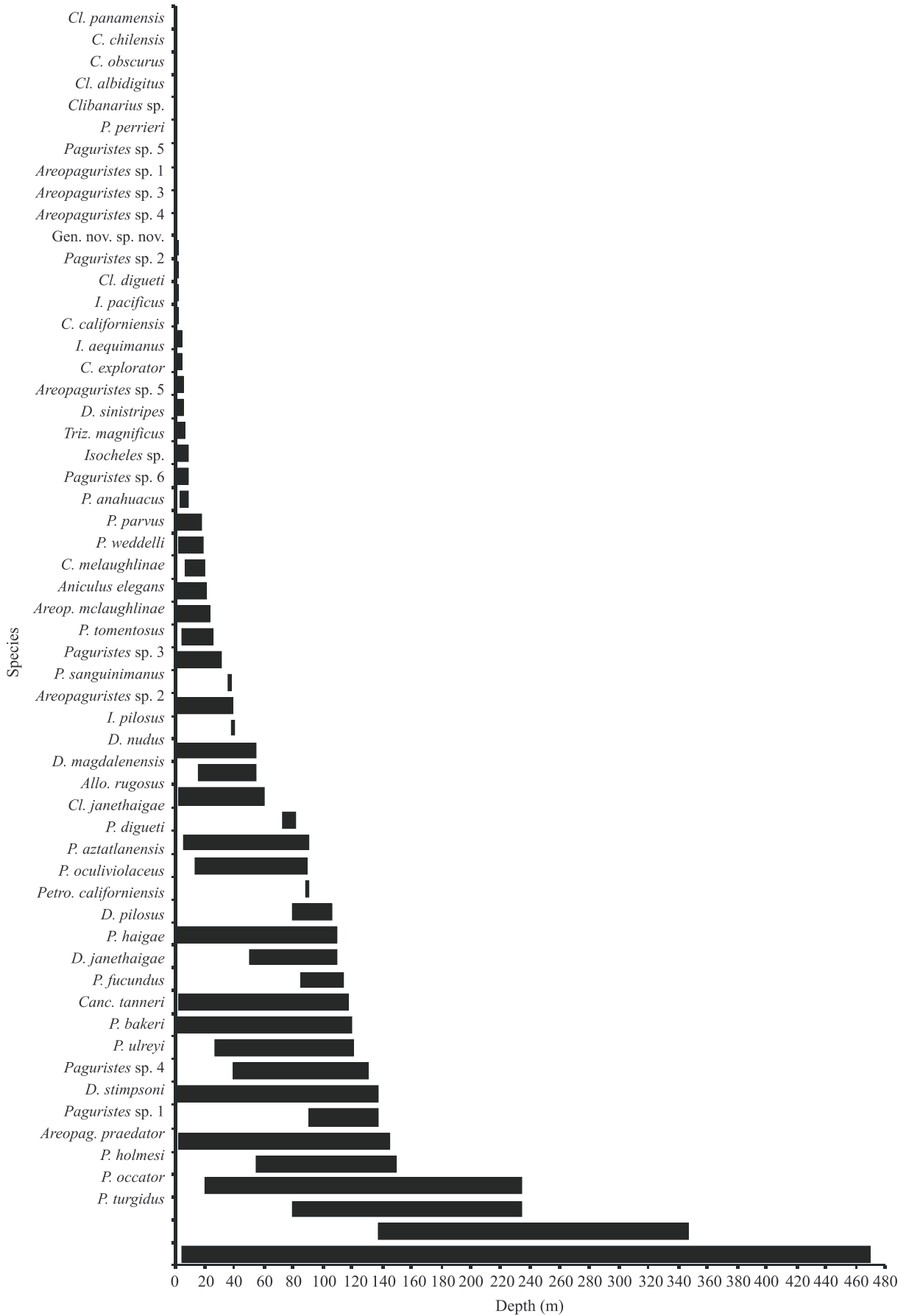


Figure 3. Bathymetric distribution of the species of Diogenidae recorded for the eastern Pacific. Species are arranged from shallow to deeper water.

Comparatively, of the 55 species recorded for the eastern Pacific region, 51 (11 genera) have been collected in subtropical water or are typical of the tropical area extending from Mexico to northern Peru. Only four species (*i.e.*, *Calcinus chilensis*, *Isocheles aequimanus*, *Paguristes fecundus* and *P. parvus*) do not enter into subtropical waters (Table II).

The lowest species richness for Diogenidae is found in the Transitional and Magellan provinces, with only one species each. The Peru-Chile Province has four. To the north, the Aleutian Province features the lowest diversity (2 species), followed by the Oregonian (3) and the Californian (7) provinces. A completely different situation is observed in the tropical eastern Pacific. The Cortés Province is by far the richest, with 42 species, followed by the Panamic (21) and the Mexican (19) provinces (Fig. 5; Table II). The highest endemicity is observed in the Cortés Province, with up to 20 undescribed species (ca 36%), but this includes 10 undescribed species (Table II) which might prove to extend their distribution further south (most likely) or to the Californian Province (less likely). Of these 20 endemics, only one (*Clibanarius digueti*) occurs in the entire Gulf of California and the Southwestern Baja California Peninsula portion of the peninsula. Four species (*Isocheles* sp., *Paguristes anahuacus*, *P. holmesi*, and *Areopaguristes* sp. 1) are found throughout the Gulf of California. The rest of the species have a much more restricted distribution (Table III). Number of endemics in the other provinces is drastically reduced. Only one in the Californian Province (*Paguristes parvus*), two in the Mexican (*Dardanus* sp. 4 and *Areopaguristes* sp. 5) and Peru-Chile (*Calcinus chilensis* and *Isocheles aequimanus*) provinces, and five in the Panamic Province (*Allodardanus rugosus*, *Calcinus obscurus*, *Clibanarius albidigitus*, *Isocheles pacificus*, and *Paguristes fecundus*). The proportion of these

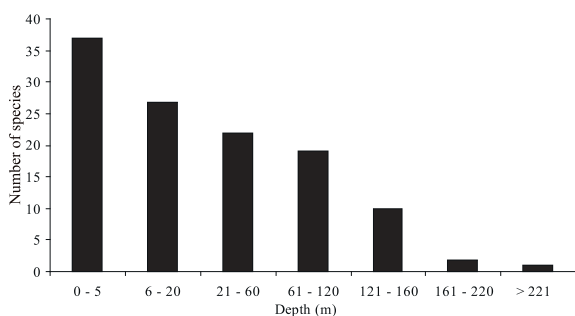


Figure 4. Number of species of Diogenidae of the eastern Pacific per depth range (depth limits: 0 to 465 m).

Table III. Species of Diogenidae endemic to the Cortés Province (Gulf of California to Magdalena Bay, on the west coast of Baja California Peninsula). Their presence in the four portions of the province is indicated with: NG, northern Gulf; CG, central Gulf; SG, southern Gulf; SWB, southwestern Baja California tip.

Species	NG	CG	SG	SWB
<i>Clibanarius digueti</i>	x	x	x	x
<i>Isocheles</i> sp.	x	x	x	
<i>Paguristes anahuacus</i>	x	x	x	
<i>Paguristes aztatlanensis</i>			x	
<i>Paguristes haigae</i>	x	x		
<i>Paguristes holmesi</i>	x	x	x	
<i>Paguristes oculiviolaceus</i>		x	x	
<i>Paguristes occator</i>	x	x	x	
<i>Paguristes perrieri</i>	x			
<i>Paguristes sanguinimanus</i>	x	x		
<i>Paguristes</i> sp. 2			x	
<i>Paguristes</i> sp. 4	x			
<i>Paguristes</i> sp. 5		x		
<i>Paguristes</i> sp. 6			x	x
<i>Areopaguristes mclaughlinae</i>			x	
<i>Areopaguristes</i> sp. 1	x	x	x	
<i>Areopaguristes</i> sp. 2			x	x
<i>Areopaguristes</i> sp. 3		x		
<i>Areopaguristes</i> sp. 4		x		
Gen. nov., sp. nov.			x	

endemics in their respective provinces, however, can be high due to the low number of species encountered (*e.g.*, the two endemics of the Peru-Chile Province account for 50% of the species).

Of the 55 species of Diogenidae currently recognized in the eastern Pacific, nine have been cited at least once on an oceanic island (Table IV). Number of species per island varies considerably, from six in the Galapagos (considering the whole island group) to only one in Cocos (Isla del Coco). No species have been recorded in all these islands, and the most frequent species is *Calcinus explorator*, present in six of these islands. Quite remarkably, the only endemic species of Diogenidae in the oceanic islands is *Dardanus spinosus*, from Clarión.

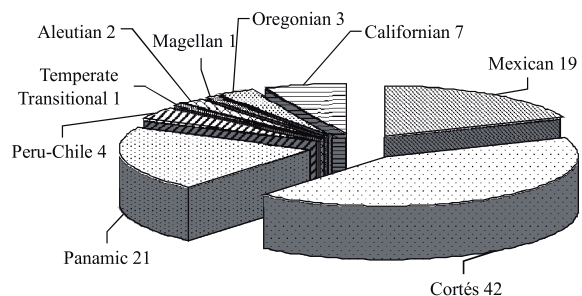


Figure 5. Number of species of Diogenidae recorded for each zoogeographic province (Arctic Province excluded) in the eastern Pacific.

Table II. Distribution of the eastern Pacific species of Diogenidae in the three subregions and nine provinces considered in this study (total: 55 species).

Species	Northern temperate subregion			Eastern tropical Pacific subregion			Southern temperate subregion		
	Aleutian (cold- temperate)	Oregonian (cold- temperate)	Californian (warm- temperate)	Cortés (sub-tropical)	Mexican (tropical)	Panamic (tropical)	Peru-Chile (warm- temperate)	Transitional (temperate)	Magellanic (cold- temperate)
<i>Allodardanus rugosus</i>	-	-	-	-	-	+	-	-	-
<i>Aniculus elegans</i>	-	-	-	+	+	+	-	-	-
<i>Calcinus californiensis</i>	-	-	-	+	+	+	-	-	-
<i>Calcinus chilensis</i>	-	-	-	-	-	-	+	-	-
<i>Calcinus explorator</i>	-	-	-	+	+	+	-	-	-
<i>Calcinus obscurus</i>	-	-	-	-	-	+	-	-	-
<i>Calcinus mclaughlinae</i>	-	-	-	+	+	+	-	-	-
<i>Cancellus tanneri</i>	-	-	-	+	+	+	-	-	-
<i>Clibanarius albidigitus</i>	-	-	-	-	-	+	-	-	-
<i>Clibanarius digueti</i>	-	-	-	+	-	-	-	-	-
<i>Clibanarius janethaigae</i>	-	-	-	+	+	+	-	-	-
<i>Clibanarius panamensis</i>	-	-	-	+	+	+	-	-	-
<i>Clibanarius</i> sp.	-	-	-	+	+	-	-	-	-
<i>Dardanus sinistripes</i>	-	-	-	-	-	+	-	-	-
<i>Dardanus nudus</i>	-	-	-	+	+	+	-	-	-
<i>Dardanus stimpsoni</i>	-	-	-	+	+	+	-	-	-
<i>Dardanus janethaigae</i>	-	-	-	+	+	-	-	-	-
<i>Dardanus magdalenensis</i>	-	-	+	+	-	-	-	-	-
<i>Dardanus spinosus</i>	-	-	-	-	+	-	-	-	-
<i>Isocheles aequimanus</i>	-	-	-	-	-	-	+	-	-
<i>Isocheles pacificus</i>	-	-	-	-	-	+	-	-	-
<i>Isocheles pilosus</i>	-	-	+	+	-	-	-	-	-
<i>Isocheles</i> sp.	-	-	-	+	-	-	-	-	-
<i>Paguristes anahuacus</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes aztatlanensis</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes bakeri</i>	-	+	+	+	-	-	-	-	-
<i>Paguristes digueti</i>	-	-	+	+	+	+	-	-	-
<i>Paguristes fecundus</i>	-	-	-	-	-	+	-	-	-
<i>Paguristes haigae</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes holmesi</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes oculiviolaecus</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes occator</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes parvus</i>	-	-	+	-	-	-	-	-	-
<i>Paguristes perrieri</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes sanguinimanus</i>	-	-	-	+	-	-	-	-	-
<i>Paguristes tomentosus</i>	-	-	-	-	-	+	+	-	-
<i>Paguristes turgidus</i>	+	+	+	+	-	-	-	-	-
<i>Paguristes ulreyi</i>	+	+	+	+	-	-	-	-	-
<i>Paguristes weddelli</i>	-	-	-	-	-	-	+	+	+
<i>Paguristes</i> sp. 1	-	-	-	+	+	+	-	-	-
<i>Paguristes</i> sp. 2	-	-	-	+	-	-	-	-	-
<i>Paguristes</i> sp. 3	-	-	-	+	+	-	-	-	-
<i>Paguristes</i> sp. 4	-	-	-	+	-	-	-	-	-
<i>Paguristes</i> sp. 5	-	-	-	+	-	-	-	-	-
<i>Paguristes</i> sp. 6	-	-	-	+	-	-	-	-	-
<i>Petrochirus californiensis</i>	-	-	-	+	+	+	-	-	-
<i>Areopaguristes mclaughlinae</i>	-	-	-	+	-	-	-	-	-
<i>Areopaguristes praedator</i>	-	-	-	+	+	+	-	-	-
<i>Areopaguristes</i> sp. 1	-	-	-	+	-	-	-	-	-
<i>Areopaguristes</i> sp. 2	-	-	-	+	-	-	-	-	-
<i>Areopaguristes</i> sp. 3	-	-	-	+	-	-	-	-	-
<i>Areopaguristes</i> sp. 4	-	-	-	+	-	-	-	-	-
<i>Areopaguristes</i> sp. 5	-	-	-	-	+	-	-	-	-
<i>Trizopagurus magnificus</i>	-	-	-	+	+	+	-	-	-
Gen. nov., sp. nov.	-	-	-	+	-	-	-	-	-

Table IV. Eastern Pacific species of Diogenidae occurring in oceanic islands (total: 9). (?) Doubtful record.

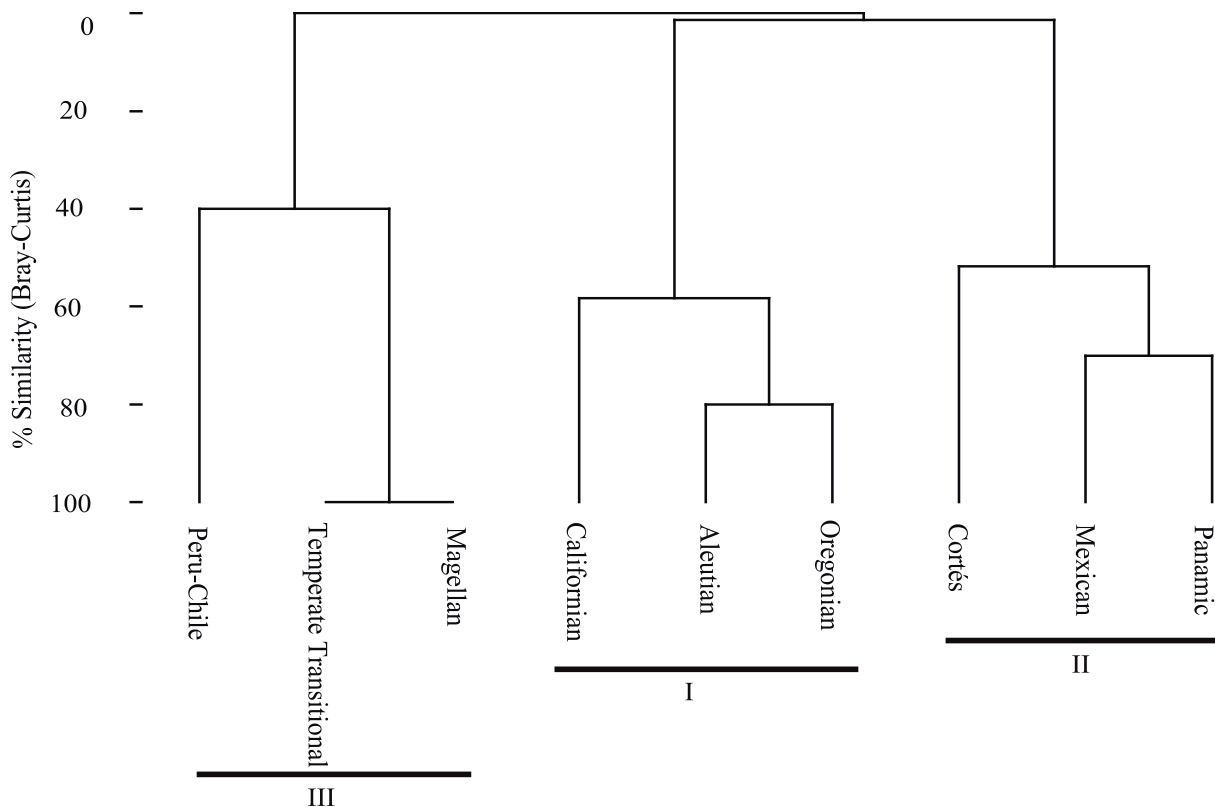
Species	Socorro	Clarión	Clipperton	Coco	Malpelo	Galapagos
<i>Aniculus elegans</i>					+	+
<i>Calcinus californiensis</i>	+(?)					
<i>Calcinus explorator</i>	+	+	+	+		+
<i>Calcinus mclaughlinae</i>	+	+	+			
<i>Cancellus tanneri</i>						+
<i>Dardanus sinistriipes</i>						+(?)
<i>Dardanus spinosus</i>		+				
<i>Petrochirus californiensis</i>						+
<i>Trizopagurus magnificus</i>					+	+

Based on the distribution of the 55 species, the dendrogram of similarity among subregions and provinces (Fig. 6; the Artic Province was omitted due to lack of records for Diogenidae) clearly shows the strong disparity between the three subregions. Within each subregion, the similarity varies considerably, with the strongest affinity between the two southernmost provinces (Temperate Transitional and Magellan), quite distinct as a group from the Peru-Chile Province (ca 40% only). A similar pattern is observed in the north, with a stronger affinity between the Oregonian and Aleutian provinces, although in this case the similarity with the Californian Province increases to ca 60%. The Mexican and Panamic provinces

are also very similar, and somewhat distinct from the Cortés Province. The strongest affinities are 70% or more between the Transitional-Magellan, Panamic-Mexican, and Oregonian-Aleutian areas. Contrary to what has been observed with other groups of Decapoda (*e.g.*, Caridea, Brachyura) (*see* Garth, 1960; Hendrickx, 1992; Wicksten and Hendrickx, 2003), there are no amphiamerican species of Diogenidae on record.

Discussion

With a total of 55 species recognized to date, the Diogenidae is one of the most diverse families

**Figure 6.** Similarity among zoogeographic provinces in the eastern Pacific based on presence-absence of species of Diogenidae in each province. I, II and III as in Fig. 1.

of decapod crustacean within the eastern Pacific. They range from the intertidal to over 465 m, and occupy virtually all habitats, with a high percentage of species associated with rocky or sandy bottoms. It should be noted, however, that a significant part of the specimens examined had no records related to the habitat in which they had been collected and some species might actually occupy a wider variety of niches. The sharp decrease in species richness observed with increasing depth denotes the affinity of Diogenidae for shallow waters, as already noted for other regions of the world (see Forest and McLay, 2001). It should be emphasized, however, that the lack of data for many species, the strong disparity of tidal ranges in the eastern Pacific coastal areas, and the presence of a wide minimum oxygen zone occurring over a considerable latitudinal range, roughly from the mid or outer continental shelf to the upper or mid slope (Brusca, 1980; Hendrickx and Serrano, 2010), have a strong influence on the proposed classification of species by bathymetric range.

As expected, the overwhelming majority of Diogenidae species in the eastern Pacific has a very strong affinity with warm waters of the subtropical and tropical provinces. The representatives of this family of hermit crabs are very rare in the higher latitudes. The review of unidentified or new, freshly collected material reveals that diversity is much higher than previously thought. As a result of the entire Mexican Diogenidae project, several new species have already been described (see Hendrickx and Esparza-Haro, 1997; Ayón-Parente and Hendrickx, 2006, 2007, 2009), and many other undescribed species have been detected and await a formal description. A clear increase of the number of species of Diogenidae in tropical and warm-temperate waters compared to higher latitudes had been previously emphasized by McLaughlin (1974) and McLaughlin *et al.* (2007).

Considering their strong affinity with warm water, the distribution of the Diogenidae within the zoogeographic provinces of the eastern Pacific should match results obtained with other groups of tropical Crustacea, particularly with the Dendrobranchiata, the Caridea and the Brachyura (Garth, 1960; Hendrickx, 1992, 1995a; Wicksten and Hendrickx, 2003). The sharp decrease of species number from the subtropical Cortés Province (42 species) to the tropical, Mexican (19 species) and Panamic (21 species) provinces, however, is contradictory with the north-south diversity gra-

dient generally observed with these other groups in the eastern tropical Pacific. One would certainly have expected a higher number of species close to the Costa Rica-northern Colombia area. This is almost certainly due to a lack of comprehensive review of the group in these localities, combined with the fact that many of the new species recognized during this study have their present distribution limited to the Gulf of California. This situation is likely to change when more material from the Panamic province is available for examination.

The endemism of the Diogenidae in the eastern Pacific is remarkable and not a single species is known from other regions of the world. This might be due to a higher speciation rate combined with a reduced dispersal capability (see Forest, 1954; Forest and McLay, 2001). Comparatively, as many as 32 species (7%) of Brachyura (except the pelagic and flotsam species) and 28 species (11%) of non-pelagic shrimps (Penaeoidea, Stenopodidea, Caridea) occurring in the eastern tropical Pacific are also found in other zoogeographic regions (Atlantic or Indo-Pacific) (Hendrickx, 1995a; Wicksten and Hendrickx, 2003). Little has been done in terms of comparing the hermit crab fauna on both sides of the American continent. According to Boschi (2000) and McLaughlin *et al.* (2005), 56 species of Diogenidae are known from the western Atlantic (vs. 55 in the eastern Pacific), belonging to nine genera. Two species of *Paguristes* from this region had been moved to *Stratiotes* by Rahayu (2005), thus leaving the former genus with a total of 35 western Atlantic species (vs. 22 species in the eastern Pacific). *Stratiotes*, a preoccupied name for a Coleoptera genus, has recently been replaced by *Areopaguristes* (see Rahayu and McLaughlin, 2010). The second most speciose genus in the western Atlantic is *Clibanarius* (six species vs. five in the eastern Pacific), while this genus is outnumbered by *Areopaguristes* (seven species) in the eastern Pacific. Including *Areopaguristes*, ten genera are known from the western Atlantic, but there are no representatives of *Allodardanus* or *Aniculus* (a single species present in the eastern Pacific). Comparatively, ten genera are also known in the eastern Pacific, but without representatives of *Bathynarius* and *Loxopagurus*, both also known from a single species in the western Atlantic. Many western Atlantic species are poorly described and a detailed revision of their taxonomic position is needed, in a similar way to what has been undertaken in the eastern Pacific. Furthermore, the discovery of a significant number of new

species along the Pacific coast of America makes any attempt of a detailed comparison between west and east American species even more difficult until further progress is made with the review of the entire Diogenidae fauna of the Americas.

Availability of shells and habitats used by Diogenidae along their distribution range might represent a significant factor for their dispersal (Bertness, 1981; Negreiros-Franzoso *et al.*, 1997; Halpern, 2004; Mantelatto *et al.*, 2004). In the eastern Pacific, data related to shell supply and to the relation between shells and the hermit species are rarely available and are mostly limited to the Gulf of California area (unpublished data). It is also often impossible to assess if records in the literature refer to the correct species of hermit crab, thus rendering any attempt of analysis very hazardous.

Forest and McLay (2001) noted that the high degree of endemicity of the Diogenidae results from their habitat and reproductive strategy. Dispersal is strongly reduced by the absence or reduction of larval stages, both in number or duration, *e.g.*, in *Paguristes frontalis*, hatching directly produces a glaucothoe which remains within the shell of the adult (Morgan, 1987); *P. eremita* features 2-3 short-lived zoea, and a glaucothoe appears after only 20-30 hours (Pike and Williamson, 1960). Very little is known about embryology and larval development of Diogenidae in the eastern Pacific. According to Hart (1937), *Paguristes turgidus* reached the glaucothoe stage in 5-8 days. Additional, unpublished data, based on material collected along the Pacific coast of Mexico indicate that *Paguristes anahuacus* presents two zoeae and reaches a glaucothoe in two days, while *Areopaguristes* sp. 1 features three zoeae and reaches the glaucothoe in five days. Although these preliminary results seem congruent with what is known in other regions of the world, further information is needed to complete our vision of Diogenidae dispersal patterns within the eastern Pacific.

On the other hand, the very low degree of endemism observed in the oceanic islands (one species only) differs from what is currently known with other decapods (*see* Garth, 1992; Hernández-Aguilera, 2002; Wicksten and Hendrickx, 2003). Potentially, dispersal of species occurring along the west coast of the Baja California Peninsula and in the Gulf of California to oceanic islands is facilitated by larval transport via the California Current and the Equatorial Countercurrent (Haedrich and Judkins, 1979; Garth, 1955, 1960; Lemaitre

and Alvarez-León, 1992; Hendrickx, 1995b). But in the case of the hermit crabs, only the distribution of *Calcinus explorator* could be explained by this process. It is also interesting to note that no species of Diogenidae from the central-west Pacific made it to the eastern Pacific oceanic islands, while several species of other decapod crustacean groups were able to cross the Pacific Ocean barrier (*e.g.*, *Synalpheus charon*, *Panulirus penicillatus*, *Hippa pacifica*, *Calappa hepatica*, *Hapalocarcinus marsupialis*); some even went one step further, to the American continent (*see* Garth, 1946, 1992; Hendrickx, 1995a; Hernández-Aguilera, 2002; Wicksten and Hendrickx, 2003).

Acknowledgments

We thank the students of the Laboratorio de Invertebrados Bentónicos and colleagues from local institutions for help provided during the collection of hermit crabs in Mexico. We also thank the following persons for facilitating access to collections, either through loans or during visits to museums: G. Davis and J.W. Martin (Natural History Museum of Los Angeles County, California), R. Lemaitre (Smithsonian Institution, Washington D.C.), P. Reinthal (UAZ), Greg Rouse and Harim Cha (SIO, La Jolla), Ardis Johnston (MCZ), G.L. Bradley (UAZ), V. Landa (CEC, Melaque), F. Alvarez and J.L. Villalobos (Instituto de Biología, UNAM), E. Felix Pico (CICIMAR, La Paz), M.S. Madrigal (Universidad del Mar, Oaxaca). One of us (MAP) thanks CONACyT, Mexico for the grant received for this study (125847). This manuscript was completed during a sabbatical stay at the Royal Belgian Institute of Natural Sciences, Brussels, Belgium, and MEH thanks the DGAPA, UNAM, Mexico for its support, and T. Backeljau (RBINS) for his hospitality. We thank M. Cordero for editing the final version of this manuscript.

References

- Ayón-Parente, M. and Hendrickx, M.E. 2006. A new species of *Stratiotes* Thomson, 1899 (Anomura, Paguroidea, Diogenidae) from the eastern tropical Pacific. *Zoosystema*, 28(2):487-497.
- Ayón-Parente, M. and Hendrickx, M.E. 2007. A new species of *Paguristes* Dana, 1851 (Anomura, Paguroidea, Diogenidae) from the Mexican Pacific. *Zootaxa*, 1470:59-68.
- Ayón-Parente, M. and Hendrickx, M.E. 2009. A review of the *Dardanus sinistripes* (Stimpson, 1859) (Decapoda, Anomura, Diogenidae) species complex with the description of five new species from the Mexican Pacific. *Zootaxa Monograph*, 2323:1-71.
- Ball, E.E. and Haig, J. 1974. Hermit crabs from the tropical eastern Pacific. I. Distribution, color and natural history of some common shallow-water species. *Bulletin of the Southern California Academy of Sciences*, 73(2):95-104.

- Benedict, J.E. 1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum. *Proceedings of the United States National Museum*, 15:1-26.
- Bertness, M.D. 1981. Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. *Ecology*, 62(2):411-425.
- Blackburn, T.M. and Gaston, K.J. 1998. Some methodological issues in macroecology. *American Naturalist*, 151:68-83.
- Boschi, E.E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. *Revista de Investigación y Desarrollo Pesquero*, 13:7-56.
- Bray, J.R. and Curtis, C.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27(4):325-349.
- Brusca, R.C. and Wallerstein, B.R. 1979. Zoogeographic patterns of idoteid isopods in the northeast Pacific with a review of shallow water zoogeography of the area. *Bulletin of the Biological Society of Washington*, 3:67-105.
- Brusca, R.C. 1980. Common Intertidal Invertebrates of the Gulf of California. The University of Arizona Press. Arizona, USA, Second Ed. 513 p.
- Espinosa-Pérez, M.C. and Hendrickx, M.E. 2006. A comparative analysis of biodiversity and distribution of shallow-water marine isopods (Crustacea-Isopoda) from polar and temperate waters in the East Pacific. *Belgian Journal of Zoology*, 136(2):219-247.
- Forest, J. 1954. Les Paguristes des côtes occidentales et méridionales d'Afrique. *Annals of the South African Museum*, 41(4):159-213.
- Forest, J. and McLay, C.L. 2001. The biogeography and bathymetric distribution of New Zealand hermit crabs (Crustacea: Anomura: Paguridea). *Journal of the Royal Society of New Zealand*, 31(4):687-720.
- Garth, J.S. 1946. Distribution studies of Galapagos Brachyura. *Allan Hancock Pacific Expeditions*, 5(11):603-638.
- Garth, J.S. 1955. The case for a warm-temperate marine fauna on the west coast of North America. p. 19-27. In: Essays in the Natural Sciences in honor of Captain Allan Hancock on the occasion of his birthday July 26, 1955. University of Southern California Press, Los Angeles. 345 p.
- Garth, J.S. 1960. Distribution and affinities of the brachyuran Crustacea. In: Symposium on the Biogeography of Baja California and adjacent seas. Part II. Marine Biotas. *Systematic Zoology*, 9(34):105-123.
- Garth, J.S. 1992. The Brachyuran crabs of the Revillagigedo Islands, Colima, México, with remarks on Insular Endemism in the Eastern Tropical Pacific. *Proceedings of the San Diego Society of Natural History*, 24:1-6.
- Glassell, S.A. 1937. The Templeton Crocker Expedition. XI. Hermit crabs from the Gulf of California and the west coast of Lower California. *Zoologica*, 22:241-263.
- Gibbons, M.J. 1997. Pelagic biogeography of the southern Atlantic Ocean. *Marine Biology*, 129:757-768.
- Haedrich, R.L. and Judkins, D.C. 1979. Macrozooplankton and its environment. p. 4-28. In: Zoogeography and diversity of plankton. S. Van der Spoel and A.C. Pierrot-Bults (eds.). Bunge Scientific Publishers, Utrecht. 410 p.
- Haig, J. 1976. *Tomopagurus macLaughlinae*, a new hermit crab from the eastern Pacific (Crustacea, Anomura, Paguridae). *Bulletin of Marine Science*, 26(1):27-32.
- Haig, J. 1977. Description of a new hermit crab (Family Paguridae) from southern California and Mexico. *Proceedings of the Biological Society of Washington*, 90(3):648-657.
- Haig, J. and Harvey, A.W. 1991. Three new species of the *Pagurus lepidus* complex (Decapoda, Anomura, Paguridae) from the eastern Pacific. *Contributions in Science, Los Angeles County National History Museum*, 430:1-11.
- Haig, J., Hopkins, T.S. and Scaland, T.B. 1970. The shallow water anomuran crab fauna of southwestern Baja California, Mexico. *Transactions of the San Diego Society of Natural History*, 16(2):13-32.
- Halpern, B.S. 2004. Habitat bottlenecks in stage-structured species: hermit crabs as a model system. *Marine Ecology Progress Series*, 276:197-207.
- Hart, J.F.L. 1937. Larval and adult stages of British Columbia Anomura. *Canadian Journal of Research*, Section D, 15(10):179-200.
- Harvey, A.W. and McLaughlin, P.A. 1991. Two new hermit crabs of the genus *Pagurus* (*provenzanoi* group) (Crustacea: Anomura: Paguridae) from the eastern Pacific, with notes on their ecology. *Contributions in Science, Los Angeles County National History Museum*, 425:13-21.
- Hendrickx, M.E. 1992. Distribution and zoogeographic affinities of decapod crustaceans of the Gulf of California, Mexico. *Proceedings of the San Diego Society of Natural History*, 20:1-11.
- Hendrickx, M.E. 1993. Crustáceos decápodos del Pacífico mexicano. p. 271-318. In: Biodiversidad Marina y Costera de México. S.I. Salazar-Vallejo and N.E. González (eds). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y CIQRO, México.
- Hendrickx, M.E. 1995a. Cangrejos. p. 565-636. In: Guía FAO para la identificación de las especies para los fines de pesca. Pacífico centro oriental. Vol. I. Plantas e Invertebrados. W. Fischer; F. Krupp; W. Schneider; C. Sommer; K.E. Carpenter and V.H. Niem (eds), FAO, Roma, Italy, 646 p.
- Hendrickx, M.E. 1995b. Introducción. p. 1-7. In: Guía FAO para la identificación de las especies para los fines de pesca. Pacífico centro oriental. Vol. I. Plantas e Invertebrados. W. Fischer; F. Krupp; W. Schneider; C. Sommer; K.E. Carpenter and V.H. Niem (eds), FAO, Roma, Italy, 646 p.
- Hendrickx, M.E. and Esparza-Haro, J.A. 1997. A new species of *Clibanarius* (Crustacea: Anomura: Diogenidae) from the eastern tropical Pacific. *Zoosystema*, 19(1):111-119.
- Hendrickx, M.E. and Harvey, A.W. 1999. Checklist of anomuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific. *Belgian Journal of Zoology*, 129:363-389.
- Hendrickx, M.E. and Serrano, D. 2010. Impacto de la zona de mínimo de oxígeno sobre los corredores pesqueros en el Pacífico mexicano. *Interciencia*, 35(1):12-18.
- Hernández-Aguilera, J.L. 2002. Crustáceos del archipiélago de Revillagigedo (Stomatopoda y Decapoda de Thalassinidae a Brachyura), Pacífico este tropical. p. 301-315. In: M.E. Hendrickx (ed), Contributions to the Study of East Pacific Crustaceans (Contribuciones al Estudio de los Crustáceos del Pacífico Este). Instituto de Ciencias del Mar y Limnología, UNAM, México, Vol. 1, 383 p.
- Holmes, S.J. 1900. Synopsis of the California stalk-eyed Crustacea. *California Academy of Sciences*, 7:1-262.
- Krebs, C.J. 1989. Ecological methodology. Harper-Collins, New York. 654 p.

- Lancellotti, D.A. and Vasquez, J.A. 1999. Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *Journal of Biogeography*, 26(5):1001-1006.
- Lemaitre, R. 1999. Crustacea Decapoda: A review of the species of the genus *Parapagurus* Smith, 1879 (Parapaguridae) from the Pacific and Indian Oceans. In: A. Crosnier (ed), Resultats des Campagnes MUSORSTOM. *Mémoires du Muséum national d'Histoire Naturelle*, 20(180):303-378.
- Lemaitre, R. and Alvarez-León, R. 1992. Crustáceos decápodos del Pacífico colombiano: Lista de especies y consideraciones zoogeográficas. *Anales del Instituto de Investigaciones Marinas de Punta de Betín*, 21:33-76.
- Magurran, A.E. 1988. Ecological diversity and its measurement. University Press. U.S.A. 169 pp.
- Mantelatto, F.L.; Martinelli, J.M. and Franzoso, A. 2004. Temporal-spatial distribution of the hermit crab *Loxopagurus loxochelis* (Decapoda: Diogenidae) from Ubatuba, Sao Paulo State, Brazil. *Revista de Biología Tropical*, 52(1):47-55.
- McLaughlin, P.A. 1974. The hermit crabs (Crustacea, Decapoda, Paguridae) of northwestern North America. *Zoologischer Verhandlungen*, 130:1-396.
- McLaughlin, P.A. 1981a. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species. Part I. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne-Edwards and Bouvier. *Bulletin of Marine Science*, 31(1):1-30.
- McLaughlin, P.A. 1981b. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species. Part II. *Rhodochirus* McLaughlin, *Phimochirus* McLaughlin. *Bulletin of Marine Science*, 31(2):329-365.
- McLaughlin, P.A. 1982. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species. Part III. *Agaricochirus* McLaughlin, *Enallopagurus* McLaughlin, and *Enallopaguropsis* McLaughlin. *Bulletin of Marine Science*, 31(2):329-365.
- McLaughlin, P.A. and Haig, J. 1993. Two new species of the Pacific component of the Provenzano group of *Pagurus* (Decapoda: Anomura: Paguridae) and a key to regional species. *Bulletin of Marine Science*, 52(2):642-668.
- McLaughlin, P.A.; Lemaitre, R. and Sorthannus, U. 2007. Hermit crab phylogeny: A reappraisal and its "fall-out". *Journal of Crustacean Biology*, 27(1):97-115.
- McLaughlin, P.A.; Camp D.K.; Eldredge, L.G.; Felder, D.L.; Goy, J.W.; Hobbs, H.H.I.; Kensley, B.; Lemaitre, R. and Martin, J.W. 2005. Order Decapoda. Names of crustaceans. p. 209-236. In: Turgeon, D. (ed.), Common and scientific names of aquatic invertebrates of the United States and Canada. American Fisheries Society Special Publication 31.
- Negreiros-Franzoso, M.L.; Franzoso, A.; Mantelatto, F.L.; Pinheiro, M.A.A. and Santos, S. 1997. Anomuran species (Crustacea, Decapoda) and their ecological distribution of Fortaleza Bay sublittoral, Ubatuba, Sao Paulo, Brazil. *Ilheringia, Série Zoologia*, 83:187-194.
- Morgan, G.J. 1987. Abbreviated development in *Paguristes frontalis* (Milne Edwards, 1836) (Anomura Diogenidae) from southern Australia. *Journal of Crustacean Biology*, 7:536-540.
- Pike, R.B. and Williamson, D.L. 1960. Larvae of decapod Crustacea of the families Diogenidae and Paguridae from the Bay of Naples. *Pubblicazioni della Stazione Zoologica di Napoli*, 31(3):493-552.
- Poupin, J. and Lemaitre, R. 2003. Hermit crabs of the genus *Calcinus* Dana, 1851 (Decapoda, Anomura; Diogenidae) from the Austral Islands, French Polynesia, with description of a new species. *Zootaxa*, 391:1-20.
- Poupin, J.; Boyko, C.B. and Guzmán, G.L. 2003. *Calcinus* hermit crabs from Easter Island, with biogeographic considerations (Crustacea: Anomura: Diogenidae). *Memoirs of Museum Victoria*, 60(1):91-97.
- Rahayu, D.L. 2005. Additions to the Indonesian fauna of the hermit crab genus *Pseudopaguristes* McLaughlin and a further division of the genus *Paguristes* Dana (Crustacea: Decapoda: Paguroidea: Diogenidae). *Zootaxa*, 831:1-42.
- Rahayu, D.L. and McLaughlin, P. 2010. *Areopaguristes*, a generic replacement name for *Stratiotes* Thomson, 1899 (Crustacea: Decapoda: Paguroidea: Diogenidae). *Zootaxa*, 2509:67-68.
- Rathbun, M.J. 1904. Decapod crustaceans of the northwest coast of North America. *Harriman Alaska Expedition Washington*, 10:1-190.
- Raz-Guzmán, A.; Sánchez, A.J.; Peralta, P. and Florido, R. 2004. Zoogeography of hermit crabs (Decapoda: Diogenidae, Paguridae) from four coastal lagoons in the Gulf of Mexico. *Journal of Crustacean Biology*, 24(4):625-636.
- Retamal, M.A. and Jara, C. 2002. La Carcinología en Chile. p. 195-208. In: M.E. Hendrickx (ed). Contributions to the Study of East Pacific Crustaceans. (Contribuciones al Estudio de los Crustáceos del Pacífico Este). Instituto de Ciencias del Mar y Limnología, UNAM, México, Vol. 1, 383 p.
- Sneath, P.H.A. and Sokal, R.R. 1973. Numerical taxonomy. The principles and practice of numerical classification. W.H. Freeman. U.S.A., 513 pp.
- Snyder-Conn, E. 1980. 19. Arthropoda Crustacea Paguroidea and Coenobitoidea (hermit crabs). p. 275-285. In: R.C. Brusca. Common Intertidal Invertebrates of the Gulf of California. University of Arizona Press, 513 p.
- Southwood T.R.E. and Henderson, P.A. 2000. Ecological Methods. Blackwell Science, London, 596 p.
- Vázquez-Domínguez, E. 2003. Diversidad y distribución de crustáceos y equinodermos y su relación con niveles de sedimentación en arrecifes coralinos. *Revista de Biología Tropical*, 51(1):183-194.
- Wicksten, M.K. 1989. Ranges of offshore decapod crustaceans in the eastern Pacific Ocean. *Transactions of the San Diego Society of Natural History*, 21(19):291-316.
- Wicksten, M.K. and M.E. Hendrickx. 2003. An updated checklist of benthic marine and brackish water shrimps (Decapoda: Penaeoidea, Stenopodidea, Caridea) from the Eastern Tropical Pacific. p. 49-76 In: M.E. Hendrickx (ed). Contributions to the Study of East Pacific Crustaceans (Contribuciones al Estudio de los Crustáceos del Pacífico Este). Instituto de Ciencias del Mar y Limnología, UNAM, México, Vol. 2, 303 pp.

Submitted 24 March 2010

Accepted 26 April 2010