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Munidopsis geyeri and *M. exuta* (Crustacea: Munidopsidae): A study of two deep-sea, amphi-Atlantic species that co-occur in the southern Gulf of Mexico

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Abstract

The history of colonization and dispersal of fauna among deep-sea chemosynthetic ecosystems remains enigmatic and poorly understood. The distribution of squat lobsters of the genus *Munidopsis* Whiteaves, 1874 can be influenced by the rich organic matter and associated organism communities of chemosynthetic ecosystems. The present work analyzed the molecular relationships and morphology of individuals from different populations of *Munidopsis exuta* Macpherson & Segonzac, 2005 and *M. geyeri* Pequegnat & Pequegnat, 1970 in such ecosystems along the Atlantic Equatorial Belt, including the Chapopote Knoll, in the southern Gulf of Mexico. *Munidopsis geyeri* is re-described based on the present findings and reference to the literature. This analysis documented the genetic distances, as well as range of variation in the diagnostic characters that support the separation of *M. exuta* and *M. geyeri*. Our results confirm that the two species coexist in seep ecosystems and have an amphi-Atlantic distribution.

Key words: Anomura, squat lobsters, Campeche Knolls, hydrothermal vent, cold seep

Introduction

The genus *Munidopsis* Whiteaves, 1874 encompasses "squat lobsters" assigned to the family Munidopsidae Ortmann, 1898, formerly Munidopsinae (Ahyong *et al.* 2010). A. Milne-Edwards (1880) placed four genera in Munidopsinae (*Orophorhynchus* A. Milne-Edwards 1880, *Galacantha* A. Milne-Edwards 1880, *Galathodes* A. Milne-Edwards 1880, *Elasmonotus* A. Milne-Edwards 1880). Subsequently, other genera and subgenera were assigned to this subfamily (e.g. *Anoplonotus* Smith, 1883; *Bathyankyristes* Alcock & Anderson, 1894). Revision of subgenera and synonymies (e.g. Alcock 1901; Benedict 1902; Faxon 1893; Henderson 1885) led to the unification of all the species under the genus *Munidopsis* on the grounds that most of the species shared morphology justifying placement under a single genus, but also because the previously applied genera were based upon character states that were apparently transitional in many species, thereby making their generic limits questionable (Chace 1940). At present, the genus *Munidopsis* encompasses 272 species (Rodríguez- Flores *et al.* 2022; WoRMS 2022). Exploration in deep-sea habitats and technological developments for small scale sampling have facilitated collections of new species, while the application of molecular phylogenetics has facilitated the recognition of cryptic species (e.g. Rodríguez-Flores *et al.* 2018b). For example, *Munidopsis subsquamosa* Henderson, 1885 previously regarded as a single species from the East Pacific Rise, is now recognized as separate from three new species (*M. bracteosa* Jones & Macpherson, 2007; *M. recta* Baba, 2005; and *M. scotti* Jones & Macpherson, 2007) on the basis of molecular analyses (Jones & Macpherson 2007).

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Most species of *Munidopsis* are distributed widely (Coykendall *et al.* 2017; Schnabel *et al.* 2011). They exhibit scavenging and opportunistic feeding behaviors (e.g. *M. albatrossae* Pequegnat & Pequegnat, 1973; Dong *et al.* 2019), usually occurring at bathyal and abyssal depths in sites that are organically enriched (Baba 2005; Chevaldonne & Olu 1996; Jones & Macpherson 2007; Kemp *et al.* 2006). Some species of *Munidopsis* are referred to as colonists (as defined by Carney 1994) of seeps and hydrothermal vents (e.g. Martin & Haney 2005; Yang *et al.* 2016).

The squat lobsters, *Munidopsis exuta* Macpherson & Segonzac, 2005 and *M. geyeri* Pequegnat & Pequegnat, 1970, occur throughout the Atlantic Ocean at depths between 1700–4151 m (Baba *et al.* 2008; Gaytán-Caballero 2009; Kilgour & Shirley 2014; Navas *et al.* 2013; Vázquez- Bader & Gracia 2016). The present study examined *M. exuta* and *M. geyeri* from abyssal depths of the southern Gulf of Mexico, with an emphasis on both molecular and morphological comparisons. We provide a re-description of *M. geyeri* based upon specimens that we examined, while also incorporating the previously unpublished description of Mayo (1974). This paper contributes new geographic records, new ecological information and ecological features of the species occurrence (e.g., habitat description and associations).

Materials and methods

Newly collected samples were obtained from the Chapopote Knoll on deep sea asphalt-associated cold seeps, in the southwestern Gulf of Mexico during cruise GeoB M67/2b of the *R/V Meteor* (2– 24 April 2006). Specimens were collected using scavenger traps deployed on the seafloor with the ROV *Quest* via the ROV's suction device. On board, specimens were fixed in absolute ethanol at 4^{o}C for 24 h, transferred to 70% ethanol and stored in labelled in glass jars. Specimens were deposited in the *Colección Nacional de Crustáceos* (CNCR), Instituto de Biología, UNAM, Mexico (CNCR24845–24869). Specimens of *M. exuta* and *M. geyeri* from different locations were requested on loan from diverse international collections and used in the comparative morphological analysis (Table 1). Morphology of specimens was examined using a stereomicroscope (Zeiss, 1.0X magnification). Re-description of *M. geyeri* followed and complemented the scheme of Mayo (1974) and followed the terminology used by Baba (2005) and Baba *et al.* (2011). The postorbital carapace length (CL) was measured in millimeters (to the nearest 0.1 mm), measured along the dorsal midline from the posterior margin of the orbit to the posterior margin of the carapace. The length of each pereopod article was measured in lateral view along its extensor margin (excluding distal spine), the breadth is measured at its widest point. Abbreviations used are: Mxp3 = maxilliped 3; P1, pereopod 1; P2–4, pereopods 2–4.

Pleonal muscle samples of specimens from different institutions were extracted from three specimens of *M. exuta*, eight specimens of *M. geyeri*, and one specimen of *Munidopsis recta* and *Munidopsis bracteosa* as comparative species and belonged (Table 2). GenBank sequences were also included (Table 2). DNA was obtained with an Epoch GenCatch DNA extraction kit and a Qiagen DNeasy kit, following manufacturer´s instructions. DNA was quantified with a Nano Drop ND-1000 Spectrophotometer (15 and 40 ng/µl readings). The Polymerase Chain Reaction (PCR) was performed with a Cetus 9600 DNA thermocycler (Pekin-Elmer Corporation, Connecticut) or a RoboCycler Gradient 96 temperature cycler; amplification used the DNA template (2 µl), 5 µl 10 buffer (supplied by the manufacturer), 5 µl $MgCl_2$ (2.5 µM), 2 µl of each primer (10 mM final concentration), 2.5 units of Taq polymerase (Taq Gold Applied Biosystem and Taq DNA Polymerase-USB), 5 µl of 2 mM stock solution of dNTPs, 1 µl of 100X BSA, and sterile H2O to a final volume of 25 µl. Primers used to amplify base pairs of the mitochondrial 12s, 16s and cytochrome c oxidase subunit 1 (COI) fragments were: 12sSf (5—GAA ACC AGG ATT AGA TAC CC—3) and 12s1R (5—AGC GAC GGG CGA TAT GTA C— 3), 16SH2 (5—AGA TAG AAA CCA ACC TGG—3) and 16SL2/16SL9 (5—TGC CTG TTT ATC AAA AAC AT—3/5—CGC CTG TTT ATC AAA AAC AT—3) (Palumbi *et al.* 1991), and gala_COIF (5—CAT CAC TWA GWT TRA TYA TTC GAG CAG AA—3) and gala_COIR (5—GAA YAG GRT CTC CTC CTC CTA C—3) (Jones & Macpherson 2007). The thermal profile was an initial denaturation at 94°C for 4 min, followed by 35 cycles of 94 C for 1 min, 55°C for 2 min, and 72 C for 3.5 min, then a final extension at 72°C for 10 min. PCR products were purified with Sephadex, a GenCatch PCR Purification kit and ExoSAP-IT for PCR Product Clean-Up. The purified template DNA was sequenced with a Big Dye^{TM} Terminator cycle sequencing reaction kit (PE Biosystems, Foster, CA) and an ABI Prism 3100 sequencer (Applied Biosystems Inc., Foster, CA). PCR products were sequenced bidirectionally from each sample with the same forward

TABLE 1. Specimens of *Munidopsis exuta* and *Munidopsis geyeri* studied. Abbreviations: *n* = number of specimens; ovig = ovigerous; juv = juvenile; F = female; M = male, Stn = sample station; D = dive; *Z*(m) = depth in meters; E = ecosystem; AS = soft abyssal substrate; HV = hydrothermal vent; CS = cold seep; ID = identification of collection; MAR = Mid-Atlantic ridge; CSIC = Centro de Estudios Avanzados de Blanes, Spain; USNM = Natural History Museum, USA; CNCR = Colección Nacional de Crustáceos, Mexico; RS-MAS = formerly UMML, Invertebrate Museum, Rosenstiel School of Marine & Atmospheric Science, University of Miami, Florida, USA; MNHN = Muséum National d´Histoire Naturelle, France; IFREMER = Institut français de Recherche pour l'exploitation de la mer; PC = personal collection; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden; BMNH = British Museum, Natural History; F = number or letter assigned to collection site in Figure 5. Dash ("–") denotes unavailable data.

M. exuta n	**Locality**	**Expedition and Stn**	**Latitude**	**Longitude**	***Z*(m)**	**E**	**ID-Collection**	**F**
1ovigF, 1juvF	Bay of Biscay	BIOGAS 5, CV40	47° 33´ N	09° 02´ W	2860	AS	CEAB CRU 2004-01	1
1juvM		BIOGAS 6, CP10	47° 30´ N	09° 04´ W	2878		CEAB CRU 2004-02	1
1ovigF	MAR	Akademik 50, 4787	30° 07´ N	42° 07´ W	3020	HV	CEAB CRU 2004-031	2
1ovgF, 1F	MAR. TAG	AMK 47, 4343	26° 08´ N	44° 49´ W	3650		CEAB CRU 2004-04	3
1ovigF	MAR. Snake Pit-Les Ruches	HYDROSNAKE, HS08	23° 22´ N	44° 57´ W	3502		Holotype MNHN Ga 4621 = MNHN IU 2014 19814	4
1F	MAR. Snake Pit-Elan	MAR93 Alvin, 2617	23° 23´ N	44° 56´ W	3500		Paratype MNHN IU 2014 19818	4
1juvF, 1juvM	Florida Escarpment	Alvin 3637, 4–5	26° 01.8´ N	84° 54.9´ W	3288	CS	CEAB CRU 2004-05	5
1juvM	Chapopote Knoll south-western Gulf of Mexico	M67/2b, 10617-5 D. 81	21° 53.94´ N	93° 26.226´ W	2919		CNCR 24866	6
1ovigF 1M		M67/2b, 10619-19 D. 82	21° 53.922´ N	93° 26.166´ W	2875		CNCR 24846 = ULLZ 8792, CNCR 24857 = ULLZ 8861	6
2F, 1M		M67/2b, 10625-13 D. 84	21° 53.994´ N	93° 26.124´ W	2916		CNCR 24867, CNCR 24869, CNCR 24868	6
1juvF	Gulf of Guinea, Regab Pockmark site	BIOZAIRE 3, CP20	05° 46.89´ S	09° 44.66´ E	3113		CEAB CRU 2004-06	7
Not analyzed	MAR. Broken Spur MAR. Logatchev	BRIDGE 1993, Alvin 2625. Record on OBIS (2022)	29° 10.2´ N 14° 45.10´ N	43° 10.3´ W 44° 57.99´ W	3056 3500	VH	E. Southward in Macpherson & Segonzac (2005); C. Fisher & C. van Dover (OBIS 2022)	8 9
	MAR. Snake Pit	BICOSE, PL568-ASP5, ASP6	23° 22´ 6.1032" N	44° 56´ 57.5016" W	3514, 3471		MNHN IU 2013 15612–MNHN IU 2013 15615	4

......*continued on the next page*

TABLE 1. (Continued)

M. exuta n	**Locality**	**Expedition and Stn**	**Latitude**	**Longitude**	***Z*(m)**	**E**	**ID-Collection**	**F**
	Gulf of Biscay	BIOGAS St. 2 and 3	47° 27′–47° 28′ N	9° 0.1′–9° 0′ W	3480–3800	AS	De Saint Laurent (1985)	10
			47° 31.8′–47° 34.9′ N	9° 28.21′–9° 40.9′ W	4050–4237			11
	MAR	Human observation on OBIS (2022)	12° N	44° W	3257–3259	VH	SERPENTINE-IFREMER BREST	a
	ZF 15N20						F. Yves & P. Briand (OBIS 2022)	
	Gulf of Biscay		47° N	9° W	2878	SB	BIOGAS VI-CNEXO L. Laubier & E. Macpherson (OBIS 2022)	b
M. geyeri n	**Locality**	**Expedition and Stn**	**Latitude**	**Longitude**	***Z*(m)**	**E**	**ID-Collection**	**F**
1juv.M	Southwestern Gulf of Mexico	Alaminos 69-A-11-92	23° 30′ N	95° 32′ W	2926–2999	AS	USNM 128812	1
4juv.F, 2juv.M	Caribbean Sea, St. Croix	Alvin DSR/V 1078	17° 94′ N	64° 81′ W	4000		USNM 231300 = ULLZ 8923	2
1F, 1M, 1juv.M	Caribbean Sea, Gonave Haiti	P-1180	18° 55′–18° 44.4′ N	73° 53′–73° 55′ W	3111–3496		UMML 32:5246 RSMAS, Miami	3
1M	Azores Islands	BIOACORES 202	37° 26.5′ N	25° 00′ W	2900		MNHN Ga 1182	4
1juv.M, 1M	Off Mauritania, Africa	EUMELI 4; CPH-15	18° 53′ N	21° 08′ W	3124		MNHN Ga 6525	5
1M	Northeastern Gulf of Mexico	Gyre DGoMB, S-41	27° 54.23′–28° 04.33′ N	86° 26.08′–86° 40.65′ W	2930–3030		USNM 310877 = ULLZ 8784	6
1juv.F	Gulf of Guinea, Regab Pockmark site	BIOZAIRE 3; CP20	05° 46.89′ S	09° 44.66′ E	3113	CS	MNHN Ga 5662 = MNHN IU 2008 13352 CEAB CRU 2004-07	7
3juv.F, 3ovig.F, 21F, 3juv.M, 19M								
1F, 3juv.M, 2M								

......continued on the next page

TABLE 1. (Continued)

M. exuta n	Locality	Expedition and Stn	Latitude	Longitude	*Z*(m)	E	ID-Collection	F
2juv 1juv 1juv 1juv	Off Gabon, Africa	BIOZ-RECUP; Mac10(152) Mac10(154) Mac10(158) Mac10(160)	05° 51´ S	09° 41.98´ E	3155		MNHN Ga 6524 MNHN Ga 6522 MNHN Ga 6523 MNHN Ga 6521	8
1M	Alaminos Canyon (AC818) Northern Gulf of Mexico	Atlantis, MPB, J2-282	26° 18´ N	94° 62´ W	2744.8		USNM 1178677 = ULLZ 8912	9
7ovig.F, 3F, 9M	Chapopote Knoll south-western Gulf of Mexico	M67/2b, 10619-19 D. 82	21° 53.92´ N	93° 26.16´ W	2875		CNCR 24847–CNCR 24853, CNCR 24845, CNCR 24855, CNCR 24856, CNCR 24854, CNCR 24858–CNCR 24865	10
Not analyzed	Florida Escarpment	Alvin 3637, 4–5	26° 01.8´ N	84° 54.9´ W	3288	CS	Macpherson & Segonzac (2005) Olu *et al*., (1996) Olu *et al*., (1997)	11
	Barbados Accretionary Prism Orenoque A & B	DIAPISUB, (1992-1993)	10° 18–24– 10° 16–23´ N	58° 46–56’– 58° 35–40´ W	1700–2080			12
	North of Zaire River channel	BIOZAIRE 1 Stn PL 81-5	05° 47.80´ S	09° 42.60´ E	3151	AS	Macpherson & Segonzac (2005)	13
		BIOZAIRE 2, Stn PL 147-10	05° 47.80´ S	09° 42.60´ E	3151			
		BIOZAIRE 3, Stn CP16 Stn CP19	05° 49.79´ S 05° 48.07´ S	09° 44.08´ E 09° 41.60´ E	3172 3184			
	Alaminos Canyon Louisiana lower slope	Record on OBIS (2022)	26° 22.46´ N	94° 30.4´ W	2200–2335		Catalogue 3523 Ch. Fisher & C. van Dover (OBIS 2022)	14
	Colombia Basin	Alaminos St. 70A10-48	14° 29.5´ N	74° 24.8´ W	4151		Pequegnat & Pequegnat (1971)	15

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TABLE 1. (Continued)

M. exuta n	Locality	Expedition and Stn	Latitude	Longitude	*Z*(m)	E	ID-Collection	F
	South of Jamaica	Alaminos St. 70A10-50	15° 50´ N	77° 24.5´ W	2650–2790			16
	Venezuela Basin	USNS BARTLETT 1301-82 St. 88, 90	13° 33.60´– 13° 26.90´ N	64° 46.90´– 64° 42.70´ W	3422–3549		Gore (1983) (RMNHD00000, BMNH 1983–353)	17
	Northeastern Gulf of Mexico	Observation on OBIS (2022)	26° 43.27´ N	84° 56.35´ W	2600	—	Felder *et al*., (2009a)	a
			25° 54.48´ N	87° 22.61´ W				b
			27° 44.21´ N	88° 17.12´ W				c
			25° 40.96´ N	89° 36.67´ W				d
	Southwestern Gulf of Mexico		23° 56.34´ N	93° 6.09´ W				e
			22° 46.42´ N	96° 23.87´ W				f
	Gulf of Guinea, Zaiango		5° S	9° E	3113	CS	M. Segonzac (OBIS 2022)	g

and reverse primers as were used in the PCR. The ten genetic vouchers, from which tissue samples were obtained, were deposited on University of Louisiana, Lafayette Zoological Collection (ULLZ, Table 2). Combined sequences were visualized and edited with Sequencher 4.1, parameters: minimum overlap 20, and minimum match 85% (Gene Codes Corporation Inc. Ann Arbor). Thirty-five new sequences were deposited in GenBank (Table 2).

Alignments for each gene segment and combined genes were obtained using ClustalW (Thompson *et al.* 1994) as implemented in Bioedit (Hall 1999). Genetic analyses were performed in MEGA X (Kumar *et al.* 2018). Pairwise distances were computed to 45 nucleotide sequences of cytochrome c oxidase subunit 1 (COI) gen fragment and to 14 combined nucleotide sequences (COI, 12S and 16S).

Analyses followed previous molecular phylogenetic analyses of galatheids with genetic distances computed by uncorrected pairwise "p" distances (number of base differences per site from between sequences, e.g. Coykendall *et al.* 2017; Machordom & Macpherson 2004; Macpherson & Robainas-Barcia 2013). The Kimura 2-parameter substitution model (K2P; Kimura 1980) for genetic distances was performed as comparative values. Frequency histograms were constructed to visualize barcoding gaps between intraspecific and interspecific genetic distances (Meyer & Paulay 2005). A second analysis inferred the molecular distances using the Neighbor-Joining method (Saitou & Nei 1987). The same group of data for pairwise distances analysis was used, including *Shinkaia crosnieri* Baba & Williams, 1998 in the analysis with combined gene fragments (12S, 16S and COI), and excluding it from the analysis of COI gene fragment to visualize the distances between similar species (Table 2). The trees were drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic trees. The evolutionary distances were computed using the p-distance method (Nei & Kumar 2000). Codon positions included were 1st + 2nd + 3rd + Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option).

TABLE 2. Specimens used in the molecular sequence analysis and sequences cited in published studies. Abbreviations: ULLZ = University of Louisiana at Lafayette Zoological Collection; CNCR = Colección Nacional de Crustáceos, UNAM, Mexico; USNM = National Collection of the Smithsonian Institution, USA; GM = Gulf of Mexico; CSea = Caribbean Sea; GG = Gulf of Guinea; GC = Gulf of California; MAR = Mid-Atlantic Ridge; EPR = East Pacific Rise; P = Pacific Ocean; CS = cold seep, HV = hydrothermal vent; WF = whale fall; AS = soft abyssal substrate; GB = GenBank accession number. Dash (–) denotes unavailable data. Publications: (1) Jones & Macpherson (2007); (2) Goffredi *et al.* (2017); (3) Coykendall *et al.* (2017); (4) Sun *et al.* (2019); (5) Yang & Yang (2008). * In GenBank as *M. antonii*.

Species/Sample site	ID-Collection or Publication	GB-12	GB-16	GB-COI
M. exuta Macpherson & Segonzac, 2005				
Chapopote Knoll, GM; CS with asphalt	CNCR 24866	OP620559	OP629188	OP628182
	CNCR 24846 = ULLZ 8792	OP620558	OP629187	OP628181
	CNCR 24857 = ULLZ 8861	OP620557	OP629186	OP628180
M geyeri Pequegnat & Pequegnat, 1970				
St. Croix, CSea; AS	USNM 231300 = ULLZ 8923	OP620555	OP629184	OP628177
Northeastern GM; AS	USNM 310877 = ULLZ 8784	OP620550	OP629179	OP628172
Regab Pockmark site, GG; CS	ULLZ 8863	OP620556	OP629185	OP628178
	ULLZ 8862	–	–	OP628179
Alaminos Canyon AC818, GM; CS	ULLZ 8912	OP620554	OP629183	OP628176
Chapopote Knoll, GM; CS with asphalt	CNCR 24845 = ULLZ 8791	OP620551	OP629180	OP628173
	CNCR 24848 = ULLZ 8794	OP620552	OP629181	OP628174
	CNCR 24853 = ULLZ 8799	OP620553	OP629182	OP628175
M. recta Baba, 2005				
EPR, 11 S; HV	USNM 1100643	OP620548	OP629177	–
M. bracteosa Jones & Macpherson, 2007	USNM 1100633	OP620549	OP629178	–
Northeastern P.; WF				

Sequences from published work

Species/Sample site	Reference	COI-Sequence
M. exuta Macpherson & Segonzac, 2005		
MAR, TAG; HV	(1)	DQ677690
M. recta Baba, 2005		
EPR, 9 N, 11 N, 17 N,18 S; HV	(1)	DQ677695
EPR, 9 N, 13 N, 21 N, 38 S, Galapagos Rift; HV	(1)	DQ677696–DQ677702
Alarcon Rise, GC; HV	(2)	KY581549
M. bracteosa Jones & Macpherson, 2007		
Endeavour Field, Northeastern P; HV	(1)	DQ677684
Mendicino Fracture Zone	(1)	DQ677685*
Northeastern P; WF	(1)	DQ677686–DQ677689*
Munidopsis sp. A Coykendall, Nizinski & Morrison, 2017		
Alaminos Canyon AC818, GM; CS	(3)	KX016552
		KX016553
M. scotti Jones & Macpherson, 2007		
Juan de Fuca, Northeastern P	(1)	DQ677703–DQ677705
Pescadero Basin, GC; HV	(2)	KY581548
M. antonii (Filhol, 1884)		
Station M, Northeastern P; HV	(1)	DQ677677, DQ677678, DQ677681, DQ677682
M. segonzaci Jones & Macpherson, 2007		
Station M, Northeastern P	(1)	DQ677683
M. tiburon Jones & Macpherson, 2007		
Monterey Bay Canyon, Northeastern P	(1)	DQ677673
M. kensmithi Jones & Macpherson, 2007		
Station M, Northeastern P	(1)	DQ677706, DQ677709
M. livida (Perrier, 1886)		
Alaminos Canyon AC818, Northeastern GM	(3)	KX016546
M. lauensis Baba & de Saint Laurent, 1992		
Southwestern P; HV		Complete genome MH717895
M. verrilli Benedict, 1902	(4)	
Southwestern P; HV		Complete genome MH717896
Shinkaia crosnieri Baba & Williams, 1998	(5)	Complete genome EU420129
Southwestern P; HV		

Molecular phylogenetic inferences

The alignment and genetic distance analysis involved 14 nucleotide sequences, each a combination of the 12S (300 basepairs), 16S (509 basepairs), and COI (503 basepairs) sequences. For the COI analysis, 45 nucleotide sequences were used (same basepair length). The resulting matrix of the evolutionary genetic divergences between 45 nucleotide sequences (Table 3) showed intergeneric distances between *Munidopsis* species and *Shinkaia crosnieri* ranging from 17.7 to 21.7% (18.7% ±0.1, mean ± SD; Fig. 1A). In contrast, pairwise comparison among species of *Munidopsis* did not show a clear barcoding gap separating intra- and interspecific groups. Intraspecific genetic distances ranged from 0 to 1.4% (0.32% ± 0.27, mean ± SD). In *M. geyeri* and *M. bracteosa* the intraspecific distances between individuals ranged from 0 to 0.4%. In contrast, between individuals of the rest of the species intraspecific distances ranged from 0 to 0.8%.

In comparing the intraspecific distances, a specimen of *M. scotti* (GenBank KY581548) from Pescadero Basin of the Gulf of California, had 1.2% and 1.4% genetic distances between the other two specimens from the same species (GenBank DQ677703–05) from Juan de Fuca Ridge in the northeastern Pacific (Table 3; Fig. 1A). The species labeled as *Munidopsis* sp. A by Coykendall *et al.* (2017) showed a distance of 0 to 0.4% to specimens of *M. geyeri*. These results are supportive of representing this species. Interspecific genetic distances ranged from 0.6 to 14.7% (5% ± 4.1, mean ± SD). *Munidopsis geyeri* and *M. bracteosa* recorded minimum interspecific divergence with a range of 0.6 to 1.2% (1% ± 0.2, mean ± SD; Table 3; Fig. 1A). By applying the K2P substitution model for the same COI alignment, we recorded the same intraspecific average distance between species (0.3% ± 0.28), slightly higher interspecific genetic distances (5.4% ± 4.6), and between *Munidopsis* species and *Shinkaia crosnieri* (20.4 to 26.2%, 21.8% ± 1.4, mean ± SD).

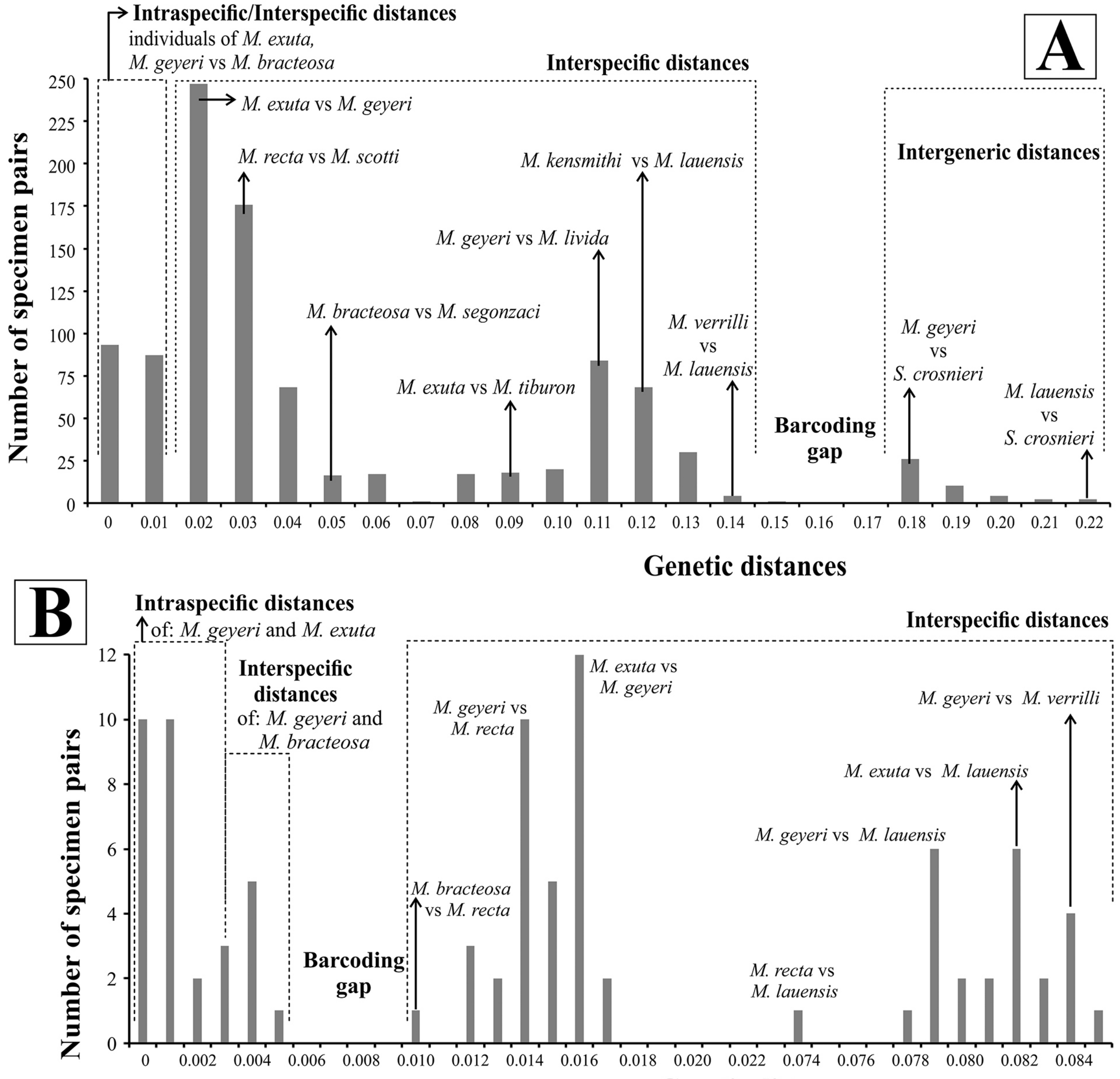

FIGURE 1. Histograms of uncorrected pairwise "p" genetic distances of *Munidopsis* analysed: A, for 45 nucleotide sequences of cytochrome c oxidase subunit 1 (COI) (same group of data used for Neighbor-Joining analysis on Fig. 2B including *Shinkaia crosnieri*). B, for 14 nucleotide sequences of combined genes (COI, 12S and 16S) (same group of data used for Neighbor-Joining analysis on Fig. 2A excluding *Shinkaia crosnieri*). Arrows show examples of specimen pairs from genetic distance. Detail of species and number of specimens used for intraspecific and interspecific distance calculations is provided in Table 3 and 4.

TABLE 3. Estimates of genetic divergence between sequences for 45 nucleotide sequences of cytochrome c oxidase subunit 1 (COI). Below the diagonal: uncorrected “p” distances, per unit, above the diagonal: Kimura 2-parameter model. Same group of data used for Neighbor-Joining analysis on Fig. 2B, including *Shinkaia crosnieri*. List of species, GenBank accession number in parenthesis: 1–8. *M. geyeri* (OP628172–OP628179), 9–10. *Munidopsis* sp. A (KX016552, KX016553), 11–16. *M. bracteosa* (DQ677684–DQ677689), 17–20. *M. exuta* (DQ677690, OP628180– OP628182), 21–29. *M. recta* (DQ677695–DQ677702, KY581549), 30–33. *M. scotti* (DQ677703–DQ677705, KY581548), 34–37. *M. antonii* (DQ677677, DQ677678, DQ677681, DQ677682), 38. *M. segonzaci* (DQ677683), 39. *M. tiburon* (DQ677673), 40. *M. livida* (KX016546), 41–42. *M. kensmithi* (DQ677706, DQ677709), 43. *M. lauensis* (MH717895), 44. *M. verrilli* (MH717896), 45. *Shinkaia crosnieri* (EU420129).

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0.002	0.002	0.002	0.002	0.002	0.004	0.004	0.004	0.002	0.006	0.006	0.008	0.008	0.008
2 0.002		0.000	0.000	0.000	0.000	0.002	0.002	0.002	0.000	0.008	0.008	0.010	0.010	0.010
3 0.002	0.000		0.000	0.000	0.000	0.002	0.002	0.002	0.000	0.008	0.008	0.010	0.010	0.010
4 0.002	0.000	0.000		0.000	0.000	0.002	0.002	0.002	0.000	0.008	0.008	0.010	0.010	0.010
5 0.002	0.000	0.000	0.000		0.000	0.002	0.002	0.002	0.000	0.008	0.008	0.010	0.010	0.010
6 0.002	0.000	0.000	0.000	0.000		0.002	0.002	0.002	0.000	0.008	0.008	0.010	0.010	0.010
7 0.004	0.002	0.002	0.002	0.002	0.002		0.004	0.004	0.002	0.010	0.010	0.012	0.012	0.012
8 0.004	0.002	0.002	0.002	0.002	0.002	0.004		0.004	0.002	0.010	0.010	0.008	0.012	0.008
9 0.004	0.002	0.002	0.002	0.002	0.002	0.004	0.004		0.002	0.010	0.010	0.012	0.012	0.012
10 0.002	0.000	0.000	0.000	0.000	0.000	0.002	0.002	0.002		0.008	0.008	0.010	0.010	0.010
11 0.006	0.008	0.008	0.008	0.008	0.008	0.010	0.010	0.010	0.008		0.000	0.002	0.002	0.002
12 0.006	0.008	0.008	0.008	0.008	0.008	0.010	0.010	0.010	0.008	0.000		0.002	0.002	0.002
13 0.008	0.010	0.010	0.010	0.010	0.010	0.012	0.008	0.012	0.010	0.002	0.002		0.004	0.000
14 0.008	0.010	0.010	0.010	0.010	0.010	0.012	0.012	0.012	0.010	0.002	0.002	0.004		0.004
15 0.008	0.010	0.010	0.010	0.010	0.010	0.012	0.008	0.012	0.010	0.002	0.002	0.000	0.004	
16 0.008	0.010	0.010	0.010	0.010	0.010	0.012	0.008	0.012	0.010	0.002	0.002	0.000	0.004	0.000
17 0.018	0.020	0.020	0.020	0.020	0.020	0.022	0.022	0.022	0.020	0.016	0.016	0.018	0.018	0.018
18 0.020	0.022	0.022	0.022	0.022	0.022	0.024	0.020	0.024	0.022	0.018	0.018	0.016	0.020	0.016
19 0.018	0.020	0.020	0.020	0.020	0.020	0.022	0.018	0.022	0.020	0.016	0.016	0.014	0.018	0.014
20 0.020	0.022	0.022	0.022	0.022	0.022	0.024	0.024	0.024	0.022	0.018	0.018	0.020	0.020	0.020
21 0.020	0.022	0.022	0.022	0.022	0.022	0.024	0.020	0.024	0.022	0.014	0.014	0.012	0.016	0.012
22 0.018	0.020	0.020	0.020	0.020	0.020	0.022	0.018	0.022	0.020	0.016	0.016	0.014	0.018	0.014
23 0.020	0.022	0.022	0.022	0.022	0.022	0.024	0.020	0.024	0.022	0.018	0.018	0.016	0.020	0.016
24 0.022	0.024	0.024	0.024	0.024	0.024	0.026	0.022	0.026	0.024	0.016	0.016	0.014	0.018	0.014

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TABLE 3. (Continued)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
25 0.022	0.024	0.024	0.024	0.024	0.024	0.026	0.022	0.026	0.024	0.020	0.020	0.018	0.022	0.018
26 0.022	0.024	0.024	0.024	0.024	0.024	0.026	0.022	0.026	0.024	0.016	0.016	0.014	0.018	0.014
27 0.020	0.022	0.022	0.022	0.022	0.022	0.024	0.020	0.024	0.022	0.014	0.014	0.012	0.016	0.012
28 0.022	0.024	0.024	0.024	0.024	0.024	0.026	0.022	0.026	0.024	0.016	0.016	0.014	0.018	0.014
29 0.022	0.024	0.024	0.024	0.024	0.024	0.026	0.022	0.026	0.024	0.016	0.016	0.014	0.018	0.014
30 0.030	0.028	0.028	0.028	0.028	0.028	0.030	0.030	0.030	0.028	0.024	0.024	0.026	0.026	0.026
31 0.032	0.030	0.030	0.030	0.030	0.030	0.032	0.032	0.032	0.030	0.026	0.026	0.028	0.028	0.028
32 0.032	0.030	0.030	0.030	0.030	0.030	0.032	0.032	0.032	0.030	0.026	0.026	0.028	0.028	0.028
33 0.024	0.024	0.024	0.024	0.024	0.024	0.026	0.026	0.026	0.024	0.022	0.022	0.024	0.024	0.024
34 0.030	0.032	0.032	0.032	0.032	0.032	0.034	0.030	0.034	0.032	0.028	0.028	0.026	0.030	0.026
35 0.032	0.034	0.034	0.034	0.034	0.034	0.036	0.032	0.036	0.034	0.030	0.030	0.028	0.032	0.028
36 0.032	0.034	0.034	0.034	0.034	0.034	0.036	0.032	0.036	0.034	0.030	0.030	0.028	0.032	0.028
37 0.032	0.034	0.034	0.034	0.034	0.034	0.036	0.032	0.036	0.034	0.034	0.034	0.032	0.036	0.032
38 0.056	0.058	0.058	0.058	0.058	0.058	0.060	0.056	0.060	0.058	0.054	0.054	0.052	0.056	0.052
39 0.082	0.080	0.080	0.080	0.080	0.080	0.082	0.078	0.082	0.080	0.088	0.088	0.086	0.090	0.086
40 0.105	0.107	0.107	0.107	0.107	0.107	0.109	0.105	0.110	0.107	0.108	0.108	0.106	0.110	0.106
41 0.110	0.112	0.112	0.112	0.112	0.112	0.114	0.114	0.114	0.112	0.110	0.110	0.112	0.108	0.112
42 0.108	0.110	0.110	0.110	0.110	0.110	0.112	0.112	0.112	0.110	0.108	0.108	0.110	0.110	0.110
43 0.125	0.125	0.125	0.125	0.125	0.125	0.127	0.123	0.124	0.125	0.125	0.125	0.124	0.127	0.124
44 0.119	0.121	0.121	0.121	0.121	0.121	0.123	0.123	0.120	0.121	0.120	0.120	0.122	0.122	0.122
45 0.181	0.183	0.183	0.183	0.183	0.183	0.181	0.181	0.182	0.183	0.183	0.183	0.181	0.181	0.181

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TABLE 3. (Continued)

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
0.008	0.018	0.020	1 0.018	0.020	0.020	0.018	0.020	0.022	0.022	0.022	0.020	0.022	0.022	0.031
0.010	0.020	0.022	2 0.020	0.022	0.022	0.020	0.022	0.024	0.024	0.024	0.022	0.024	0.024	0.029
0.010	0.020	0.022	3 0.020	0.022	0.022	0.020	0.022	0.024	0.024	0.024	0.022	0.024	0.024	0.029
0.010	0.020	0.022	4 0.020	0.022	0.022	0.020	0.022	0.024	0.024	0.024	0.022	0.024	0.024	0.029
0.010	0.020	0.022	5 0.020	0.022	0.022	0.020	0.022	0.024	0.024	0.024	0.022	0.024	0.024	0.029
0.010	0.020	0.022	6 0.020	0.022	0.022	0.020	0.022	0.024	0.024	0.024	0.022	0.024	0.024	0.029
0.012	0.022	0.024	7 0.022	0.024	0.024	0.022	0.024	0.027	0.027	0.027	0.025	0.027	0.027	0.031
0.008	0.022	0.020	8 0.018	0.024	0.020	0.018	0.020	0.022	0.022	0.022	0.020	0.022	0.022	0.031
0.012	0.023	0.025	9 0.023	0.025	0.025	0.023	0.025	0.027	0.027	0.027	0.025	0.027	0.027	0.031
0.010	0.020	0.022	10 0.020	0.022	0.022	0.020	0.022	0.024	0.024	0.024	0.022	0.024	0.024	0.029
0.002	0.016	0.018	11 0.016	0.018	0.014	0.016	0.018	0.016	0.020	0.016	0.014	0.016	0.016	0.024
0.002	0.016	0.018	12 0.016	0.018	0.014	0.016	0.018	0.016	0.020	0.016	0.014	0.016	0.016	0.024
0.000	0.018	0.016	13 0.014	0.020	0.012	0.014	0.016	0.014	0.018	0.014	0.012	0.014	0.014	0.027
0.004	0.018	0.020	14 0.018	0.020	0.016	0.018	0.020	0.018	0.022	0.018	0.016	0.018	0.018	0.027
0.000	0.018	0.016	15 0.014	0.020	0.012	0.014	0.016	0.014	0.018	0.014	0.012	0.014	0.014	0.027
	0.018	0.016	16 0.014	0.020	0.012	0.014	0.016	0.014	0.018	0.014	0.012	0.014	0.014	0.027
0.018		0.006	17 0.004	0.006	0.018	0.016	0.018	0.020	0.020	0.020	0.018	0.020	0.020	0.029
0.016	0.006		18 0.002	0.008	0.016	0.014	0.016	0.018	0.018	0.018	0.016	0.018	0.018	0.035
0.014	0.004	0.002	19	0.006	0.014	0.012	0.014	0.016	0.016	0.016	0.014	0.016	0.016	0.033
0.020	0.006	0.008	20 0.006		0.020	0.018	0.020	0.022	0.022	0.022	0.020	0.022	0.018	0.035
0.012	0.018	0.016	21 0.014	0.020		0.002	0.004	0.002	0.006	0.002	0.000	0.002	0.002	0.031
0.014	0.016	0.014	22 0.012	0.018	0.002		0.002	0.004	0.004	0.004	0.002	0.004	0.004	0.033
0.016	0.018	0.016	23 0.014	0.020	0.004	0.002		0.006	0.006	0.006	0.004	0.006	0.006	0.035
0.014	0.020	0.018	24 0.016	0.022	0.002	0.004	0.006		0.008	0.004	0.002	0.004	0.004	0.033
0.018	0.020	0.018	25 0.016	0.022	0.006	0.004	0.006	0.008		0.008	0.006	0.008	0.008	0.037
0.014	0.020	0.018	26 0.016	0.022	0.002	0.004	0.006	0.004	0.008		0.002	0.004	0.004	0.033
0.012	0.018	0.016	27 0.014	0.020	0.000	0.002	0.004	0.002	0.006	0.002		0.002	0.002	0.031
0.014	0.020	0.018	28 0.016	0.022	0.002	0.004	0.006	0.004	0.008	0.004	0.002		0.004	0.033

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TABLE 3. (Continued)

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
0.014	0.020	0.018	29 0.016	0.018	0.002	0.004	0.006	0.004	0.008	0.004	0.002	0.004		0.033
0.026	0.028	0.034	30 0.032	0.034	0.030	0.032	0.034	0.032	0.036	0.032	0.030	0.032	0.032	
0.028	0.030	0.036	31 0.034	0.036	0.032	0.034	0.036	0.034	0.038	0.032	0.032	0.034	0.034	0.002
0.028	0.030	0.036	32 0.034	0.036	0.032	0.034	0.036	0.034	0.038	0.034	0.032	0.034	0.034	0.002
0.024	0.026	0.028	33 0.026	0.028	0.028	0.026	0.028	0.030	0.030	0.030	0.028	0.030	0.030	0.012
0.026	0.024	0.026	34 0.024	0.030	0.026	0.024	0.026	0.028	0.028	0.028	0.026	0.028	0.028	0.032
0.028	0.026	0.028	35 0.026	0.032	0.028	0.026	0.028	0.030	0.030	0.030	0.028	0.030	0.030	0.034
0.028	0.026	0.028	36 0.026	0.032	0.028	0.026	0.028	0.030	0.030	0.030	0.028	0.030	0.030	0.034
0.032	0.030	0.032	37 0.030	0.036	0.028	0.026	0.028	0.030	0.030	0.030	0.028	0.030	0.030	0.034
0.052	0.050	0.048	38 0.050	0.056	0.050	0.048	0.048	0.052	0.048	0.052	0.050	0.052	0.052	0.054
0.086	0.090	0.088	39 0.090	0.096	0.086	0.084	0.084	0.088	0.084	0.086	0.086	0.088	0.088	0.094
0.106	0.108	0.105	40 0.107	0.109	0.100	0.102	0.104	0.102	0.106	0.102	0.100	0.102	0.097	0.112
0.112	0.112	0.114	41 0.116	0.118	0.112	0.110	0.110	0.114	0.110	0.114	0.112	0.114	0.114	0.112
0.110	0.110	0.112	42 0.114	0.116	0.110	0.108	0.108	0.112	0.108	0.112	0.110	0.112	0.112	0.110
0.124	0.127	0.125	43 0.127	0.133	0.120	0.122	0.120	0.122	0.125	0.122	0.120	0.118	0.121	0.114
0.122	0.118	0.119	44 0.121	0.123	0.125	0.127	0.127	0.127	0.127	0.127	0.126	0.124	0.127	0.122
0.181	0.191	0.187	45 0.187	0.187	0.179	0.181	0.181	0.181	0.181	0.181	0.178	0.181	0.177	0.187

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TABLE 3. (Continued)

31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
0.033	0.033	0.024	0.031	0.033	0.033	1 0.033	0.059	0.088	0.116	0.121	0.119	0.141	0.133	0.209
0.031	0.031	0.024	0.033	0.035	0.035	2 0.035	0.061	0.085	0.118	0.124	0.121	0.141	0.136	0.212
0.031	0.031	0.024	0.033	0.035	0.035	3 0.035	0.061	0.085	0.118	0.124	0.121	0.141	0.136	0.212
0.031	0.031	0.024	0.033	0.035	0.035	4 0.035	0.061	0.085	0.118	0.124	0.121	0.141	0.136	0.212
0.031	0.031	0.024	0.033	0.035	0.035	5 0.035	0.061	0.085	0.118	0.124	0.121	0.141	0.136	0.212
0.031	0.031	0.024	0.033	0.035	0.035	6 0.035	0.061	0.085	0.118	0.124	0.121	0.141	0.136	0.212
0.033	0.033	0.026	0.035	0.037	0.037	7 0.037	0.064	0.088	0.121	0.126	0.124	0.143	0.138	0.209
0.033	0.033	0.026	0.031	0.033	0.033	8 0.033	0.059	0.083	0.116	0.126	0.124	0.138	0.138	0.209
0.033	0.033	0.027	0.035	0.038	0.038	9 0.038	0.064	0.088	0.122	0.127	0.124	0.139	0.135	0.211
0.031	0.031	0.024	0.033	0.035	0.035	10 0.035	0.061	0.085	0.118	0.124	0.121	0.141	0.136	0.212
0.027	0.027	0.022	0.029	0.031	0.031	11 0.035	0.057	0.095	0.118	0.122	0.119	0.141	0.134	0.212
0.027	0.027	0.022	0.029	0.031	0.031	12 0.035	0.057	0.095	0.118	0.122	0.119	0.141	0.134	0.212
0.029	0.029	0.024	0.027	0.029	0.029	13 0.033	0.055	0.092	0.116	0.124	0.122	0.138	0.136	0.210
0.029	0.029	0.024	0.031	0.033	0.033	14 0.037	0.059	0.097	0.121	0.119	0.122	0.144	0.136	0.210
0.029	0.029	0.024	0.027	0.029	0.029	15 0.033	0.055	0.092	0.116	0.124	0.122	0.138	0.136	0.210
0.029	0.029	0.024	0.027	0.029	0.029	16 0.033	0.055	0.092	0.116	0.124	0.122	0.138	0.136	0.210
0.031	0.031	0.027	0.025	0.027	0.027	17 0.031	0.052	0.097	0.118	0.124	0.122	0.144	0.131	0.224
0.037	0.037	0.029	0.027	0.029	0.029	18 0.033	0.050	0.095	0.116	0.126	0.124	0.141	0.133	0.218
0.035	0.035	0.026	0.025	0.027	0.027	19 0.031	0.052	0.097	0.118	0.129	0.126	0.143	0.136	0.218
0.037	0.037	0.029	0.031	0.033	0.033	20 0.037	0.059	0.104	0.121	0.131	0.129	0.151	0.138	0.218
0.033	0.033	0.029	0.027	0.029	0.029	21 0.029	0.052	0.092	0.109	0.124	0.122	0.133	0.141	0.207
0.035	0.035	0.027	0.025	0.027	0.027	22 0.027	0.050	0.090	0.111	0.122	0.119	0.136	0.144	0.210
0.037	0.037	0.029	0.027	0.029	0.029	23 0.029	0.050	0.090	0.113	0.121	0.119	0.134	0.144	0.209
0.035	0.035	0.031	0.029	0.031	0.031	24 0.031	0.055	0.095	0.111	0.127	0.124	0.136	0.144	0.210
0.039	0.039	0.031	0.029	0.031	0.031	25 0.031	0.050	0.090	0.116	0.122	0.119	0.141	0.144	0.210
0.033	0.035	0.031	0.029	0.031	0.031	26 0.031	0.054	0.092	0.111	0.126	0.124	0.136	0.144	0.209
0.033	0.033	0.029	0.027	0.029	0.029	27 0.029	0.052	0.093	0.109	0.124	0.122	0.134	0.142	0.205
0.035	0.035	0.031	0.029	0.031	0.031	28 0.031	0.055	0.095	0.111	0.127	0.124	0.131	0.139	0.210

......*continued on the next page*

TABLE 3. (Continued)

31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
0.035	0.035	0.031	0.029	0.031	0.031	29 0.031	0.055	0.095	0.106	0.126	0.124	0.136	0.144	0.204
0.002	0.002	0.012	0.033	0.035	0.035	30 0.035	0.057	0.102	0.123	0.124	0.122	0.126	0.136	0.218
	0.004	0.014	0.035	0.037	0.037	31 0.037	0.059	0.099	0.126	0.127	0.124	0.128	0.139	0.221
0.004		0.014	0.035	0.037	0.037	32 0.037	0.059	0.104	0.126	0.127	0.124	0.128	0.134	0.221
0.014	0.014		0.031	0.033	0.033	33 0.033	0.054	0.102	0.125	0.121	0.119	0.138	0.138	0.212
0.034	0.034	0.030		0.002	0.002	34 0.006	0.035	0.102	0.114	0.119	0.117	0.129	0.149	0.224
0.036	0.036	0.032	0.002		0.004	35 0.008	0.037	0.105	0.111	0.119	0.119	0.131	0.152	0.227
0.036	0.036	0.032	0.002	0.004		36 0.008	0.037	0.100	0.116	0.122	0.119	0.131	0.152	0.227
0.036	0.036	0.032	0.006	0.008	0.008	37	0.037	0.105	0.111	0.114	0.112	0.129	0.155	0.221
0.056	0.056	0.052	0.034	0.036	0.036	38 0.036		0.095	0.116	0.079	0.076	0.116	0.139	0.215
0.092	0.096	0.094	0.094	0.096	0.092	39 0.096	0.088		0.140	0.129	0.124	0.131	0.142	0.239
0.114	0.114	0.113	0.104	0.102	0.106	40 0.102	0.106	0.125		0.141	0.141	0.168	0.160	0.236
0.114	0.114	0.110	0.108	0.108	0.110	41 0.104	0.074	0.116	0.126		0.006	0.138	0.147	0.250
0.112	0.112	0.108	0.106	0.108	0.108	42 0.102	0.072	0.112	0.126	0.006		0.136	0.142	0.253
0.116	0.116	0.123	0.116	0.118	0.118	43 0.116	0.106	0.118	0.147	0.124	0.122		0.162	0.262
0.124	0.120	0.123	0.132	0.134	0.134	44 0.136	0.124	0.125	0.141	0.130	0.126	0.141		0.258
0.189	0.189	0.183	0.192	0.194	0.194	45 0.190	0.185	0.201	0.201	0.210	0.212	0.217	0.215	

The analysis with the combined sequences (COI, 12S and 16S) showed lower genetic distances, intraspecific distances of *M. geyeri* and *M. exuta* individuals ranged from 0 to 0.3% (0.1% ± 0.09, mean ± SD; Fig. 1B, Table 4), interspecific distance between *M. verrilli* Benedict, 1902, *M. lauensis* Baba & de Saint Laurent, 1992, *M. bracteosa*, *M. geyeri*, *M. recta* and *M. exuta* species was an average of 3.7 ± 3.3% (mean ± SD; ranged from 0.3 to 8.4%; Fig. 1B, Table 4). At this resolution differences between evident morphologically differentiated groups of species showed distances up to 8.5% (like *M. geyeri* with *M. verrilli*; Fig. 1B).

TABLE 4. Estimates of evolutionary divergence between sequences for 14 nucleotide combined sequences (COI, 12S and 16S). Below the diagonal: uncorrected "p" distances, per unit, above the diagonal: Kimura 2-parameter model. Same group of data used for Neighbor-Joining analysis on Fig. 2A, excluding *Shinkaia crosnieri.* List of species, GenBank accession number in parenthesis: 1. *M. lauensis* (MH717895), 2. *M. verrilli* (MH717896), 3. *M. bracteosa* (DQ677684), 4–10. *M. geyeri* (OP628172–OP628179; OP620550–OP620556; OP629179–OP629185), 11. *M. recta* (DQ677695), 12–14. *M. exuta* (OP628180–OP628182; OP620557–OP620559; OP629186–OP629188).

1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0.0905	0.0833	0.0841	0.0844	0.0841	0.0841	0.0850	0.0856	0.0864	0.0789	0.0842	0.0860	0.0878
2 0.0839		0.0872	0.0881	0.0892	0.0890	0.0890	0.0899	0.0905	0.0914	0.0918	0.0889	0.0890	0.0908
3 0.0778	0.0809		0.0031	0.0039	0.0039	0.0039	0.0039	0.0040	0.0048	0.0102	0.0142	0.0126	0.0142
4 0.0785	0.0816	0.0031		0.0008	0.0008	0.0008	0.0008	0.0008	0.0016	0.0134	0.0157	0.0142	0.0157
5 0.0787	0.0826	0.0039	0.0008		0.0000	0.0000	0.0000	0.0000	0.0008	0.0142	0.0166	0.0150	0.0166
6 0.0785	0.0824	0.0039	0.0008	0.0000		0.0000	0.0000	0.0000	0.0008	0.0142	0.0165	0.0150	0.0165
7 0.0785	0.0824	0.0039	0.0008	0.0000	0.0000		0.0000	0.0000	0.0008	0.0142	0.0165	0.0150	0.0165
8 0.0793	0.0832	0.0039	0.0008	0.0000	0.0000	0.0000		0.0000	0.0008	0.0143	0.0159	0.0143	0.0159
9 0.0798	0.0837	0.0039	0.0008	0.0000	0.0000	0.0000	0.0000		0.0008	0.0144	0.0160	0.0144	0.0160
10 0.0805	0.0845	0.0047	0.0016	0.0008	0.0008	0.0008	0.0008	0.0008		0.0152	0.0168	0.0152	0.0168
11 0.0739	0.0848	0.0101	0.0132	0.0140	0.0140	0.0140	0.0141	0.0142	0.0150		0.0118	0.0118	0.0134
12 0.0785	0.0824	0.0140	0.0155	0.0163	0.0163	0.0163	0.0157	0.0158	0.0165	0.0117		0.0016	0.0031
13 0.0801	0.0824	0.0124	0.0140	0.0148	0.0148	0.0148	0.0141	0.0142	0.0150	0.0117	0.0016		0.0031
14 0.0816	0.0840	0.0140	0.0155	0.0163	0.0163	0.0163	0.0157	0.0158	0.0165	0.0132	0.0031	0.0031	

The Neighbor Joining analysis, based the genetic distances obtained from the combined gene fragments analysis (12S, 16S, COI), resulted on the optimal tree with the sum of branch length equal to 0.27 (Fig. 2A). While the analysis to COI gene fragment resulted on the optimal tree with the sum of branch length equal to 0.48 (Fig. 2B).

In both cases there were a total of 1312 positions in the final dataset. On the combined gene fragments tree, specimens of *M. geyeri* from different sites in the Atlantic Ocean grouped in a single clade with *M. bracteosa* from the northeastern Pacific Ocean as the sister group. *Munidopsis exuta* grouped in a single clade with *M. recta* from the east Pacific Ocean. *Munidopsis lauensis* and *M. verrilli* (from the southwestern Pacific Ocean) grouped as a sister group *M. geyeri–M. bracteosa* and to the *M. exuta–M. recta* groups. *Shinkaia crosnieri* constituted the sister group of the rest of the clades. Analysis of the COI gene fragment recognized the groups of *M. geyeri* and *M. bracteosa*, where *Munidopsis* sp. A (Coykendall *et al.* 2017) was integrated to the *M. geyeri* group. *Munidopsis scotti* (a widespread species) was the sister group to the four species mentioned above, they all are close in morphology. They are followed by *M. antonii* (Filhol, 1884), *M. segonzaci* Jones & Macpherson, 2007*, M. tiburon* Jones & Macpherson, 2007 (from the eastern Pacific Ocean)*,* and *M. livida* (Perrier, 1886) (from the Atlantic Ocean). *Munidopsis lauensis* and *M. kensmithi* Jones & Macpherson, 2007 were grouped with *M. verrilli* and are considered the basal group (all these species occur in the Pacific Ocean; Fig. 2B).

The average value of the intraspecific genetic distances of the *Munidopsis* specimens (0.3% ± 0.27) matched with the average values recorded previously for the genera (0.4 ± 0.3; Jones & Macpherson 2007). These agreed with the Superfamily Galatheoidea Samouelle, 1819 (Table 5). In accord with Munididae Ahyong, Baba, Macpherson & Poore, 2010 intraspecific values were within range (0.1 to 0.3%) and, they were slightly lower compared with Galatheidae Samouelle, 1819 values (0.3 to 1.4%).

Divergence values were minimal between individuals of the species *M. geyeri* (from the Atlantic Ocean) and *M. bracteosa* (from the northeastern Pacific Ocean). These did not exceed 0.04%, whilst individuals of other species ranged from 0 to 0.08% (*M. exuta, M. recta, M. scotti,* and *M. antonii*, Fig. 1A). The interspecific genetic distance recorded on *M. geyeri* and *M. bracteosa* recorded an average of 1% ± 0.2 (Table 3). The sequence of *M. geyeri* from the northern Gulf of Mexico (USNM 310877 = ULLZ 8784) recorded genetic distance values of 0.6 and 0.8% with *M. bracteosa* (all sequences; Table 4).

The studies of bathyal galatheids of the Indo-Pacific region that compare *Paramunida* Baba, 1988 of Munididae and *Leiogalathea* Baba, 1969 of Munidopsidae Ortmann, 1898; support similar patterns of diversification to those described in shallow-water galatheids (Cabezas *et al.* 2012; Rodríguez-Flores *et al.* 2020). The morphological homogeneity, the low intraspecific divergences, and low phylogenetic support of some genera has been explained by a set of rapid radiation events that left no signs of evolutionary splitting or divergence of taxa, by stasis, or by constraints in its morphological evolution (Cabezas *et al.* 2009; Machordom & Macpherson 2004).

The low genetic divergence of *M. geyeri* and *M. bracteosa*, could be an example of vicariance related to the Panamanian seaway closure (Schmittner *et al.* 2004). Species are genetically close and share similar niches in geographically separated areas (Faure *et al.* 2015; Hiller & Lessios 2019). A possible past wide-distribution pattern of *M. bracteosa* with a higher genetic flow that accounts for the low species divergences and/or population extinction in the Atlantic should be considered. Other cold seep species (e.g. lamellibrachid tube worms) display a slow evolutionary rate (Mcmullin *et al.* 2003). Nevertheless, our complete understanding of these sibling species, *M. geyeri* and *M. bracteosa*, needs an integrative analysis. The relevance of chemosynthetic associated ecosystem scenarios would greatly contribute to future studies (Jones & Macpherson 2007).

The sequence analysis of gene fragments of specimens collected in different localities on both sides of the Atlantic, support the differences between *M. exuta* and *M. geyeri*, displaying low intraspecific genetic distances (1.8 to 2.4%; Table 3). These results are congruent with previous records, as *M. exuta* and *M. recta*, the latter from the east Pacific Ocean (2.0%; Coykendall *et al.* 2017), and *Paramunida* species range (with a minimum of 1.7%; Table 5). The average interspecific genetic distance was relatively low (5% ± 4.1) in comparison with other families of galatheids (8.6 to 17.2%), and within *Munidopsis* (9.2 to 18.1%; Table 5). These results showed the difficulty in finding a clear barcoding gap separating intra and interspecific groups, which has been suggested in species of *Munida* Leach, 1820 by Macpherson & Machordom (2005). This could be resolved by adding morphological and molecular analysis of abyssal species, including those from chemosynthetic ecosystems form both the Atlantic and Pacific oceans (Coykendall *et al.* 2017; Jones & Macpherson 2007; Marin 2020). It would also suggest that the genus *Munidopsis* might be constituted of different and independent evolutionary lineages (Ahyong *et al.* 2011).

The genetic distance between morphologically well-differentiated species, such as *M. geyeri* and *M. livida,* is relatively high, 10.5 to 11% (Table 3). Both species co-occur in the Caribbean Sea (Gonave Bay, Haiti, and south of Jamaica; Mayo 1974; Pequegnat & Pequegnat 1971), in the northern Gulf of Mexico (Alaminos Canyon as *Munidospis* sp. A in Coykendall *et al.* 2017) and in the Gulf of Guinea (Regab Pockmark; Macpherson & Segonzac

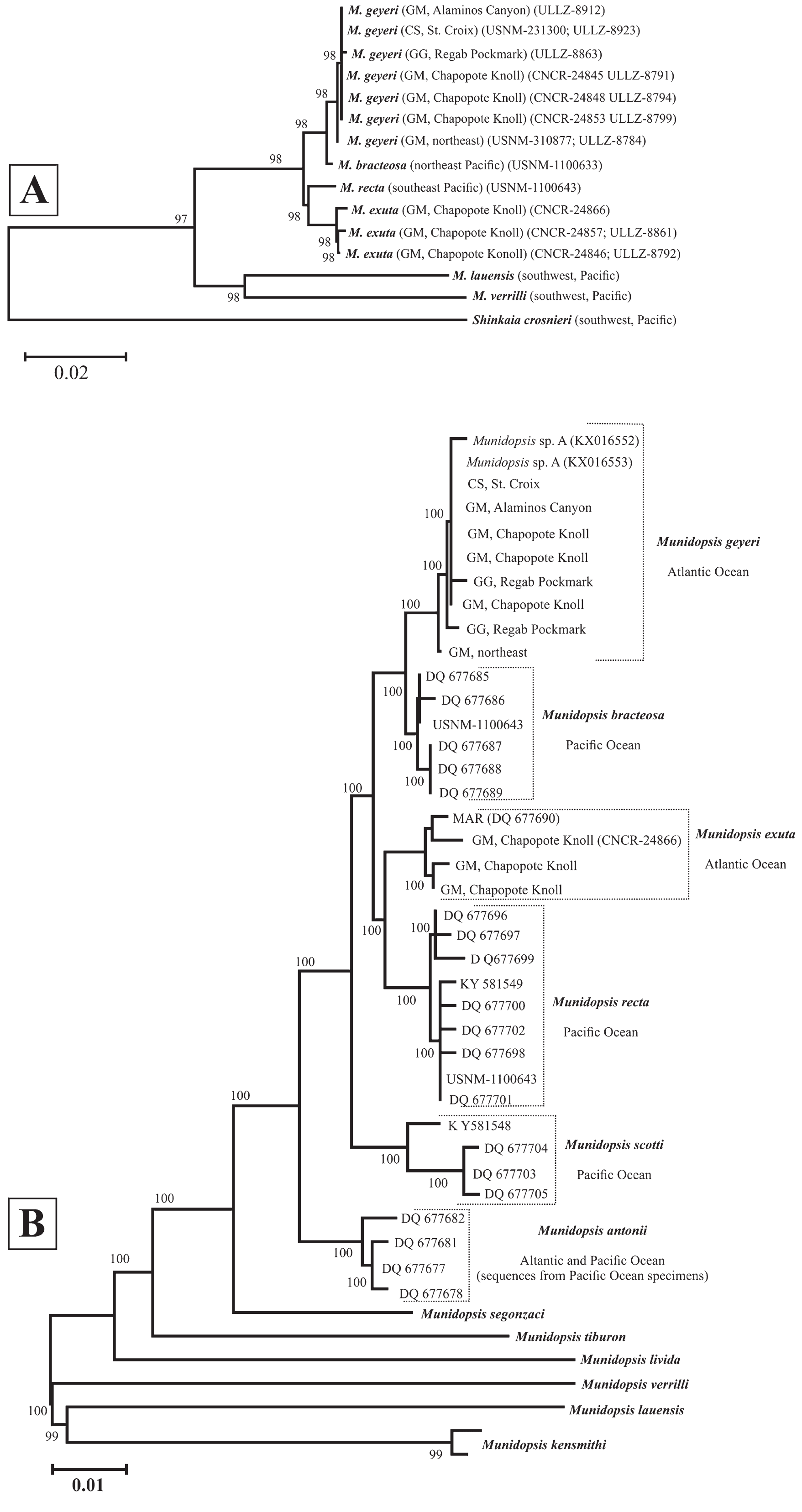

FIGURE 2. Relationships of analyzed *Munidopsis* species inferred using the Neighbor-Joining method and uncorrected "p" genetic distances. A, involved nucleotide sequences of combined fragment genes (COI, 12S and 16S) (same group of data used for histogram on Fig. 1B including *Shinkaia crosnieri*); and B, with nucleotide sequences of cytochrome c oxidase subunit 1 (COI) (same group of data used for histogram on Fig. 1A excluding *Shinkaia crosnieri*). The percentage of the bootstrap is indicated in each node.

TABLE 5. Intra and interspecific COI genetic distances (in percentage). SD = standard deviation of the mean. Dash ("–") denote unavailable data. References: 1. Machordom & Macpherson (2004); 2. Cabezas *et al.* (2011); 3. Rodríguez-Flores *et al.* (2018a); 4. Rodriguez-Flores *et al.* (2017); 5. Macpherson & Robainas-Barcia (2015); 6. Macpherson & Robainas-Barcia (2013); 7. Cabezas *et al.* (2008); 8. Macpherson & Machordom (2005); 9. Cabezas *et al.* (2009); 10. Macpherson *et al.* (2017); 11. Coykendall *et al.* (2017); 12. Cabezas *et al.* (2012); 13. Macpherson & Machordom (2001); 14. Rodríguez-Flores *et al.* (2018b); 15. Jones & Macpherson (2007); 16. Poore & Andreakis (2011); 17. Costa *et al.* (2007); 18. Ocampo *et al.* (2013); 19. Puillandre *et al.* (2011); 20. Hiller & Lessios (2019); 21. Dong *et al.* (2019).

Taxa	Intraspecific Mean ± SD	Intraspecific Range	Interspecific Mean ± SD	Interspecific Range	Ref.
Uncorrected "p" distances, per unit					
Galatheoidea Samouelle, 1819 **Galatheidae** Samouelle, 1819 (Intergeneric: 14 ± 1, 12.4–15.2, Ref. 6)					
Alainius Baba, 1991	0.3	0.2–0.5	—	—	1
Allogalathea Baba, 1969	—	—	13.4 ± 1.3	10.9–15.5	2
Coralliogalathea Baba & Javed, 1974	0.8 ± 0.5	0.3–1.3	13.1 ± 2.2	6.7–15.1	3
Fennerogalathea Baba, 1988	0.7 ± 0.7	0–1.7	9.7 ± 1.2	7.6–10.7	4
Galathea Fabricius, 1793	—	—	17.2 ± 2.2	6.3–24.6	5
Lauriea Baba, 1971	1.4 ± 1.7	0–5.2	9.1 ± 1.4	5.2–10.6	6
Triodonthea Macpherson & Robainas-Barcia, 2013	—	1.0–1.8	—	—	6
	—	1.2–1.6	—	—	6
Macrothea Macpherson & Cleva, 2010					
Galatheoidea Munididae Ahyong, Baba, Macpherson & Poore, 2010 (Intergeneric: 18.2 ± 1.8, 8.7–24.4, Ref. 1, 7, 9)					
Agononida Baba & de Saint Laurent, 1996	0.1	0–0.3	16.5	14–17.9	1
Babamunida Cabezas, Macpherson & Machordom, 2008	—	—	—	15.4–15.5	7
Munida Leach, 1820	0.2 ± 0.02	0–1.22	13.4 ± 3.1	2.8–19.5	1, 8–11
Onconida Baba & de Saint Laurent, 1996	0.3	0.2–0.5	8.6	8.4–8.9	1
Paramunida Baba, 1988	0.2	0 –1.4	13	1.7–16.9	1, 9, 12
Plesionida Baba & de Saint Laurent, 1996	—	—	—	10.8	9
Raymunida Macpherson & Machordom, 2000	0.2	0–2.1	11.01	7.3–13.2	1, 13
Galatheoidea Munidopsidae Ortmann, 1898 (Intergeneric: 18.7 ± 0.1, 17.7–21.7, This study)					
Munidopsis Whiteaves, 1874	—	—	15.7 ± 1.1	14.5–17	14
	—	—	18.1 ± 4.46	2.7–25	11
	0.4 ± 0.3	0–0.6	9.2 ± 3.3	—	15
	0.3 ± 0.27	0–1.4	5 ± 4.1	0.6–14.7	This study
Chirostyloidea Ortmann, 1892 **Chirostylidae** Ortmann, 1892					
Uroptychus Henderson, 1888	—	—	4.4	—	16
Kimura two-parameter (K2P)					
Decapoda Latreille, 1802 (Intrageneric: 19.8 ± 0.2, 11.3–49.9)					
	0.5 ± 0.05	0–2.57	17.2 ± 0.2	4.9–23.7	17
Brachyura Latreille, 1802 **Pinnotheroidea** De Haan, 1833 **Pinnotheridae** De Haan, 1833 (Intergeneric: 20–24.6, Ref. 18)					
Calyptraeotheres Campos, 1990	0.9 ± 0.4	0–2.2	17	15–19	18
Chirostyloidea Eumunididae A. Milne Edwards & Bouvier, 1900					
Eumunida Smith, 1883	—	0–3.3	—	4.3–16	19
Galatheoidea Porcellanidae Haworth, 1825					
Megalobrachium Stimpson, 1858	—	—	15.4 ± 6.3	4.6–24.7	20
Galatheoidea Munidopsidae (Intergeneric: 21.8 ± 1.4, 20.4–26.2, This study)					
Munidopsis Whiteaves, 1874	0.4	—	2.2 ± 1.19	1.4–4	21
	0.3 ± 0.28	0–1.4	5.4 ± 4.6	0.6–16.8	This study

2005). Perrier (1886) placed *M. livida* into the genus *Elasmonotus* and then *Orophorhynchus* by Milne Edwards & Bouvier (1894) on the basis of general morphology characters: a robust carapace and pereiopod 2 that exceeds the chelipeds. Most species of *Munidopsis* included in the current analysis belong to *Orophorhynchus* group, with a low genetic distance between species (less than 11%). Coykendall *et al.* (2017) recorded mean genetic distances of 18.7% between *Munidopsis* species within the northwestern Atlantic and Gulf of Mexico from different depths and ecosystems. A complete analysis of the species in the *Orophorhynchus* group is needed to recognize the close morphology among the species *M. geyeri* and *M. bracteosa* in contrast to *M. livida* and *M. geyeri* that are morphologically well differentiated species (Ahyong *et al.* 2011).

Using the K2P substitution model, we recorded a similar intraspecific average of genetic distances with the p-distances analysis. Interspecific divergences (5.4% ± 4.6; Table 3) and intergeneric divergence between species of *Munidopsis* and *Shinkaia crosnieri* (21.8% ± 1.4; Table 3) were not dissimilar to groups of *Munidopsis* of the west Pacific (2.2% ± 1.19; Table 5; Dong *et al.* 2019). The interspecific average for the *Munidopsis* species is lower than the values recorded for other decapods (17%; Table 5) but are within the ranges recorded (from 4.3 to 24.7%; Table 5). As already noted, a more comprehensive molecular phylogenetic study of the abyssal *Munidopsis* spp. is required to clarify the taxonomy of this group, as occurs in other groups of squat lobsters, such as the chirostylid genus *Eumunida* Smith, 1883 (Puillandre *et al.* 2011).

Based on this study, *Munidopsis exuta* and *M. geyeri* extend their distributional range. For both species we suggest an amphi-Atlantic distribution pattern where the metapopulations connect following a stepping-stone pattern (van Dover *et al.* 2002; Kimura & Weisss 1964). The number and size of eggs suggest a lecithotrophic larval development for both species (egg size: 2.23–2.36 mm and 2.6 mm respectively; Macpherson & Segonzac 2005). Lecithotrophic larval development restricts dispersal, however rich organic matter sites exemplified by chemosynthesis-based ecosystems could provide settlement rich in organic matter locations for the larvae in its dispersal. These could be potentially connected through organic enriched sites along the Equatorial Atlantic Belt (Levin *et al.* 2016; Vrijenhoek 1997).

The literature provides examples of taxa that benefit from the organic rich chemosynthetic based ecosystems connecting along the Equatorial Atlantic Belt including mussels (*Bathymodiolus boomerang* Cosel & Olu, 1998 and *Gigantidas childressi* (Gustafson, Turner, Lutz & Vrijenhoek, 1998)), clams (*Abyssogena southwardae* Krylova, Sahling & Janssen, 2010), gastropods (*Cordesia provannoides* Warén & Bouchet, 2009 and *Phymorhynchus cingulatus* (Dall, 1890)), polynoid polychaetes (*Branchipolynoe seepensis* Pettibone, 1986), sea cucumbers (*Chiridota heheva* Pawson & Vance, 2004), ophiuroids (*Ophioctenella acies* Tyler, Paterson, Sibuet, Guille, Murton & Segonzac, 1995), and the alvinocarid caridean shrimps of the genus *Alvinocaris* Williams, 1988 (Arellano *et al.* 2014; Cordes *et al.* 2007; Olu *et al.* 2010; Teixeira *et al.* 2013). A recent study (Hernández-Ávila *et al.* 2015) described a novel larval development model with lecithotrophic early larval stages of caridean shrimps (including *Alvinocaris muricola* Williams, 1988) hatching with a large lipid reserve. These larvae lack mouth appendages limiting the larva to feed. The mouthparts appear later in its development as an ecological strategy that extends the dispersal. A similar example connecting vents and cold seep ecosystems is seen in larvae and postlarvae of bresiliid vent shrimps (Hernández-Ávila *et al.* 2015; Lunina & Vereshchaka 2014), and bathymodiolid mussels (Arellano *et al.* 2014).

Integrative studies using ecological, paleogeographic and phylogenetic data are required to improve our understanding of the connectivity of abyssal species. Adding the life history stages will strengthen the models and predictions required in deep sea spatial management (Cordes *et al.* 2010; Coykendall *et al.* 2017 Olu *et al.* 2010; Teixeira *et al.* 2013) for future sustainable resources exploitation (Hilário *et al.* 2015).

Taxonomic account

Family Munidopsidae Ortmann, 1898

Munidopsis Whiteaves, 1874

Munidopsis exuta Macpherson & Segonzac, 2005

(Figs 3; 4; 5A)

Munidopsis subsquamosa.—de Saint Laurent, 1985: 475 (not *M. subsquamosa* Henderson, 1885),
Munidopsis crassa.—Segonzac, 1992: 596 (not *M. crassa* Smith, 1885).

Munidopsis geyeri.—Macpherson & Segonzac, 2005: 26 (not *M. geyeri*, Florida Escarpment organisms: 1 male, 17.6 mm, 1 female, 10.2 mm).

Munidopsis exuta Macpherson & Segonzac, 2005: 22–25, tab. 2, fig. 5 (description, distribution and ecology).—Macpherson & Segonzac, 2006: 442, figs 1, 2, 3 (description); Jones & Macpherson 2007: 479, tab. 1, fig. 12 (phylogenetic analysis); Baba *et al.*, 2008: 141 (list of taxa); Martin, 2011: 184 (distribution list); Coykendall *et al.*, 2017: tab. 4, fig. 4 (phylogenetic analysis); Dong *et al.*, 2019: 3, tab. 1, fig. 6 (phylogenetic analysis).

Type material examined. Holotype: ovigerous female, 34.7 mm (MNHN Ga 4621 = MNHN IU 2014 19814), Mid-Atlantic Ridge, vent site Snake Pit-Les Ruches, HYDROSNAKE, Stn HS08, 23 22.15′ N, 45 57.1′ W, 3502 m, 26.06.1988. Paratype: 1 female, 32.0 mm (MNHN IU 2014 19818), Mid-Atlantic Ridge, vent site Snake Pit-Elan, MAR93, Alvin Dive 2617, Stn PLM09, 23 22.1′ N, 44 56.9′ W, 3500 m, 18.06.1993.

Additional material examined. *Soft abyssal substrate ecosystems*: Bay of Biscay, BIOGAS 5, Stn CV40, 47 33′ N, 09 02′ W, 2860 m, 15.06.1974: 1juv. female, 18.2 mm, 1ovig. female, 29.2 mm (CEAB CRU 2004-01, Fig. 3F, 3G). BIOGAS 6, Stn CP10, 47 30′ N, 09 04′ W, 2878 m, 21.10.1974: 1 juv. male, 17.1 mm (CEAB CRU 2004-02). *Hydrothermal vent ecosystems*: Mid-Atlantic Ridge, vent site, Akademik 50, Stn 4787, 30 07′ N, 42 07′ W, 3020 m: 1 ovig. female, 20.5 mm (CEAB CRU 2004-03, Fig. 3C). Mid-Atlantic Ridge, vent site TAG, AMK 47, Stn 4343, 26 08′ N, 44 49′ W, 3650 m, 26.06.2002: 1ovig. female, 39.5 mm, 1 female, 31.6 mm (CEAB CRU 2004-04). *Cold seep ecosystems*: Florida Escarpment, ALVIN 3637, 4–5, 26 01.8′ N, 84 54.9′ W, 3288 m, 30.10.2000: 1 juv. female, 10.2 mm, 1 male, 17.6 mm (CEAB CRU 2004-05, Fig. 3D, E). Southern Gulf of Mexico, Chapopote Knoll, Dive 81 Stn GeoB10617-5, 21 53.94′ N, 93 26.226′ W, 2919.2 m, 11.04.2006: 1 juv. male, 13.3 mm (CNCR 24866). Dive 82 Stn GeoB10619-19, 21 53.922′ N, 93 26.166′ W, 2875 m, 12.04.2006: 1 ovig. female, 41.2 mm (CNCR 24846 = ULLZ 8792, Fig. 3B), 1 male, 25.72 mm (CNCR 24857 = ULLZ 8861, Fig. 3A). Dive 84, Stn 10625-13, 21 53.994′ N, 93 26.124′ W, 2916 m, 15.04.2006: 2 females, 28.5 mm (CNCR 24867), 32.6 mm (CNCR 24869), 1 male, 28.6 mm (CNCR 24868). Gulf of Guinea, Regab Pockmark site, BIOZAIRE 3, Stn CP20, 05 46.89′ S, 09 44.66′ E, 3113 m, 02.01.2004: 1 juv. female, 8.3 mm (CEAB CRU 2004-06).

Remarks. The specimens of *Munidopsis exuta* collected at Chapopote Knoll (n = 6) match the original description of the species; nevertheless, some variations are observed. The rostrum is horizontal or slightly upcurved (upcurved in the holotype from 3502 m depth). The antennal spine is present (left and right sides) in one specimen (CNCR 24867) and only the right antennal spine in another specimen (CNCR 24857 = ULLZ 8861, Fig. 3A), being always smaller than the first lateral spine of the carapace (absent in the holotype and specimens from Bay of Biscay and Mid-Atlantic Ridge). Apart of the two well-developed conical epigastric spines (in adults), some specimens (50%) present spine-like tubercles on the gastric region (CNCR 24857 = ULLZ 8861, Fig. 3A; CNCR 24846 = ULLZ 8792, Fig. 3B, CNCR 24868). The specimens from the Florida Escarpment (in the northeastern Gulf of Mexico) and the Regab Pockmark site (Gulf of Guinea) match the diagnostic identification of *M. exuta* with regards the shape of the rostrum, the absence of antennal spines, and the shape of the dactylus on the walking legs. These diagnostic characters are detected on juvenile organisms of all localities. Figure 4 shows a comparison between juvenile specimens of *M. exuta* and *M. geyeri*.

Ecology. *Munidopsis exuta* has been recorded on soft abyssal substrates and in the immediate vicinity of active hydrothermal vent structures (Macpherson & Segonzac 2005). The specimens of *M. exuta* analyzed in this study were collected at three cold seep sites, two in the Gulf of Mexico (Chapopote Knoll, in the southern Gulf of Mexico and in the Florida Escarpment in the northeastern Gulf of Mexico), and one specimen from a cold seep site in the Regab Pockmark in the Gulf of Guinea. Those specimens from Chapopote Knoll were collected from the main asphalt field (continuous asphalt flow habitat), asphalt fragments (breccia with chemosynthetic influence habitat) and gas seepage habitats.

At the Mid-Atlantic Ridge hydrothermal vents *M. exuta* was collected at the base of an active edifice in a baited trap, together with a nephropid lobster *Thymopides laurentae* Segonzac & Macpherson, 2003, and a macrurid fish *Coryphaenoides armatus* (Hector, 1875), but also at the base of an inactive site among empty shells of mytilid bivalves (Macpherson & Segonzac 2006). *Munidopsis exuta* was also collected along with *M. geyeri* on two cold seep ecosystems: Regab Pockmark and Chapopote Knoll (at breccia influenced by chemosynthesis). Morphological similarities among specimens through video identification were limited by the lack of close-up video by the ROV in Chapopote Knoll. The wide-angle images recorded a random distribution pattern among Chapopote Knoll's seafloor habitats.

Geographical distribution. Our records extend the known distribution of *M. exuta* from Bay of Biscay and the

Mid-Atlantic Ridge to the Gulf of Mexico and the Gulf of Guinea from 2860 to 4237 m depth (Fig. 5A). Within the Gulf of Mexico (Felder *et al.* 2009b) the distribution extends from the north-northeastern (NNE; Florida Escarpment) to the south-southwestern (SSW; Chapopote Knoll) cold seep sites. The species displays an amphi-Atlantic distribution and matches the pattern described by Schnabel *et al.* (2011) and Navas *et al.* (2013).

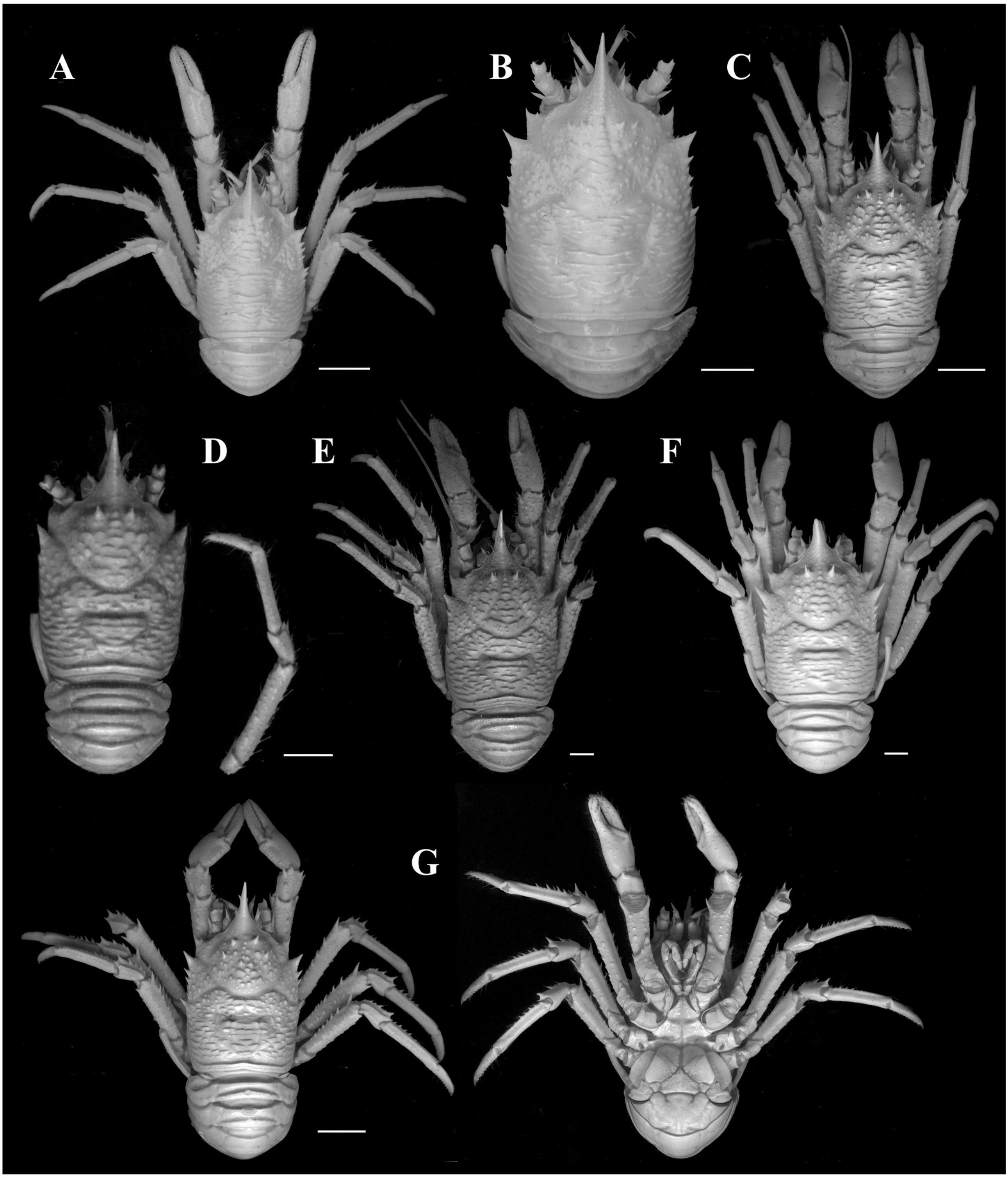

FIGURE 3. *Munidopsis exuta* Macpherson & Segonzac, 2005. A, male, from Chapopote Knoll (CNCR 24857 = ULLZ 8861); B, ovigerous female, Chapopote Knoll (CNCR 24846 = ULLZ 8792); C, ovigerous female, Mid-Atlantic Ridge (CEAB CRU 2004-03); D, juvenile female and E, juvenile male, Florida Escarpment (CEAB CRU 2004-05); F, juvenile female, and G, ovigerous female, Bay of Biscay (CEAB CRU 2004-01). Scale bar = 10 mm in A, B, C, G; 5 mm in D, E, F.

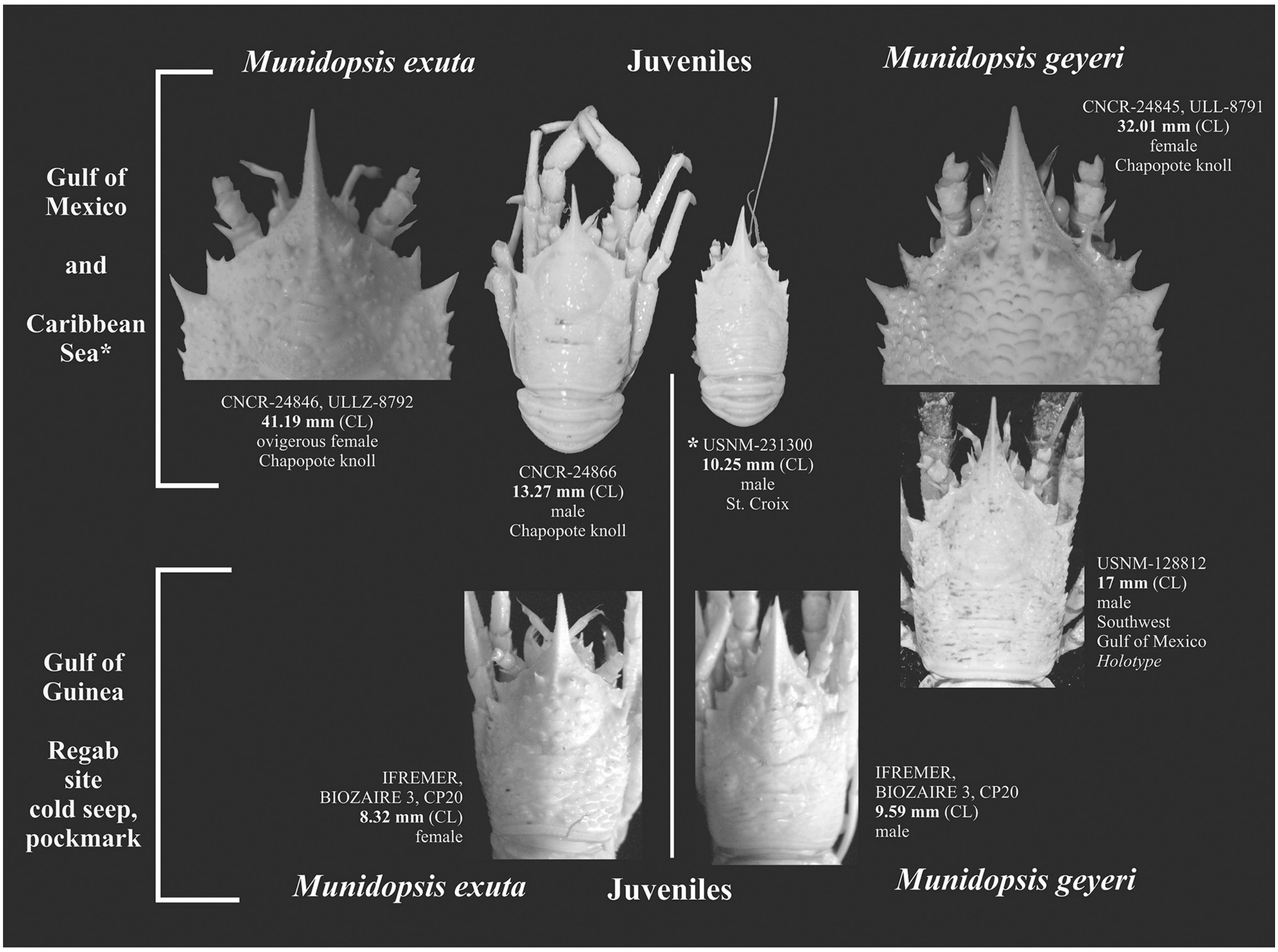

FIGURE 4. Morphological comparison between *Munidopsis exuta* and *Munidopsis geyeri* juveniles. CL = carapace length.

Munidopsis geyeri Pequegnat & Pequegnat, 1970
(Figs 4, 5B, 6)

Munidopsis subsquamosa.—Ambler, 1980: 25–26.

Munidopsis cf. *subsquamosa*.—Turnipseed *et al.*, 2004: 123.

Munidopsis geyeri.—Wicksten & Packard, 2005: 1761 (not *Munidopsis subsquamosa* synonym).

Munidopsis sp.—Olu *et al.*, 1996: 371 (table), 372.—Olu *et al.*, 1997: 209, 834 (table).—Cordes *et al.*, 2007: 643, 647 (table), 649.

Munidopsis sp. A.—Coykendall *et al.*, 2017: 267–270, tabs 1, 4, fig. 4 (phylogeny).

Munidopsis geyeri Pequegnat & Pequegnat, 1970: 139, 149–151, figs 5–1, 5–2, 5–9, 5–10, (key, description and table); 1971: 5 (key), 19 (distribution remarks).—Mayo, 1974: 28, 431 (table), 38 (key), 144–154, figs 20–21 (description and ecology).—Gore, 1983: 202 (table), 208 (taxonomic remarks, discussion), 213 (zoogeography).—Navas *et al.*, 2003: 201, 217 (key and list).—Baba, 2005: 163, fig. 76 (taxonomic remarks and distribution).—Macpherson & Segonzac, 2005: 25–26, fig. 6 (taxonomic remarks, distribution and ecology). —Baba *et al.*, 2008: 142 (list of taxa).—Felder *et al.*, 2009a: 1066, 1094 (checklist).—Gaytán-Caballero, 2009: 1–146 (taxonomy, biology and ecology).—Olu *et al.*, 2009: 2386, 2390, 2391, tabs 2, 6, 7, (ecology, local distribution, density and diet).—Olu *et al.*, 2010: 4, 5, 7, tab. 3 (biogeography).—Navas *et al.*, 2013: 3505, 3507 (biogeography).—Kilgour & Shirley, 2014: 406, tab. 4, fig. 12H (reproductive biology).—Vázquez-Bader & Gracia, 2016: 23 (list).

Type material examined. Holotype: juv. male, 17 mm (USNM 128812), southwestern Gulf of Mexico, Stn 69-A-11-92, 2330′N, 9532′W, 2926–2999 m, 27.08.1969.

Additional material examined. *Soft abyssal substrate ecosystems*: Caribbean Sea, San Croix, Alvin DSR/V

Stn 1078, 1794′N, 6481′W, 4000 m, 05.12.1980: 4 juv. female, 2 juv. male, 2.97–10.25 mm (USNM 231300 = ULLZ 8923). Gonave Bay, Haiti, Stn P-1180, 1855′–1844.4′ N, 7353′–7355′W, 3111–3496 m, 01.07.1970: 1 female, 27.1 mm, 1 male, 21.8 mm, 1 juv. male, 18.9 mm (UMML 32: 5246). Azores Islands, BIOACORES Stn 202, 3726.5′N, 2500′W, 2900 m, 06.11.1971: 1 male, 36.9 mm (MNHN Ga 1182). Off Mauritania, Africa, EUMELI 4 Stn CPH-15, 1853′N, 2108′W, 3124 m, 01.06.1992: 1 juv. male, 11.2 mm, 1 male, 21.2 mm (MNHN Ga 6525). Northeastern Gulf of Mexico, Gyre DGoMB, Stn S-41, 2754.23´N–2804.33´N, 8626.08´W–8640.65´W, 2930–3030 m, 09.06.2000: 1 male, 23.2 mm (USNM 310877 = ULLZ 8784). *Cold seep ecosystems*: Gulf of Guinea, Regab Pockmark site, BIOZAIRE 3, Stn CP20, 0546.89′S, 0944.66′E, 3113 m, 02.01.2004, 1 juv. female, 12.9 mm; 3 juv. females 17.68–19.49 mm, 3 ovig. females, 33.5–43.3 mm, 21 females, 20.1–38.5 mm, 3 juv. males, 17.6–19.6 mm, 19 males, 24.5–38.8 mm (five broken; MNHN Ga 5662 = MNHN IU 2008 13352); 1 female, 28.8 mm, 3 juv. males, 8.3–19.0 mm, 2 males, 28.8–31.1 mm (CEAB CRU 2004-07, Fig. 6A; ULLZ 8863, ULLZ 8862). Off Gabon, BIOZ-RECUP Mac10 (160), (158), (154), (152), 0551′S, 0941.98′E, 3155 m, 01–06.02.2003: 5 juv., 3.2–6.4 mm (MNHN Ga 6521–MNHN Ga 6524). Northwestern Gulf of Mexico, Alaminos Canyon (AC818), ATLANTIS, MPB Stn J2-282, 2618′N, 9462′W, 2744.8 m, 01.07.2007: 1 male, 27.9 mm (USNM 1178677 = ULLZ 8912). Southwestern Gulf of Mexico, Chapopote, Dive 82 Stn GeoB10619-19, 2153.922′N, 9326.166′ W, 2875 m, 12.04.2006: 7 ovig. females, 31.0–47.4 mm (CNCR 24847, CNCR 24848 = ULLZ 8794, CNCR 24849–CNCR 24852, CNCR 24853 = ULLZ 8799), 3 females, 27.0–32.0 mm (CNCR 24845 = ULLZ 8791, CNCR 24855, CNCR 24856, Fig. 6B), 9 males, 24.2–38.5 mm (CNCR 24854, CNCR 24858– CNCR 24865).

Diagnosis. Carapace slightly longer than broad (length-width ratio >1.2), 2 well-developed epigastric spines bearing spine-like tubercles and non-sharp tubercles through carapace, as well as ridges (setiferous scale-like on anterior half, and longer interrupted transverse ridges on posterior half). Anterior margin with antennal spine subequal to anterolateral (first spine on lateral margin) and this one directed slightly forward; second spine of lateral margin well-developed, bigger than anterolateral spine. Rostrum form as isosceles triangle (broad at base, distally somewhat narrowed), dorsally well carinated and lateral margins bearing small teeth. Cornea relatively reduced (moderately broader than the eyestalk) having distomesial eye-spine. Basal article of antennular peduncle bearing well developed dentate process, ending in a distomesial tubercle, and 2 spines in distolateral and distodorsal position. Absence of denticulate carina on mesial margin of P1. P2 over-reaching P1. P2–4 dactyli strongly curved distally. Epipods present only on P1. Pleon spineless, posteromedian margin of pleonite 6 weakly convex, not produced.

Redescription. Carapace slightly longer than broad (length-width ratio >1.2), pentagonal, wide at distal region; lateral margins slightly convex; cervical groove well-defined, gastric region with two well-developed conical epigastric spines, anterior branchial region with some spine-like tubercles (one to eight surrounding epigastric spines) and scale-like ridges elsewhere; posterior part of carapace with interrupted, elevated ridges; short setae across carapace (Fig. 6C, 6D). Anterior margin of carapace oblique, bearing sharp antennal spine similar in size to anteriorly directed anterolateral (first spine on lateral margin) (Fig. 6E). Second spine of lateral margin well developed, larger than anterolateral, originating just behind anterior branch of cervical groove. Usually 2 or 3 more spines (up to 6 spines on lateral margin of carapace). Posterior margin of carapace with a continuous double ridge along with setae (Fig. 6D). Rostrum forming isosceles triangle (broad at base, distally somewhat narrowed, Fig. 6F), strongly upturned distally, proximal half somewhat straight. Median carina well defined on dorsal region, ridges scale-like and small tubercles that increase in number proximally, ventral region smooth. Lateral margins bearing small teeth. Rostrum usually one-half carapace length, sometimes less (in smaller specimens).

Pleon weakly tuberculate, tubercles apparent on pleura (Fig. 6C), with some isolated setae; pleonites 2–4 bearing 2 elevated transverse ridges; pleonite 5 and pleonite 6 with scattered scale-like tubercles, anterior edge with row of rounded teeth and continuous line of short setae (Fig. 6B, D). Pleonite 6 with well-defined posterolateral lobes, posteromedian margin weakly convex, not produced or overhanging the posterolateral lobes (Fig. 6G). Protopod of uropod with posterolateral margin in 3 lobes bearing scale-like tubercles and setae; posterior lobe with group of denticles and sharp teeth separated by notch. Telson wider than long (wide/length ratio usually 1.43, range 1.28–1.69), composed of 8 to 10 plates (usually 8), armed with scale-like tubercles with setae scattered over surface (Fig. 6G). Several short, calcified setae on margin (except proximal one).

Thoracic sternum bearing transversal depressions between each sternite, anterior margins between coxae of P1 serrate; small scale-like tubercles with setae along forward edge. Sternite 3 complete, slightly narrow forming apposed lobe bearing anteromedian process at either side of slightly deep median groove (Fig. 6H).

Ocular peduncles slightly movable, wide at proximal region, bearing small tubercles and setae. Cornea relatively reduced (moderately broader than the eyestalk), armed with an elongate and sharp distomesial eye-spine directed slightly forward (sometimes directed anterolaterally) and covering less than one-half of the ocular (cornea, Fig. 6E).

Antennule basal article somewhat tuberculate, inflated laterally; dentate process well developed, ending in a distomesial tubercle (sometimes as small spine) and 2 sharp spines, distolateral and distodorsal, of almost equal size (Fig. 6I). Setae of extended flagellum barely reaching tip of rostrum.

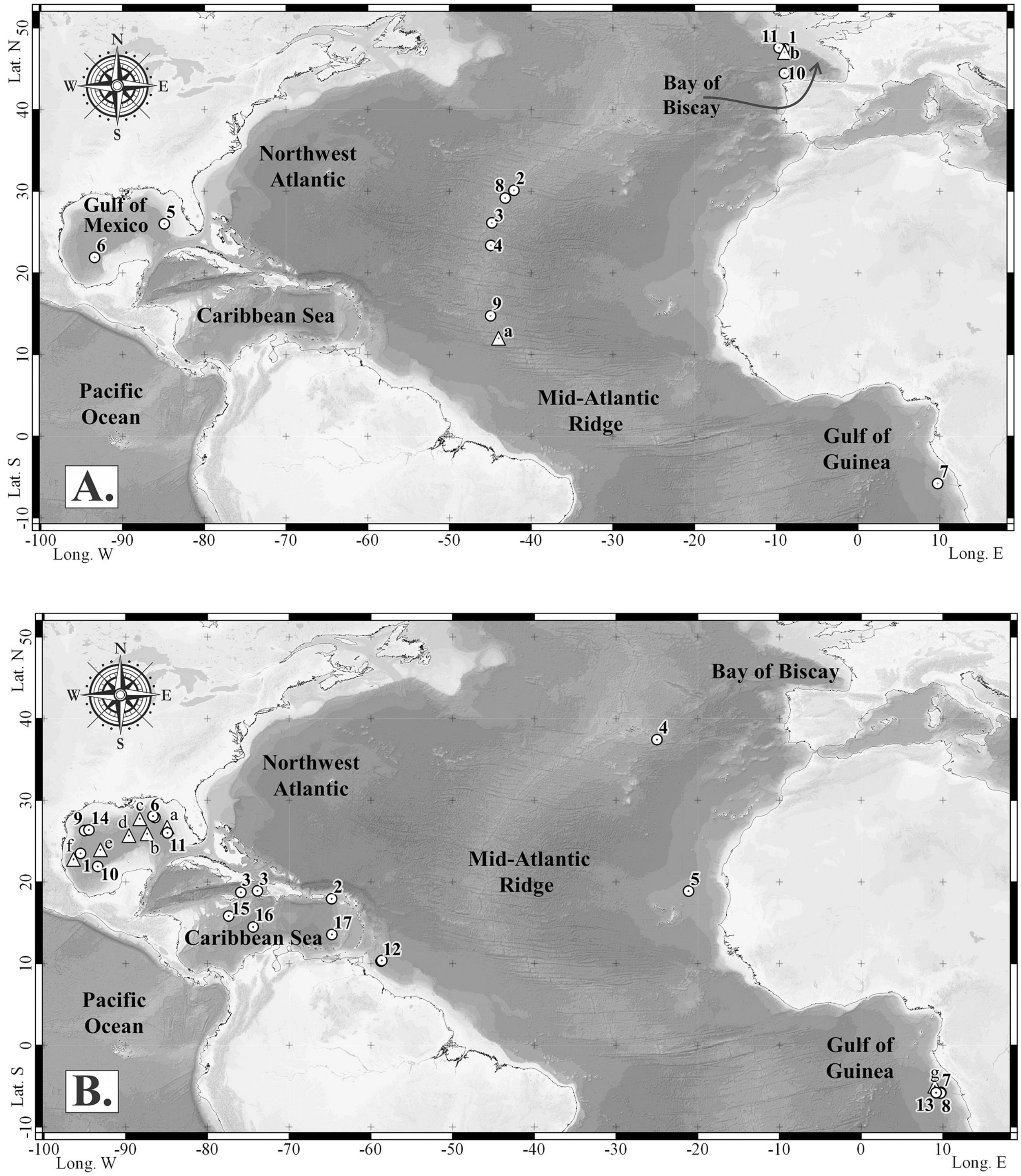

FIGURE 5. Geographic distribution of A, *Munidopsis exuta* and B, *M. geyeri*. Numbers with circles represent specimens analyzed in this study, letters with triangles represent populations not examined on this study. See Table 1. Base map from UNINMAR (2020).

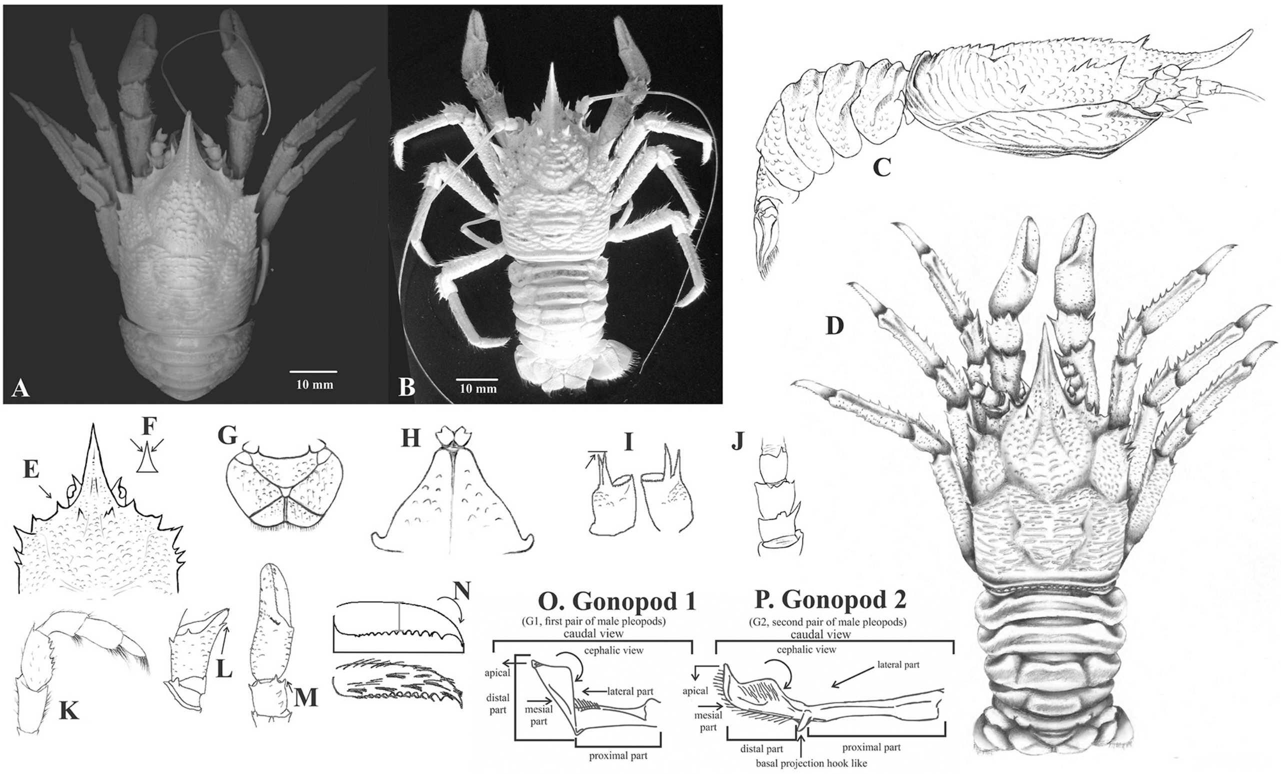

FIGURE 6. *Munidopsis geyeri* Pequegnat & Pequegnat, 1970. Specimens from A, Regab Pockmark site (Gulf of Guinea; CEAB CRU 2004-07) and B. Chapopote Knoll (Gulf of Mexico; CNCR 24856). C, lateral and D, dorsal view. Morphological features: E, distal part of cephalothorax, antennal spine; F, shape of rostrum; G, antennular peduncle, distolateral and distodorsal spines; H, anntenal peduncle; I, third maxilliped; J, thoracic sternite; K, carpus of cheliped; L, ischium of cheliped, dorsolateral spine; M, dactylus, strongly curved at the end of extensor margin, number of teeth on flexor margin; N, telson; O, gonopod 1 (G1); P, gonopod 2 (G2).

Antennal peduncle bearing small tubercles, usually decreasing in number by article 4. Article 1 broad, armed with two triangular teeth, often ventromesial tooth sharper and longer, while lateral tooth is broad. Article 2 with distomesial tubercle and elongated distolateral spine barely reaching one-half of article 3; dorsal region bearing a tooth on proximal margin. Article 3 with small tubercles or spines around distal margin, usually larger denticle in lateral and mesial margins armed with smaller teeth (Fig. 6J). Flagellum long, approximately 4 times carapace length.

Third maxilliped articles bearing small tubercles and some setae. Basis with mesial ridge armed with 2–7 (usually 5 teeth), ischium with mesial denticulate carina (range 15–27 teeth) and with small spine on extensor distal margin. Merus armed with distal spine on extensor margin, sometimes also with tubercles or small spines. Flexor margin with (1–6) usually 4 well developed spines and smaller spines or tubercles also. Carpus usually unarmed, setae thicker in mesial region, as well as in propodus and dactylus (Fig. 6K).

P1 (cheliped) with epipod, article surfaces armed with tubercles and spines associated with setae. Ischium armed with dorsolateral spine and one smaller mesial spine, as well as scattered tubercles (Fig. 6L). Merus smaller than chela, armed with scale-like tubercles more apparent in dorsal region, 4 distal spines: distomesial, distodorsal, distolateral, and distoventral, and middorsal spines (range 2–8), decreasing in length proximally region. Carpus slightly narrow (length:width ratio 1.1–1.6) armed with tubercles on dorsal region and variable distal ornamentation (usually 4 spines: lateral, dorsolateral, adjacent to propodus joint and mesial, Fig. 6M). Chela narrow, not slender (width:length ratio usually 0.28; range 0.24–0.45), dorsoventrally compressed in distal region and somewhat inflated in proximal region, armed with scale-like tubercles bearing row of rounded teeth and continuous short setae along forward edge. Propodus pollex (fixed finger) without denticulate carina on mesial margin. Tips of dactylus (movable finger) and pollex spooned, margins dentate.

P2–P5 lacking epipods. P2–P4 similar in shape, with tubercles and spines associated with setae, slender and slightly narrow (measured on P2: ratio of total pereiopod length/merus width 9– 13), armed with tubercles, spines, and setae. Ischium bearing dorsal blunt teeth and projections. P2 usually over-reaching P1 or nearly same size. Merus slightly longer than propodus, with well-developed distal spines in extensor and flexor margins, dorsomesial ridge usually with 6 spines decreasing in length proximally region (range 0–11), along with tubercles and setae arranged in lines. Carpus bearing enlarged spines at dorsomesial angle of distal margin, usually followed by row of 3 smaller spines and ridge of tubercles; tubercles scattered through carpus, decreasing on flexor surface. Propodus bearing two mobile spines on distal flexor region and with several raised longitudinal rows of small tubercles on flexor surface and more apparent ridges on extensor surface; variable number of spines (range 0–8) along with setae. Dactylus moderately slender (ratio of dactylus width measured at mid-length/total dactylus length: range 0.17–0.26, usually 0.21–0.22), length approximately 3/4 propodus length, strongly curved at the end of extensor margin, and ending in a brown claw. Flexor margin with a row of proximally diminishing low dactylus teeth (range 12–17, usually 14), each with corneous spinule projecting from anterior edge. Distal tooth remote from the terminal claw (end of dactylus) and much closer to penultimate tooth (Fig. 6N). P5 armed with small tubercles on lateral margin, small and blunt teeth on ventral margin. Propodus and dactylus distal region bearing elongated setae. Male pleopods as Figure 6O (gonopod 1, G1) and Figure 6P (gonopod 2, G2).

Color. White with golden setae, cornea orange.

Size. Maximum CL 47.41 mm ovigerous female (CNCR 24848) from Chapopote Knoll, southwestern Gulf of Mexico, CL 38.51 mm female and CL 38.79 mm male (IFREMER) from Regab Pockmark, Gulf of Guinea. Juveniles (gonopods immature) present a CL between 2.17 mm and 20.00 mm.

Remarks. The morphological similarity between *M. geyeri* and *M. subsquamosa* was noted since the first description of *M. geyeri*, Pequegnat & Pequegnat (1970) recognized the following differences: *M. subsquamosa* with a mobile eyestalk, pleon armed with granules and three denticulate spines on merus of third maxilliped. Those differences were considered insufficient to support the specific difference between species and fell into synonymy (e.g. Ambler 1980; Wicksten & Packard 2005). Mayo (1974) and Gore (1983) compared the species and the original description by Henderson (1888) along with *M. pallida* Alcock, 1894 (as *M. subsquamosa* var. *pallida* Alcock & Anderson, 1894), with emphasis on the carapace spine-like tubercles (more than 2 epigastric spines in *M. subsquamosa*), the appearance of the cardiac region (less apparent), the length and orientation of the rostrum (usually 1/3 of the carapace length, almost straight), and the direction of the second spine of the carapace margin (anterolateral). Baba (2005) reviewed *M. pallida* in detail and compared it with the holotype of *M. geyeri*, concluding that the principal difference between the species lays in the strong distal curvature on P2–P4 dactyli and the greater proximity of the ultimate flexor marginal process to the penultimate than to the tip of the article in *M. geyeri*. Similarly, five species from the Pacific Ocean (*M. abyssicola* Baba, 2005*, M. panamae* Baba, 2005*, M. petila* Baba, 2005*, M. producta* Baba, 2005 and *M. recta*) resemble *M. geyeri* morphologically. These can easily be distinguished by the P2–P4 dactylus curvature and dactylus/propodus length ratio (*M. panamae* and *M. recta* by a slightly curved dactylus, ratio 0.68–0.75, *M. petila* with a ratio of 0.71–0.72, *M. producta* 0.64, and *M. abyssicola* 0.55) as well as shape and direction of the rostrum. *Munidopsis bracteosa* and *M. scotti* (Jones & Macpherson 2007) are morphologically similar to *M. geyeri*. These species can be differentiated by a produced posteromedian lobe in pleonite 6 on *M. bracteosa*, whereas *M. scotti* has a carapace armed with more than two gastric spines, rostrum weakly carinate and almost straight. Other Atlantic Ocean species are similar to *M. geyeri*: *M. crassa* differs by >20 spines on the carapace and >4 spines on the lateral margins, and a produced posteromedian lobe on pleonite 6 (as pointed out by Mayo 1974). *Munidopsis hirtella* Macpherson & Segonzac, 2005 and *M. exuta* differ from *M. geyeri* by a spine-like rostrum, posterolateral lobes of pleonite 6 overreaching the transverse posteromedian margin, P2–P4 dactylus length similar to the propodus, a larger number of gastric spines in *M. hirtella*, and the absence of well-developed antennal spines in *M. exuta* (Fig. 4).

The morphological intraspecific variability of *M. geyeri* was recorded in 24 juveniles and 70 adults (35 females, 9 of which were ovigerous, and 35 males), and among individuals of the same size. More than half of the reviewed characters varied both in juveniles and adults. This variability led us to re-describe *M. geyeri*. The re-description follows Baba (2005), Gore (1983), Macpherson & Segonzac (2005), Pequegnat & Pequegnat (1970), Pequegnat & Pequegnat (1971) and Mayo (1974) description of three specimens (one female, one male and one juvenile) and the specimens analyzed herein.

Biology. Sexual dimorphism on lateral margin of telson, with more dense setae in males. Males and females are not significantly different in size in the Chapopote Knoll population (t-test, df = 22, t = 1.239, p = 0.2285, n = 24; Gaytán-Caballero 2009) and with those from the northern Gulf of Mexico (t-test, df = 9, t = -1.023, p = 0.333, n =

11; Kilgour & Shirley 2014). Ovigerous females were sampled form the Regab Pockmark site in January (Gulf of Guinea), and from Chapopote Knoll in April (Gulf of Mexico), no ovigerous females have been sampled from June through August, and December in the northern Gulf of Mexico (Kilgour & Shirley 2014). Other isolated sampled specimens prevent recognition of the existence of ovigerous females form the sites. Ovigerous females from Chapopote Knoll, carry up to 140 embryonated eggs with an average size of 2.36 mm (2.36 ± 0.22; *n* = 590). In the Regab Pockmark site embryonated eggs have an average size of 2.23 mm (2.23 ± 0.14; *n* = 21). Based on the number and size of eggs in *Munidopsis geyeri* this study suggests that this species could have lecithotrophic larvae.

Ecology. Microscopic filamentous epizoans were recorded attached to the body surfaces, appendages and setae in specimens from Gonave Bay (Mayo 1974). Parasites found on *M. geyeri* include the branchial bopyrid isopod (in female from the Venezuela Basin; Gore 1983) and Cirripedia (Superorder: Rhizocephala Müller, 1862) on the pleonal ventral region (six specimens from the Regab Pockmark and in one male form Chapopote Knoll: CNCR-24854).

As mentioned above, *M. geyeri* was collected along with *M. livida*. It co-occurs with *M. colombiana* Pequegnat & Pequegnat, 1971*, M. crassa, M. aries* (Milne Edwards, 1880) and *M. reynoldsi* (Milne Edwards, 1880) in the Colombia Basin (Pequegnat & Pequegnat 1971). It co- occurs with *M. bermudezi* Chace, 1939 in the Venezuela Basin (Gore 1983) and the Alaminos Canyon in the northeastern Gulf of Mexico (Coykendall *et al.* 2017). It co-occurs with *M. hirtella* at the Regab Pockmark in the Gulf of Guinea. In Chapopote Knoll, *M. geyeri* was randomly distributed co-occurring with *M. exuta* and background fauna. The specimens were more abundant on the asphalt and the active seeping sites than in the background habitats. On the asphalt, the species coexists with typical seep biota including tube worms (*Escarpia laminata* Jones, 1985), mussels (*Bathymodiolus heckerae* Turner, Gustafson, Lutz & Vrijenhoek *in* Gustafson, Turner, Lutz & Vrijenhoek, 1998 and *B. brooksi* Gustafson, Turner, Lutz & Vrijenhoek, 1998), ophiuroids (*Ophioctenella acies*), caridean shrimps (*Alvinocaris muricola*), holothurians (*Chiridota heheva*), encrusting sponges, and demersal fishes (*Pachycara* Zugmayer, 1911). Similarly, in the Regab Pockmark site *M. geyeri* specimens have been recorded in vesicomyid clusters empty shells on the periphery of the pockmark and co-occur with holothurids and other seep biota. The species is more abundant in active seeps (Olu *et al.* 2009). Association with *M. exuta* in Regab Pockmark is difficult to confirm due to a single recorded juvenile female (Table 1).

Geographical distribution. The known geographic distribution of *Munidopsis geyeri* is extended to the northwestern (NW) and to the south-southwestern (SSW) Gulf of Mexico (Felder *et al.* 2009b), and off Mauritania, Africa (Fig. 5B). *Munidopsis geyeri* displays an amphi-Atlantic distribution (Navas *et al.* 2013; Schnabel *et al.* 2011). The species is known from the wider Caribbean Sea, the Gulf of Guinea, off Mauritania in the northwestern Africa, and the Azores Islands (Fig. 5B) at depths of 1700 to 4151 m. Mayo (1974) calculated the occurrence of the species to a depth range of 2790–4151 m for three Caribbean Sea specimens (off Gonave, Haiti) based on the greatest depth of occurrence, at the shallowest station, to the least depth at the deepest station.

Discussion

The morphological variability of the species of the genus *Munidopsis,* previously discussed by Chace (1942), is herein exemplified for *Munidopsis exuta* and *M. geyeri*. The specimens examined display individual variability in each species, but the characters measured following the criteria proposed by Baba (2005) allow clear separation of the two species. High-resolution ROV photography and close-up assisted in differentiating the species' general morphology and diagnostic characters during the exploratory dives. The presence and absence of characters and measurements allowed us to identify as *M. exuta,* the juvenile specimens from the Florida Escarpment (Gulf of Mexico) and those from the Regab Pockmark site (Gulf of Guinea). This species was described based on seven specimens (Macpherson & Segonzac 2005). In the present study we analyzed 10 more individuals (4 juveniles, 2 ovigerous females, 2 females and 2 males) and offer an insight to the biology and ecology of the species. The shape and quantity of eggs recorded were similar in ovigerous females of *M. exuta* and *M. geyeri* (Gaytán-Caballero 2009; Kilgour & Shirley 2014). The size and number of eggs suggest lecithotrophic larval development and dispersion strategy in the amphi-Atlantic geographic distribution.

Pequegnat and Pequegnat (1970) described *Munidopsis geyeri* from a juvenile (17 mm carapace length). The description was based in 16 characters in nine body structures. The characters that described the juvenile are rendered obsolete today. The sampling of adult individuals and study of specimens from different locations confirm the variability mentioned by Gore (1983) that led to synonymy of this species in the past. Revisiting these characters in the current analysis that included juvenile and adult specimens helped to identify the specificity despite the variability recorded. The two transverse ridges on pleonites 2–4, a diagnostic character described by Mayo (1974), is absent in some juveniles, having ridges only on pleonites 2 and 3. This study proposes five characters as diagnostic characters based on homogeneity and range of variation of the distolateral and distodorsal spines of the antennular peduncle that are almost equal in size; the dactylus of P2–P4 moderately slender (ratio of width at mid-length to length 0.22, range 0.17–0.26); chela narrow, not slender (length/width ratio 0.28, range 0.24–0.35); pleonite 6 with the posteromedian margin weakly convex, not produced or overhanging the posterolateral lobes; the telson wider than long (width/length ratio usually 1.43, range 1.28–1.69). Most of these characters are important in comparing, differentiating species and describing new ones (Baba 2005; Macpherson & Segonzac 2005).

The sampling strategy is an important factor. Very few specimens of *M. geyeri* have been collected from benthic trawls from soft abyssal substrate. New tools and technology, e.g., manned submersibles and ROVs, help to collect in the small spatial scale and the rocky substrates. These tools help to document with video and images providing an insight of the species habitat selectivity and distribution patterns. These tools helped place the traps that provided 19 and 56 *M. geyeri* specimens from the Chapopote Knoll and Regab Pockmark sites, respectively, in contrast with 6 specimens obtained in trawls in the Venezuela Basin (Gore 1983).

Morphological and molecular genetic distances deliver information that support identification in addition to the diagnostic characters, highly variable, that characterize each of the co-occurring species, *M. exuta* and *M. geyeri*. The genetic homogeneity measured between individuals from the populations of the two species at both sides of the Atlantic Ocean was confirmed. The fragments of genes analyzed limit a complete inference at the population level. Our results confirm that both species, *M. exuta* and *M. geyeri* have an amphi-Atlantic distribution pattern connected by chemosynthetic ecosystems serving as stepping-stones in the Atlantic Tropical Equatorial Belt.

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References

Ahyong, S.T., Andreakis, N. & Taylor, J. (2011) Mitochondrial phylogeny of the deep-sea squat lobsters, Munidopsidae (Galatheoidea). *Zoologischer Anzeiger*, 250, 367–377.
https://doi.org/10.1016/j.jcz.2011.06.005

Ahyong, S.T., Baba, K., Macpherson, E. & Poore, G.C.B. (2010) A new classification of the Galatheoidea (Crustacea: Decapoda: Anomura). *Zootaxa*, 2676 (1), 57–68.
https://doi.org/10.11646/zootaxa.2676.1.4

Alcock, A. (1894) Natural history notes from H. M. Indian marine survey steamer “Investigator”, commander R. F. Hoskyn, R. N., commaning. Series II. No. 1. On the results of the deep- sea dredging during the season 1890–91. *Annals and Magazine of Natural History*, Series 6 (13), 321–334.
https://doi.org/10.1080/00222939408677707

Alcock, A. (1901) *A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian Marine Survey Ship Investigator*. Trustees of the Indian Museum, Calcutta, 286 pp.

Alcock, A. & Anderson, A.R.S. (1894) Natural history notes from H.M. Indian marine survey steamer “Investigator”, commander C.F. Oldham, R.N., commanding. Series II, No. 14. An account of a recent collection of deep-sea Crustacea from the Bay of Bengal and Laccadive Sea. *Journal of the Asiatic Society of Bengal (Natural History)*, 63, 141–185.

Ambler, J.W. (1980) Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters. *Fishery Bulletin*, 78 (1), 13–34.

Arellano, S.M., Van Gaest, A.L., Johnson, S.B., Vrijenhoek, R.C. & Young, C.M. (2014) Larvae from deep-sea methane seeps disperse in surface waters. *Proceedings of the Royal Society B*, 281(1786), 1–8.
https://doi.org/10.1098/rspb.2013.3276

Baba, K. (1969) Four new genera with their representatives and six new species of the Galatheidae in the collection of the Zoological Laboratory, Kyushu University, with redefinition of the genus *Galathea*. *Ohmu*, 2 (1), 1–32.

Baba, K. (1988) Chirostylid and Galatheid Crustaceans (Decapoda: Anomura) of the “Albatross” Philippine Expedition, 1907–1910. *Researches on Crustacea*, Special Number 2, 1–186.
https://doi.org/10.18353/rcrustaceasn.2.0_1

Baba, K. (2005) Deep-sea chirostylid and galatheid crustaceans (Decapoda: Anomura) from the Indo-Pacific, with a list of species. *Galathea Reports*, 20, 1–317.

Baba, K., Ahyong, S.T. & Macpherson, E. (2011) Morphology of marine squat lobsters. *In*: Poore, G.C.B., Ahyong, S.T. & Taylor, J. (Eds.), *The Biology of squat lobsters*. CSIRO Publishing, Melbourne and CRC Press, Boca Raton, Florida, pp. 1–37.

Baba, K. & de Saint Laurent, M. (1992) Chirostylid and Galatheid crustaceans (Decapoda: Anomura) from active thermal vent areas in the southwest Pacific. *Scientia Marina*, 56 (4), 321–332.

Baba, K., Macpherson, E., Poore, G.C.B., Ahyong, S.T., Bermudez, A., Cabezas, P., Lin, C., Nizinski, M., Rodrigues, C. & Schnabel, K.E. (2008) Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura-families Chirostylidae, Galatheidae and Kiwaidae). *Zootaxa*, 1905 (1), 1–220.
https://doi.org/10.11646/zootaxa.1905.1.1

Baba, K. & Williams, A.B. (1998) New Galatheoidea (Crustacea, Decapoda, Anomura) from hydrothermal systems in the west Pacific Ocean: Bismarck Archipelago and Okinawa trough. *Zoosystema*, 20 (2), 143–156.

Benedict, J.E. (1902) Descriptions of a new genus and forty-six new species of crustaceans of the Family Galatheidae, with a list of the known marine species. *Proceedings of the United States National Museum*, 26 (1311), 243–334.
https://doi.org/10.5479/si.00963801.26-1311.243 Cabezas, P., Macpherson, E. & Machordom, A. (2008) A new genus of squat lobster (Decapoda: Anomura: Galatheidae) from the Southwest Pacific and Indian Ocean inferred from morphological and molecular evidence. *Journal of Crustacean Biology*, 28 (1), 68–75.
https://doi.org/10.1651/07-2823r.1

Cabezas, P., Macpherson, E. & Machordom, A. (2009) Morphological and molecular description of new species of squat lobster (Crustacea: Decapoda: Galatheidae) from the Solomon and Fiji Islands (South-West Pacific). *Zoological Journal of the Linnean Society*, 156 (3), 465–493.
https://doi.org/10.1111/j.1096-3642.2008.00492.x

Cabezas, P., Macpherson, E. & Machordom, A. (2011) *Allogalathea* (Decapoda: Galatheidae): a monospecific genus of squat lobster? *Zoological Journal of the Linnean Society*, 162 (2), 245– 270.
https://doi.org/10.1111/j.1096-3642.2010.00681.x

Cabezas, P., Sanmart, I., Paulay, G., Macpherson, E. & Machordom, A. (2012) Deep under the sea: unraveling the evolutionary history of the deep-sea squat lobster *Paramunida* (Decapoda, Munididae). *Evolution*, 66 (6), 1878–1896.
https://doi.org/10.1111/j.1558-5646.2011.01560.x

Carney, R.S. (1994) Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. *Geo-Marine Letters*, 14, 149–159.
https://doi.org/10.1007/BF01203726

Chace, F.A. Jr. (1939) Reports on the scientific results of the first Atlantis expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. Preliminary descriptions of one new genus and seventeen new species of decapod and stomatopod. *Memorias de la Sociedad Cubana de Historia Natural*, 13, 31–54.

Chace, F.A. Jr. (1940) The ATLANTIS expedition to the West Indies in 1938 and 1939 under the joint auspices of the University of Havana and Harvard University. *Woods Hole Oceanography Institute Contribution*, 274, 1–8.

Chace, F.A. Jr. (1942) The anomuran Crustacea I Galatheidae Reports on the scientific results of the Atlantic expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. *Torreia*, 11, 1–106.

Chevaldonne, P. & Olu, K. (1996) Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent and cold-seep communities: a review. *Proceedings of the Biological Society of Washingtoniological society of Washington*, 109, 286–

298.

Cordes, E.E., Becker, E.L., Hourdez, S. & Fisher, C.R. (2010) Influence of foundation species, depth, and location on diversity and community composition at Gulf of Mexico lower-slope cold seeps. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 57(21–23), 1870– 1881.
https://doi.org/10.1016/j.dsr2.2010.05.010

Cordes, E.E., Carney, S.L., Hourdez, S., Carney, R.S., Brooks, J.M. & Fisher, C.R. (2007) Cold seeps of the deep Gulf of Mexico: community structure and biogeographic comparisons to Atlantic Equatorial Belt seep communities. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(4), 637–653.
https://doi.org/10.1016/j.dsr.2007.01.001

Costa, F.O., deWaard, J.R., Boutillier, J., Ratnasingham, S., Dooh, R.T., Hajibabaei, M. & Hebert, P.D.N. (2007) Biological identifications through DNA barcodes: the case of the Crustacea. *Canadian Journal of Fisheries and Aquatic Sciences*, 64 (2), 272–295.
https://doi.org/10.1139/F07-008

Coykendall, D.K., Nizinski, M.S. & Morrison, C.L. (2017) A phylogenetic perspective on diversity of Galatheoidea (*Munida*, *Munidopsis*) from cold-water coral and cold seep communities in the western north Atlantic Ocean. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 137, 258–272.
https://doi.org/10.1016/j.dsr2.2016.08.014

Dong, D., Xu, P., Li, X.Z. & Wang, C. (2019) *Munidopsis* species (Crustacea: Decapoda: Munidopsidae) from carcass falls in Weijia Guyot, west Pacific, with recognition of a new species based on integrative taxonomy. *PeerJ*, 7, 1–20.
https://doi.org/10.7717/peerj.8089

von Dover, C.L., German, C.R., Speer, K.G., Parson, L.M. & Vrijenhoek, R.C. (2002) Evolution and biogeography of deep-sea vent and seep invertebrates. *Science*, 295 (5558), 1253–1257.
https://doi.org/10.1126/science.1067361

Faure, B., Schaeffer, S.W. & Fisher, C.R. (2015) Species distribution and population connectivity of deep-sea mussels at hydrocarbon seeps in the Gulf of Mexico. *PLoS ONE*, 10 (4), 1–19.
https://doi.org/10.1371/journal.pone.0118460

Faxon, W. (1893) Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross", during 1891. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 24 (7), 149–220.

Felder, D.L., Álvarez, F., Goy, J.W. & Lemaitre, R. (2009a) Decapoda (Crustacea) of the Gulf of Mexico, with Comments on the Amphionidacea. *In*: Felder, D.L. & Camp, D.K. (Eds.), *Gulf of Mexico Origins, Waters, and Biota. Vol. 1. Biodiversity*. Texas A&M University Press, College Station, Texas, pp. 1019–1104.

Felder, D.L., Camp, D.K. & Tunnell, J.W. (2009b) An introduction to Gulf of Mexico biodiversity assessment. *In*: Felder, D.L. & Camp, D.K. (Eds.), *Gulf of Mexico Origin, Waters, and Biota*. Texas A&M University Press, Texas, pp. 1–14.

Gaytán-Caballero, A. (2009) *Munidopsis geyeri Pequegnat & Pequegnat, 1970 asociado al volcán de asfalto (sur del Golfo de México) y su vinculación con las poblaciones del Atlántico*. Universidad Nacional Autónoma de México, Ciudad de México, 147 pp.

Goffredi, S.K., Johnson, S., Tunnicliffe, V., Caress, D., Clague, D., Escobar, E., Lundsten, L., Paduan, J.B., Rouse, G., Salcedo, D.L., Soto, L.A., Spelz-Madero, R., Zierenberg, R. & Vrijenhoek, R. (2017) Hydrothermal vent fields discovered in the southern Gulf of California clarify role of habitat in augmenting regional diversity. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20170817.
https://doi.org/10.1098/rspb.2017.0817

Gore, R.H. (1983) Notes on rare species of *Munidopsis* (Anomura: Galatheidae) and *Ethusina* (Brachyura: Dorippidae) collected by the USNS Bartlett in the Venezuela Basin, Caribbean Sea. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 135, 200–217.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.

Henderson, J.R. (1885) Diagnoses of new species of Galatheidae collected during the "Challenger" expedition. *Annals and Magazine of Natural History*, Series 5, 16 (96), 407–421.
https://doi.org/10.1080/00222938509459908

Henderson, J.R. (1888) Report on the Anomura Collected by H.M.S. Challenger during the years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, Zoology*, 27 (1), 1–221.

Hernández-Ávila, I., Cambon-Bonavita, M.A. & Pradillon, F. (2015) Morphology of first zoeal stage of four genera of alvinocaridid shrimps from hydrothermal vents and cold seeps: implications for ecology, larval biology and phylogeny. *PLoS ONE*, 10 (12), e0144657.
https://doi.org/10.1371/journal.pone.0144657

Hilário, A., Metaxas, A., Gaudron, S.M., Howell, K.L., Mercier, A., Mestre, N.C., Ross, R.E., Thurnherr, A.M. & Young, C. (2015) Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. *Frontiers in Marine Science*, 2, 1–14.
https://doi.org/10.3389/fmars.2015.00006

Hiller, A. & Lessios, H.A. (2019) Marine species formation along the rise of Central America: the anomuran crab *Megalobra-*

chium. *Molecular Ecology*, 29 (2), 413–428.
https://doi.org/10.1111/mec.15323

Jones, J.W. & Macpherson, E. (2007) Molecular phylogeny of the East Pacific squat lobsters of the genus *Munidopsis* (Decapoda: Galatheidae) with the descriptions of seven new species. *Journal of Crustacean Biology*, 27 (3), 477–501.
https://doi.org/10.1651/S-2791.1

Kemp, K.M., Jamieson, A.J., Bagley, P.M., McGrath, H., Bailey, D.M., Collins, M.A. & Priede, I.G. (2006) Consumption of large bathyal food fall, a six-month study in the NE Atlantic. *Marine Ecology Progress Series*, 310, 65–76.
https://doi.org/10.3354/meps310065

Kilgour, M.J. & Shirley, T.C. (2014) Reproductive biology of galatheoid and chirostyloid (Crustacea: Decapoda) squat lobsters from the Gulf of Mexico. *Zootaxa*, 3754 (4), 381–419.
https://doi.org/10.11646/zootaxa.3754.4.3

Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
https://doi.org/10.1007/BF01731581

Kimura, M. & Weisss, G.H. (1964) The stepping-stone model of population structure and the decrease of genetic correlation with distance. *Genetics*, 49 (4), 561–576.
https://doi.org/10.1093/genetics/49.4.561

Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35 (6), 1547– 1549.
https://doi.org/10.1093/molbev/msy096

Leach, W.E. (1820) Galatéadées. *Dictionnaire des Sciences Naturelles, Paris*, 18, 48–56. Levin, L.A., Baco, A.R., Bowden, D.A., Colaco, A., Cordes, E.E., Cunha, M.R., Demopoulos, A.W.J., Gobin, J., Grupe, B.M., Le, J., Metaxas, A., Netburn, A.N., Rouse, G.W., Thurber, A.R., Tunnicliffe, V., Van Dover, C.L., Vanreusel, A. & Watling, L. (2016) Hydrothermal vents and methane seeps: rethinking the sphere of influence. *Frontiers in Marine Science*, 3, 1–23.
https://doi.org/10.3389/fmars.2016.00072

Lunina, A.A. & Vereshchaka, A.L. (2014) Distribution of hydrothermal alvinocaridid shrimps: effect of geomorphology and specialization to extreme biotopes. *PLoS ONE*, 9 (3), 92802.
https://doi.org/10.1371/journal.pone.0092802

Machordom, A. & Macpherson, E. (2004) Rapid radiation and cryptic speciation in squat lobsters of the genus *Munida* (Crustacea, Decapoda) and related genera in the South West Pacific: Molecular and morphological evidence. *Molecular Phylogenetics and Evolution*, 33 (2), 259– 279.
https://doi.org/10.1016/j.ympev.2004.06.001

Macpherson, E. & Machordom, A. (2001) Phylogenetic relationships of species of *Raymunida* (Decapoda: Galatheidae) based on morphology and mitochondrial cytochrome oxidase sequences, with the recognition of four new species. *Journal of Crustacean Biology*, 21 (3), 696–714.
https://doi.org/10.1163/20021975-99990168

Macpherson, E. & Machordom, A. (2005) Use of morphological and molecular data to identify three new sibling species of the genus *Munida* Leach, 1820 (Crustacea, Decapoda, Galatheidae) from New Caledonia. *Journal of Natural History*, 39 (11), 819–834.
https://doi.org/10.1080/00222930400002473

Macpherson, E. & Robainas-Barcia, A. (2013) A new genus and some new species of the genus *Lauriea* Baba, 1971 (Crustacea, Decapoda, Galatheidae) from the Pacific and Indian Oceans, using molecular and morphological characters. *Zootaxa*, 3599 (2), 136–160.
https://doi.org/10.11646/zootaxa.3599.2.2

Macpherson, E. & Robainas-Barcia, A. (2015) Species of the genus *Galathea* Fabricius, 1793 (Crustacea, Decapoda, Galatheidae) from the Indian and Pacific Oceans, with descriptions of 92 new species. *Zootaxa*, 3913 (1), 1–335.
https://doi.org/10.11646/zootaxa.3913.1.1

Macpherson, E., Rodríguez-Flores, P.C. & Machordom, A. (2017) New sibling species and new occurrences of squat lobsters (Crustacea, Decapoda) from the western Indian Ocean. *European Journal of Taxonomy*, 343, 1–61.
https://doi.org/10.5852/ejt.2017.343

Macpherson, E. & Segonzac, M. (2005) Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheidae) from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. *Zootaxa*, 1095 (1), 1–60.
https://doi.org/10.11646/zootaxa.1095.1.1

Macpherson, E. & Segonzac, M. (2006) *Munidopsis exuta* Macpherson & Segonzac, 2005. *In*: Desbruyères, D., Segonzac, M. & Bright, M. (Eds.), Handbook of deep-sea hydrothermal vent fauna. *Denisia*, 18, Biologiezentrum, pp. 442.

Marin, I. (2020) Northern unicorns of the depths: Diversity of the genus *Munidopsis* Whiteaves, 1874 (Decapoda: Anomura: Munidopsidae) in the northwestern Pacific Ocean, with descriptions of three new species along the Russian coast. *Progress in Oceanography*, 183, 102263.
https://doi.org/10.1016/j.pocean.2020.102263

Martin, J. (2011) *Les invertébrés marins du golfe de Gascogne la Manche orientale*. Quae, Versailles Cedex, 176 pp.

Martin, J.W. & Haney, T.A. (2005) Decapod crustaceans from hydrothermal vents and cold seeps: a review through 2005. *Zoo-*

logical Journal of the Linnean Society, 145 (4), 445–522.
https://doi.org/10.1111/j.1096-3642.2005.00178.x

Mayo, B.S. (1974) *The systematics and distribution of the deep-sea genus Munidopsis (Crustacea, Galatheidae) in the west Atlantic Ocean*. University of Miami, Coral Gables, Florida, 433 pp.

Mcmullin, E.R., Hourdez, S., Schaeffer, S.W. & Fisher, C.R. (2003) Phylogeny and biogeography of deep sea vestimentiferan tubeworms and their bacterial symbionts. *Symbiosis*, 34, 1–41.

Meyer, C.P. & Paulay, G. (2005) DNA barcoding: error rates based on comprehensive sampling. *PLoS Biology*, 3(12), 1–10.
https://doi.org/10.1371/journal.pbio.0030422

Milne-Edwards, A. (1880) Report on the results of dredging in the Gulf of Mexico and in the Caribbean Sea, 1877, ’78, ’79, by the U.S. Coast Survey Steamer “Blake”. VIII. Études préliminaires sur les crustacés. *Bulletin of Museum Comparative Zoology, Harvard College*, 8 (1), 1–68.

Milne Edwards, A. & Bouvier, E.L. (1894) Considerations génerales sur la famille des Galathéidés. *Annales des Sciences Naturelles, Zoologie et biologie animale*, 7(16), 191–327.
https://doi.org/10.5962/bhl.title.10042

Navas, G.R., Bermúdez, A., Ángel-Yunda, C. & Campos, N. (2013) Afinidades biogeográficas de los galateoideos (Decapoda: Anomura) del Caribe y Pacífico colombiano. *Revista MVZ Córdoba*, 18(2), 3501–3511.
https://doi.org/10.21897/rmvz.174

Navas, G.R., Bermúdez, A., Cruz, N. & Campos, N.H. (2003) Galatéidos (Decapoda, Anomura, Galatheidae) del Caribe Colombiano, incluyendo doce primeros registros. *Boletín de Investigaciones Marinas y Costeras—INVEMAR*, 32, 183–218.
https://doi.org/10.25268/bimc.invemar.2003.32.0.266

Nei, M. & Kumar, S. (2000) *Molecular evolution and phylogenetics*. Oxford University Press, New York, 333 pp.

OBIS (2022) Ocean Biogeographic Information System. UNESCO, IODE. Available from: https://mapper.obis.org/ (accessed 10 May 2022)

Ocampo, E.H., Robles, R., Terossi, M., Nuñez, J.D., Cledón, M. & Mantelatto, F.L. (2013) Phylogeny, phylogeography, and systematics of the american pea crab genus *Calyptraeotheres* Campos, 1990, inferred from molecular markers. *Zoological Journal of the Linnean Society*, 169 (1), 27–42.
https://doi.org/10.1111/zoj.12045

Olu, K., Caprais, J.C., Galéron, J., Causse, R., von Cosel, R., Budzinski, H., Ménach, K. Le, Roux, C. Le, Levach, D., Khripounoff, A. & Sibuet, M. (2009) Influence of seep emission on the non-symbiont-bearing fauna and vagrant species at an active giant pockmark in the Gulf of Guinea (Congo-Angola margin). *Deep-Sea Research Part II: Topical Studies in Oceanography*, 56 (23), 2380–2393.
https://doi.org/10.1016/j.dsr2.2009.04.017

Olu, K., Cordes, E.E., Fisher, C.R., Brooks, J.M., Sibuet, M. & Desbruye, D. (2010) Biogeography and potential exchanges among the Atlantic Equatorial Belt cold-seep faunas. *PLoS ONE*, 5 (8), 1–11.
https://doi.org/10.1371/journal.pone.0011967

Olu, K., Lanc, S., Sibuet, M., Fiala-Medioni, A. & Dinetj, A. (1997) Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. *Deep Sea Research Part I: Oceanographic Research Papers*, 44 (5), 811–841.
https://doi.org/10.1016/S0967-0637(96)00123-9

Olu, K., Sibuet, M., Harmegnies, F., Foucher, J.P. & Fiala-Medioni, A. (1996) Spatial distribution of diverse cold seep communities living on various diapiric structures of the southern Barbados prism. *Progress in Oceanography*, 38 (4), 347–376.
https://doi.org/10.1016/S0079-6611(97)00006-2

Ortmann, A.E. (1898) Crustacea, Malacostraca. *In*: Gerstäcker, A. & Ortmann, A.E. (Eds.), *Die Klassen und Ordnungen der Arthropoden wissenschaftlich dargestellt in Wort und Bild*. Verlagshandlung, Leipzig, pp. 1057–1168.

Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) *The simple fool’s guide to PCR*. *Department of Zoology and Kewalo Marine Laboratory, Special Publication*. University of Hawaii, Honolulu, 44 pp.

Pequegnat, L.H. & Pequegnat, W.E. (1970) Deep-sea anomurans of superfamily Galatheoidea with descriptions of three new species. *In*: Pequegnat, W.E. & Chace, F.A. Jr. (Eds.), *Contributions on the Biology of the Gulf of Mexico*. Texas A & M University Oceanographic studies, Houston, Texas, pp. 125–170.

Pequegnat, L.H. & Pequegnat, W.E. (1971) *Contributions of the Biology of the Gulf of Mexico. New species and new records of Munidopsis (Decapoda: Galatheidae) from the Gulf of Mexico and Caribbean Sea*. Texas A & M University Oceanographic Studies, Houston, Texas, 24 pp.

Pequegnat, W.E. & Pequegnat, L.H. (1973) *Munidopsis albatrossae*, a new species of deep-sea Galatheidae (Decapoda, Anomura) from the eastern Pacific Ocean. *Crustaceana*, 24 (2), 163– 168.
https://doi.org/10.1163/156854073X00335

Perrier, E. (1886) *Les explorations sous-marines*. Hachette & Cie, Paris, 352 pp.

Poore, G.C.B. & Andreakis, N. (2011) Morphological, molecular and biogeographic evidence support two new species in the *Uroptychus naso* complex (Crustacea: Decapoda: Chirostylidae). *Molecular Phylogenetics and Evolution*, 60 (1), 152–169.
https://doi.org/10.1016/j.ympev.2011.03.032

Puillandre, N., Macpherson, E., Lambourdière, J., Cruaud, C., Boisselier-Dubayle, M.C. & Samadi, S. (2011) Barcoding type

specimens helps to identify synonyms and an unnamed new species in *Eumunida* Smith, 1883 (Decapoda: Eumunididae). *Invertebrate Systematics*, 25 (4), 322– 333.
https://doi.org/10.1071/IS11022

Rodríguez-Flores, P.C., Buckley, D., Macpherson, E., Corbari, L. & Machordom, A. (2020) Deep- sea squat lobster biogeography (Munidopsidae: *Leiogalathea*) unveils Tethyan vicariance and evolutionary patterns shared by shallow-water relatives. *Zoologica Scripta*, 49 (3), 340–356.
https://doi.org/10.1111/zsc.12414

Rodriguez-Flores, P.C., Machordom, A. & Macpherson, E. (2017) Three new species of squat lobsters of the genus *Fennerogalathea* Baba, 1988 (Decapoda: Galatheidae) from the Pacific Ocean. *Zootaxa*, 4276 (1), 46–60.
https://doi.org/10.11646/zootaxa.4276.1.2

Rodríguez-Flores, P.C., Macpherson, E., Buckley, D. & Machordom, A. (2018a) High morphological similarity coupled with high genetic differentiation in new sympatric species of coral-reef squat lobsters (Crustacea: Decapoda: Galatheidae). *Zoological Journal of the Linnean Society*, 185 (4), 984–1017.
https://doi.org/10.1093/zoolinnean/zly074

Rodríguez-Flores, P.C., Macpherson, E. & Machordom, A. (2018b) Three new species of squat lobsters of the genus *Munidopsis* Whiteaves, 1874, from Guadeloupe Island, Caribbean Sea (Crustacea, Decapoda, Munidopsidae). *Zootaxa*, 4422 (4), 569–580.
https://doi.org/10.11646/zootaxa.4422.4.7

Rodríguez-Flores, P.C., Macpherson, E. & Machordom, A. (2022) New species of deep-sea squat lobsters (Decapoda: Anomura: Galatheoidea) from Guadeloupe, French West Indies, unveiled through integrative taxonomy. *Journal of Crustacean Biology*, 42 (1), 1–14.
https://doi.org/10.1093/jcbiol/ruab070

de Saint Laurent, M. (1985) Remarques sur la distribution des Crustacés Décapodes. *In*: Laubier, L. & Monniot, C. (Eds.), *Peuplements profonds du Golfe de Gascogne campagnes Biogas*. Institut Français de Recherche pour l'Exploitation de la Mer, Plouzane, pp. 469–478.

Saitou, N. & Nei, M. (1987) The Neighbor-Joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, 4 (4), 406–425.
https://doi.org/10.1093/oxfordjournals.molbev.a040454

Samouelle, G. (1819) *The Entomologist's useful compendium; or an introduction to the knowledge of British insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linn, and the modern method of arranging the classes Crustacea, Myriapoda, spiders, mites, and insects from their affinities and structure, according to the views of Dr. Leach. Also an explanation of the terms used in entomology; a calendar of the times of appearance, and usual situations of near 3000 species of British insects; with instructions for collecting and fitting up objects for the microscope*. Thomas Boys, London, 496 pp.
https://doi.org/10.5962/bhl.title.34177

Schmittner, A., Sarnthein, M., Klnkel, H., Bartoli, G., Bickert, T., Crucifix, M., Crudeli, D., Groeneveld, J., Kosters, E., Mikolajewicz, U., Millo, C., Reijmer, J., Schafer, P., Schmidt, D., Schneider, B., Schulz, M., Steph, S., Tiedemann, R., Weinelt, M. & Zuvela, M. (2004) Global impact of the panamanian seaway closure. *Eos Transactions American Geophysical Union*, 85 (49), 526.
https://doi.org/10.1029/2004EO490010

Schnabel, K.E., Cabezas, P., McCallum, A., Macpherson, E., Ahyong, S.T. & Baba, K. (2011) Worldwide distribution patterns of squat lobsters. *In*: Poore, G.C.B., Ahyong, S.T. & Taylor, J. (Eds.), *The Biology of squat lobsters*. CSIRO Publishing, Melbourne and CRC Press, Boca Raton, Florida, pp. 149–182.

Segonzac, M. (1992) Les peuplements associés l'hydrothermalisme océanique du Snake Pit (dorsale médio-atlantique; 23°N, 3480 m): composition et microdistribution de la mégafaune. *Comptes Rendus de l'Académie des Sciences de Paris*, Série III, 314, 593–600.

Smith, S.I. (1883) Preliminary report on the Brachyura and Anomura dredged in deep water off the south coast of New England by the United States Fish Commission in 1880, 1881 and 1882. *Proceedings of the United States Natural Museum*, 6 (343), 1–57.
https://doi.org/10.5479/si.00963801.6-343.1

Smith, S.I. (1885) On some new or little-known decapod Crustacea, from recent fish commission dredging off the east coast of the United States. *Proceedings of the United States Natural Museum*, 7 (455), 493–511.
https://doi.org/10.5479/si.00963801.455.493

Sun, S., Sha, Z. & Wang, Y. (2019) The complete mitochondrial genomes of two vent squat lobsters, *Munidopsis lauensis* and *M. verrilli*: Novel gene arrangements and phylogenetic implications. *Ecology and Evolution*, 9 (22), 12390–12407.
https://doi.org/10.1002/ece3.5542

Teixeira, S., Olu, K., Decker, C., Cunha, R.L., Fuchs, S., Hourdez, S., Serrao, E.A. & Arnaud- Haond, S. (2013) High connectivity across the fragmented chemosynthetic ecosystems of the deep Atlantic Equatorial Belt: efficient dispersal mechanisms or questionable endemism? *Molecular Ecology*, 22 (18), 4663–4680.
https://doi.org/10.1111/mec.12419

Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence

alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22 (22), 4673–4680.
https://doi.org/10.1093/nar/22.22.4673

Turnipseed, M., Jenkins, C.D. & Van Dover, C.L. (2004) Community structure in Florida Escarpment seep and Snake Pit (Mid-Atlantic Ridge) vent mussel beds. *Marine Biology*, 145, 121–132.
https://doi.org/10.1007/s00227-004-1304-z

UNINMAR (2020) Unidad Informática Marina. Colección de las inmersiones de la campaña Marum. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Available from: http://uninmar.icmyl.unam.mx/search?query=Marum (accessed 10 May 2022)

Vázquez-Bader, A.R. & Gracia, A. (2016) Diversity and distribution of Chirostyloidea and Galatheoidea (Decapoda, Anomura) in the southern Gulf of Mexico. *ZooKeys*, 2016, 1–30.
https://doi.org/10.3897/zookeys.612.9492

Vrijenhoek, R.C. (1997) Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. *Journal of Heredity*, 88 (4), 285–293.
https://doi.org/10.1093/oxfordjournals.jhered.a023106

Whiteaves, J.F. (1874) On recent deep-sea dredging operations in the Gulf of St. Lawrence. *American Journal of Science*, s3–7 (39), 210–219.
https://doi.org/10.2475/ajs.s3-7.39.210

Wicksten, M.K. & Packard, J.M. (2005) A qualitative zoogeographic analysis of decapod crustaceans of the continental slopes and abyssal plain of the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers*, 52 (9), 1745–1765.
https://doi.org/10.1016/j.dsr.2005.04.006

WoRMS (2022) World Register of Marine Species. *Munidopsis* Whiteaves, 1874. Flanders Marine Institute. Available from: http://www.marinespecies.org/aphia.php?p=taxdetails&id=106836 (accessed 10 May 2022)

Yang, C.-H., Tsuchida, S., Fujikura, K., Fujiwara, Y., Kawato, M. & Chan, T.-Y. (2016) Connectivity of the squat lobsters *Shinkaia crosnieri* (Crustacea: Decapoda: Galatheidae) between cold seep and hydrothermal vent habitats. *Bulletin of Marine Science*, 92 (1), 17–31.
https://doi.org/10.5343/bms.2015.1031

Yang, J.S. & Yang, W.J. (2008) The complete mitochondrial genome sequence of the hydrothermal vent galatheid crab *Shinkaia crosnieri* (Crustacea: Decapoda: Anomura): A novel arrangement and incomplete tRNA suite. *BMC Genomics*, 9 (257), 1–13.
https://doi.org/10.1186/1471-2164-9-257