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The Crustacean Society Journal of Crustacean Biology (2021) XX(XX), 1–14. https://doi.org/10.1093/jcbiol/ruab070 Version of Record, first published online XXXXX, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN. LSID: urn: lsid: zoobank.org: pub: BDCBD888-8BB7-4BE4-AA24-F8976ADB93DF

New species of deep-sea squat lobsters (Decapoda: Anomura: Galatheoidea: Munididae) from Guadeloupe, French West Indies, unveiled through integrative taxonomy

	Paula C. Rodríguez-Flores ^{1,2,3,} , Enrique Macpherson ^{2,} and Annie Machordom ^{3,}		
¹ Def.	partment of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge MA 02138, USA; ² Centre d'Estudis Avançats de Blanes (CEAB-CSIC), C. acc. Cala Sant Françesc 14 17300 Blanes, Girona, Spain; and ³ Museo Nacional de Ciencias Naturales (MNCN-CSIC), José Gutiérrez Abascal, 2, 28006 Madrid, Spain	1.05	
	Correspondence: P.C. Rodríguez-Flores; e-mail: paularodriguezflores@g.harvard.edu	1.90	
	(Received 19 September 2021; accepted 21 November 2021)		
ABSTRACT			
	During two deep-sea expeditions off the island of Guadeloupe, French West Indies, several specimens belonging to <i>Munida</i> Leach, 1820 and <i>Munidopsis</i> Whiteaves, 1874 (Galatheoidea,	1.95	
	Munididae) were collected. Further study, integrating morphological and molecular data, in-		
	two to <i>Munidopsis</i> . <i>Munida anteae</i> n . sp . is morphologically closely related to the Atlantic species	1.100	
	M. microphthalma A. Milne-Edwards, 1880. Both species can be easily distinguished morpho-		
	logically and represent independent evolutionary lineages. The closest relative to Munidopsis		
	<i>balconi</i> n. sp. is <i>M. glabra</i> Pequegnat & Williams, 1995 from the Gulf of Mexico. They can		

be distinguished by the armature of the carapace and perciopods, among other differences.	1 105
Munidopsis pholidota n. sp. is sister to M. squamosa (A. Milne-Edwards, 1880) and both are con-	1.105
sidered cryptic species, distinguished only by molecular characters and subtle morphological	
differences like the number of epipodites. Our phylogenetic results show some monophyletic	
groups within <i>Munidopsis</i> and <i>Munida</i> , and the existence of morphological convergences.	
Key Words Crustacea cruptic species mitochondrial genes morphological stasis Western	1.110

Key Words: Crustacea, cryptic species, mitochondrial genes, morphological stasis, Western Atlantic region

1.45 INTRODUCTION

With large areas still to be explored, the diversity of the vast ocean, particularly the deep sea (from 200 m onwards) remains underestimated (Schnabel et al., 2020). High costs on both time and resources in exploration and sampling these habitats account 1.50 for this but, even though thousands of new species have been described in the last 40 years of ocean exploration (Vrijenhoek, 2009). Squat lobsters are one of the most abundant and diverse crustacean deep-sea inhabitants and it is estimated that only around a third of the extant diversity is described (Appeltans et al., 1.55 2012). The use of integrative taxonomy has improved our knowledge on the diversity of squat lobsters, since it has allowed to recognize sibling species and cryptic taxa that otherwise would have been overlooked with the use of morphological characters only (e.g., Poore & Andreakis, 2012). Recent expeditions have increased

1.60 the available material of deep-sea squat lobsters (e.g., Richer de Forges *et al.*, 2013) and new species of squat lobsters are being recurringly described (e.g., Vázquez-Bader *et al.*, 2014; Macpherson *et al.*, 2016; Poupin & Corbari, 2016; Rodríguez-Flores *et al.*, 2018) in relatively well-studied regions like the Caribbean Sea and the Gulf of Mexico.

More than 30 squat lobster species belonging to the family Munididae Ahyong, Baba, Macpherson & Poore, 2010 and over 50 species to Munidopsidae Ortmann, 1898 (Wicksten & 1.120Packard, 2005; Baba et al., 2008) have been recorded from the Caribbean Sea and the Gulf of Mexico, harboring the richest species diversity after the Indo-West Pacific region (Schnabel et al., 2011). Representatives of these two families have been collected by several expeditions to the region (e.g., A. Milne-Edwards, 1.125 1880; Benedict, 1902; Chace, 1942; Pequegnat & Pequegnat, 1970, 1971; Mayo, 1974) and more recently from the coasts of Florida to Brazil (e.g., Pequegnat & Williams, 1995; Tavares & Campinho, 1998; de Melo-Filho & de Melo, 2001; Campos et al., 2005; Cardoso et al., 2014; Poore, 2014; Vázquez-Bader 1.130 et al., 2014; Poupin & Corbari, 2016; Macpherson et al., 2016). Both families are highly speciose, with more than 400 species in

- 2.5the case of Munididae and nearly 300 species in Munidopsidae (Baba et al., 2008, 2009; Ahyong et al., 2010; Rodríguez-Flores et al., 2019; Schnabel, 2020). Several studies have pointed out that there is a need for taxonomic revision of supraspecific taxa within these families (Ahyong et al., 2011; Rodríguez-Flores et al., 2019;
- AQ5.10 Miranda et al., 2021), and most species have unknown phylogenetic placement. Thanks to integrative taxonomy studies, however, genetic data of several squat lobster species are available in public databases (e.g., Rodríguez-Flores et al., 2019; Dong et al., 2021), allowing us to perform comparisons among species and propose 2.15 phylogenetic relationships.

During the molecular revision of the material collected during two surveys in the island of Guadeloupe, French West Indies (Poupin, 1994; Poupin & Corbari, 2016), we observed several cryptic and/or incorrectly identified species of Munida

- 2.20 and Munidopsis. After the morphological comparison with type material and the analysis of molecular data, we found three new species: one species of Munida closely related to M. microphthalma A. Milne-Edwards, 1880, and two species of Munidopsis morphologically related to *M. squamosa* (A. Milne-Edwards, 1880).
- 2.25 We herein 1) described the new Munida and Munidopsis species using morphological characters and molecular markers (COI, 16S), 2) redescribed the holotype of M. squamosa, and 3) investigated the phylogenetic placement of these species in a squat lobster's phylogenetic framework focused on the West Atlantic 2.30 species.

MATERIAL AND METHODS

- The terminology used for the descriptions follows Baba et al. 2.35(2009). The size of the specimens is indicated by the postorbital carapace length. Measurements of appendages are taken on dorsal (pereiopod 1), lateral (antennule, pereiopods 2-4), and ventral (antenna) midlines. Ranges of morphological and meristic variations are included in the description. Abbreviations used: Mxp, max-
- 2.40 illiped; P1, pereiopod 1 (cheliped); P2-4, pereiopods 2-4 (walking legs 1-3); M, male; F, female; ovig., ovigerous. The examined material is deposited in the Muséum national d'Histoire naturelle, Paris, France (MNHN) and the Museum of Comparative Zoology, Cambridge, USA (MCZ). 2.45

We used tissue from one pereiopod per specimen to extract genomic DNA with DNeasy kit (Qiagen, Hilden, Germany) following manufacturer's protocol, and adding RNase, with a previous proteinase K digestion overnight. Partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) and 16S 2.50 ribosomal RNA (16S) were amplified by polymerase chain reac-

- tion (PCR) using the combination of several primers: LCO 1490 (Folmer et al., 1994), tenuiCOIFwint (Rodríguez-Flores et al., 2019), COI-H (Machordom et al., 2003);16SAR/16SBR (Palumbi et al., 1991), and 16S1471/16S1472 (Crandall & Fitzpatrick,
- 2.55 1996), respectively. The amplified fragments were purified using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA). We sequenced both strands using BigDye Terminator in an ABI 3730 genetic analyzer at SECUGEN (Madrid, Spain). Forward and reverse DNA sequences obtained for each specimen were checked 2.60
- and assembled using the program Sequencher v.5.4 (Gene Code Corporation, Ann Arbor, MI, USA) and aligned using MAFFT (Katoh et al., 2002) with a posterior manual correction using AliView alignment editor (Larsson, 2014).
- Uncorrected p-distances between species were calculated using 2.65 PAUP v.4.0a (build 169) (Swofford, 2002). Some sequences from related species obtained in previous studies (Coykendall et al., 2017; Mantelatto et al., 2018; Rodríguez-Flores et al., 2018, 2019, Dong et al., 2021) were retrieved from GenBank and employed for comparisons. 2.70
- Phylogenetic analyses were performed with the COI data matrix, which included a larger number of taxa, using 2.72

MrBayes v3. 2. 1 (Huelsenbeck & Ronquist, 2001). We selected 2.75 Munida microphalma A. Milne-Edwards, 1880 was selected as the outgroup for rooting the Munidopsis tree (MK138925) and Munidopsis nitida (A. Milne-Edwards, 1880) (MN397923) as outgroup of the Munida tree. To estimate posterior probabilities, four Markov Chains Monte Carlo (MCMC) were 2.80 run for 2×10^7 generations, sampling trees and parameters every 20,000 generations. The initial 25% generations were discarded as burn-in. Bayesian analyses were run in CIPRES portal (Miller et al., 2010). We also ran maximum-likelihood analyses in the IQtree web server (http: //iqtree.cibiv.univie. 2.85 ac.at/). Branch support analyses were run with 1,000 iterations. The phylogenetic trees were plotted and edited in FigTree v1. 4. 2 (Rambaut, 2012). Posterior probabilities from the Bayesian Inference and bootstrap support from ML were included in the final tree. 2.90

TAXONOMY

2.95 Family Munididae Ahyong, Baba, Macpherson & Poore, 2010

Munida Leach, 1820

Munida anteae n. sp.

Fig. 1

Munida? microphthalma – Poupin & Corbari, 2016: 40, fig. 10c.

2.105

2.100

Material examined: Holotype. Guadeloupe, KARUBENTHOS 2015, stn. DW4511, 8 June 2015, 16°13.9'N, 61°51.5'W, 630-660 m: 1 F 5.0 mm (MNHN-IU-2013-18893).

2.110 Etymology: The name refers to the R/V Antea, on which the cruise KARUBENTHOS was carried out.

Description: Carapace: 1.2× longer than wide. Ridges mostly interrupted, some scale-like, with conspicuously short non-iridescent 2.115 setae. Gastric region with pair of small epigastric spines, without parahepatic spines. Postcervical spine on each side. Frontal margins oblique. Lateral margins slightly convex. Anterolateral spine small, at anterolateral angle, clearly not reaching level of sinus between rostrum and supraocular spines. Second marginal spine 2.120 before cervical groove as long as preceding one. Branchial margins with 4 spines. Rostrum spiniform, about $0.5 \times$ as long as remaining carapace, straight, horizontal. Supraocular spines reaching midlength of rostrum, not reaching end of corneas, subparallel, slightly directed upwards.

Sternum: Surface of thoracic 4-6 sternites smooth, few striae on sternite 4 only. Anterior margin of sternite 4 clearly narrower than third. Sternite 3, $5.5 \times$ wider than long.

2.130 Abdomen: Somite 2 with row of 6 spines on anterior ridge, with transverse posterior ridge; somites 3-4 each with uninterrupted transverse ridge on tergite behind anterior ridge; posteromedian margin of somite 6 straight.

2.135 Eyes: Ocular peduncles as long as broad. Cornea not dilated. Maximum corneal diameter one-fourth distance between bases of anterolateral spines.

Antennule: Article 1 (distal spines excluded) conspicuously long, 2.140 about $0.4 \times$ carapace length, $2.5 \times$ longer than wide (excluding spines), clearly overreaching end of corneas, with 2 distal spines, 2.142



3.60

right P2, lateral view (**G**); right P3, lateral view (**H**); right P4, lateral view (**I**). Scale bars: A, E, F, H, I = 2.0 mm; B, C, D, G = 1.0 mm. mesial spine shorter than lateral; 2 spines on lateral margin, proximal one short, at midlength of segment, distal one long, not PI: Subequal in length, about 2.2× carapace leng some scattered non-iridescent uniramous seta

3.65 *Antenna*: Article 1 with short distomesial spine clearly not reaching end of article 2. Article 2 with subequal distomesial and distolateral spines, both exceeding article 3 falling short of end of article 4. Article 3 unarmed.

reaching end of distolateral spine.

3.70 Mxp 3: Ischium about 1.5× length of merus measured along dorsal margin, distoventrally with spine; merus with 2 spines on flexor margin, distal smaller; extensor margin unarmed.

P1: Subequal in length, about $2.2 \times$ carapace length, with few scales,
some scattered non-iridescent uniramous setae. Merus armed
with row of spines, strongest spines on mesial and distal margins,
reaching proximal quarter of carpus. Carpus $2.5 \times$ longer than
heigh, as long as palm; palm slightly shorter than fingers, with sev-
eral spines along mesial and dorsal margins. Palm slightly shorter
than fingers, with some spines along mesial and lateral margins,
dorsal surface unarmed. Fingers unarmed, except basal spine on
movable finger, distally curving crossing, ending in sharp point.3.135

3.130

P2-4: Moderately long, slender, with numerous plumose setae and some iridescent non-plumose setae along extensor margin of each 3.142

showing left antennular and antennal peduncles, ventral view (C); right Mxp3, lateral view (D); right P1, dorsal view (E), right P2 lateral view (F); dactylus of

- 4.5 article. P2 about 2.2× carapace length. Meri decreasing in length posteriorly (P3 merus 0.8 length of P2 merus, P4 merus 0.7 length of P3 merus); P2 merus as long as carapace, ~8× as long as broad, 1.5× longer than P2 propodus; P3 merus 6.5× longer than broad, 1.2× longer than P3 propodus; P4 merus 4.5× as long as broad,
- 4.10 as long as P4 propodus; P4 merocarpal articulation ending at level of anterior branch of cervical groove. Extensor margins of meri with row of 9 or 10 proximally diminishing spines on P2–3, unarmed on P4; flexor margins with strong distal spine followed by row of 5 or 6 proximally diminishing spines; lateral surfaces
- 4.15 unarmed. Carpi with 1 or 2 spines on extensor margin; lateral surface with several granules sub-paralleling extensor margin on P2–3; flexor margin with distal spine. Propodi 7.5–7.8 (P2–3) –7.0 (P4)× as long as broad; extensor margin unarmed; flexor margin with 5–7 slender movable spines. Dactyli slender, length 0.6–0.7×
- 4.20 length of propodi; flexor margin with 8–10 movable spinules along entire length; P2 dactylus 6× longer than wide.

Distribution: Guadeloupe, Caribbean Sea, depth 630 to 660 m.

- 4.25 Genetic data: COI and 16S. GenBank Accession numbers XXXX-XXXX
- *Remarks: Munida anteae* **n. sp.** belongs to the group of species having the maximum corneal diameter one-fourth the distance between bases of the anterolateral spines, second abdominal segment with spines, lateral parts of the posterior thoracic sternites without granules, a spiniform rostrum, article 1 of the antennular segment markedly elongated with the distomesial spine clearly shorter than the distolateral spine, distomesial spine of the antennal article
- 4.35 2 not exceeding the end of the fourth article, and dactylus with corneous spines on the entire flexor margin. Morphologically, the closest relative is *M. microphthalma* A. Milne-Edwards, 1880 from the Caribbean Sea (type locality), Brazil, south of Iceland, Bay of Biscay, NW Iberian Peninsula, Middle Atlantic Bight, Canary and
- 4.40 Cape Verde islands at 677–2,094 m (de Melo-Filho & de Melo, 1992; García-Raso et al., 2018). The occurrences of this species in the Pacific Ocean are dubious (Baba et al., 2008). A comparison of type material of *M. microphthalma* from Yucatán (1 F, MNHN Ga 960) and Martinica (1 M, MNHN Ga 959), and additional ma-
- 4.45 terial from Brazil (1 ovig. F) (see de Melo-Filho & de Melo, 2001) with the new species revealed that the two species can be distinguished morphologically and genetically. *Munida microphthalma* has five spines on the branchial margin of the carapace, whereas there are only four in the new species. Furthermore, the anterolateral
- 4.50 spine of the carapace is very small in the new species, being clearly more developed in *M. microphthalma*. The epigastric region has several pairs of spines in *M. microphthalma*, whereas there is only one pair in *M. anteae*. Article 1 of the antennular peduncle is clearly slenderer in the new species. The distal portion, from the lateral
- 4.55 spines to the base of the distal spines, is more than twice longer than wide in *M. anteae*, being as long as wide in *M. microphthalma*. The distal spines of the second segment of the antennal peduncle exceed the third segment in *M. anteae*, whereas these spines never reach the end of the third segment in *M. microphthalma*.
- 4.60 The two species are genetically very different. The genetic divergence ranges were 12% in 16S and 16–17% in COI.

Munida anteae **n. sp.** is also closely similar to *M. victoria* de Melo-Filho, 1996, from Espirito Santo, Brazil, from a depth of 960 m. The two species can be easily differentiated by similar characters distinguishing the new species and *M. microphthalma* (see de Melo-Filho, 1996). There is unfortunately no available molecular data from *M. victoria*. The new species is also very similar to *M. oblongeta*. Coherea March and Science Science Science Science Science

4.65

- *longata* Cabezas, Macpherson & Machordom, 2009 from the Solomon Islands. Both species can nevertheless be distinguished
 4.70 morphologically and genetically. Article 1 of the antennular ped-
- 4.72 uncle is slenderer in *M. oblongata* than in the new species. The P1 palm is slightly shorter than the fingers in the new species, whereas

it is clearly larger in M. oblongata. The P1 carpus is $2.5 \times \text{longer}$ 4.75 than high in the new species, whereas it is four times longer than high in M. oblongata.

The interspecific p-distance between both species is 9% for the 16S (*M. oblongata* GenBank Accession number EU417978, no data for COI).

Family Munidopsidae Ortmann, 1898

Figs. 2, 3

Munidopsis squamosa. -Poupin, 1994: 39.

4.90

4.95

4.80

Material examined: Holotype: POLKA, station without number, west coast of Guadeloupe, Basse Terre, January 1993, 500 m: ovig. F 14.3 mm (MNHN-IU-2014-23830).

Etymology. After Rémy Balcon, Head of Operations at GENAVIR, in recognition for his continuous support for the explorations of the Tropical Deep-Sea Benthos program.

Description. Carapace: Slightly longer than broad, widest at midlength; quadrangular, moderately convex across. Dorsal surface squamate; 2 thick epigastric protuberances; hepatic and anterior branchial areas with small scales, some acute granules. Regions well delineated by deep furrows including distinct anterior and posterior cervical grooves. Posterior cardiac region weakly triangular, preceded by deep transverse depression across. Posterior margin unarmed. Rostrum acutely triangular, 0.3× carapace length, width 4.105



 Figure 2. Munidopsis balconi n. sp. holotype, ovig. F 14. 3 mm
 4.140

 (MNHN-IU-2014-23830). Carapace and abdomen, dorsal view (A); carapace and abdomen, lateral view (B).
 4.142



Figure 3. Munidopsis balconi n. sp. holotype, ovig. F 14. 3 mm (MNHN-IU-2014-23830). Carapace, anterior part, dorsal view (A); sternal plastron (B); telson
 5.50 (C); Cephalic region, showing left antennular and antennal peduncles, ventral view (D); right Mxp3, lateral view (E); right P1, dorsal view (F); right P2 lateral
 5.120 view (G); dactylus of right P2, lateral view (H); dight P3, lateral view (I); right P4, lateral view (J). Scale bars: A, B, C, D, E, H = 2.0 mm; F, G, I, J = 4.0 mm.

0.3× anterior width of carapace, directed slightly upwards, dorsally carinate, lateral margins straight. Frontal margin with orbit slightly
5.55 concave behind ocular peduncle, limited laterally by rounded process, then slightly transverse toward anterolateral spine of carapace. Lateral margins slightly convex; anterolateral spine broad; anterior branchial margin with 2 broad spines; broad spine behind lateral end of posterior cervical groove. Pterygostomian flap smooth, with
5.60 minute rugosities, anteriorly acute.

Sternum: As long as broad, maximum width at sternite 7. Sternite 3 moderately broad, 2× wider than long, anterolaterally angular, anterior margin with median notch flanked by 2 lobes. Sternite 5.65
4 narrowly elongated anteriorly; surface depressed in midline, smooth; greatest width 3× that of sternite 3, 1.5× wider than long.

Abdomen: Smooth, unarmed; tergites 2, 3 each with 2 slightly elevated transverse ridges, anterior more elevated than posterior; tergites 4–6 lacking posterior ridge; tergite 6 with weakly produced posterolateral lobes and nearly transverse posteromedian margin.
5.72 Telson composed of 8 plates; 1.8× as wide as long.

Eye: Peduncle scarcely movable, with small tubercular process mediodorsally; cornea subglobular, as wide as eyestalk; blunt spine between eye and antennal peduncle.

Antennule: Article 1 of peduncle with dorsolateral and distolateral spines; distomesial margin slightly produced, granular.

Antenna: Peduncle slightly exceeding eye; article 1 with strong 5.130 distomesial spine, reaching end of article 2, distolateral angle rounded; article 2 with well-developed distolateral spine, distomesial blunt; articles 3, 4 unarmed.

5.125

5.140

Mxp3: Surface smooth, with few granules. Ischium as long as 5.135 merus measured on extensor margin; flexor margin of merus with 2 spines and several granules, proximal spine stronger than distal; extensor margin with small distal spine; 19 or 20 corneous denticles on crista dentata.

P1: Stout, granular, exceeding P2, with numerous minute granules and scales, each scale with few short setae, $1.5 \times$ longer than 5.142

5

RODRÍGUEZ-FLORES ET AL

6.5 carapace. Merus 2.5× carpus length, with some distal stout spines. Carpus 1.2× longer than broad, with some acute distal granules, few acute granules along dorsal side, some spines may be present along mesial margin. Palm unarmed, slender, slightly longer than carpus, 1.2× longer than broad. Fingers unarmed, 1.4×
6.10 longer than palm, opposable margins nearly straight, not gaping, spooned; fixed finger without denticulate carina on distolateral margin.

P2-4: Stout, coarsely granular, nearly devoid of setae, some-6.15 what compressed laterally, slightly decreasing in size posteriorly. P2 merus moderately elongated, $0.5 \times$ carapace length, nearly $3.0 \times$ longer than high and $1.5 \times$ length of P2 propodus. Extensor margin of P2-4 meri carinate, with small granules along entire border, distal part slightly flat, ending in thick spine; flexor 6.20 margin granular. Carpi with thick distal spine on extensor margin, granular carina along lateral side. P2-4 propodi 3.1-3.6× as long as high, triangular in cross section, unarmed. Dactyli 0.7-0.9× length of propodi; distal claw short, moderately curved; flexor margin distally curved, with 9-11 minute teeth decreasing in size 6.25 proximally, each with slender corneous spine, last tooth as close to penultimate tooth as to dactylar claw.

Epipods present on P1 and P2.

6.30 Distribution.

Guadeloupe, Caribbean Sea; depth 500 m.

Genetic data: COI and 16S. GenBank Accession numbers XXXX-XXXX.

6.35

Remarks: Munidopsis balconi n. sp. belongs to the group of species having a rostrum without lateral spines, triangular and dorsally carinated, the orbit slightly delimited by antennal spine or process two epigastric spines or protuberances, the abdominal seg-6.40 ments unarmed, the telson with eight plates, one dorsal eye-spine, tubercle-like, and the P2 not reaching the end of the P1. This specimen was initially identified as *M. squamosa* (Poupin, 1994); however, a comparison with Guadeloupe specimens (Poupin & Corbari, 2016) and the examination of the type material and 6.45 other material of *M. squamosa* from MCZ demonstrated that they can be distinguished by some important characters. The armature of the carapace surface is tuberculate in M. squamosa, whereas it is squamate in the new species. The eyes have The dorsomesial surface of the eye cornea has a large blunt granular projection 6.50 reaching midlength of rostrum in M. squamosa, whereas the eyes only have a small tubercular process mediodorsally in the new species. The P1-4 have numerous spines, tubercles, and projections in the meri to propodi of *M. squamosa*, whereas these articles are barely smooth, with a few granules and small spines, in the new 6.55 species. The epipods are present in the P1-3 in *M. squamosa*, but only in P1, 2 in M. balconi n. sp. Munidopsis balconi n. sp. is larger in size than M. squamosa.

These two species diverge on 18–19% for the COI and 13% for the
6.60 16S. The closest western Atlantic relative of the new species is M. glabra Pequegnat & Williams, 1995, from the continental slope of the northwestern Gulf of Mexico. The two species can be differentiated as follows. The dorsal carapace surface is smooth in M. glabra, but clearly squamate in M. balconi n. sp. The front
6.65 margin has one antennal spine in M. glabra the spine is absent in

- M. balconi n. sp. Epipods are present in the P1-3 of M. glabra, but present only in the P1, 2 in M. balconi n. sp. The Mxp3 has two strong, nearly subequal spines along the flexor margin of the merus in M. glabra, whereas these spines are smaller and proximally larger than distally in the new species.
- 6.72 *Munidopsis balconi* **n. sp**. also resembles *M. mandelai* Macpherson, Amon & Clark, 2014 from the southwestern Indian Ocean and

 M. hemingi Alcock & Anderson, 1899 from southwestern India.
 6.75

 Munidopsis balconi n. sp. can be distinguished from these two species by having an eye dorsal spine that overreaches the cornea (not overreaching the cornea in M. mandelai and in M. hemingi) and the presence of blunt epigastric processes in the new species (well-developed epigastric spines in the other two species).
 6.80

The new species also resembles to M. tasmaniae Ahyong & Poore, 2004 from deep water of southeastern Australia. The two species can be clearly distinguished by the following characters. The pair of epigastric processes are blunt, flattened, and thicker in M. tasmaniae, but much smaller and thinner in the new species. The ornamentation of the carapace, abdomen, and appendages is overall more finely tuberculate in M. tasmaniae, whereas it is covered by large scales in the new species. The Mxp 3 merus and carpus has spines along the extensor margin in M. tasmaniae, but these margins are only armed with the distal spine in the new species.

There is unfortunately no genetic data available for *M. tasmaniae*, *M. mandelai*, and *M. hemingi*.

Munidopsis pholidota n. sp.

6.95

6.105

Figs. 4, 6B

Material examined: Holotype. Guadeloupe, KARUBENTHOS 2015, stn. DW4611, 24 June 2015, 16°20'N, 60°52'W, 263–242 6.100 m: 1 M 3.9 mm (MNHN-IU-2016-2365).

Etymology: From the Greek pholidotós, meaning "scale bearing."

Description: Carapace:

Slightly longer than broad, widest at midlength; quadrangular, moderately convex across. Dorsal surface heavily sculptured; thick protuberances on gastric area; hepatic and anterior branchial areas with scales and some acute granules. Regions well delineated by deep furrows including distinct anterior and posterior cervical 6.110 grooves. Posterior cardiac region preceded by deep transverse depression. Posterior margin unarmed. Rostrum widely triangular, width 0.3× anterior width of carapace, directed slightly upwards, dorsally carinate, lateral margins straight; 0.3× carapace length. Frontal margin with orbit nearly transverse behind ocular ped-6.115 uncle, anterolaterally directed on lateral part, outer orbital spine/ process (antennal spine) absent; tuberculate projections lateral to rostrum between eyes, fused with rostrum and eye projections. Lateral margins straight; anterolateral spine broad, acute; anterior branchial margin with broad small spine; broad spine behind lat-6.120 eral end of posterior cervical groove. Pterygostomian flap smooth, with rugosities, anteriorly acute.

Sternum: As long as broad, maximum width at sternite 7. Sternite 3 moderately broad, 2.5× wider than long, anterolaterally rounded, 6.125 anterior margin nearly straight. Sternite 4 narrowly elongated anteriorly; surface depressed in midline, smooth; greatest width 2.9× that of sternite 3, 1.9× wider than long.

Abdomen: Smooth, unarmed; tergites 2, 3 each with 2 slightly ele-
vated transverse ridges, anterior ridge more elevated than pos-
terior one, covered by granules and scales; tergites 4–6 lacking
posterior ridge; tergite 6 with weakly produced posterolateral
lobes and nearly transverse posteromedian margin. Telson com-
posed of 8 plates; $1.5 \times$ as wide as long.6.130

Eye: With short peduncle fused to carapace, covered with granules; cornea subglobular, mesial surface with large granular projection.

The closest western Atlantic relative of the Article 1 of peduncle with dorsolateral and distolateral spines; distomesial margin slightly produced and granular. 6.142

6



Figure 4. Munidopsis pholidota n. sp. holotype, M 3.9 mm (MNHN-IU-2016-2365). Carapace, dorsal view (A); carapace, lateral view (B); sternal plastron (C); telson (D); cephalic region, showing left antennular and antennal peduncles, ventral view (E); left Mxp3, lateral view (F); right P1, dorsal view (G); right P2, lateral view (I); merus and carpus of right P3, lateral view (J); right P4, lateral view (K). Scale bars: A, B, G, H, J, 7.135 K = 1.0 mm; C, D, E, F, I = 0.5 mm.

Antenna: Peduncle slightly exceeding eye; article 1 with strong distomesial spine, not reaching end of article 2, distolateral angle acute; articles 2, 3 with well-developed distolateral spine, distomesial corner blunt; article 4 unarmed.

Mx\$\$\pi\$3: Surface with granules. Ischium as long as merus measured on
extensor margin; flexor margin of merus with 2 spines and several
granules, proximal spine stronger than distal; extensor margin with
small distal spine; 19 or 20 corneous denticles on crista dentata.7.140

7.72

7.70

RODRÍGUEZ-FLORES ET AL

- 8.5 P1: Stout, with numerous minute granules and scales, each scale with few short setae, 1.5× longer than carapace. Merus 2.5× carpus length, with some spines on mesial and lateral margins and a few distal stout spines. Carpus 1.4× longer than broad, with some distal stout spines, few acute granules along dorsal side.
- 8.10 Palm slender, slightly longer than carpus, 1.6× longer than broad, with some acute proximal spines on mesial margin. Fingers unarmed, 0.7× longer than palm, opposable margins nearly straight, not gaping, spooned; fixed finger without denticulate carina on distolateral margin.
 8.15
 - P2-4: Stout, coarsely granular, nearly devoid of setae, slightly compressed laterally, slightly decreasing in size posteriorly. P2 merus moderately elongated, $0.5 \times$ carapace length, nearly $3.0 \times$ longer than high, $1.5 \times$ length of P2 propodus. Extensor margin of
- 8.20 P2–4 meri carinate, with small granules along entire border, distal part slightly flat, ending in thick spine; flexor margin granular. Carpi with thick distal spine on extensor margin, granular carina along lateral side. Propodi 3.1–3.6× as long as high, triangular in cross section, unarmed. Dactyli 0.7–0.9× length of propodi; distal
- 8.25 claw short, moderately curved; flexor margin distally curved, with 8 minute teeth decreasing in size proximally, each with slender corneous spine, ultimate tooth as close to penultimate tooth as to dactylar claw.
- 8.30 Epipods present on P1 and P2.

Distribution: Guadeloupe, French West Indies; depth 242-263 m.

Genetic data: COI and 16S. GenBank Accession numbers 8.35 XXXX-XXXX

Remarks: Munidopsis pholidota n. sp. belongs to the group of species having triangular rostrum without lateral spines, with frontal margin with 2 granular projections lateral to rostrum, and often fused with rostrum and eye projections, orbit slightly excavated but without antennal (outer orbital) spine, the eyes with large granular projection, the abdominal segments unarmed, and the telson with 8 plates. This species is closely related to M. squamosa (see remarks for M. squamosa).

8.45

Munidopsis squamosa (A. Milne Edwards, 1880)

Figs. 5, 6C–E

- Orophorhynchus squamosus A. Milne Edwards, 1880: 58 (Martinique, 350 m).
 - Elasmonotus squamosus A. Milne Edwards & Bouvier, 1894: 282 (key). — A. Milne Edwards & Bouvier, 1897: 99, pl. 8, figs. 4–6 (Martinique, St. Lucia, 212–350 m). — Young, 1900: 414 (key). Munidopsis squamosa – Benedict, 1902: 276 (key), 327 (list). —
- 8.55 Doflein & Balss, 1913: 173 (list), 178 (table). Chace, 1942: 73 (key). Pequegnat & Pequegnat, 1970: 138 (key); 1971: 4 (key). Poupin, 1994: 39 (French West Indies, 212–500 m). Boschi, 2000: 98 (list). Baba *et al.*, 2008: 163 (catalogue). Poupin & Corbari, 2016: 51, fig. 12d (Guadeloupe, 385–399 m).
- 8.60 Material examined. Holotype. Off Martinique, 12 February 1879, 14°29'10°N, 61°5'47°W, 350 m: 1 M broken, 4 mm (MCZ CRU-4756). Other material. Off St. Lucia, 16 February 1879, 13°50.3'N, 61°3.8'W, 212 m: F 3.5 mm (MCZ CRU-9784). Guadeloupe, KARUBENTHOS 2015, stn. DW4634, 27, June 2015, 15°48'N,
- 8.65 61°26'W, 310–304 m: ovig. F 3.5 mm (MNHŇ-IU-2016-2340). stn. CP4543, 13 June 2015, 16°40'N 61°34'W, 385–399 m: ovig. F 3.9 mm (MNHN-IU-2013-18901).

Description. Carapace: Slightly longer than broad, widest at midlength; quadrangular, moderately convex across. Dorsal surface heavily sculptured; thick protuberances on gastric, posterior branchial, cardiac regions; hepatic and anterior branchial areas with scales and some acute granules. Regions well delineated by

deep furrows including distinct anterior and posterior cervical grooves. Posterior cardiac region preceded by deep transverse depression. Posterior margin unarmed. Rostrum widely triangular, width 0.3× anterior width of carapace, directed slightly upwards, dorsally carinate, lateral margins straight; 0.3× carapace length. Frontal margin with orbit concave behind ocular peduncle, outer orbital spine/process (antennal spine) absent; tuberculate projections lateral to rostrum between eyes, fused with rostrum and eye projections. Lateral margins straight; anterolateral spine broad, small; anterior branchial margin with broad small spine; broad branchial spine behind lateral end of posterior cervical groove.
8.85

Abdomen: Smooth, unarmed; tergites 2, 3 each with 2 slightly ele-
vated transverse ridges, anterior more elevated than posterior
ridge; tergite 6 with weakly produced posterolateral lobes and
nearly transverse posteromedian margin. Telson composed of 7 or
8 plates; 1.5× as wide as long.8.95

Eye: With short peduncle fused to carapace, covered with granules; cornea subglobular, mesial surface with large granular projection.

Antennule: Article 1 of peduncle with dorsolateral and distolateral 8.105 spines; distomesial margin slightly produced and granular.

Antenna: Peduncle slightly exceeding eye; article 1 with strong distomesial spine, not reaching end of article 2, distolateral angle acute; article 2, 3 with well-developed distolateral spine, 8.110 distomesial non-acute; article 4 unarmed.

Mxp3: Surface with granules. Ischium as long as merus measured on extensor margin; flexor margin of merus with 3 acute spines, medial stronger, and several granules; extensor margin with small 8.115 distal spine; 19 or 20 corneous denticles on crista dentata.

P1:Stout, with numerous minute granules and scales, each
scale with few short setae, $1.5 \times$ longer than carapace. Merus
 $2.5 \times$ carpus length, with some spines at all surfaces including
a few distal stout spines. Carpus $1.4 \times$ longer than broad, with
some distal stout spines, a few acute granules along dorsal side.
Palm with some acute proximal spines, slender, slightly longer
than carpus, $1.6 \times$ longer than broad. Fingers unarmed, $0.7 \times$
longer than palm, opposable margins nearly straight, not gaping,
spooned; fixed finger without denticulate carina on distolateral
margin.8.120

P2-4 (lost in holotype, description of material from Guadeloupe): Stout, coarsely granular, devoid of setae, cylindrical in cross section, 8.130 slightly decreasing in size posteriorly. P2 merus stout, 0.5× carapace length, nearly $2.0 \times$ longer than high, $1.5 \times$ length of P2 propodus. Extensor margin of P2-4 meri carinate, with small granules along entire border, distal part slightly flat, 8.135 ending in thick spine; flexor margin granular. Carpi with thick distal spine on extensor margin, granular carina along lateral side. Propodi 3.1-3.6× as long as high, triangular in cross section, unarmed. Dactyli 0.7-0.9× length of propodi; distal claw short, moderately curved; flexor margin distally curved, 8.140 with 8 minute teeth decreasing in size proximally, each with slender corneous spine, ultimate tooth as close to penultimate 8.142 tooth as to dactylar claw.

8



- **Figure 5.** Munidopsis squamosa (A. Milne-Edwards, 1880). A, D, F,G., holotype, M 4 mm (MCZ CRU-4756), B, C, E, F 3.5 mm. (MCZ CRU-9784). H, I., ovig. F 3.5 mm (MNHN-IU-2016-2340). Carapace, dorsal view (A); carapace, dorsal view (B); carapace, lateral view (C); sternal plastron (D); telson (E); cephalic region, showing left antennular and antennal peduncles, ventral view (F); right Mxp3 (G); merus and carpus of right P2, lateral view (H); right P2, lateral view (I). Scale bars = 1 mm.
- 9.55
- *Epipods present on P1–3. Distribution.* Martinique, St. Lucia, and Guadeloupe, Caribbean Sea; depth 212–399.

Genetic data: COI and 16S. GenBank Accession numbers 9.60 XXXX-XXXX

Remarks. Munidopsis squamosa was described by A. Milne Edwards (1880) in his preliminary report on the crustaceans collected by the Blake while trawling in the Caribbean Sea and Gulf of Mexico. The formal report of the *Blake* was published later (A. Milne-Edwards & Bouvier 1897). The species was nevertheless

9.65 Milne-Edwards & Bouvier 1897). The species was nevertheless not collected again until much later by Mayo (1974), who exhaustively revised *Munidopsis* from the Caribbean Sea and the Gulf of Mexico, including *M. squamosa* from the Yucatán Channel and the Dominican Republic. This work, a dissertation, remains unpublished, and a redescripton of *M. squamosa* is needed using the char-

9.70 lished, and a redescripton of *M. squamosa* is needed using the characters currently employed for the taxonomy of Munidopsidae.

9.72 Munidopsis squamosa belongs to the group of species having

triangular rostrum without lateral spines, with frontal margin with two granular projections lateral to rostrum, and often fused with rostrum and eye projections, orbit slightly excavated but without antennal (outer orbital) spine, the eyes with large granular projection, the abdominal segments unarmed, the telson with 9.130 eight plates and epipods on P1, 2 or P1-3. This group includes small and uncommon species from the Atlantic and the Pacific oceans: M. amapa Poore, 2014 and M. brasilia Poore, 2014, and M. bajacalifornia Poore, 2014, and M. papanui Schnabel & Bruce, 2006, respectively. The species of this group can be distinguished 9.135 from each other by the armature pattern of the carapace (spines versus tubercules or scales), the armature on the pereiopods and the fusion of the rostrum with the eye peduncles and ocular projections (Fig. 6). The closest relative to M. squamosa is M. pholidota n. sp. Molecular

9.125

 The closest relative to M. squamosa is M. phohdola n. sp. Molecular
 9.140

 comparison among specimens collected in Guadeloupe (Poupin & Corbari, 2016) revealed differences for genetic markers within
 9.142



Figure 6.Rostrum and frontal margin of the carapace, dorsal view. Munidopsis amapa Poore, 2014 from Guadeloupe Island, KARUBENTHOS, DW4599,10.40M 3.9 mm (MNHN-IU-2016-2446) (**A**); M. pholidota **n. sp.** holotype M 3.9 mm (MNHN-IU-2016-2365) (**B**); M. squamosa (A. Milne-Edwards, 1880) ovig F
3.5 mm (MNHN-IU-2016-2340) (**C**); M. squamosa (A. Milne-Edwards, 1880) ovig F 3.9 mm (MNHN-IU-2013-18901) (**D**); M. squamosa (A. Milne-Edwards, 1880) holotype M broken 4.0 mm (MCZ CRU-4756) (**E**). Scale bars: A, B, C, D = 0.4 mm, E = 1 mm.10.110

specimens identified as *M. squamosa*. Further comparisons with the description and illustrations provided by Mayo (1974) and with the holotype and specimens deposited in the MCZ demonstrates that *M. pholidota* **n. sp.** and *M. squamosa* can be distinguished by subtle morphological characters. The epipods are present in the P1, 2 in the new species, but in the P1–3 in *M. squamosa*. The orbit is shallowly excavated in *M. squamosa* but transverse in the new species. The anterolateral angle of the carapace presents an acute spine in the new species, whereas this spine is blunt and small in *M. squamosa*. The anterior margin of the third sternite is nearly straight in the new species, but with a median notch and two lateral lobes in *M. squamosa*.

- 10.55 Specimens from Guadeloupe belonging to both species diverged on 5.5% for the COI and 1% for the 16S. The genetic divergence of these species with *M. amapa* was 15% for the COI and from 11 to 12% for the 16S. There is unfortunately no genetic data available for the other species.
- 10.60
 Phylogenetic placement of new species of Munida and Munidopsis Results from the molecular phylogenetics analyses of Munididae, including close morphologically related species and other species from the Atlantic revealed that Munida anteae n. sp. represent a highly divergent lineage (Fig. 7). In spite of the morphological
- 10.65 highly divergent lineage (Fig. 7). In spite of the morphological resemblance between *Munida anteae* and *M. microphthalma*, the latter was more related with a clade including *M. valida* Smith, 1883 and *M. sanctipauli* Henderson, 1885 from the West Atlantic, and an eastern Atlantic clade is recovered as monophyletic. It is noteworthy that the clade that includes the new species is not
- 10.70 is noteworthy that the clade that includes the new species is not phylogenetically close to the cluster from the eastern Atlantic, suggesting different evolutionary histories and lineage independence.

10.72 gesting different evolutionary histories and lineage independence.

In the case of Munidopsidae, Munidopsis squamosa and M. pholidota **n. sp.** were phylogenetically close, forming a clade clustered 10.115 with M. amapa with high Bayesian posterior probability and ML bootstrap support (Fig. 7B). This relationship was also congruent with morphology, these species having several similarities in the morphological characters used to distinguish taxa. The phylogenetic placement of M. balconi n. sp. in relation to other species of 10.120 Munidopsis with available molecular data was still unknown, since this lineage was recovered as a part of an unsupported polytomy. This clade includes other species from the Atlantic plus M. dispar Dong Gan & Li, 2021 described from deep water in the Pacific, which has also a densely tuberculated carapace. Our reconstruc-10.125 tion also showed that other species of Munidopsis recorded from Guadeloupe (e.g., Munidopsis turgida Rodríguez-Flores, Macpherson & Machordom, 2018, M. granulens Mayo, 1972, and M. corniculata Rodríguez-Flores, Macpherson & Machordom, 2018) represent highly divergent unrelated lineages, also considering the new spe-10.130 cies described herein. Munidopsis granulens and M. turgida were clustered together, M. senticosa was sister to a species complex including M. barbarae (Boone, 1927), and M. corniculata constituted a lineage with dubious phylogenetic position.

10.135

DISCUSSION

The species diversity of *Munida* and *Munidopsis* in the Caribbean Sea has been increased by the three new species, which are highly supported by phylogenetic analyses and morphological dissimilarities. Squat lobsters are characterized by a high degree 10.142

West

- 11.5 of morphological convergence and stasis, characteristics more common in species of Munididae, as pointed out in Munida by Machordom & Macpherson (2004), and in related genera (Agononida Baba & de Saint Laurent, 1996, Paramunida Baba, 1988, Sadayoshia Baba, 1969) by several other studies (Cabezas et al.,
- 11.10 2012; Macpherson & Baba, 2012; Poore & Andreakis, 2012). Although the molecular phylogenetic relationships show morphologically cohesive groups in some cases (e.g., the clade including Munidopsis amapa, M. squamosa, and M. pholidota), our phylogenetic reconstructions revealed that most morphological characters em-
- 11.15 ployed to distinguish species present convergent states. This is the case of Munida microphthalma versus M. anteae, in which the existence of a reduced orbit and its relative size to the rostral spine seems to be convergent, whereas the armature pattern of the carapace and abdomen and the relative length of pereiopods are 11.20 characters shared by all the species from the monophyletic eastern

Atlantic lineage (Fig. 7). Munidopsis balconi n. sp. as contrasted against M. squamosa is an-

other example of evolutionary convergence in squat lobsters (Fig. 7), in which the existence of carapace sculpture, the reduction of

- 11.25 the ocular orbits, the number and existence of epipods on pereiopods, and the presence of eye spines seem to be morphological homoplasies. In the case of Munidopsis, the existence of such a great morphological diversification appears to be more common than a pattern of morphological stasis like in many species of 11.30 Munida (Machordom & Macpherson, 2004). Several authors have highlighted the high morphological disparity of the genus (e.g., Baba, 2005; Ahyong et al., 2011), which is coupled in some cases
 - with low genetic divergences (Jones & Macpherson, 2007; Dong et al., 2019).
- 11.35 Either the high degree of morphological convergence or the high morphological diversification make difficult the establishment of new taxa in the absence of molecular data and phylogenetic analyses (Rodríguez-Flores et al., 2019). For instance, the sister species, Munidopsis squamosa and M. pholidota, are hardly distinguish-
- 11.40 able when only using morphological characters; however, cryptic species are not commonly found in this family (but see Rodríguez-Flores et al., 2020). Moreover, several previous works have indicated the polyphyletic nature of both Munida (Machordom & AQ6 Macpherson, 2004; Rodríguez-Flores et al., 2019; Miranda et al.,
- 11.45 2021) and Munidopsis (Ahyong et al., 2011). Ongoing studies including a more complete taxonomic sampling and analyses of several molecular markers indicate that both are composite taxa, including multiple ancient lineages at genus level (Rodríguez-Flores, 2021; Machordom et al., unpublished data).
- 11.50 New species of Munida and Munidopsis are described each year (Rodríguez-Flores et al., 2018; Dong et al., 2019, 2021; Macpherson et al., 2020). Considering that only a small part of the deep sea is explored, the known diversity of squat lobsters would constitute just the peak of the iceberg (Appeltans et al.,
- 11.55 2012). Moreover, some of these squat lobster species are only known from the holotype or the type locality (e.g., Macpherson et al., 2016, Rodríguez-Flores et al., 2018), which is evidence of either uncommonness (endemic species or only found in a few seamounts), low abundances, or lack of exhaustive exploration of the
- 11.60 deep-sea floor. The deep sea is of high interest as a source of several desirable resources, like the polymetallic nodules (Vanreusel et al., 2016). Therefore, efforts in taxonomy and exploration should be increased in order to get to know these uncommon and vulnerable species to preserve them before any potential impact of 11.65
- human activity on their populations and habitats.

ACKNOWLEDGMENTS

We thank our colleagues who made specimens available for study: 11.70 P. Bouchet, L. Corbari, and P. Martin-Lefèvre, all from the MNHN, Paris, and J. Poupin (Ecole Navale, Brest, France). Thanks also to 11.72

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Figure 7. Phylogenetic placement of A. Munida anteae n. sp. (A) and Munidopsis new species (B) according to Bayesian analyses of COI partial marker. Asterisks indicate nodes supported also by ML analyses (bootstrap support >70). Colours at nodes indicate values for posterior probabilities 11.130 (see legend). GenBank accession numbers or voucher codes for the species analyzed in this study are at the tips of each branch.

Ricardo García for his help with the laboratory work. We are also 11.135 indebted to all the chief scientists of KARUBENTHOS 2015 cruise (https: //doi.org/10.17600/15005400), including the captains, crew, and scientists who sorted out material and provided the specimens used in this study. We thank A. Baldinger for his assistance when revising the MCZ collection. Thanks to the Editor-11.140 in-Chief and to the two anonymous reviewers for their helpful comments, corrections and suggestions on the manuscript. This study 11.142

- 12.5 was partially supported by a project of the Ministry of Economy, Industry and Competitiveness (CTM2014-57949-R) and by the GALETTE project (Galatheoidea lobster adaptations to deep sea environments), co-founded by CNRS (France) and CSIC (Spain)
 (2018FR0053). PCRF was provided graduate student support by
- 12.10 (2010) ROOSS). FORF was provided graduate student support by the The Crustacean Society Fellowship Student Award (2020) and is currently funded by the E.O. Wilson Biodiversity Postdoctoral Fellowship at the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.
- 12.15

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