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

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#### Abstract

During two deep-sea expeditions off the island of Guadeloupe, French West Indies, several specimens belonging to Munida Leach, 1820 and Munidopsis Whiteaves, 1874 (Galatheoidea, Munididae) were collected. Further study, integrating morphological and molecular data, indicated that some of the specimens belonged to three undescribed species, one to Murida and two to Munidopsis. Munida anteae n. sp. is morphologically closely related to the Atlantic species M. microphthalma A. Milne-Edwards, 1880. Both species can be easily distinguished morphologically and represent independent evolutionary lineages. The closest relative to Munidopsis balconin. sp. is M. glabra Pequegnat \& Williams, 1995 from the Gulf of Mexico. They can be distinguished by the armature of the carapace and pereiopods, among other differences. Munidopsis pholidota n. sp. is sister to M. squamosa (A. Milne-Edwards, 1880) and both are considered cryptic species, distinguished only by molecular characters and subtle morphological differences like the number of epipodites. Our phylogenetic results show some monophyletic groups within Munidopsis and Munida, and the existence of morphological convergences.


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

## INTRODUGTION

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 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., 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 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 \& Packard, 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, 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 et al., 2014; Poupin \& Corbari, 2016; Macpherson et al., 2016). Both families are highly speciose, with more than 400 species in
the 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; 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 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 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). We herein 1) described the new Munida and Munidopsis species using morphological characters and molecular markers (COI, $16 \mathrm{~S}), 2$ ) 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 species.

## MATERIAL AND METHODS

The terminology used for the descriptions follows Baba et al. (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, maxilliped; 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).

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 16 S ribosomal RNA (16S) were amplified by polymerase chain reaction (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, 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 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 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.
Phylogenetic analyses were performed with the COI data matrix, which included a larger number of taxa, using

MrBayes v3. 2. 1 (Huelsenbeck \& Ronquist, 2001). We selected Munida micropthalma 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 run for $2 \times 10^{7}$ 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. 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.

## TAXONOMY

Family Munididae Ahyong, Baba, Macpherson \& Poore, 2010
Munida Leach, 1820

## Munida anteae n. sp.

Fig. 1
Munida? microphthalma -Poupin \& Corbari, 2016: 40, fig. 10c.
Material examined: Holotype. Guadeloupe, KARUBENTHOS 2015, stn. DW4511, 8 June 2015, $16^{\circ} 13.9^{\prime} \mathrm{N}, 61^{\circ} 51.5^{\top} \mathrm{W}, 630-660$ m: 1 F 5.0 mm (MNHN-IU-2013-18893).

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

Description: Carapace: $1.2 \times$ longer than wide. Ridges mostly interrupted, some scale-like, with conspicuously short non-iridescent 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 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.

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.

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

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


Figure 1. Munida anteae n. sp. holotype, F 5.0 mm (MNHN-IU-2013-18893). Carapace and abdomen, dorsal view (A); sternal plastron (B); cephalic region, showing left antennular and antennal peduncles, ventral view $(\mathbf{C})$; right Mxp3, lateral view $(\mathbf{D})$; right P1, dorsal view $(\mathbf{E})$, right P2 lateral view $(\mathbf{F})$; dactylus of right P 2, lateral view $(\mathbf{G})$; right P 3 , lateral view $(\mathbf{H})$; right P 4 , lateral view $(\mathbf{I})$. Scale bars: A, E, F, H, I $=2.0 \mathrm{~mm} ; \mathrm{B}, \mathrm{C}, \mathrm{D}, \mathrm{G}=1.0 \mathrm{~mm}$.
mesial spine shorter than lateral; 2 spines on lateral margin, proximal one short, at midlength of segment, distal one long, not reaching end of distolateral spine.

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.

Mxp 3: Ischium about $1.5 \times$ 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 several 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.

P2-4: Moderately long, slender, with numerous plumose setae and some iridescent non-plumose setae along extensor margin of each
article. P2 about $2.2 \times$ carapace length. Meri decreasing in length posteriorly ( P 3 merus 0.8 length of P 2 merus, P 4 merus 0.7 length of P3 merus); P2 merus as long as carapace, $\sim 8 \times$ as long as broad, $1.5 \times$ longer than P2 propodus; P3 merus $6.5 \times$ longer than broad, $1.2 \times$ longer than P 3 propodus; P 4 merus $4.5 \times$ as long as broad, 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 $\mathrm{P} 2-3$, unarmed on P 4 ; flexor margins with strong distal spine followed by row of 5 or 6 proximally diminishing spines; lateral surfaces 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 $(\mathrm{P} 4) \times$ as long as broad; extensor margin unarmed; flexor margin with 5-7 slender movable spines. Dactyli slender, length $0.6-0.7 \times$ length of propodi; flexor margin with $8-10$ movable spinules along entire length; P 2 dactylus $6 \times$ longer than wide.

Distribution: Guadeloupe, Caribbean Sea, depth 630 to 660 m .
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 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 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 ( $1 \mathrm{M}, \mathrm{MNHN}$ Ga 959), and additional material from Brazil (l 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 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 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.

The two species are genetically very different. The genetic divergence ranges were $12 \%$ in 16 S and $16-17 \%$ in COI.

Munida anteae $\mathbf{n}$. sp. is also closely similar to M. victoria de MeloFilho, 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. oblongata Cabezas, Macpherson \& Machordom, 2009 from the Solomon Islands. Both species can nevertheless be distinguished morphologically and genetically. Article 1 of the antennular peduncle is slenderer in M. oblongata than in the new species. The Pl palm is slightly shorter than the fingers in the new species, whereas
it is clearly larger in M. oblongata. The Pl carpus is $2.5 \times$ longer 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
Munidopsis Whiteaves, 1874
Munidopsis balconi n. sp.
Figs. 2, 3
Munidopsis squamosa. -Poupin, 1994: 39.

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, $0.3 \times$ carapace length, width


Figure 2. Munidopsis balconi n. sp. holotype, ovig. F 14. 3 mm (MNHN-IU-2014-23830). Carapace and abdomen, dorsal view (A); carapace and abdomen, lateral view $(\mathbf{B})$.


Figure 3. Munidopsis balconin. sp. holotype, ovig. F 14.3 mm (MNHN-IU-2014-23830). Carapace, anterior part, dorsal view (A); sternal plastron (B); telson (C); Cephalic region, showing left antennular and antennal peduncles, ventral view (D); right Mxp3, lateral view $(\mathbf{E})$; right P1, dorsal view $(\mathbf{F})$; right P2 lateral view $(\mathbf{G})$; dactylus of right P 2 , lateral view $(\mathbf{H})$; dight P 3 , lateral view $(\mathbf{I})$; right P 4 , lateral view $(\mathbf{J})$. Scale bars: $\mathrm{A}, \mathrm{B}, \mathrm{C}, \mathrm{D}, \mathrm{E}, \mathrm{H}=2.0 \mathrm{~mm} ; \mathrm{F}, \mathrm{G}, \mathrm{I}, \mathrm{J}=4.0 \mathrm{~mm}$.
$0.3 \times$ anterior width of carapace, directed slightly upwards, dorsally carinate, lateral margins straight. Frontal margin with orbit slightly 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 minute rugosities, anteriorly acute.

Sternum: As long as broad, maximum width at sternite 7. Sternite 3 moderately broad, $2 \times$ wider than long, anterolaterally angular, anterior margin with median notch flanked by 2 lobes. Sternite 4 narrowly elongated anteriorly; surface depressed in midline, smooth; greatest width $3 \times$ that of sternite $3,1.5 \times$ 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. Telson composed of 8 plates; $1.8 \times$ 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 distomesial spine, reaching end of article 2, distolateral angle rounded; article 2 with well-developed distolateral spine, distomesial blunt; articles 3, 4 unarmed.

Mxp3: Surface smooth, with few 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.

P1: Stout, granular, exceeding P2, 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 distal stout spines. Carpus $1.2 \times$ 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, $1.2 \times$ longer than broad. Fingers unarmed, $1.4 \times$ 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, somewhat 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 margin granular. Carpi with thick distal spine on extensor margin, granular carina along lateral side. P2 -4 propodi $3.1-3.6 \times$ as long as high, triangular in cross section, unarmed. Dactyli $0.7-0.9 \times$ length of propodi; distal claw short, moderately curved; flexor margin distally curved, with 9-11 minute teeth decreasing in size proximally, each with slender corneous spine, last tooth as close to penultimate tooth as to dactylar claw.

## Epipods present on P1 and P2.

## Distribution. <br> Guadeloupe, Caribbean Sea; depth 500 m. <br> Genetic data: COI and 16S. GenBank Accession numbers XXXX-XXXX.

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 segments 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 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 reaching midlength of rostrum in M. squamosa, whereas the eyes only have a small tubercular process mediodorsally in the new species. The Pl-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 species. The epipods are present in the $\mathrm{P} 1-3$ in $M$. squamosa, but only in $\mathrm{P} 1,2$ in M. balconi $\mathbf{n}$. sp. Munidopsis balconi $\mathbf{n}$. sp. is larger in size than M. squamosa.

These two species diverge on 18-19\% for the COI and 13\% for the 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 $\mathbf{n}$. sp. The front margin has one antennal spine in M. glabra the spine is absent in M. balconi n. sp. Epipods are present in the $\mathrm{Pl}-3$ of $M$. glabra, but present only in the Pl , 2 in M. balconi $\mathbf{n}$. 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.

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. 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 (welldeveloped epigastric spines in the other two species).

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.

Figs. 4, 6B
Material examined: Holotype. Guadeloupe, KARUBENTHOS 2015, stn. DW4611, 24 June 2015, $16^{\circ} 20^{\prime} \mathrm{N}, 60^{\circ} 52^{\prime} \mathrm{W}, 263-242$ m: 1 M 3.9 mm (MNHN-IU-2016-2365).

## Etymology: From the Greek pholidōtós, 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 grooves. Posterior cardiac region preceded by deep transverse depression. Posterior margin unarmed. Rostrum widely triangular, width $0.3 \times$ anterior width of carapace, directed slightly upwards, dorsally carinate, lateral margins straight; $0.3 \times$ carapace length. Frontal margin with orbit nearly transverse behind ocular peduncle, 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 lateral 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, $2.5 \times$ wider than long, anterolaterally rounded, anterior margin nearly straight. Sternite 4 narrowly elongated anteriorly; surface depressed in midline, smooth; greatest width $2.9 \times$ that of sternite $3,1.9 \times$ wider than long.

Abdomen: Smooth, unarmed; tergites 2, 3 each with 2 slightly elevated transverse ridges, anterior ridge more elevated than posterior 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 composed of 8 plates; $1.5 \times$ as wide as long.

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.


Figure 4. Munidopsis pholidota $\mathbf{n}$. sp. holotype, M 3.9 mm (MNHN-IU-2016-2365). Carapace, dorsal view (A); carapace, lateral view (B); sternal plastron $(\mathbf{C})$; telson $(\mathbf{D})$; cephalic region, showing left antennular and antennal peduncles, ventral view $(\mathbf{E})$; left Mxp3, lateral view $(\mathbf{F})$; right P , dorsal view $(\mathbf{G})$; right P 2 , lateral view $(\mathbf{H})$; dactylus of right P2, lateral view $(\mathbf{I})$; merus and carpus of right P3, lateral view (J); right P4, lateral view ( $\mathbf{K}$ ). Scale bars: A, B, G, H, J, $\mathrm{K}=1.0 \mathrm{~mm} ; \mathrm{C}, \mathrm{D}, \mathrm{E}, \mathrm{F}, \mathrm{I}=0.5 \mathrm{~mm}$.

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.

Mxp3: 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.

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 on mesial and lateral margins and a few distal stout spines. Carpus $1.4 \times$ longer than broad, with some distal stout spines, few acute granules along dorsal side. Palm slender, slightly longer than carpus, $1.6 \times$ longer than broad, with some acute proximal spines on mesial margin. Fingers unarmed, $0.7 \times$ 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, 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 P 2 propodus. Extensor margin of 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 $3.1-3.6 \times$ as long as high, triangular in cross section, unarmed. Dactyli $0.7-0.9 \times$ length of propodi; distal 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.

Epipods present on P1 and P2.
Distribution: Guadeloupe, French West Indies; depth 242-263 m.
Genetic data: COI and 16S. GenBank Accession numbers 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).

## 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). 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).

Material examined. Holotype. Off Martinique, 12 February 1879, $14^{\circ} 29^{\prime} 10^{\prime} \mathrm{N}, 61^{\circ} 5^{\prime} 47^{\prime} \mathrm{W}, 350 \mathrm{~m}: 1 \mathrm{M}$ broken, 4 mm (MCZ CRU-4756).

Other material. Off St. Lucia, 16 February 1879, $13^{\circ} 50.3^{\prime} \mathrm{N}$, $61^{\circ} 3.8^{\prime \prime} \mathrm{W}, 212 \mathrm{~m}:$ F 3.5 mm (MCZ CRU-9784). - Guadeloupe, KARUBENTHOS 2015, stn. DW4634, 27, June 2015, $15^{\circ} 48^{\circ}$ N, $61^{\circ} 26^{\prime}$ W, $310-304 \mathrm{~m}$ : ovig. F 3.5 mm (MNHN-IU-2016-2340). stn. CP4543, 13 June 2015, $16^{\circ} 40^{\prime} \mathrm{N} 61^{\circ} 34^{\prime} \mathrm{W}, 385-399 \mathrm{~m}$ : 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 $0.3 \times$ anterior width of carapace, directed slightly upwards, dorsally carinate, lateral margins straight; $0.3 \times$ 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. Pterygostomian flap smooth, with rugosities, anteriorly acute.

Sternum: As long as broad, maximum width at sternite 7. Sternite 3 moderately broad, $2.5 \times$ wider than long, anterolaterally rounded, anterior margin with median notch flanked by 2 lobes. Sternite 4 narrowly elongated anteriorly; surface depressed in midline, smooth; greatest width $2.9 \times$ that of sternite $3,1.9 \times$ wider than long.

Abdomen: Smooth, unarmed; tergites 2, 3 each with 2 slightly elevated transverse ridges, anterior more elevated than posterior, covered by granules and scales; tergites 4-6 lacking posterior ridge; tergite 6 with weakly produced posterolateral lobes and nearly transverse posteromedian margin. Telson composed of 7 or 8 plates; $1.5 \times$ as wide as long.

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 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, 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 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.

P2-4 (lost in holotype, description of material from Guadeloupe): Stout, coarsely granular, devoid of setae, cylindrical in cross section, slightly decreasing in size posteriorly. P2 merus stout, $0.5 \times$ 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, ending in thick spine; flexor margin granular. Carpi with thick distal spine on extensor margin, granular carina along lateral side. Propodi $3.1-3.6 \times$ as long as high, triangular in cross section, unarmed. Dactyli $0.7-0.9 \times$ length of propodi; distal 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.


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 $(\mathbf{B})$; carapace, lateral view $(\mathbf{C})$; sternal plastron $(\mathbf{D})$; telson $(\mathbf{E})$; cephalic region, showing left antennular and antennal peduncles, ventral view (F); right Mxp3 (G); merus and carpus of right P 2 , lateral view $(\mathbf{H})$; right P 2 , lateral view $(\mathbf{I})$. Scale bars $=1 \mathrm{~mm}$.

Epipods present on P1-3. Distribution. Martinique, St. Lucia, and Guadeloupe, Caribbean Sea; depth 212-399.

Genetic data: COI and 16S. GenBank Accession numbers 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 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 characters currently employed for the taxonomy of Munidopsidae. 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 eight plates and epipods on $\mathrm{Pl}, 2$ or $\mathrm{Pl}-3$. 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 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 comparison among specimens collected in Guadeloupe (Poupin \& Corbari, 2016) revealed differences for genetic markers within


Figure 6. Rostrum and frontal margin of the carapace, dorsal view. Munidopsis amapa Poore, 2014 from Guadeloupe Island, KARUBENTHOS, DW4599, M 3.9 mm (MNHN-IU-2016-2446) (A); M. pholidota $\mathbf{n .}$ 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 $4.0 \mathrm{~mm}(\mathrm{MCZ}$ CRU-4756) (E). Scale bars: A, B, C, D $=0.4 \mathrm{~mm}, \mathrm{E}=1 \mathrm{~mm}$.
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 $\mathrm{Pl}-3$ 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.

Specimens from Guadeloupe belonging to both species diverged on $5.5 \%$ for the COI and $1 \%$ for the 16 S . The genetic divergence of these species with M. amapa was $15 \%$ for the COI and from 11 to $12 \%$ for the 16 S . There is unfortunately no genetic data available for the other species.

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 $\mathbf{n}$. sp. represent a 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 phylogenetically close to the cluster from the eastern Atlantic, suggesting different evolutionary histories and lineage independence.

In the case of Munidopsidae, Munidopsis squamosa and M. pholidotan. sp. were phylogenetically close, forming a clade clustered 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 $\mathbf{n}$. sp. in relation to other species of 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 reconstruction 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 species 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.

## 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
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., 2012, Macpherson \& Baba, 2012, Poore \& Andrakis, 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 employed 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 characters shared by all the species from the monophyletic eastern Atlantic lineage (Fig. 7).

Munidopsis balconi $\mathbf{n}$. sp. as contrasted against M. squamosa is another example of evolutionary convergence in squat lobsters (Fig. 7), in which the existence of carapace sculpture, the reduction of 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).

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 distinguishable when only using morphological characters; however, cryptic species are not commonly found in this family (but see RodríguezFlores et al., 2020). Moreover, several previous works have indicated the polyphyletic nature of both Munida (Machordom \& Macpherson, 2004; Rodríguez-Flores et al., 2019; Miranda et al., 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 (RodríguezFlores, 2021; Machordom et al., unpublished data).

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 eep-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 human activity on their populations and habitats.

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Figure 7. Phylogenetic placement of A. Munida anteae n. sp. (A) and Munidopsis new species $(\mathbf{B})$ 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 (see legend). GenBank accession numbers or voucher codes for the species analyzed in this study are at the tips of each branch.

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