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# A morphological, phylogenetic and phylogeographic reappraisal of the land crabs *Gecarcinus quadratus* De Saussure, 1853, and *G. lateralis* Fréminville in Guérin, 1832 (Decapoda: Gecarcinidae). Are they different species?

IA ATZIMBA TOLEDANO-CARRASCO[1,2], JOSÉ LUIS VILLALOBOS[1*] & FERNANDO ÁLVAREZ[1]
[1] *Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, 04510 Ciudad de México, México*
[2] *iaia@comunidad.unam.mx; https://orcid.org/0000-0001-6918-2509*
[3] *falvarez@unam.mx; http://orcid.org/0000-0002-7347-5483*
[*] *Corresponding author. hiriart@unam.mx; http://orcid.org/0000-0001-6810-2300*

## Abstract

Land crabs of the genus *Gecarcinus* are distributed along both versants of the American continent. At some point four species were recognized: *G. lateralis*, *G. nobilii*, *G. quadratus*, and *G. ruricola*. Taxonomically, several authors have tried to differentiate *Gecarcinus lateralis* from the Atlantic coast and *G. quadratus* from the Pacific coast. Because morphologic characters used showed high intra-population variability, identification were very difficult. Consequently, these two species have occasionally been considered synonyms. To establish the degree of genetic difference between them a molecular analysis was performed with both species, *G. lateralis* and *G. quadratus*, including Mexican Pacific and Atlantic specimens, using the mitochondrial COI and 16S genes. The maximum clade credibility and maximum likelihood trees showed two clades with high support values, one corresponding to the Gulf of Mexico population and the other one to the Pacific coast population, with a genetic distance of 6.1%. The within-clade average distance for the Atlantic populations (*G. lateralis*) was 1.1% and 0.2% for those of the Pacific coast (*G. quadratus*). This supports the status of *G. quadratus* as a valid species, not as a synonym of *G. lateralis*. The estimated time of divergence between both species ranged between 2.3 to 4.3 million years, coinciding with the proposed closure of the Isthmus of Panama. Morphologically, some populations show high variability in somatic characters, whereas sexual appendices of males of both species showed very little variation. Color in life, shape of sternite 3, and shape and degree of coverage of the abdomen of thoracic sternites, in both sexes, are traits that can be used to differentiate both species.

**Key words:** taxonomy, phylogeny, phylogeography, molecular dating, semi-terrestrial crabs

## Introduction

The family Gecarcinidae H. Milne-Edwards 1837, is composed of semi-terrestrial crabs distributed in the tropical coastal plains of the Americas and in the southwestern Pacific region (Guinot *et al*. 2018). They inhabit mangrove forests, as well as inland areas adjacent to salt marshes, estuaries and coastal lagoons, where they play a significant role in the structuring and functioning of the coastal ecosystem, processing organic litter, recycling nutrients and aerating the soil (Jones *et al.* 1994; Sherman 2003; Griffiths *et al*. 2007; McGaw *et al*. 2019).

The genus *Gecarcinus* Leach 1814, is widely distributed in the American Continent. Currently, it contains four species. Two occur along the coast of the eastern Pacific: *G. quadratus* De Saussure, 1853, from the eastern coast of the Gulf of California, Mexico to Peru (Hendrickx 1995; Cuesta *et al.* 2007; Toledano-Carrasco 2019), and *G. nobilii* Perger & Wall, 2014, in Ecuador and Colombia. The other two inhabit the western Atlantic coast: *G. lateralis* Fréminville in Guérin, 1832, occurs from Florida, USA to Venezuela (Toledano-Carrasco 2019), and *G. ruricola* (Linnaeus, 1758) is distributed from Florida, USA, to Nicaragua, including the Caribbean islands (Rathbun 1918; Chace & Hobbs 1969; Perger & Wall 2014). The taxonomic status of *G. quadratus* has remained questionable, as it has been regarded by some authors as a junior synonym of *G. lateralis* (Türkay 1973; Perger & Wall 2014). Rathbun (1918), Powers (1977), von Prahl & Manjarrés (1984), and Abele & Kim (1986) tried to distinguish both species based on morphological characters that are highly variable within populations, such as the shape of the merus of the

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third maxilliped, the degree of coverage of maxillipeds with respect to the epistome of the buccal cavity, and the number of longitudinal rows of spines on the dactyli of pereiopods. This has led to misidentifications. For example, specimens of *G. lateralis* from northeast Mexico were identified as *G. ruricola* in some scientific collections. Due to this variable morphology, Türkay (1970) considered *G. quadratus* as a subspecies of *G. lateralis*; nevertheless, after reviewing the type specimens, he concluded that they were synonymous. Later, Perger & Wall (2014) followed this idea and erected *G. nobilii*, including only three species as valid within the genus (*G. lateralis*, *G. ruricola* and *G. nobilii*) and suggesting the need of molecular analyses including different populations of *Gecarcinus*.

The aim of this study is to evaluate the taxonomic status of *G. quadratus* as a separate species, distinct from *G. lateralis*, employing molecular and morphological characters of specimens from the Pacific and Atlantic coasts of Mexico. Also, we re-evaluate the records of *G. ruricola* from Mexico with a view to recognize possible misidentifications.

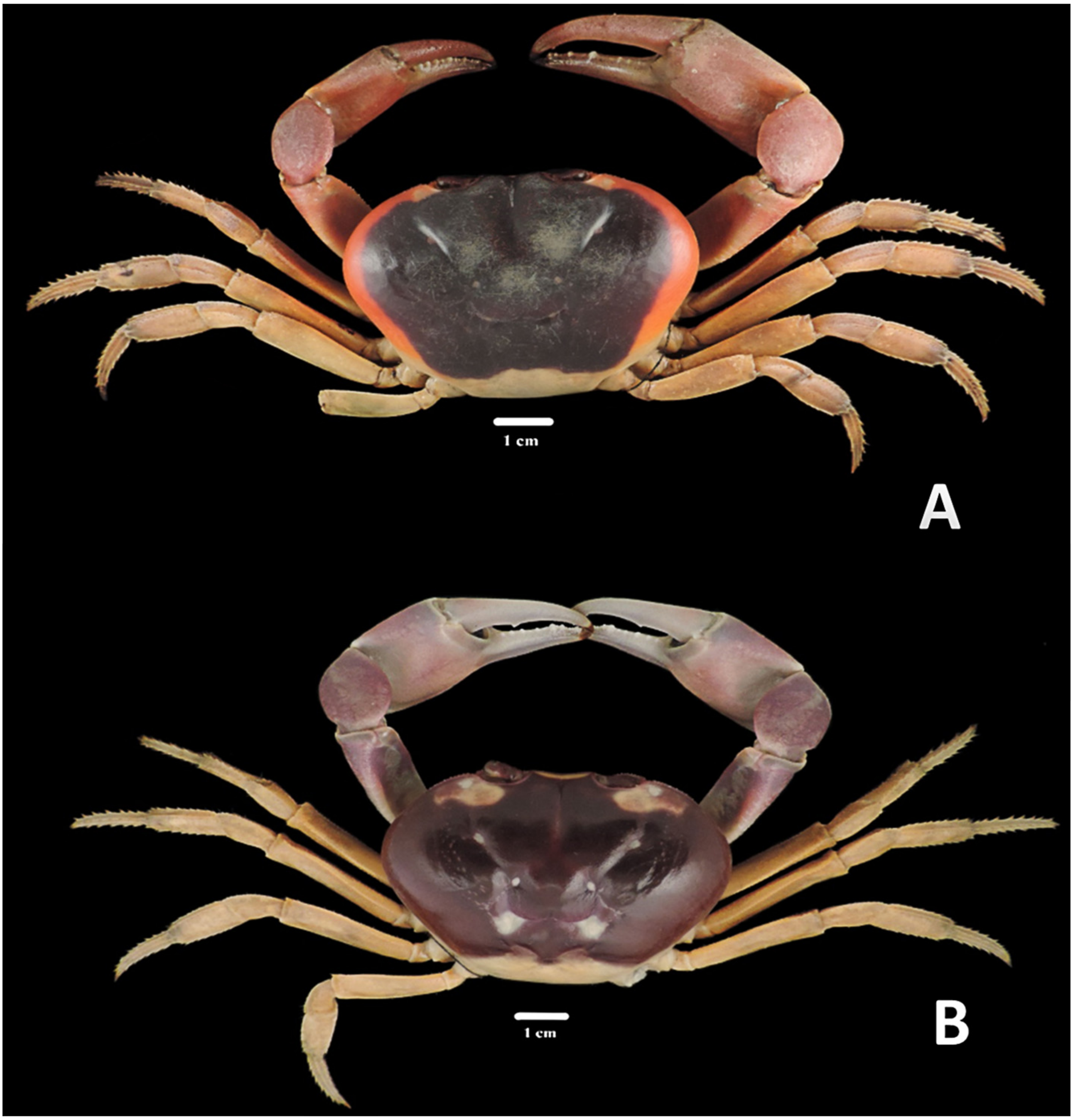

**FIGURE** 1. Dorsal view of: A) *Gecarcinus lateralis* from Río Prieto, Veracruz (CNCR 33942) and B) *G. quadratus* from Barra de Boca del Cielo, Chiapas (CNCR 34630).

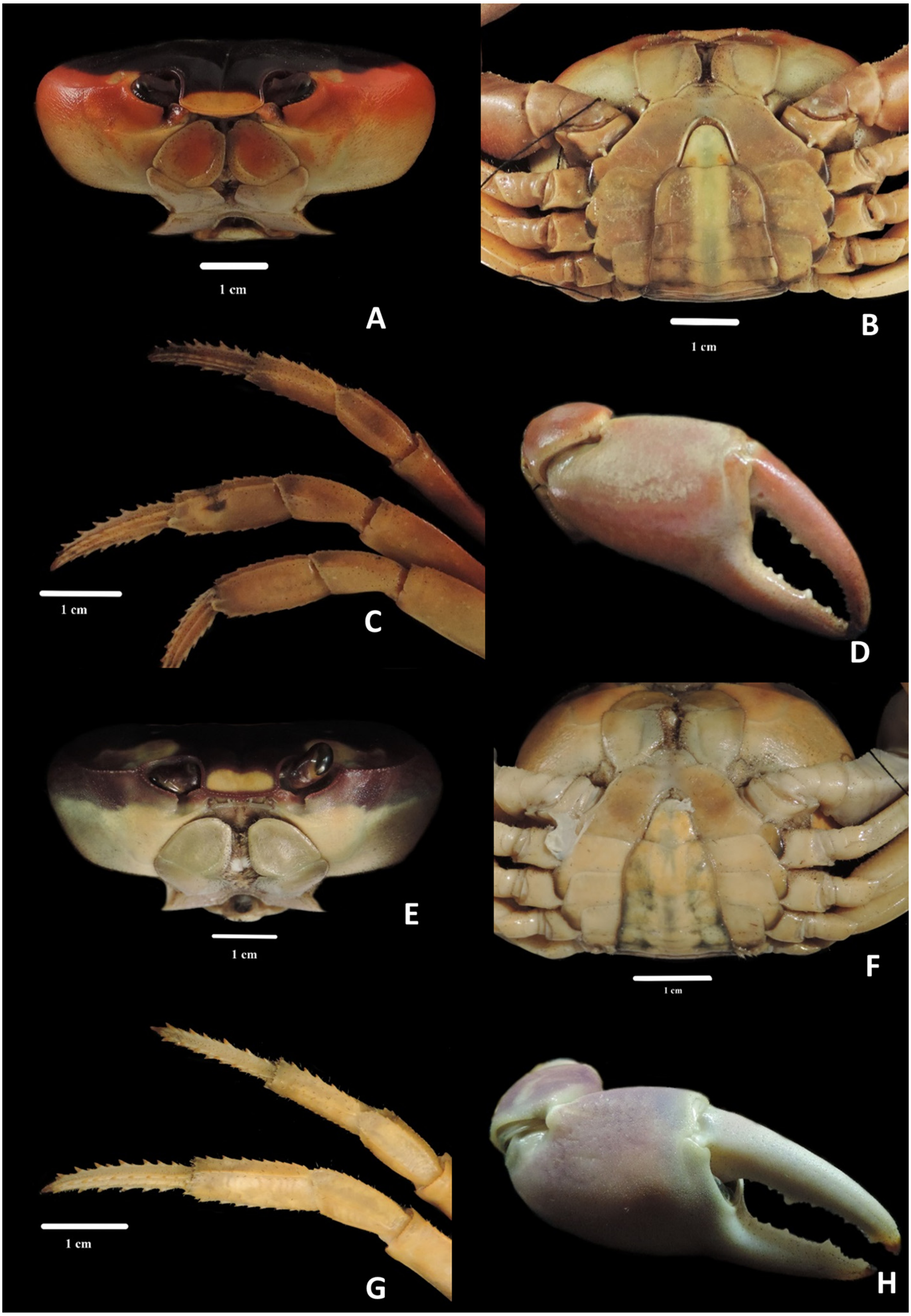

**FIGURE 2.** *Gecarcinus lateralis* from Río Prieto, Veracruz (CNCR 33942): A) frontal view, B) ventral vie, C) rows of spines in the dactyli of the pereiopods, D) major chela. *Gecarcinus quadratus* from Boca del Cielo, Chiapas (CNCR 34630): E) frontal view, F) ventral view, G) rows of spines in the dactyli of the pereiopods, H) major chela.

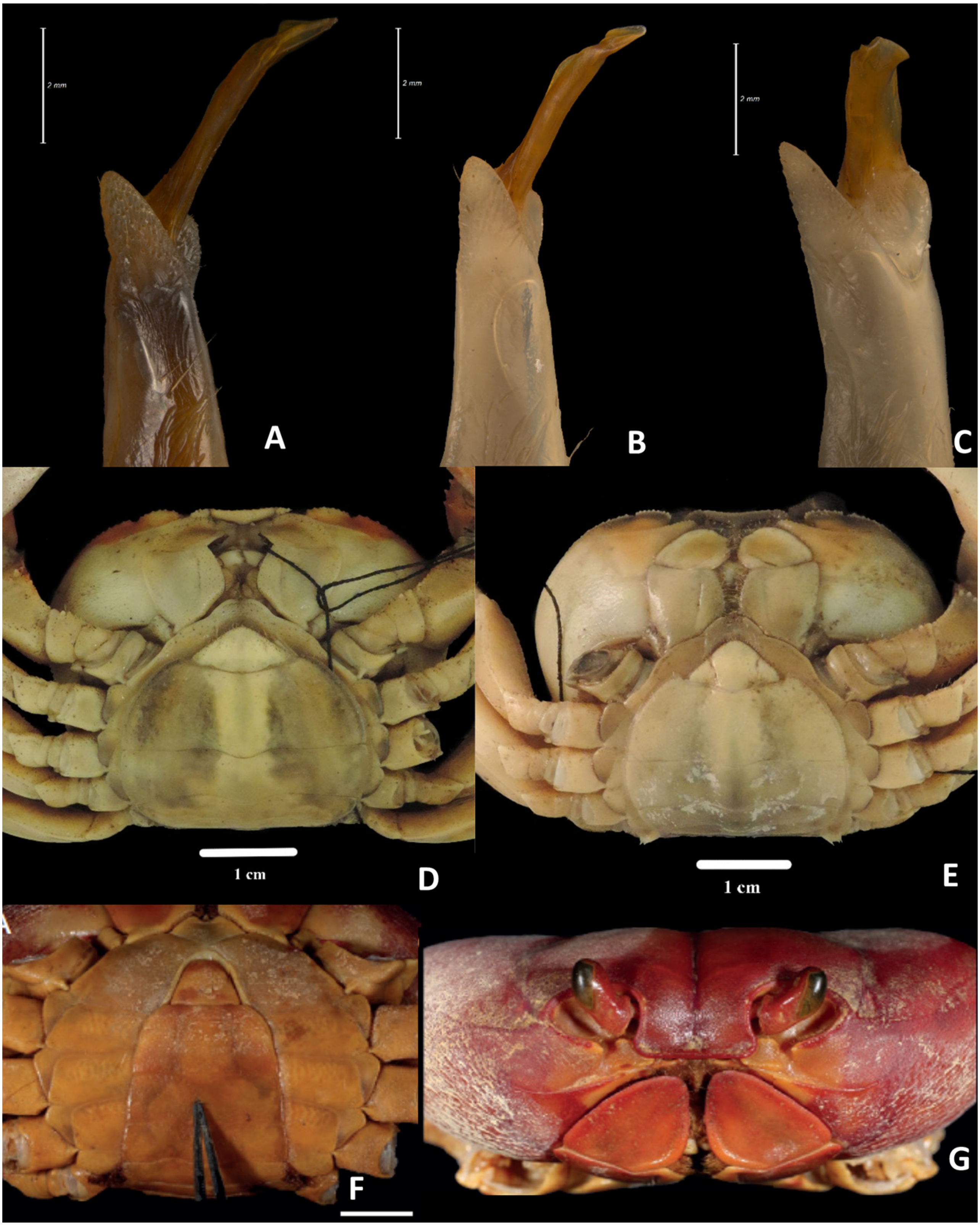

**FIGURE 3.** Left male first gonopod (G1): Cephalic view, A) *G. lateralis* from Río Prieto, Veracruz (CNCR 33942); B) *G. quadratus* from Boca del Cielo, Chiapas (CNCR 34630). Lateral view, C) *G. quadratus* from Boca del Cielo, Chiapas (CNCR 34630). Ventral surface, D) *G. lateralis* female from Barra de Sontecomapan, Veracruz (CNCR 33943); E) *G. quadratus* female from Playa Higuera Blanca, Nayarit (CNCR 34012); F) *G. ruricola* male from Cuba (MNHN-IU-2017-8392). Frontal view, G) *G. ruricola* from Cuba (MNHN-IU-2017-8392) (*G. ruricola* photos modified from Guinot *et al*., 2018).

## Materials and methods

### ***Specimens available and morphological characters***

Fifty-six crabs belonging to *Gecarcinus* and one to *Johngarthia* Türkay, 1970, were analyzed, most of them (45) deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, Universidad Nacional Autónoma de México. The other specimens included were: 10 crabs from the Colección Carcinológica del Laboratorio de Entomología y Artrópodos, Escuela de Biología, Universidad Autónoma de Nuevo León (CCLEA) and one crab from the Colección de Crustáceos de Yucatán (CCY), Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México. The samples came from 23 different localities along the Mexican Pacific and Atlantic coasts. Additionally, four sequences (two COI, two 16S) of *G. lateralis* from Costa Rica and two (COI, 16S) from Panama, courtesy of F. Mantelatto (UNESP, Brazil), were included as well as a sequence of *G. ruricola* from Cuba, obtained from tissue of two pereiopods donated by C. Schubart (Universität Regensburg, Germany). The morphological description of the material examined was based on the terminology proposed by Perger & Wall (2014) for the frontal and orbital structures. Guinot (1979) and Guinot *et al*. (2018) were followed regarding the ventral sternites and sutures that separate each somite. We followed Toledano-Carrasco (2019) for the gonopod description. The synonymy is restricted to the taxonomically important changes in each species. Measurements are in millimeters.

Organisms were morphologically compared and measured to find new characters that could correctly differentiate both species. A photographic catalog of the specimens was made taking three different views of the body, dorsal, ventral and frontal. The left first pleopod or male gonopod (G1), was photographed with a LEICA DFC490 camera adapted to a Leica Z16APOA dissection microscope. Photos of *G. ruricola* were reproduced from Guinot *et al.* (2018). The following abbreviations were used: carapace length (CL), measured along the midline, from the frontal to the posterior margin; carapace width (CW), measured across the carapace at its widest point.

### ***DNA sequencing***

Genomic DNA was isolated from the gills or muscle tissue of specimens previously preserved in 70-80% ethanol, following the protocol of the “Animal and Fungi DNA Preparation Kit, L pack” Kit. Polymerase chain reaction (PCR) was performed to amplify two mitochondrial genes, under the protocol of the MyTaq Kit. A fragment (~ 635 base pairs (bp)) of the cytochrome c oxidase subunit I (COI) gene was amplified using the primers LCO1490 (5´-GGTCAACAAATCATAAAGATATTGG-3´) and HCO2198 (5´-TAAACTTCAGGGTGACCAAAAAATCA-3´) (Folmer *et al*. 1994). The PCR conditions were denaturation for 45 s at 94°C, annealing for 45 s at 48°C and extension for 1 s at 72°C (35 cycles), followed by a final extension for 8 min at 72°C.

A fragment (~ 539 base pairs (bp)) of the 16S rRNA gene was obtained using the primers 16Sa (5´-CGCCTGTTTACTAAAAACAT-3´), 16Sb (5´-CCGGTCTGAACTCAGATCACGT-3´) (Daniels *et al*. 2006) and 16SA-L2510 (5´-CGCCTGTTTATCAAAAACAT-3´), 16SB-H3080 (5´-CCGGTCTGAACTCAGATCACGT-3´) (Kang *et al*. 2015). For the first set of primers the PCR program was: denaturation for 40 s at 95°C, annealing for 40 s at 48-50°C and extension for 40 s at 72°C (35 cycles), and final extension for 10 min at 72°C. For the second set of primers, the PCR program was: denaturation for 1 min at 94°C, annealing for 1 min at 50°C and extension for 1 min at 72°C (35 cycles), followed by a final extension for 8 min at 72°C. Sequences were obtained by automated sequencing on an Applied Biosystems 3500 xL sequencer and were aligned manually, COI sequences with the aid of ClustalW implemented in MEGA 7.0.26 (Kumar *et al*. 2016) and 16S rRNA sequences with the algorithm L-INS-i, in MAFFT v7.397 (Katoh & Standley 2013), after verification with the complementary strand. Additional 16S and COI sequences were downloaded from GenBank, for 16S an organism from Punta Delgada, Veracruz (accession number AJ130804.2.), and for both genes, sequences of *Johngarthia lagostoma* (H. Milne-Edwards, 1837) were included (accession numbers: KT159739.1 and KM578842.1). Finally, *Cardisoma guanhumi* Latreille, 1828, was used as outgroup (accession numbers: MF490171.1 and MF490075.1).

### ***Phylogenetics and phylogeographic analysis***

Analyses were carried out separately for the COI and the 16S rRNA genes. The best fitting models for sequence evolution datasets were determined with jModelTest 2.1.10 (Darriba *et al*. 2012), selected by the Akaike information criterion with correction (AICc). The model for the first codon position of the COI gene was SYM+1, F81 for the second and GTR for the third, while the model chosen for the 16S rRNA gene was GTR+G. A partitioned

Bayesian inference analysis was performed with Mr. Bayes 3.2.2 on XSEDE (Ronquist *et al*. 2012) and the search was run with four chains for 100 million generations, with trees sampled every 10,000 generations. The sample of trees resulting was used to get the maximum clade credibility tree (MCC) in Tree Annotator v1.10.0 (Suchard *et al.* 2018); the first 10,000 trees were discarded since a stationary distribution was reached, these values were collected with Tracer v1.6. (Rambaut *et al*. 2014). The maximum-likelihood (ML) analysis was performed with the RAxML, implemented in Cyberinfrastructure for Phylogenetic Research (CIPRES) (Miller *et al*. 2010), using the default parameters and the GTR+G+I model of evolution. The bootstrap was automatically determined during the run. The trees were observed and edited in Fig Tree v1.4.3 (Rambaut 2014).

Intraspecific and interspecific divergences were calculated with the COI gene sequences, using the Kimura-two-parameter (K2P) substitution model (Kimura 1980), implemented in MEGA 7.0.26. The number of variable sites, the haplotype diversity (Hd), and the nucleotide diversity (π), for each gene, were calculated with the same program. The haplotype network of the COI gene was constructed using the Median-Joining algorithm (Bandelt *et al*. 1999) with Network 10.1.0.0 (https://www.fluxus-engineering.com/sharenet_rn.htm).

The approximate time of divergence was estimated by considering the COI substitution rates of 1.4% and 2.6% per million years, published for snapping shrimps belonging to the genus *Alpheus* from the Isthmus of Panama (Knowlton *et al*. 1993; Knowlton & Weigt 1998).

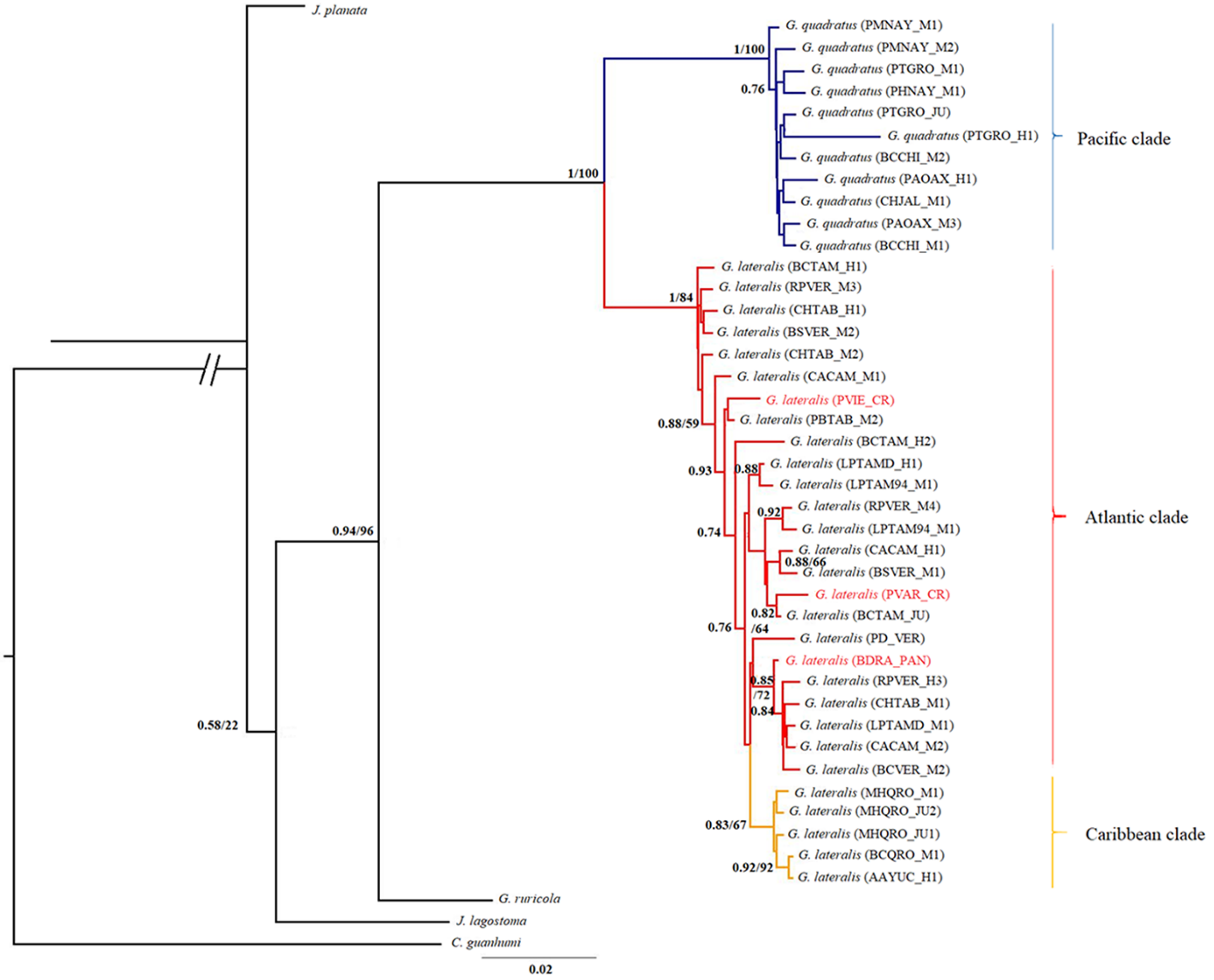

**FIGURE 4.** Maximum clade credibility tree based on Bayesian inference (BI) for *Gecarcinus*, *Johngarthia* and the outgroup, *Cardisoma guanhumi*, using the concatenated matrix of the 16S and COI genes. Probability values at the nodes refer to support values for BI and maximum likelihood (ML). In the assigned key for Mexican specimens, the last letter indicates the sex of the organism: male (M), female (H) or juvenile (JU), followed by the individual number. The organisms highlighted in red in the Atlantic Clade correspond to specimens from Costa Rica and Panama. See the locality list in table 1.

## Results

### *Phylogenetics and phylogeography*

A total of 40 COI sequences were included in the phylogenetic analysis: 11 of *G. quadratus*, 28 of *G. lateralis*, and one of *G. ruricola* (Table 1). A 635-bp segment of COI was amplified and aligned; 113 positions were variable and 55 parsimoniously informative, 20 different haplotypes were identified, 16 for *G. lateralis* and four for *G. quadratus*. For the 16S gene, the 539-bp fragment had 101 polymorphic sites, 30 of which were informative, and nine haplotypes, five for *G. lateralis* and four for *G. quadratus*, were found (Table 2).

According to the K2P genetic distance matrix, *G. quadratus* and *G. lateralis* differed by 6.1%, while intraspecifically the distances were 1.1% for *G. lateralis* and 0.2% for *G. quadratus* (Table 3). The genetic distance between *G. lateralis* populations from the Gulf of Mexico and the Caribbean Sea was 0.6%. *Gecarcinus ruricola* differed by 10.1% from *G. quadratus* and 9.6% from *G. lateralis* (Table 3).

Divergence time was estimated by using the average genetic distance between both the Pacific and the Atlantic clades, 6.1%, and the COI mutation rates of 1.4% and 2.6% per million years, resulted in a time interval ranging from 2,346,153 to 4,357,142 years.

The phylogenetic tree based on the concatenated matrix of both genes (1,174 bp), was constructed using BI with the support values from BI and ML analyses. In all the analyses the separation of *G. quadratus* and *G. lateralis* as different clades was strongly supported; the specimens from Costa Rica (Puerto Vargas-PVAR_CR) and Panama (Bocas del Toro-BDRA_PAN) appeared immersed with those from the Gulf of Mexico. In addition, *G. lateralis* from the Caribbean grouped together next to the Gulf of Mexico specimens. The clade formed by *G. quadratus* and *G. lateralis* appears related to *G. ruricola* from Cuba. They, in turn are recovered as a sister clade of *Johngarthia lagostoma*, however, the branch support values were low. *Johngarthia planata* (Stimpson, 1860) is recovered as a separate clade, but only 16S sequences could be obtained for this species (Fig. 4).

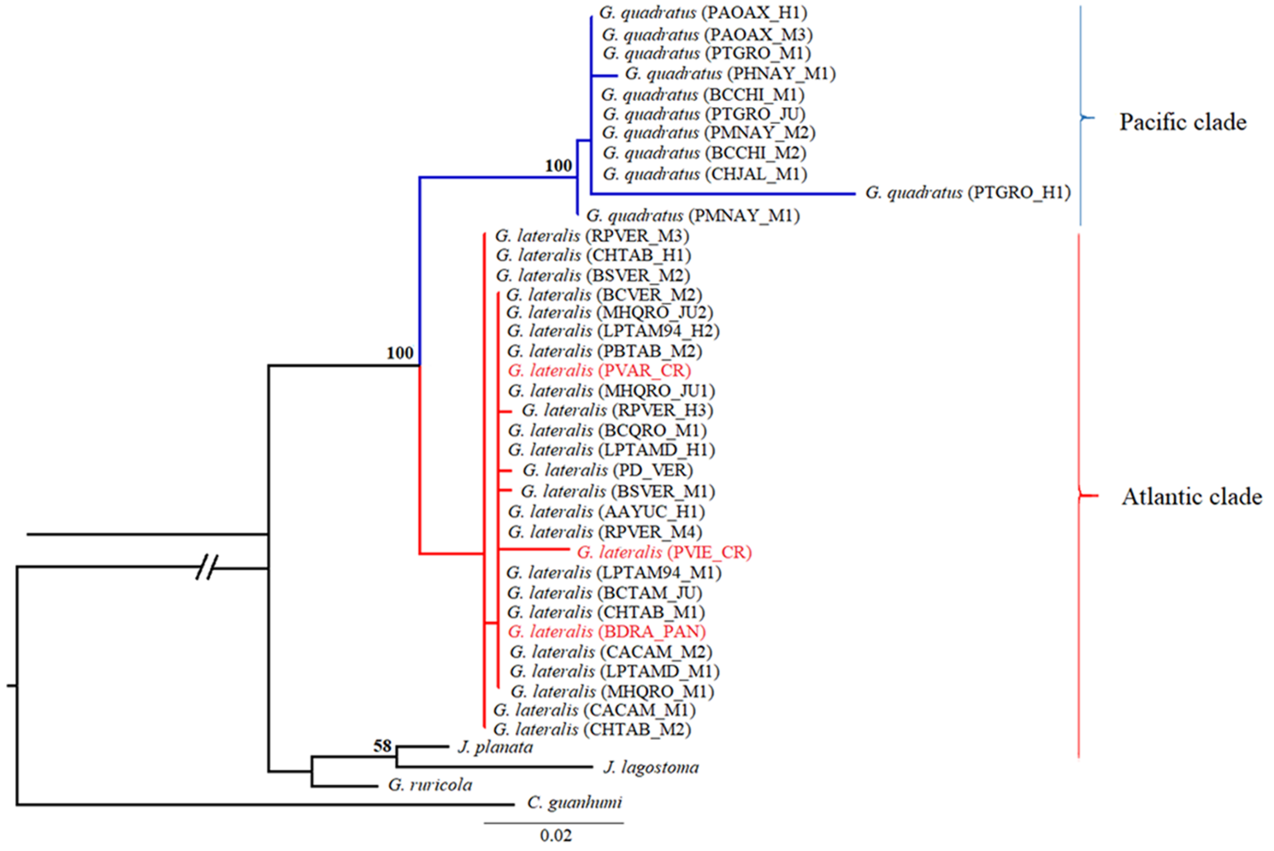

**FIGURE 5.** Maximum likelihood tree (ML) for *Gecarcinus*, *Johngarthia* and the outgroup, *Cardisoma guanhumi*, using the 16S gene. Probability values at the nodes represent support values for likelihood (ML). In the assigned key for Mexican specimens, the last letter indicates whether the organism is male (M), female (H) or juvenile (JU) followed by the individual number. The organisms highlighted in red in the Atlantic Clade correspond to specimens from Costa Rica and Panama. See the locality list in table 1.

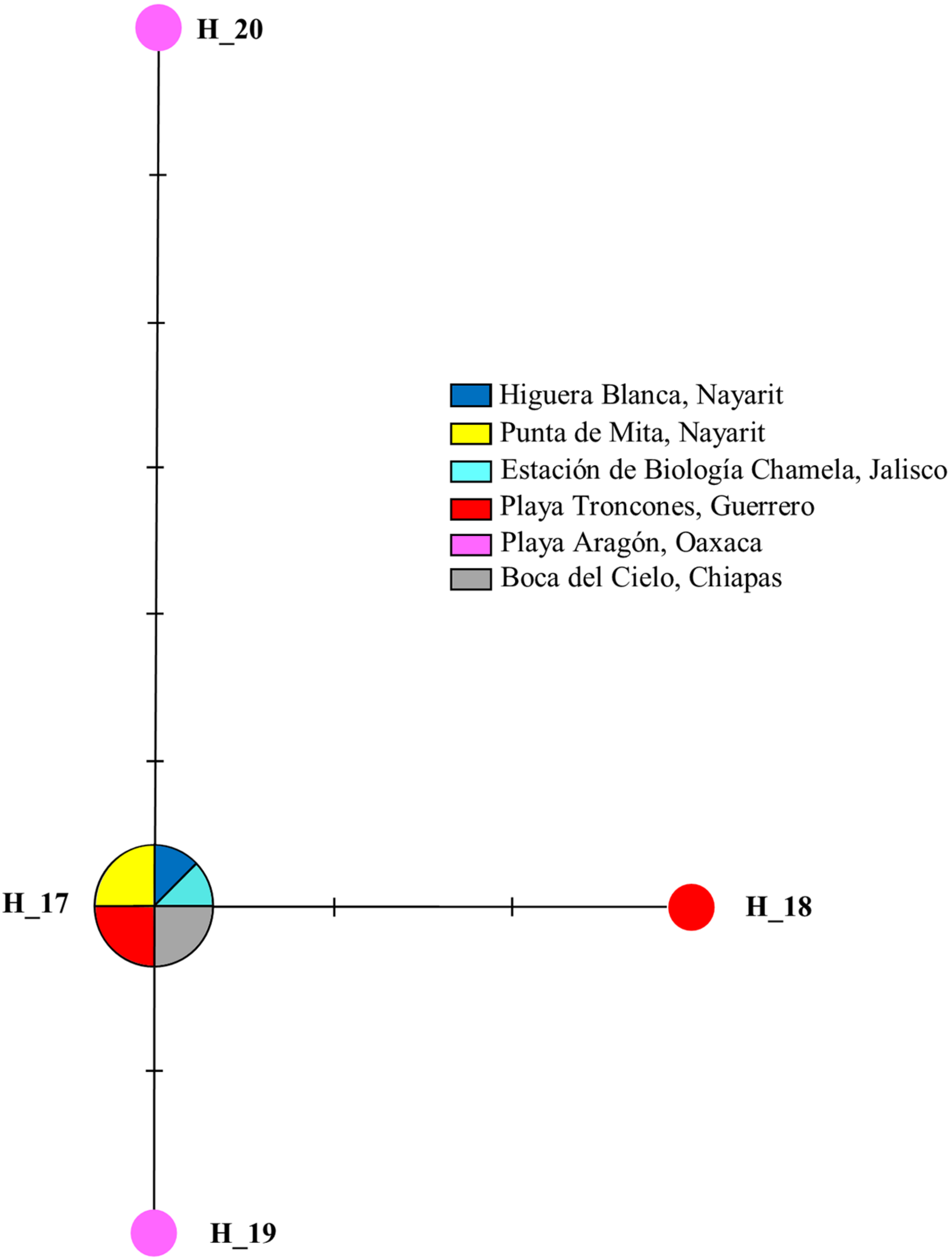

**FIGURE 6.** Median-joining network for *Gecarcinus quadratus* based on the alignment of the mitochondrial gene COI. Each middle line indicates one mutational step between haplotypes. Circles represent different haplotypes and their diameters the frequency of each.

**TABLE 1.** Data of the organisms that were sequenced for both genes, including the catalogue number in the respective biological collections or the accession number in GenBank, the locality, the key assigned for each individual in phylogenetic and phylogeographic analyses. In the assigned key, the last letter indicates whether the organism is male (M), female (H) or juvenile (JU) followed by the individual number. The dashes represent sequences that could not be obtained, either because they could not be amplified or they were not available in GenBank.

| Catalogue no./ accession number | Locality | State of Mexico/ Country | Key assigned for COI | Haplotype of COI | Key assigned for 16S |
|---|---|---|---|---|---|
| **CNCR 19003** | Playa Troncones | Guerrero | PTGRO_H1 | H_17 | PTGRO_H1 |
| | | | PTGRO_M1 | H_18 | PTGRO_M1 |
| | | | PTGRO_JU | H_17 | PTGRO_JU |
| CNCR 34013 | Playa Aragón | Oaxaca | PAOAX_H1 | H_20 | PAOAX_H1 |
| | | | PAOAX_M3 | H_19 | PAOAX_M3 |
| **CNCR 33941** | Punta Mita | Nayarit | PMNAY_M1 | H_17 | PMNAY_M1 |
| | | | PMNAY_M2 | H_17 | PMNAY_M2 |
| **CNCR 34012** | Playa Higuera Blanca | | PHNAY_M1 | H_17 | PHNAY_M1 |
| CNCR 34630 | Barra de Boca del Cielo | Chiapas | BCCHI_M1 | H_17 | BCCHI_M1 |
| | | | BCCHI_M2 | H_17 | BCCHI_M2 |
| CNCR 34846 | Estación Biología Chamela | Jalisco | CHJAL_M1 | H_17 | CHJAL_M1 |
| C86-7182 | La Laguna | Tamaulipas | BCTAM_H1 | H_3 | - |
| | | | BCTAM_H2 | H_9 | - |
| | | | BCTAM_JU | H_7 | BCTAM_JU |
| C86-07094 | La Pesca | | LPTAM94_H2 | H_5 | LPTAM94_H2 |
| | | | LPTAM94_M1 | H_11 | LPTAM94_M1 |
| FD | | | LPTAMD_M1 | H_13 | LPTAMD_M1 |
| | | | LPTAMD_H1 | H_6 | LPTAMD_H1 |
| C86-06601 | Barra de Cazones | Veracruz | BCVER_M2 | H_14 | BCVER_M2 |
| CNCR 33942 | Río Prieto | | RPVER_H3 | H_13 | RPVER_H3 |
| | | | RPVER_M3 | H_3 | RPVER_M3 |
| | | | RPVER_M4 | H_12 | RPVER_M4 |
| CNCR 33943 | Barra de Sontecomapan | | BSVER_M1 | H_10 | BSVER_M1 |
| | | | BSVER_M2 | H_3 | BSVER_M2 |
| AJ130804.2 (GenBank) | Punta Delgada | | - | | PDVER |
| C86-06495 | Playa Bruja | Tabasco | PBTAB_M2 | H_3 | PBTAB_M2 |
| C86-06500 | Chiltepec | | CHTAB_H1 | H_3 | CHTAB_H1 |
| | | | CHTAB_M1 | H_15 | CHTAB_M1 |
| | | | CHTAB_M2 | H_3 | CHTAB_M2 |
| CNCR 34011 | Cayo Arcas | Campeche | CACAM_H1 | H_8 | - |
| | | | CACAM_M1 | H_4 | CACAM_M1 |
| | | | CACAM_M2 | H_13 | CACAM_M2 |
| YUC-CC-255-11-001024 | Arrecife Alacranes | Yucatan | AAYUC_H1 | H_1 | AAYUC_H1 |
| CNCR 34010 | Mahahual | Quintana Roo | MHQRO_M1 | H_2 | MHQRO_M1 |
| | | | MHQRO_JU1 | H_2 | MHQRO_JU1 |
| | | | MHQRO_JU2 | H_2 | MHQRO_JU2 |
| CNCR 30834 | Isla Cayo Norte Menor, Banco Chinchorro | | BCQRO_M1 | H_1 | BCQRO_M1 |

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

**TABLE 1. (Continued)**

| Catalogue no./ accession number | Locality | State of Mexico/ Country | Key assigned for COI | Haplotype of COI | Key assigned for 16S |
|---|---|---|---|---|---|
| CCDB1520 | Puerto Viejo, Limón | Costa Rica (Atlantic) | PVIE_CR | H_3 | PVIE_CR |
| CCDB1109 | Puerto Vargas, Parque Nacional Cahuita | Costa Rica | PVAR_CR | H_16 | PVAR_CR |
| CCDB2553 | Bocas del Drago, Bocas del Toro | Panama | BDRA_PAN | H_13 | BDRA_PAN |
| AM_Gruricola | Playa Larga | Cuba | G_ruricolaCU |  | G_ruricolaCU |
| CNCR 19002 | Playa Troncones | Guerrero | - |  | J_planata |
| KT159739.1<br>KM578842.1<br>(GenBank) | - | - | J_lagostoma |  | J_lagostoma |

In general, clades obtained in the MCC tree for COI under the BI method showed high branch supports compared to those of ML (Fig. 4). Topologies of the 16S and COI fragments presented some discrepancies, particularly with regard to the position of *G. ruricola* relative to other *Gecarcinus* and *Johngarthia*. For the 16S tree under ML, clades from the Atlantic slope had low support values, while those from the Pacific formed a polytomy, excluding only one specimen from Punta Mita, Nayarit (Fig. 5).

Overall, Atlantic populations were genetically more diverse than those from the Pacific. For the COI gene, a total of 28 polymorphic sites and 16 haplotypes were obtained for *G. lateralis* with a Hd = 0.5233 and Π= 0.0099. For the 16S gene, eight polymorphic sites and five haplotypes were obtained with a Hd = 0.498 and Π= 0.0016. The Pacific populations of *G. quadratus* had eight polymorphic sites and four haplotypes for COI with a Hd = 0.491 and Π= 0.0023. For the 16S gene, 15 polymorphic sites were calculated. As a result, the degree of polymorphism was higher (Π=0.0055) than for COI. However, the number of haplotypes and consequently the haplotype diversity had the same values (Tables 2, 3).

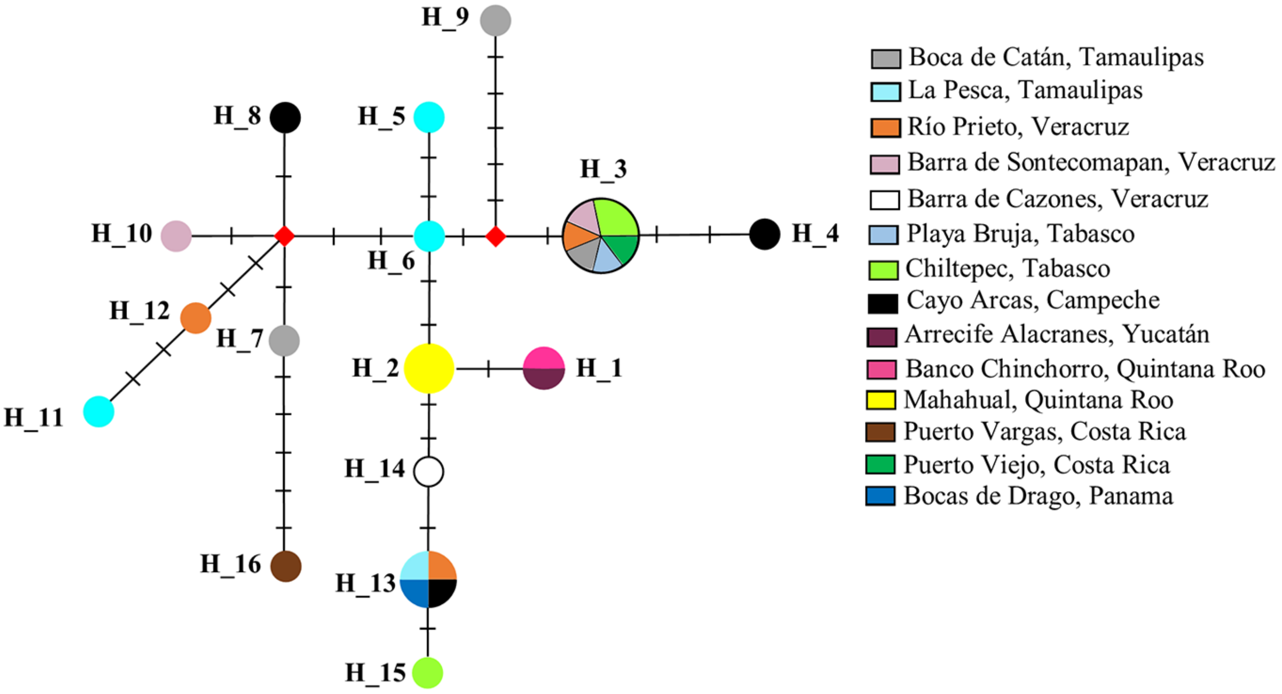

**FIGURE 7.** Median-joining network for *Gecarcinus lateralis* based on the alignment of the mitochondrial gene COI. Small red rhombuses correspond to missing or hypothetical haplotypes. Each middle line indicates one mutational step between haplotypes. Circles represent different haplotypes and their diameters their frequency of appearance.

The haplotype network for the Pacific coast populations showed haplotype H_17 to be the most common one in eight individuals and distributed in five localities. Playa Troncones and Playa Aragón were the localities with two haplotypes, while the rest had one haplotype (Fig. 6; Table 1). In the Atlantic, the most frequent haplotype was H_3 with seven individuals, distributed in six localities, followed by the H_13 with four individuals in four localities. Playa Brujas, Tabasco (H_3) and Barra de Cazones (H_14) had one haplotype because only one individual was sequenced. In the Caribbean region, two haplotypes (H_1 and H_2) were found distributed in three localities, Mahahual and Banco Chinchorro in Quintana Roo and Arrecife Alacranes in Yucatán, of which H_2, had more organisms (Fig. 7; Table 1).

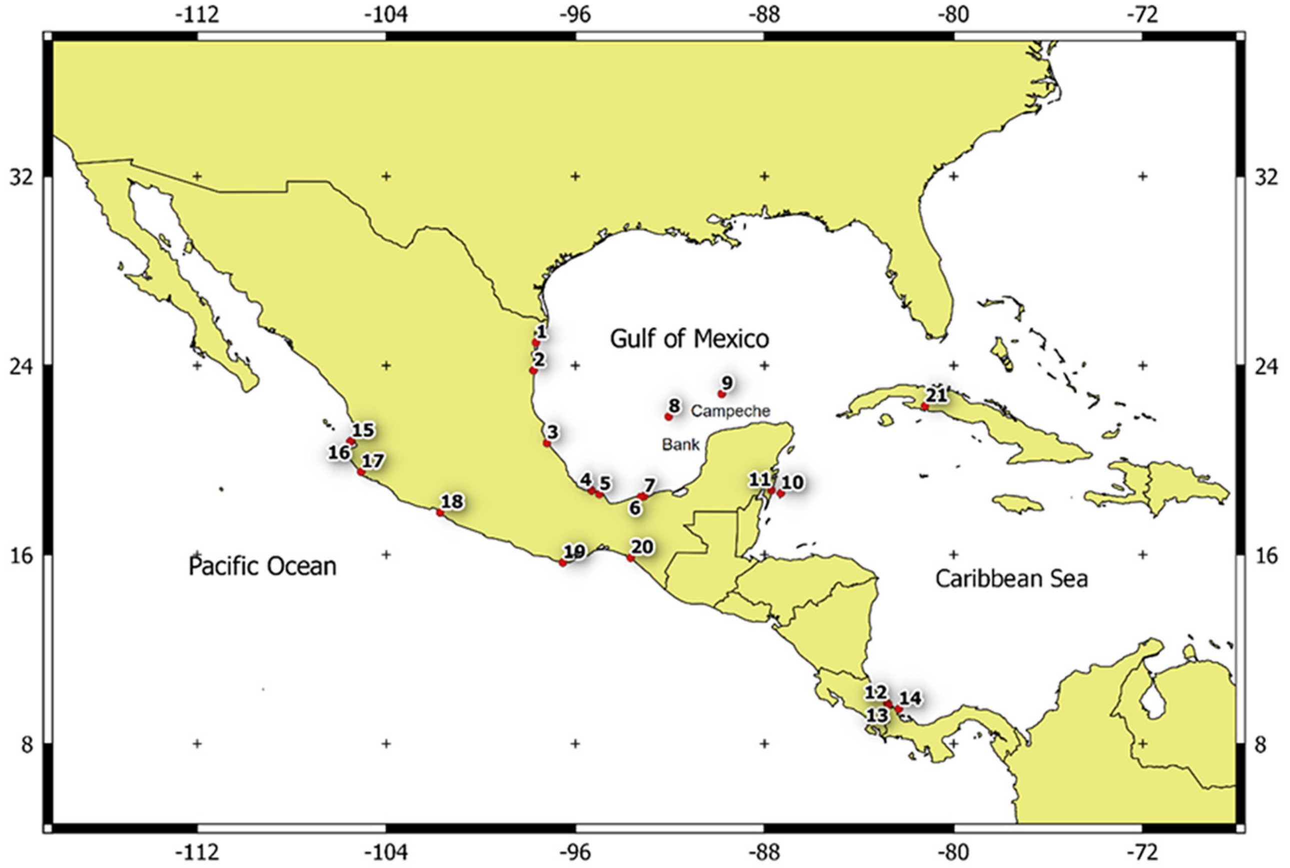

**FIGURE 8.** Localities of *Gecarcinus lateralis* and *G. quadratus* analized. 1) Boca de Catán, Tamaulipas. 2) La Pesca, Tamaulipas. 3) Barra de Cazones, Veracruz. 4) Río Prieto, Veracruz. 5) Barra de Sontecomapan, Veracruz. 6) Chiltepec, Tabasco. 7) Playa Bruja, Tabasco. 8) Cayo Arcas, Campeche. 9) Arrecife Alacranes, Yucatán. 10) Banco Chinchorro, Quintana Roo. 11) Mahahual, Quintana Roo. 12) Puerto Vargas, Costa Rica. 13) Puerto Viejo, Costa Rica, 14) Bocas del Drago, Panamá. 15) Playa Higuera Blanca, Nayarit. 16) Punta Mita, Nayarit. 17) Estación de Biología Chamela, Jalisco. 18) Playa Troncones, Guerrero. 19) Playa Aragón, Oaxaca. 20) Boca del Cielo, Chiapas. 21) Playa Larga, Cuba.

## Taxonomy

Descriptions were based on 23 *G. lateralis* and 33 *G. quadratus* from Mexico. A diagnosis of *Gecarcinus* is provided followed by complete descriptions of both species.

## Genus *Gecarcinus* Leach 1814

**Diagnosis.** Carapace transversely oval with branchial regions inflated. Pterygostomian regions glabrous. Anterior part of lateral border marked by marginal line. Fronto-orbital border 1/2 or less than 1/2 greatest breadth of carapace. Front strongly deflexed, frontal edge horizontal, from 1/5 to 1/8 the greatest breadth of carapace. Orbits deep, not much wider than high, outer angle obtuse, not prominent, inner angle as stout angular tooth touching inferior angle of front; a deep U-shaped sinus next to it. Eyes nearly filling orbits (Rathbun 1918). Proepistome hardly discernible, inserted under lower margin of narrow front (Guinot *et al*. 2018). Epistomal edge sometimes covered by third maxillipeds. Oral cavity subcircular or rhomboid, wider in the middle, margins with dense strip of bristles; third maxillipeds separated, central opening rhomboid, exposing mandibles; ischium and merus broad, subequal in length, merus suboval, hiding short and robust palp, the latter articulated in the middle of anterior margin of merus. Exognath hidden behind ischium, without flagellum, shorter than ischio-meral articulation. Chelipeds sturdy, almost smooth, in adults can be slightly or evidently different in size and robustness (smaller and weaker in females); internal surface of palm of major chela with or without tuberculated longitudinal ridge. Robust ambulatory appendages, second pair longest, last 3 joints armed with spines, dactyli with 4-6 longitudinal rows. First male pleopod (G1) semi-cylindrical, terminal apical element more than 1/3 of G1 length, extending distally well beyond apex, as narrow, chitinous, semi-cylindrical structure, open with longitudinal furrow in lateral view, distal end widening in caudal and cephalic views. Main axis of G1 with suture mostly visible in mesial view, distal portion of cephalic surface, ending in finger-like projection, pointed and elongated or rounded and relatively short, directed apically or cephalically, ornamented with slender bristles extending distally (Fig. 3A, B) (Toledano-Carrasco 2019). In lateral view, distal portion of main axis excavated, ending in two projections, a corneous process and finger-like projection of cephalic surface; the former extending distally, rectangular, smoothly ribbed, ending obliquely with cephalic margin reaching beyond caudal one, the latter sharply triangular, about 1/2 as long as the former (Fig. 3C). In caudal view, excavation of G1 main axis evident, corneous process inclined mesially. In cephalic view, apical plate directed distolaterally, fused to distal end of lateral surface, apically concave; marginal suture along cephalic surface of main axis (Fig. 3A, B) (Toledano-Carrasco 2019).

Sternal surface of carapace with bands of short setae between sternites 4–5. Sternite 1 as small triangular tooth, not separated by suture from sternite 2; sternite 2 semi-ovate or trapezoidal; suture 2/3 straight, weakly marked, or V-shaped and well-developed; sternites 3–4 completely fused with straight or convex, obliquely directed lateral margins, thus not restricted at level of first pereopods (P1). Sternites 5–7 with similar shape, sutures well defined. Sternite 8 totally hidden when pleon is folded (Figs. 2B, F; 3D, E, F), posterior emargination reaching sternite 7 at level of narrow median bridge situated at level of suture 7/8. Another weak median bridge present at level of suture 6/7 (*G. ruricola*) or traces of it (*G. lateralis, G. quadratus*). Male genital orifice completely sternal (Guinot, 1979). Sternites 3–4 with sterno-pleonal rim well-marked or rounded and slightly marked. Locking structure formed by button covered with setae in *G. ruricola* and *G. quadratus* (Köhnk *et al*. 2017; Guinot *et al*. 2018). Abdomen subtriangular in males, semi-circular in females, with 7 articulated somites in both sexes (Figs. 2B, F; 3D, E, F) (Toledano-Carrasco 2019). Margins of abdomen with dense tufts of hydrophilic setae, facing row of setae on adjacent portions of last sternites (Bliss 1963; Wolcott 1984), Müller's channel absent (De Oliveira 2014).

**Remarks.** Guinot *et al*. (2018) reexamined all gecarcinid morphological characters, and divided the family Gecarcinidae into two subclades. The first clade included: *Cardisoma* Latreille, 1828, *Discoplax* A. Milne-Edwards, 1867, and *Tuerkayana* Guinot *et al.*, 2018; the second subclade, with a higher degree of terrestriality, included: *Gecarcinus* Leach, 1814, *Gecarcoidea* H. Milne-Edwards, 1837, and *Johngarthia* Türkay, 1970. Among the important characters shared by *Gecarcinus* and *Johngarthia* is the stridulatory apparatus, which is used to produce sounds when these crabs are disturbed in their retreats (Abele *et al*. 1973). The sound is produced when oblique rows of rugosities on the subhepatic region are rubbed against the tuberculated internal margin of the merus of the cheliped in *G. quadratus*, or against a longitudinal tuberculated ridge on the internal surface of the palm of the major cheliped in *G. lateralis* (Klaassen 1973; Abele *et al*. 1973).

The ability to absorb water from the substrate is well developed in *Gecarcoidea natalis* (Pocock, 1889) and *Gecarcinus lateralis*, in which setal tufts extend along the first three pleonal somites and on the coxa of P5 to establish a connection with the pericardial sacs (Bliss 1963, 1968; Greenaway 1988). In *Gecarcinus ruricola* and *Gecarcoidea lalandii* H. Milne Edwards, 1837, the posterior margin of sternite 7 is lined with dense hydrophilic setae in contact with tufts of setae on the coxa of P5 and pleonal somites 1-3 (Guinot *et al*. 2018).

### *Gecarcinus lateralis* Fréminville in Guérin, 1832

(Figs. 1A; 2A-D; 3A, D)

*Gecarcinus lateralis* Fréminville in Guérin 1832: 7, pl. 5, figs. 1, 1a–b.
*Ocypoda lateralis*.—Fréminville 1835: 224.
*Gecarcinus lateralis*.—H. Milne-Edwards 1837: 27, pl. 18, figs. 1–6. De Saussure 1858: 440.
*Geocarcinus lateralis*.—Young 1900: 239.
*Gecarcinus lateralis*.—Rathbun 1918: 355. Chace & Hobbs 1969: 198.
*Gecarcinus (Gecarcinus) lateralis lateralis*.—Türkay 1970: 337.
*Gecarcinus (Gecarcinus) lateralis*.—Türkay 1973: 974.
*Gecarcinus lateralis*.—Powers 1977: 139.
*Gecarcinus (Gecarcinus) lateralis lateralis*.—von Prahl & Manjarrés 1984: 158.
*Gecarcinus lateralis*.—Abele & Kim 1986: 661. Hernández-Aguilera 1996: 92. Schubart *et al*. 2006: 195. Ng e*t al*. 2008: 215. Felder *et al*. 2009: 1088. Low *et al*. 2013: 101. Perger & Wall 2014: 97. Hermoso-Salazar & Arvizu-Coyotzi 2015: 21. Guinot *et al*. 2018: 568-570. Toledano-Carrasco 2019: 18-22. Ng *et al*. 2019: 99-100.

**Material examined.** MEXICO. Tamaulipas: 2 females, 1 juvenile, CCLEA C86–07182, Municipality San Fernando, La Laguna, Boca de Catán, Apr 04, 2014, coll. G. Rodríguez; 1 female, CCLEA, C86–07094, Municipality Soto La Marina, La Pesca, Oct 20, 2014, coll. G. Rodríguez; 1 male, 1 female, CCLEA C86–07094 jar D, same locality and collector data as previous, Sept 24, 2016.– Veracruz: 1 male, CCLEA C86–06601, Municipality Cazones, Barra de Cazones, Jan 24, 2015, coll. G. Rodríguez; 2 males, 1 female, CNCR 33942, Municipality Ángel R. Cabada, Río Prieto, coll. anonymous; 2 males, CNCR 33943, Municipality Catemaco, Barra de Sontecomapan, Apr 24, 2017, colls. I. Toledano, E. Moreno, J.L. Villalobos.– Tabasco: 1 male, CCLEA C86-06495, Municipality Paraíso, Playa Bruja, Oct 14, 2006, coll. G. Rodríguez; 1 male, 1 female, CCLEA, C86-06500, Municipality Paraíso, Chiltepec, Apr 06, 2007, coll. G. Rodríguez.– Campeche: 2 males, 1 female, CNCR 34011 Cayo Arcas, Apr 06, 2017, coll. anonymous; 1 female, CCY YUC-CC-255-11-001024, Municipality Progreso, Arrecife Alacranes, Aug 01, 2009, coll. C. Cinthya Delgado.– Quintana Roo: 1 male, 2 juveniles, CNCR 34010, Municipality Othón P. Blanco, Playa Mahahual, Mar 12, 2017, coll. Anonymous; 1 male, CNCR 30834, Isla Cayo Norte Menor, Banco Chinchorro, Mar 28, 2013, coll. anonymous.

**Diagnosis.** Male abdomen triangular; telson campanulate, narrower than sixth abdominal somite, lateral margins slightly marked, tip rounded. Sixth somite with convex lateral margins, forming lateral shoulder (Fig. 2B). Female abdomen subcircular, completely or almost completely covering thoracic sterna; telson triangular, as wide as posterior margin of sixth somite, lateral margins straight, smooth (Fig. 3D). Antero-lateral margins of sternite 3 slightly convex, those of sternite 4 straight, with slight concavity (Figs. 2B, 3D). Shallow endostomial ridges delimiting efferent branchial channel, poorly defining this region. Third maxilliped with merus generally concealing epistome. Adult male chelae different in size and robustness; inner surface of palm of major chela with longitudinal tuberculated ridge, used as stridulatory plectrum.

**Description.** Based on adult male with G1 well developed (54.3 mm CL, 71.7 mm CW). Carapace transversely oval, wider anteriorly, strongly arched at level of branchial regions, anterolateral margin incipient, posterior portion of external orbital angle slightly marked, armed with minuscule granules. Regions well defined, delimited by shallow grooves. Branchial regions prominent. Fronto-orbital margin about 1/2 of maximum carapace width (Fig. 1A). Front about 1/4 length of carapace, deflexed, surface slightly concave, occasionally straight, inferior margin granulated, raised from surface, straight, generally concealing basal segments of antennules; frontal lobes poorly defined (Fig. 2A).

Orbits delimited by well defined, smooth superior border. Infra-orbital margin granulated, interrupted by deep notch, continued as triangular plate forming mesial lobe. Suborbital ridge well marked (stridulating crest of Guinot *et al*. 2018), extending from superior border of epistome to subhepatic suture. Surface of anterolateral wall of carapace reticulated (pars strident). Third maxillipeds not closing completely, leaving rhomboidal gap; merus covering epistome anteriorly, anterior border with medial notch, occasionally straight; ischium longer than merus, subequal in width. Palp short, hidden and articulated behind merus, directed laterally (Fig. 2A). Short exognath hidden behind ischium.

Strong heterochely in males, subequal chelipeds in females; fingers longer than palm, with corneous tips; longitudinal rows of granules throughout surface; cutting margins bearing 6–8 irregularly spaced blunt teeth; dactyl slightly curved inwards; fingers gapping (Fig. 2D). Internal surface of palm swollen, with distinct longitudinal ridge along midsection, used as stridulatory plectrum, internal depression next to articulation with carpus. Carpus subtriangular, dorso-mesial margin smooth in large organisms, spinulous in small ones. Merus elongated, subtriangular, internal border granulated.

Pereiopods (2–4) long, slender, with short setae; merus elongated, surface striated; carpus subtriangular, shorter than propodus, or almost of same length in fifth pair, dorsal margin toothed; propodus shorter than dactyl, dorsal and ventral margins formed by short, slender spines; dactyli armed with 4–6 rows of spines, those on lateral carina poorly developed to absent (Fig. 2C).

Male and female abdomen as in species diagnosis.

Male G1, as in genus diagnosis (Fig. 3A).

Female (39 mm CL, 33–50 mm CW), with gonopore on sixth plate of thoracic sternum, protruding. Ring around operculum oval, with sharp edges; operculum a large, oval, protruding lobe.

*Coloration*. Dorsal surface of carapace dark, lateral margins orange, posteriorly light cream. Chelipeds and lower portion of front orange (Fig. 1A)

**Measurements.** Males: 28.6–49.1 mm CL; 33.9–64.5 mm CW. Females 27.3–39 mm CL, 33–50 mm CW.

**Remarks.** The authorship of the species was attributed to Fréminville (1835) for many years who originally named organisms from the French West Indies: Marie-Galante, La Désirade, Guadeloupe and Martinique, as *Ocypode lateralis.* However, Low *et al.* (2013) reported that Guérin in 1832 had already used the name "*Gecarcinus lateralis* Freminv." in his *Iconographie du Règne animal* by G. Cuvier and, hence, he must be recognized as the author of the species.

### *Gecarcinus quadratus* De Saussure 1853

(Figs. 1B; 2E–H; 3B, C, E)

*Gecarcinus quadratus* De Saussure 1853: 360. Rathbun 1918: 358. Garth 1948:58.
*Gecarcinus (Gecarcinus) lateralis quadratus*.—Türkay 1970: 338. von Prahl & Manjarrés 1984: 155.
*Gecarcinus quadratus*.—Ng *et al*. 2008: 215. Arzola-González *et al*. 2010: 187.
*Gecarcinus lateralis*.—Perger & Wall 2014: 97.
*Gecarcinus quadratus*.—Guinot *et al*. 2018: 568-570. Toledano-Carrasco 2019: 22-26. Ng *et al*. 2019: 99-100.

**Material examined.** MEXICO. Sinaloa: 8 males, 2 females, CNCR 362, Municipality Mazatlán, Isla Venados, May 30, 1974, colls. M.C. Chávez, C.A. Martínez.– Nayarit: 2 males, CNCR 33941, Municipality Bahía de Banderas, Punta de Mita, Apr 21, 2017, Coll. Anonymous; 1 male, CNCR 34012, Municipality Bahía de Banderas, Playa Higuera Blanca, Jul 07, 2017, coll. J.L. Villalobos.– Jalisco: 1 female, CNCR 3514, Municipality La Huerta, Playa La Rosada, Bahía de Chamela, Jun 16, 1984, coll. A. Cantú; 1 female, CNCR 3517, Municipality La Huerta, Salinas, Bahía de Chamela, Jun 15, 1984, colls. J.C. Nates, J.L. Villalobos, A. Cantú; 1 male, CNCR 34846, Municipality La Huerta, Estación de Biología Chamela, Instituto de Biología, UNAM, no date, coll. anonymous.– Michoacán: 1 male, CNCR 11736, Municipality Aquila, Playa de Maruata, Jun 20, 1990, coll. M.S. García; 2 females, CNCR 25629, Municipality Lázaro Cárdenas, Río Popoyuta, cerca desembocadura, Jul 12, 1986, coll. A. Raz Guzman; 3 males, 2 females, CNCR 6158, Municipality Aquila, Monte del Oro, km 175 carretera Tecomán-Playa Azul, Mar 03, 1986, coll. R. Lamothe, L.J. Rangel.– Guerrero: 1 male, 1 female, 1 juvenile, CNCR 19003, Municipality La Unión de Isidoro Montes de Oca, Playa Troncones, N of Zihuatanejo, Jan 01, 2001, coll. C. Candelaria.– Oaxaca: 1 male, 1 female, CNCR 34013, Municipality Santa María Tonameca, Playa Aragón, Jan 01, 2017, coll. anonymous; 1 male, 1 female, CNCR 3031, Municipality Santa María Colotepec, Playa El Carrizalillo, Puerto Escondido, Sep 08, 1983, coll. A. Cantú.– Chiapas: 2 males, CNCR 34630, Municipality Tonalá, Barra de Boca del Cielo, Mar 08, 2018, colls. J.L. Villalobos, I. Toledano, E. Moreno.

**Diagnosis.** Male abdomen triangular; telson triangular, lateral margins straight continuous with those of sixth abdominal somite, slightly marked, tip moderately rounded. Sixth somite with posterior margin as broad as telson or slightly wider, lateral margins forming continued straight margin with telson (Fig. 2F). Female abdomen subcircular, not covering thoracic sternum completely; telson triangular, narrower than posterior margin of sixth somite, lateral margins slightly concave with faint vertical suture at middle (Fig. 3E). Antero-lateral margins of sternites 3-4 widely convex at junction of third maxillipeds, gently concave at level of articulation of first pereiopods (Figs. 2F, 3E). Endostomial ridges (Davie *et al*. 2015) delimiting efferent branchial channel. Third maxilliped with merus not reaching epistome.

**Description.** Carapace transversely oval, wider anteriorly, strongly arched at level of branchial regions, anterolateral margin thin. Regions well-defined, delimited by shallow grooves. Branchial regions prominent. Fronto-orbital margin about half of maximum carapace width (Fig. 1B). Front about 1/4 length of carapace, deflexed, surface slightly concave; inferior margin lightly granulated, not raised from surface, straight, leaving visible basal segments of antennules; frontal lobes poorly defined (Fig. 2E).

Orbits delimited by well defined, smooth, superior border. Infra-orbital margin granulated, interrupted by deep notch, continued as subrectangular or low subtriangular plate forming mesial lobe; area of contact between internal angle of front and mesial lobe of infraorbital margin of variable width (Perger & Wall 2014), reaching superior border of epistome. Suborbital ridge softly marked, short, extending laterally from superior border of epistome, not reaching subhepatic suture. Third maxillipeds not closing completely, leaving rhomboidal gap; merus not reaching epistome, anterior border straight, occasionally with shallow emargination or discontinuity; ischium with scattered setae on mesial margin, subequal in width to merus, but longer than it (Fig. 2E). Palp short, hidden, articulated behind merus, directed laterally. Exognath hidden behind ischium, without flagellum, not reaching ischium-merus articulation.

Chelipeds in both sexes subequal or similar, evident heterochely in largest males. Chelae with fingers longer than palm, with corneous tips, surface with longitudinal rows of pits and granules, more evident dorsally; cutting margins with distinct subacute tubercles along fingers length, dactyl slightly curved inwards, with 8-10 irregularly spaced small blunt teeth, largest tooth on proximal half; fixed finger with 11-12 irregularly spaced small blunt teeth, largest tooth on distal half; fingers gapping (Fig. 2H). Palm with internal surface smooth, swollen, without tuberculated longitudinal ridge, internal depression next to articulation with carpus. Carpus subtriangular, dorso-mesial margin smooth in large organisms or with spinules in small ones. Merus elongated, subtriangular, inner surface striated, used as stridulatory plectrum.

Pereiopods long, slender with short setae; merus elongated, surface striated, dorsal ridge distally spinulated; carpus subtriangular, shorter than propodus, or almost of same length in fifth pair, distal half of dorsal ridge spinulated; propodus shorter than dactyl, dorsal, ventral and lateral ridges armed with short, thin spines; dactyli armed with 6 rows of spines (Fig. 2G), 5 rows in juveniles.

Male and female abdomen as in species diagnosis.

Male G1, as in genus diagnosis (Fig. 3B, C).

*Coloration.* Dorsal surface of carapace dark purple, posterior and postero-lateral margins yellow or slightly orange, as well as the ambulatory appendages. Yellow or light orange patches above orbits, and on lower part of front. Chelipeds purple, carpus and merus darker (Fig. 1B).

**Measurements.** Males: 35.8–54.3 mm CL; 44.9–71.7 mm CW. Females 33– 51.8 mm CL; 38.7–63.9 mm CW.

**Remarks.** With the resurrection of *G. quadratus* as a distinct species and geminate analogue from the western Atlantic of *G. lateralis*, new morphologic and genetic analyses including the eastern Pacific *G. nobilii* are necessary. According to Perger & Wall (2014), *G. nobilii* is distinguished from *G. lateralis* because the former has a particular coloration: carapace without lighter anterolateral and posterior patches on the light lateral margin, carpus and palm of chelipeds homogeneously red or white. Additionally, the frontal width is distinctly greater than the distance between the mesial ends of the suborbital cristae. Also, the width of the mesial lobe of the infraorbital margin at point of contact with the carapace front is longer than the shortest distance between the carapace front and the mesial end of the suborbital crista (Perger & Wall 2014).

## Discussion

### *Phylogenetics and phylogeography*

The two sequenced genes, 16S and COI, showed low variability (haplotype and nucleotide diversity) in *G. lateralis* and *G. quadratus*; however, using COI alone it was possible to distinguish two well-supported clades, corresponding to the Atlantic and Pacific specimens. The genetic distance (6.1%) with COI between *G. lateralis* and *G. quadratus* was high in comparison to the within species distance (1.1% and 0.2%, respectively), establishing a clear difference between the two species (Table 3). Similar values in the COI have been obtained in studies with trans-isthmian species, for example, *Aratus pisonii* H. Milne Edwards, 1853, and *A. pacificus* Thiercelin & Schubart, 2014, had distances ranging between 4.5 and 5.7% (Thiercelin & Schubart 2014). Cryptic new species of the gecarcinid genus *Gecarcoidea* were erected with smaller distance values, *G. humei* (Wood-Mason, 1874) had an average distance of 1.47% and 2.07% from *G. lalandii* and *G. natalis*, respectively (Lai *et al.* 2017).

Within the Atlantic coast populations of *Gecarcinus lateralis*, we detected significant departures in terms of genetic distances. The specimens from Boca de Catan, Tamaulipas, Mexico (BCTAM_H2) and those from Puerto Vargas, Costa Rica (PVAR_CR) differ between 2.1 and 2.9% from the rest, suggesting that more than one species of *Gecarcinus* might occur along the Atlantic coast.

Divergence time of the Atlantic and Pacific lineages was estimated at 2.3–4.3 million years ago (mya) which coincides with the closure of the Isthmus of Panama that has been dated by several authors in different time ranges: Collins (2003) 4 mya, Coates & Obando (1996) 2.8–3.1 mya, and Jackson & O´dea (2013) and Weir *et al.* (2009) 3–4 mya; however, the exact time of the closure of the Isthmus remains in dispute.

*Gecarcinus lateralis* from the southwestern Gulf of Mexico and Mexican Caribbean (Arrecife Alacranes, Mahahual and Banco Chinchorro) were genetically very homogeneous and clearly different from the Atlantic populations (La Laguna, La Pesca, Barra de Cazones, Río Prieto, Barra de Sontecomapan, Playa Bruja and Chiltepec). This could indicate the presence of barriers formed by currents inside the Gulf of Mexico, causing a weak connection between the the Bank of Campeche keys (Arcas, Triángulos and Arenas) and the western portion of the gulf, as has been suggested by Johnson *et al*. (2013), Sanvicente-Añorve *et al*. (2014), Jordán-Dahlgren (2002) and Oliveira *et al*. (2018). In the case of *G. ruricola*, it was interesting to note that higher genetic distances separate it from *G. lateralis* and *G. quadratus* (9.6% and 10.1%, respectively) than from *Johngarthia lagostoma* (8%), suggesting that further analyses should be conducted to evaluate the generic divisions.

Within *G. lateralis* some clades were recovered with strong branch supports, relating organisms from the Atlantic of Central America to those from Mexico and not revealing significant differences. In contrast, in *G. quadratus* only one clade was well-supported, the rest formed a large polytomy that, in addition to the genetic distances, highlight the homogeneous genetic makeup of these populations. *Gecarcinus lateralis* from Cayo Arcas showed greater genetic affinity with other localities from the Gulf of Mexico rather than with those of Arrecife Alacranes (Fig. 4), which is also considered part of the Campeche Bank Reef System, this is consistent with observations of Sanvicente-Añorve *et al*. (2014), who suggested that the connection between the keys Arcas, Triángulos and Arenas was higher than with Alacranes (Fig. 8).

The haplotype network obtained for *G. lateralis* showed a complex structure due to the 16 haplotypes obtained for only 28 individuals (Fig. 7; Table 2). This haplotype diversity can be associated with geological events that have occurred during the Neogene (23 mya to present). Two of the vicariant mechanisms that have been considered very important are: 1) the closing of the Isthmus of Panama in the Pliocene, originating sister or geminate species as in the case of *Gecarcinus lateralis* and *G. quadratus*, and 2) the periodic glaciations throughout the Neogene, leading to sea level fluctuations and climate changes that fragmented populations that were later connected again. Virtually, all species in the Gulf of Mexico experienced the effects of glaciations, with the most recent event ending 12,000 years ago (Neigel 2009).

**TABLE 2.** Genetic diversity of mitochondrial COI and 16S genes for *Gecarcinus lateralis* and *G. quadratus* populations. N: number of sequences used, K: number of polymorphic sites, H: number of haplotypes, Hd: haplotype diversity, π: nucleotide diversity.

| Gene | Species | N | K | H | Hd | Π |
|---|---|---|---|---|---|---|
| COI | *G. lateralis* | 28 | 28 | 16 | 0.918 | 0.0099 |
| COI | *G. quadratus* | 11 | 8 | 4 | 0.491 | 0.0023 |
| 16S | *G. lateralis* | 26 | 8 | 5 | 0.498 | 0.0016 |
| 16S | *G. quadratus* | 11 | 15 | 4 | 0.491 | 0.0055 |

In contrast, in *G. quadratus*, four haplotypes were found for 11 individuals from Nayarit to Chiapas (Fig. 6; Table 3). This pattern could be the result of either: 1) a higher natural connectivity among populations along the Pacific coast, or 2) population reductions that produced bottlenecks reducing the genetic variability. Arnaud *et al.* (2000), proposed that some causes of bottlenecks in marine populations can be epidemiological problems, environmental changes or human impact.

**TABLE 3.** K2P pairwise nucleotide divergences for COI. Values are given in average percentages.

| | *C. guanhumi* | *G. quadratus* | *G. lateralis* | *G. ruricola* |
|---|---|---|---|---|
| *G. quadratus* | 21.1 | 0.2 | | |
| *G. lateralis* | 21.6 | 6.1 | 1.1 | |
| *G. ruricola* | 19.2 | 10.1 | 9.6 | |
| *J. lagostoma* | 18.6 | 12.8 | 11.8 | 8 |

### *Morphology*

The examined crabs from Mexico showed a consistent coloration; however, Perger & Wall (2014) reported crabs from the Atlantic coast of Costa Rica with a coloration similar to *G. quadratus* from Mexico, suggesting that coloration was not a good character to separate species. Unfortunately, specimens sheltered in biological collections lose their coloration over the years, hindering the correct identification of old preserved specimens. However, according to Bruce (1975) and Knowlton (1986), live coloration patterns are useful to distinguish among problematic decapod species that differ slightly in their morphology. For instance, in cryptic species of hermit crabs (e.g., Malay & Paulay 2009), spiny lobsters (Ravago & Juinio-Meñez 2003), porcelain crabs (Hiller *et al*. 2006) and the blue crab of Christmas Island *Tuerkayana celeste* (Ng & Davie 2012), congruent genetic and coloration differences have been observed.

The shape of sternite 3, as well as the shape of the abdomen and its width, were constant characters in both species and were not size-dependant. These differences were more evident in males (Figs. 2B, F). Overall, the abdomen of *G. lateralis* females exhibited in most cases an enlarged sixth somite (Figs. 3D, E). This character has been used to distinguish species within the genus *Discoplax* A. Milne Edwards, 1867, in which there was a slight variation in the shape of the sixth somite in males (Ng & Shih 2015).

There are strong morphological differences between *Johngarthia* and *Gecarcinus* that have already been noted by several authors (e.g., Türkay 1970; Cuesta *et al*. 2007; Perger *et al*. 2011). Additionally, Guinot *et al*. (2018) observed differences in the abdomen locking apparatus; in *G. ruricola* and *G. quadratus* (see Köhnk *et al*. 2017) there is a button, while in *Johngarthia* there is a large, oblique prominence, both structures covered with setae (Guinot & Bouchard, 1998, as *G. planatus* = *Johngarthia planata*); but in both genera the pleonal sockets are not delineated, so the locking is no longer functional.

In this study we observed significant differences among *G. ruricola, G. quadratus* and *G. lateralis*. In the former, the body regions and the frontal lobes are well-defined and divided by a deep median groove, in contrast, these are poorly defined in the two other species (Figs. 2A, E; 3G). Regarding the thoracic sternum, in *G. ruricola*, sternite 2 is semi-ovate and the lateral margins of sternite 3 are poorly arched, while in the other two species, sternite 2 is trapezoidal and the lateral margins of sternite 3 are convex, being strongly arched in *G. quadratus*. Also, *G. ruricola* has a sternite with a well-developed V-shaped suture 2/3 and its congeneric species show a horizontal and faint suture (Figs. 2B, F; 3D–F). In *G. ruricola*, there is a weak triangular median bridge at level of suture 6/7 and a very narrow one at level of suture 7/8, while in *G. quadratus* and *G. lateralis* only some traces of such bridges remain and in *Johngarthia* the bridges are indistinct (Guinot *et al*. 2018).

Although in many brachyuran species the morphology of the male gonopod is a key character to distinguish among species (Guinot 1979; Brandis *et al.* 1999; McLay & Becker 2015), in the *Gecarcinus* group there is very little morphological variation, not enough to distinguish among species.

All the genetic analyses and morphological observations made by Guinot *et al.* (2018) suggest that a new genus, which includes *G. lateralis*, *G. quadratus* and *G. nobilii*, should be erected, since *G. ruricola* shows significant differences when compared to its congeneric species and to *Johngarthia*.

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