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Gecarcinus ruricola (Linnaeus, 1758), the 'black land crab' of San Andrés Archipelago, Colombia: two females having laid their eggs in the sea are setting off again for return migration (Gabriela Dominguez, MFA/Filmmaker, bluelizardstudio.co).

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ABSTRACT

Detailed adult morphologies of the largest living brachyuran crabs have been surprisingly neglected. This is exemplified by the type genus of the family Gecarcinidae H. Milne Edwards, 1837, *Gecarcinus* Leach, 1814, and by its type species, the charismatic land crab *G. ruricola* (Linnaeus, 1758), remarkable for its considerable size, its ecological, economic and cultural importance throughout the Caribbean region. *Gecarcinus* currently includes three other terrestrial species: *G. lateralis* Fréminville *in* Guérin, 1832, distributed on the American continent and in the Caribbean Islands; *G. quadratus* Saussure, 1853 and *G. nobilii* Perger & Wall, 2014 only on the American continent. In the context of an ongoing revision of the Gecarcinidae by the first two authors, *Gecarcinus* revealed not monophyletic, which is supported by morphological and molecular data. *Gecarcinus* new status is redefined to include only *G. ruricola*; the three remaining species are transferred to a new genus, *Hartnollius* n. gen., with the following combinations: *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., *H. quadratus* (Saussure, 1853) n. comb. and *H. nobilii* (Perger & Wall, 2014) n. comb. We designate here a neotype for *Cancer ruricola* Linnaeus, 1758. Molecular data highly support that morphological differences observed through *G. ruricola* distribution (position of merus mxp3 in relation to frontal margin, position of extremity of sterno-pleonal cavity in relation to thoracic sternal suture 2/3) are due to intraspecific variability. Previous references to *G. ruricola* in Florida and Nicaragua are found to be erroneous, *G. ruricola* proving to be a specifically insular species. The case of *Gecarcinus depressus* Saussure, 1857, described from Haiti, is documented.

KEY WORDS
Gecarcinus n. status,
Hartnollius lateralis n. comb.,
H. quadratus n. comb.,
H. nobilii n. comb.,
terrestriality,
ICZN,
phenotypic variations,
geographical distribution,
insularity,
genetics,
neotype,
new combinations,
new genus.

RÉSUMÉ

Le charismatique Gecarcinus ruricola *(Linnaeus, 1758), espèce type de* Gecarcinus *Leach, 1814, avec désignation d'un néotype et données génétiques, et nouvelle attribution générique,* Hartnollius *n. gen., pour les trois espèces restantes du genre (Crustacea, Brachyura, Gecarcinidae).*

La morphologie adulte détaillée des crabes brachyoures vivants de grande taille a été étonnamment négligée. L'illustration en est donnée ici par le genre type de la famille des Gecarcinidae H. Milne Edwards, 1837, *Gecarcinus* Leach, 1814, et par son espèce type, le charismatique crabe terrestre *G. ruricola* (Linnaeus, 1758), remarquable par sa taille considérable, son importance écologique, économique et culturelle dans toute la région des Caraïbes. *Gecarcinus* comprend actuellement trois autres espèces terrestres : *G. lateralis* Fréminville *in* Guérin, 1832, réparti sur le continent américain et dans les îles des Caraïbes ; *G. quadratus* Saussure, 1853 et *G. nobilii* Perger & Wall, 2014, uniquement sur le continent américain. Dans le contexte d'une révision en cours des Gecarcinidae par les deux premiers auteurs, *Gecarcinus* s'est révélé non monophylétique, ce qui est confirmé par les données morphologiques et moléculaires. *Gecarcinus* n. status est redéfini pour inclure uniquement *G. ruricola* ; les trois espèces restantes sont transférées dans un nouveau genre, *Hartnollius* n. gen., avec les combinaisons suivantes : *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., *H. quadratus* (Saussure, 1853) n. comb. et *H. nobilii* (Perger & Wall, 2014) n. comb. Nous désignons ici un néotype pour *Cancer ruricola* Linnaeus, 1758. Les données moléculaires démontrent avec une valeur de soutien élevée que les différences morphologiques observées dans la distribution de *G. ruricola* (position du mérus mxp3 par rapport au bord frontal, position de l'extrémité de la cavité sterno-pléonale par rapport à la suture sternale thoracique 2/3) sont dues à une variabilité intraspécifique. Les précédentes références à *G. ruricola* en Floride et au Nicaragua se révèlent erronées, *G. ruricola* s'avérant être une espèce spécifiquement insulaire. Le cas de *Gecarcinus depressus* Saussure, 1857, décrit de Haïti, est documenté.

MOTS CLÉS
Gecarcinus n. status,
Hartnollius lateralis n. comb.,
H. quadratus n. comb.,
H. nobilii n. comb.,
terrestrialité,
ICZN,
variations phénotypiques,
distribution géographique,
insulatité,
génétique,
néotype,
combinaisons nouvelles,
genre nouveau.

INTRODUCTION

The detailed adult morphologies of the largest brachyuran crabs have surprisingly been ignored and received little close scrutiny. This is the case for the two largest brachyurans, namely the largest-shelled *Pseudocarcinus gigas* (Lamarck, 1818) that has only recently undergone a thorough morphological review by Ng & Davie (2020) resulting in the establishment of a new family, Pseudocarcinidae Ng & Davie, 2020; and the largest living arthropod (by its leg-span) *Macrocheira kaempferi* (Temminck, 1836) that has also required an in-depth study resulting in the formal re-establishment of Macrocheiridae Dana, 1851 (Guinot *et al.* 2022). The present article examines the case of the type species of the genus *Gecarcinus* Leach, 1814, the land crab *G. ruricola* (Linnaeus, 1758), which can reach more than 120 mm in carapace width (see Fig. 1) and is remarkable by its ecological, economic and even cultural importance throughout the Caribbean region. Other gecarcinid species also play important ecological role on tropical islands (Lindquist *et al.* 2009).

The genus *Gecarcinus* belongs to the ancestrally marine lineage of brachyuran crabs, the Gecarcinoidea H. Milne Edwards, 1837, generally called 'land crabs', sometimes 'semi-terrestrial crabs' (see Burggren & McMahon 1988), although they are not the best brachyurans adapted to life on land (Hartnoll 1988a), which are the 'primary' freshwater crabs. Land crabs are currently referred to as Gecarcinidae H. Milne Edwards, 1837 (for the authorship see Guinot *et al.* 2018, appendix p. 602), widely if not almost invariably considered to be simply a family subordinate to the Grapsoidea MacLeay, 1839 (e.g. Wang *et al.* 2021, 2023; Kong *et al.* 2025). Molecular studies of Schubart *et al.* (2000a; 2000b: 184) provided 'evidence' for a close relationship between grapsid and gecarcinid crabs, even suggesting that Gecarcinidae evolved within Grapsidae. As a result of the identification and critical examination of reliable fossils for deep time calibrations, Luque *et al.* (2024: 16, fig. 1), regard the phylogenetic position of Gecarcinidae as 'contentious' with respect to other families within Grapsoidea. Similarly, in more recent works such as that of Wolfe *et al.* (2024: fig. 4), using new and published sequences of 10 genes spanning 88 families for the reconstruction of the evolutionary history of Brachyura, Gecarcinidae is maitained within Grapsoidea. However, Cuesta *et al.* (2002) suggested that the larval characters might distinguish them from the rest of the grapsoid families. We are convinced, in agreement with Cuesta *et al.* (2002), that the adult morphology, with unique characters, argues for a suprafamilial status, Gecarcinoidea H. Milne Edwards, 1837, completely distinct from the Grapsoidea. The species of *Gecarcinus* and allied have 5-6 zoeal stages and one megalopal stage (Hartnoll & Clark 2006; Cuesta *et al.* 2007: table 5). According to Rice (1980), the zoea does not have advanced characters, with an evolutionary level similar to that of the more basal Grapsidae MacLeay, 1839 and Ocypodidae Rafinesque, 1815, and certainly less advanced than that of other Thocatotremata.

Gecarcinoids evolved to live mainly on land; the juveniles and adults live on land. Brooding females must hatch larvae at sea (Fig. 21A), which, after a typical planktotrophic pelagic life, head for the mainland as megalopae or first crab stages; then, females set off again towards the forests for the return migration (Fig. 21B). *Gecarcinus ruricola* exhibits a high degree of terrestriality, with the level of terrestrial adaptation of adults varying substantially between species, both morphologically and behaviourally (e.g. burrowing to hide from predator, mating and feeding). The transition to terrestrial environment also requires multiple and important morphological, physiological and biological adaptations, with the evolution of new structures, in particular expansion of the branchial cavity and modifications of the branchial epithelium, with the membrane lining the chamber being mooth and simply vascularised (e.g. Bliss 1968; Copeland 1968; Diaz & Rodríguez 1977; Taylor & Davies 1982; Burggren & McMahon 1988; Farrelly & Greenaway 1992, 1993; Adamczewska & Morris 2000; Hartnoll & Clark 2006; Hartnoll *et al.* 2006a, 2007, 2014; Hartnoll 2015; Watson-Zink 2021). Osmoregulatory genes play a role in how land crabs adapt to the unique selective challenges that accompany a terrestrial life (Watson-Zink *et al.* 2024 preprint). The period during which crabs migrate from residential to reproductive areas is critical because individuals are more vulnerable to stressful conditions, especially species occupying anthropised islands.

Hartnoll (1988a, b, 2015) and Hartnoll and collaborators (Hartnoll *et al.* 2006a, b, 2007, 2009, 2010, 2014) have made major contributions to our understanding of many aspects of the biology of gecarcinoids: how these animals manage to live on land and how they are among the most land-adapted forms. *Gecarcinus ruricola* is the most terrestrial of the land crabs throughout the Caribbean region: its megalopa (instead of the crab stage 1) is the landward migration stage, so it is the most terrestrially adapted megalopa described to date for locomotion on land (Hartnoll & Clark 2006: 162). *G. ruricola* (and *Johngarthia* species as well) appears therefore unique in that the megalopa migrates inland into fully terrestrial habitats before moulting to the first crab instar; this is unlike other gecarcinids, in which the moult into the first crab stage occurs either in water or, at least, in moist adjacent habitats (Hartnoll & Clark 2006, see fig. 2 showing pink swarms of *G. ruricola* megalopae in Providence Island emerging from the sea, crossing the coast road and entering the forest). There are also reports in 2007 of land megalopae from the Cayman Islands (most likely *G. ruricola*), with millions of them heading inland and disappearing within three days (Hartnoll *et al.* 2006a). On Saba, Van der Hoeven & Walters (1998) described first crabs (which may have been megalopae) as occurring in shelter near the sea.

The genus *Gecarcinus* currently comprises four species: the type species *G. ruricola* (Linnaeus, 1758), *G. lateralis* Fréminville *in* Guérin, 1832, *G. quadratus* Saussure, 1853, and *G. nobilii* Perger & Wall, 2014. The taxonomy of *Gecarcinus* had not been thoroughly revised since Türkay (1970), who had already divided the genus into two subgenera, *Gecarcinus* (*Gecarcinus*) and *Gecarcinus* (*Johngarthia*) by that time. The genus *Johngarthia* Türkay, 1970, with *G. planatus* Stimpson, 1860 as the type species, later elevated to generic status (Türkay 1987), currently consists of seven species. The contributions of Perger *et al.* (2011) with the new species *Johngarthia cocoensis* Perger, Vargas & Wall, 2011, of Perger & Wall (2014) with the new species *Gecarcinus nobilii* Perger & Wall, 2014, and of Perger (2019) with the new species *Johngarthia oceanica* Perger, 2019, have significantly improved our understanding of the taxonomic diversity of gecarcinoids. Hartnoll *et al.* (2006a: 316) pointed out that, despite its ecological and economic interest, *G. ruricola* has been very little studied, whereas the other species of *Gecarcinus* (now *Hartnollius* n. gen.), in particular *H. lateralis* n. comb., which is widespread in Caribbean islands and also along adjacent mainland coasts, is much better known.

The most studied species for its biology, physiology, ecology and behaviour is *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., so that it is impossible to cite here all the references relating to it (see e.g. Bliss & Sprague 1958; Bliss 1968, 1979; Bliss *et al.* 1978; Britton *et al.* 1982; Burggren & McMahon 1988). *Gecarcinus ruricola* is the most widely exploited land crab for human consumption in the Western Caribbean, notably in the San Andrés Archipelago (Hartnoll *et al.* 2006a; Baine *et al.* 2007), where it plays an important ecological role and even has cultural significance. But in other parts of the Caribbean and in other areas of its wide distribution, the most exploited land crab is *Cardisoma guanhumi* (Latreille *in* Latreille, Le Peletier, Serville & Guérin, 1828) (Hostetler *et al.* 1999; Maitland 2002; Hernández-Maldonado & Campos Campos 2015).

Taxonomists have acknowledged the close affinities between *Gecarcinus ruricola* and *G. lateralis*, which are often sympatric, but have not recognised that their own unique features, discernible in some taxonomic keys, could be indicative of two distinct genera, as e.g. by Rathbun (1918: 351), Türkay (1970: 335), and Chace & Hobbs (1969: 194-200). The brief description by Prahl & Manjarrés (1984a: 151, 155, figs 1, 2, 3.1, as *Gecarcinus* (*Gecarcinus*) *ruricola*) provided some of the characters that distinguish *G. ruricola* from the other *Gecarcinus*, such as the first male gonopod, which is a notable feature. Guinot *et al.* (2018: fig. 7A-D) showed the distinctive characters (front, mxp3, pleon, thoracic sternum) of *G. ruricola*, but did not go further as it was not the focus of that work. Poupin (2018: 223, 224), referring only to photographs, highlighted some morphological differences between *G. ruricola* and *G. lateralis*.

As a continuation of Guinot *et al.* (2018) and as part of the ongoing revision of the Gecarcinidae H. Milne Edwards, 1837 by the first two authors, the morphological study of the four species of *Gecarcinus* surprisingly showed that it is not monophyletic, with *G. ruricola* significantly distinguishable from the three other congeneric species. This discovery therefore requires their exclusion from *Gecarcinus* and a new generic assignment for these non-congeneric taxa, namely the establishment of a new genus, *Hartnollius* n. gen., which includes *G. lateralis*, *G. quadratus* and *G. nobilii*. The numerous specimens of *G. ruricola* deposited in the historical collection of the MNHN and those obtained on loan from various institutions allow us to highlight the characters that distinguish it from the three species of *Hartnollius* n. gen.

The differential features between *Gecarcinus* new status and *Hartnollius* n. gen. are highlighted in Table 1. The morphological study is supported by a molecular analysis that shows a genetic difference between *G. ruricola* and its previously congeneric species (Toledano-Carrasco *et al.* 2021). This preliminary genetic analysis based on the mitochondrial 16S rRNA and COI genes recovers the two major groups of gecarcinoids proposed by Guinot *et al.* (2018) and suggests that, although *Gecarcinus ruricola* is the sister group of *Hartnollius* n. gen., the genetic distance between the two is high enough to consider them different genera, with *G. ruricola* being closer to *Johngarthia* than to *Hartnollius* n. gen. (see below and Fig. 16). A diagnosis is provided for the genera *Gecarcinus* new status and *Hartnollius* n. gen. as well as for each species: *H. lateralis* n. comb., *H. quadratus* n. comb. and *H. nobilii* n. comb.

Recognition of a new status for *Gecarcinus* must be preceded by a comprehensive revision of its type species *G. ruricola*, with the designation of a neotype, and be based on sufficient material to detect possible phenotypic variations.

To our knowledge, the identity of *Gecarcinus ruricola* across its range has not been questioned: no morphological differences, apart from the various colour patterns, have been pointed to date, and intraspecific variations have not been reported. One of the most informative and striking feature of all American gecarcinids is the shape of the mxp3. In the literature on *G. ruricola*, no mentions of high degree of variability in this feature has been made, and only a more or less significant extension of the mxp3 has occasionally been reported. And, indeed, the most variable character, at first sight, that we observed in *G. ruricola* from various regions is the mxp3, namely its degree of its forwards extension. Therefore, this character required further investigation. Another crucial feature is the anterior border of mxp3 merus. Türkay (1974: fig. 2a-c, as *Gecarcinus* (*Gecarcinus*) *lateralis*) showed that in *Hartnollius lateralis* n. comb. the emargination of the anterior border of the merus varies, even in the type series: the outline of the merus does not only depend on the islands (Guadeloupe and Martinique), but, moreover, the shape is not the same on the mxp3 on each side of the individual. A disparity between the two mxp3 is sometimes also encountered in *G. ruricola* (Figs 4D; 6H) and in one of the syntypes of *Gecarcinus depressus* Saussure, 1857 from Haiti (Fig. 8C) that seems to be a *G. ruricola* (see below).

Most of other morphological characters (except colour morphs) of *Gecarcinus ruricola* do not appear to be variable. However, we found another morphological variation, namely the distance between the extremity of the sternopleonal cavity and the sternal thoracic suture 2/3. In the Zapata Swamp (Ciénaga de Zapata), southern Matanzas Province of Cuba, which harbours a black and a yellow morphs, similar frequency in both sexes and between years, similar mean values of cephalotorax length and width according to the year, and a similar cheliped-body weight relationship were demonstrated (Acevedo 1989). In the past, *G. ruricola* was one of the most common crabs in Puerto Rico (Ledrú 1863). Recent description of the natural history of *G. ruricola* in Puerto Rico by Rodríguez-Fourquet *et al.* (2025) showed a male-biased population, a stable population where all size classes were present with, however, few small individuals, the absence of juveniles being explained by different activity pattern, refugees, or habitat differences. Currently, the population size is low (estimated at 678 individuals when based on the rare occasions that this crab is seen) compared to the common *Cardisoma guanhumi* and the populations of *G. ruricola* in other Caribbean islands such as San Andrés Islands (Colombia) and Cuba.

Due to limited taxonomic studies and the lack of previous genetic analyses in *Gecarcinus ruricola*, it has not been possible to assess so far the degree of differentiation across its distribution area as in the case of *Cardisoma guanhumi*. The latter exhibits a degree of differentiation, although modest, over its range along the Brazilian coast and does not appear to encounter obstacles to gene flow populations, and without the organisation into significant evolutionarily units. Genetic flow between populations of *C. guanhumi* is accomplished by the dispersal capacity of its larvae, probably amplified through coastal currents, and leads to a homogenisation of the genetic compositions of the populations (Oliveira-Neto *et al.* 2008). But the case of *C. guanhumi* is different from that of *G. ruricola*: the former preferentially inhabits mangroves and is limited to less than 5 km from the sea; *G. ruricola* is found further from the sea, up to 1000 m in Jamaica (Britton *et al.* 1982), and, in the San Andrés Archipelago (Hartnoll *et al.* 2006a), it inhabits forest environments, and is therefore forced to a longer migration. Migration may have an effect on relative allele frequencies. In a rather close species, *Johngarthia lagostoma* (H. Milne Edwards, 1837), mitochondrial DNA sequence analyses have revealed the genetic structure and diversity on the four islands where it occurs (Ascension Island and three Brazilian oceanic islands) and have shown that three discrete significant evolutionary units should be considered, but not implying taxonomic changes (Rodríguez-Rey *et al.* 2016). In populations of *Hartnollius lateralis* n. comb. from Mexico, some genetic differentiation has also been observed, especially between populations from the southwestern Gulf of Mexico-Mexican Caribbean and from the Atlantic populations (Toledano-Carrasco *et al.* 2021). This could be due to the presence of currents that form soft barriers between the Bank of Campeche keys (Arcas, Triangles and Arenas) and the western portion of the Gulf as mentioned already by other authors (see Toledano-Carrasco *et al.* 2021).

Having observed some variable traits in the *Gecarcinus ruricola* from the MNHN collection, in most part in dry condition and therefore not ensuring detailed examination, and, although Rathbun (1918) who had in her hands many *G. ruricola* from both the mainland and islands reported no variation, we have assembled a large collection of the species for our study, in particular thanks to loans from the NHM and NMNH. The objective of our examination of a wide range of *G. ruricola* material is to determine whether there are sets of populations whose members share morphological attributes absent from other geographically separated populations, or whether they are groups actually or potentially interbreeding populations that are phylogenetically distinct from, but reproductively compatible with, other such groups. Combining multiple approaches would be essential to determine whether *G. ruricola* (gene flow or reproductive isolation?) constitutes a distinct, independently evolving lineage deserving recognition as a unique, taxonomically valid species. Most of the material was collected too long ago to be suitable for genetic analysis, and therefore we had to rely almost exclusively on morphological characters and, moreover, on faded coloured crabs, which does not allow for precise identification of the different morphs. Thanks to the successful 16S rRNA and COI sequences in the final phase of our research from two individuals of G. *ruricola* collected during the Karubenthos 3 Expedition in 2024 in Guadeloupe and one individual from Cuba, genetic data could be integrated, which supports that these morphological differences are solely due to intraspecific variability.

MATERIAL AND METHODS

Terminology essentially follows Guinot *et al.* (2018) and Davie *et al.* (2015a). Measurements are provided in millimetres, being taken at the maximum of the carapace (including rostrum and lateral teeth if present) and are reported as carapace length (cl) × width (cw), respectively. The thoracic somites are numbered from 1 to 8. Pleonal somites are numbered from 1 to 6. Thoracic sternal sutures are designated by the number of the two thoracic sternites that they involve, and thus are numbered from 1/2 to 7/8.

ABBREVIATIONS AND SYMBOLS

Institutions

ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia;
BLSZ	Barbados Laboratory of Systematic Zoology, Barbados;
CNCR	Colección Nacional de Crustáceos del Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), México;
ICZN	International Code of Zoological Nomenclature, here referred to as "*Code*";
LACM	Natural History Museum of Los Angeles County, Los Angeles;
MNHN	Muséum national d'Histoire naturelle, Paris;
MHNG	Muséum d'Histoire naturelle de Genève, Geneva;
MZUSP	Museu de Zoologia da Universidade de São Paulo (ex USU, Museu Nacional, Universidade Federal do Rio de Janeiro), São Paulo;
NHM	Natural History Museum, formerly British Museum (Natural History) BM (NH), London;
NKML	Naturkundemuseum, Leipzig;
NMNH	National Museum of Natural History; (Smithsonian; Arthropoda Collection, USNM), Washington, DC;
SGN	Senckenberg Research Institute and Natural History Museum, Frankfurt;
SNSD MTD	Senckenberg Naturhistorische Sammlungen, Staatliches Museum für Tierkunde, Dresden;
ULLZ	University of Louisiana at Lafayette Zoological Collection, Lafayette;
UWI	University of the West Indies, Barbados;
ZMH	Zoologisches Museum Hamburg, Hamburg;
ZRC	Zoological Reference collection, Lee Kong Chian Natural History Museum, Singapore.

Expedition

MNHN-ARBig-LPRig	Muséum national d'Histoire naturelle-Agence régionale de la Biodiversité Îles de Guadeloupe-La Planète Revisitée Îles de Guadeloupe.

Morphology

♀	female;
♂	male;
G1	male first pleopod;
G2	male second pleopod;
mxp3	external maxillipeds;
P2-P5	pereiopods 2-5 (first to fourth ambulatory legs, respectively).

Genetics

BI	Bayesian inference;
bp	basepairs;
COI	cytochrome oxidase subunit 1;
K2P	Kimura two-parameter;
ML	Maximum-likelihood;
16S	16S rRNA.

Other abbreviations

CAA	"Catalogue of Articulated animals: Crustaceans, Arachnids, Insects, received, donated, exchanged or bought" (Catalogue des Animaux articulés: Crustacés, Arachnides, Insectes, reçus, donnés, échangés ou achetés), housed in the MNHN Entomology Collection;
coll.	collected by;
det.	identified by;
leg.	donated by;
rev.	revised by;
vid.	examined by.

DNA EXTRACTION

For the samples ZMH-K65343 and MNHN-IU-2024-4640, the fragments for COI had a length of 900 bp (base pairs) using the primer combination COL6E (5'-ATGCAACGATGATTCTTTTCTAC-3') (Schubart *et al.* 2022) /COH900 (5'-ATAATTATTGCWRTYCCHAC-3') (Schubart *et al.* 2022), and for 16S the length was 610 bp with the primer combination 16L29 (5'-YGCCTGTTTATCAAAAACAT-3') (Schubart *et al.* 2001, as 16L2) /16HLeu (5'-CATATTATCTGCCAAAATAG-3') (Schubart 2009). For the sample MNHN-IU-2024-7258, the fragment for COI had a length of 846 bp (base pairs) using the primer combination COL6 (5'-TYTCHACAAAYCATAAAGAYATYGG-3') (Schubart 2009) / COH900 (5'-ATAATTATTGCWRTYCCHAC-3') (Schubart *et al.* 2022), and for 16S the length was 430 bp with the primer combination 16L29 (5'-YGCCTGTTTATCAAAAACAT-3') (Schubart *et al.* 2001, as 16L2)/ 16H11 (5'-AGATAGAAACCRACCTGG-3') (Schubart 2009). The general PCR profile was: initial step 4 min at 94°C, denaturation for 45 s at 94°C, annealing for 1 min at 47°C and extension for 1 min at 72°C (40 cycles), followed by a final extension for 5 min at 72°C. The PCR products were sent to Macrogen Europe for sequencing. For the analyses the longest sequences were matched to the rest (658 bp for COI and 559 for 16S).

MOLECULAR ANALYSES

Two concatenated phylogenetic trees were performed based on Bayesian Inference and Maximum Likelihood methods using fragments of the mitochondrial genes COI and 16S rRNA. For this aim, 14 sequences of each gene were manually aligned in MAFFT v7.397 (Katoh & Standley 2013) with the method L-INS-i. The sequences of *Hartnollius* n. gen. were recycled from Toledano-Carrasco *et al.* (2021), while the sequences of *Cardisoma guanhumi* Latreille, 1828, *Discoplax michalis* Ng & Shih, 2015, *Discoplax longipes* A. Milne-Edwards, 1867, *Tuerkayana magnum* (Ng & Shih, 2014), *Tuerkayana* *latens* Ng & Shih, 2023, *Johngarthia lagostoma* and *Ocypode rotundata* Miers, 1882 were obtained from GenBank (see Table 2, under *Genetics*). The sequences of *Gecarcinus ruricola* were obtained for the purpose of this work (see methods in the section above). *Ocypode rotundata* was included as outgroup.

For the analysis under BI the best-fitting models for sequence evolution datasets were identified using jModelTest 2.1.10 (Darriba *et al.* 2012), with selection based on the Akaike Information Criterion with correction (AICc). For the COI gene, the selected models were SYM+G for the first codon position, F81 for the second, and GTR+G for the third, as well as for the 16S gene. The partitioned BI analysis was conducted using Mr. Bayes 3.2.2 (Ronquist *et al.* 2012), running four chains for 10 000 000 generations with tree sampling every 1000 generations. The ML phylogenetic analysis was performed using IQ-TREE v1.6.12 (Nguyen *et al.* 2015), with 1000 replicates of Ultrafast Bootstrap (Hoang *et al.* 2018) to assess branch support. ModelFinder (Kalyaanamoorthy *et al.* 2017) was automatically employed by the program to determine the best-fit substitution models. The selected models were: TNe+G4 for the first codon position of the COI gene, F81+F for the second, TN+F for the third, and TIM3+F+G4 for the 16S gene. Trees were visualized and edited with Fig Tree v1.4.3 (Rambaut 2014). Intraspecific and interspecific divergences were calculated from COI gene sequences using the Kimura two-parameter (K2P) substitution model (Kimura 1980), implemented in MEGA 7.0.26.

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
Subsection THORACOTREMATA Guinot, 1977
Superfamily GECARCINOIDEA H. Milne Edwards, 1837

Family GECARCINIDAE H. Milne Edwards, 1837

NOMENCLATURE. — In the newly created Thoracotremata Guinot, 1977, a superfamily rank Gecarcinoidea was proposed by Guinot (1977a: 406; 1977b: 1050; 1978: 287). The family-group name Gécarciniens H. Milne Edwards, 1837 meets all the criteria of availability in accordance with the provisions of the *Code* (ICZN 1999, Art. 11.7, 11.7.2). However, although authority of H. Milne Edwards is explicitly recognised by many carcinologists and despite that Türkay (1970: 335), Prahl & Manjarrés (1983: 32; 1984a: 151) and Tavares (1989: in the title and p. 5, 21) formally assigned authorship to H. Milne Edwards (1837a), the Gecarcinidae continued to be attributed to MacLeay (1838: 63) by most authors, e.g. by Ng *et al.* (2008: 30, 214), Guinot *et al.* (2013: 40, table 7), Ng & Davie (2012: 89), Ng & Shih (2014: 112; 2015: 383; 2023: 2), Davie *et al.* (2015b: 1117), Ng (2017: 2). Authorship of the family-group name Gecarcinidae was already discussed in detail by Guinot *et al.* (2018: 602) and Tavares & Mendonça Jr (2022: 9), and is hereby – and we hope – definitively – ascribed to H. Milne Edwards (1837a).

Genus *Gecarcinus* Leach, 1814 new status

Gecarcinus Leach, 1814: 430. — Toledano-Carrasco *et al.* 2021 *pro parte*: 221, fig. 5.

Gecarcinus of all authors, except for references to *Gecarcinus ruricola*, see under this name.

Geocarcinus – Miers 1886: 217 (incorrect emendation of *Gecarcinus* Leach, 1814). — Young 1900: 236, 237.

TYPE SPECIES. — *Cancer ruricola* Linnaeus, 1758, by subsequent designation by H. Milne Edwards (1837b: pl. 24), see Figs 1-4, 6; 10A, D; 11A; 16-18; 21, Table 1.

OTHER INCLUDED SPECIES. — None.

EMENDED DIAGNOSIS

Carapace

Carapace much broader than long, globular, with hepatic, subhepatic and branchial regions markedly inflated, even vaultlike; widest part of carapace considerably ahead of antero-lateral angles of mesogastric region; area lateral to the orbits proportionally very large, with fronto-orbital distance in adults about two-fifths carapace width (near half the carapace width in half-grown individuals). Dorsal surface with well-pronounced grooves: cervical groove very deep, terminating anteriorly in a pit near orbital angle; median (or urogastric) groove very deep; longitudinal mesogastric groove very deep, rising towards frontal margin, making certain regions well defined, such as e.g. the gastric and cardiac regions. Numerous striae along lateral margins of carapace. Front long, strongly produced and deflexed, proportionally narrow and slightly widening underneath, with concave lateral margins and upturned lower margin. Mesial lobe of infraorbital margin elongated, curved around ventrolateral edge of front, covered by front edge. Antero-lateral margins rounded; proximally with a short row of more or less marked granules, well pronounced in small and medium-sized male individuals and in females, then tending to largely disappear in very large-sized individuals; then margins smooth.

Cephalic structures

Antennules very small, folded obliquely. Antennae very short, visible but markedly recessed. Orbits small, englobed in carapace, deep; outer angle not marked. Eyestalks relatively short, curved.

Proepistome, epistome and pterygostome

Proepistome not completely covered by triangular median process of subfrontal plate, thus visible. Epistome developed, with one median crest and a lateral crest on each side. Buccal cavity rhomboid. Subhepatic and pterygostomial region glabrous, with many striae.

Mxp3

Mxp3 (when applied well against buccal cavity) with anterior margin of merus reaching only the epistome or advancing either to the level of the antennules or to the frontal margin (see *Phenotypic variations*, under *Gecarcinus ruricola*); leaving between them a narrow rhomboid gap, in which mandibles are exposed. Ischium and merus very unequal, their articulation clearly oblique; ischium smaller and merus elongated, strongly obliquely directed; with marked longitudinal groove. Merus triangular, narrowing anteriorly, with anterior margin

Fig. 1. — *Gecarcinus ruricola* (Linnaeus, 1758), dorsal view: **A**, ♂ 66.4 × 95 mm, Cuba, dry, MNHN-IU-2000-10953 (= MNHN-B10953), with homomorph chelipeds; **B**, ♂ 66.2 × 93.3 mm, Cuba, dry, MNHN-IU-2000-10955 (= MNHN-B10955), with conspicuous heterochely and heterodonty. Scale bars: 50 mm. Credits: MNHN-Soubzmaigne.

TABLE 1. — Morphological differences between *Gecarcinus* Leach, 1814 new status, monospecific with *G. ruricola* (Linnaeus, 1758) as type species, and *Hartnollius* n. gen. with *H. lateralis* (Fréminville *in* Guérin, 1832) n. comb. as type species.

Morphological characters	***Gecarcinus ruricola* (Linnaeus, 1758)**	***Hartnollius* n. gen. (male of *H. nobilii* n. comb. not examined)**
Size	largest size known, males with cw 123 mm (Van der Hoeven & Walters 1998)	maximum size generally lower
Carapace	much broader than long, globulous; widest part of carapace considerably ahead of antero-lateral angles of mesogastric region hepatic, subhepatic and branchial regions markedly inflated, even vaulted-like	broader than long, widest part of carapace being in line with antero-lateral angles of mesogastric region all regions less swollen, carapace flatter
Fronto-orbital distance	approximately two-fifths carapace width in adults	about half of maximum carapace width in adults
Carapace dorsal surface	cervical and median (or urogastric) grooves very deep; longitudinal mesogastric groove very deep, rising towards frontal margin	all grooves similar but less deep
Subhepatic and pterygostomial striae	present, numerous, but stridulation not mentioned	present, used as stridulatory pars stridens
Anterolateral margin of carapace in males	entire, rounded, not delimitated, except for short denticular proximal ridge in young adults	entire, not as rounded, joining exorbital angle, with more or less marked junction
Front	long, narrow, strongly produced and deflexed	shorter and broader, less produced and less deflexed
Proepistome	not completely covered by subfrontal plate, thus visible	completely covered by subfrontal plate, thus not visible
Antenna	very short, visible but markedly recessed	very short but completely exposed, visible
Orbit	small, englobed in carapace in large adults, deep; outer angle not marked	orbit typical; with more or less marked angle at anterolateral margin
Mesial lobe of infraorbital margin	elongated, concave, covered by frontal margin	angular, just joining frontal margin, completely exposed
Mxp3 (when applied well against oral cavity)	much developed, directed obliquely, reaching either frontal margin, or antennular cavities, or only epistome merus and ischium greatly unequal, their articulation distinctly oblique	smaller, not reaching epistome, except in *H. quadratus* n. comb. merus and ischium subequal, their articulation only slightly oblique
Mxp3 ischium	small, not much longer than wide, with marked longitudinal groove	small, barely smaller than merus, without longitudinal groove (only a trace)
Mxp3 merus	distinctly longer than wide, suboval, directed obliquely meri of both sides nearly or completely joining	relatively more elongated, directed only slightly obliquely meri of both sides not joining distally, except in *H. quadratus* n. comb.
Anterior margin of mxp3 merus	entire, not emarginate, without notch or fissure	variously emarginate, with more or less distinct notch; in *H. quadratus* n. comb. with only very small notch, or margin slightly concave
Mxp3 palp	entirely concealed, not visible	last mobile article(s) visible
Mxp3 exopod	suboval plate well visible, with lateral dense setae	narrower plate, largely concealed by fringe of thick setae
Male chelipeds	equal or slightly subequal, occasionally may be distinctly unequal in large individuals	very unequal, especially in old males
Major cheliped	usually not or sligtlhly gaping	usuallly moderately gaping
Merus and carpus of male cheliped of adults	merus with distinctly curved internal surface; matked denticles on inner lower margin carpus with denticles, may be spiniform, on inner upper margin	merus with normal internal surface; smooth (*H. lateralis* n. comb.) or with only small granules on inner lower margin (*H. quadratus* n. comb., *H. nobilii* n. comb.); carpus smooth (*H. lateralis* n. comb., *H. quadratus* n. comb.) or with denticles on inner upper margin (*H. nobilii* n. comb.)
Ambulatory legs (P3)	very spiny	less spiny
Propodus	with lateral carinae bearing four rows of prominently, similarly developed spines	with unequally developed lateral carinae bearing four rows of weakly developed spines
Dactylus	with lateral carinae bearing six rows of prominently, similarly developed spines	with four rows of small equal spines (*H. lateralis* n. comb., *H. nobilii* n. comb.) or six rows of small unequal spines (*H. quadratus* n. comb.)
Sterno-pleonal cavity	long, its extremity ending very close to sternal suture 2/3	shorter, its extremity not close to sternal suture 2/3

Table 1. — Continuation.

Morphological characters	***Gecarcinus ruricola*** **(Linnaeus, 1758)**	***Hartnollius*** **n. gen. (male of** ***H. nobilii*** **n. comb. not examined)**
Male pleon	lateral margins only with sparse setae	lateral margins with fringe of setae
Pleonal locking structures in males	setose prominence about in middle of sternite 5	setose prominence closer to suture 4/5 (not known in *H. nobilii* n. comb.)
Thoracic sternum suture 2/3	wide at level of somite 5, not restricted at level of P1 present, V-shaped	narrowing at level of somite 5, thus restricted at level of P1 present, practically straight, barely concave
G1	G1 tapering at its extremity, with unequal setae at its tip; apex rather long; laterally, a very long, narrow horny tube, completely rolled up on itself, with the opening displaced towards its distal extremity	G1 tapering at its extremity, with unequal setae at its tip; apex shorter; laterally, either a very long, narrow, horny tube, more or less curved, not folded and open all along (*H. lateralis* n. comb., *H. quadratus* n. comb.)
Vulvae	obliquely directed, with rigid operculum	oriented nearly horizontally, with rigid operculum

entire, not emarginate; meri of both sides more or less joining medially; palp inserted below merus: palp with first article fused to merus internal surface and with two mobile distal articles concealed, not visible. Exopod of mxp3 completely concealed, apex not reaching ischium-merus articulation, as well visible suboval plate, with lateral dense setae; without flagellum.

Chelipeds

Adult male chelipeds massive but not extraordinarily enlarged, equal or slightly to moderately subequal, possibly distinctly unequal in large individuals; narrowly gaping; heterochely and heterodonty usually not or slightly marked, possibly occasionally pronounced (Fig. 1B); occlusal margins of fingers with small, spaced teeth on both sides; in the rare cases of greatly uneven chelipeds (heterochely), a more pronounced gap and pronounced heterodonty (Fig. 1B). Merus with curved internal surface and with marked denticles on inner lower margin; carpus with conspicuous denticles on upper margin. Sexual dimorphism moderate.

Ambulatory legs

Very spiny. P3 propodus with lateral carinae bearing four rows of prominently and similarly developed spines; dactylus with lateral carinae bearing six rows of prominently and similarly developed spines.

Sterno-pleonal cavity and pleon

Sterno-pleonal cavity completely glabrous, long; its extremity ending either very close to suture 2/3 and even almost exceeding it, sometimes very slightly distant, with marked ridge around telson. Male pleon rather long, with all somites free plus telson; margins only with sparse setae; somite 6 with convex margins.

Thoracic sternum, locking pleonal structures and setal tufts

Thoracic sternum wide (especially at level of somite 5); sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed; sternite 2 semi-ovate with convex margins; suture 2/3 present, V-shaped; suture 3/4 absent, without lateral trace; sternites 3 + 4 completely fused, with convex, obliquely directed margins, thus not restricted at level of P1; sutures 4/5 to 7/8 interrupted; sternites 5-7 similarly shaped, sutures well defined; suture 7/8 rather short; sternite 8 not developed medially, totally hidden when pleon is folded; posterior emargination reaching sternite 7 at level of narrow median bridge at level of suture 7/8; another weak median bridge at level of suture 6/7; deep median line only along sternite 7.

Locking pleonal structure as rather large prominence about in middle of sternite 5, but pleonal sockets not delineated, so no longer functional.

Setal tufts of more or less dense hydrophilic setae located along first pleonal somites margins and at junction of pleon with carapace.

Male gonopore and penis

Male gonopore and penis at level of suture 7/8, emerging rather far from P5 coxo-sternal condyle.

G1 and G2

G1 tapering at its extremity, with unequal setae at its tip; apex rather long (called 'palp', see Türkay 1970: 336, fig. 1a-f); laterally, a very long, narrow horny tube (called 'Terminalanhang' by Türkay 1970: 334, or appendix) completely rolled up on itself, with the opening displaced towards its distal extremity, and clearly exceeding G1 tip; several horny setae at its base. G2 tiny, without flagellum.

Vulvae

Protruding, obliquely directed, normally occluded by a rigid calcified immobile operculum (see Hartnoll 1968).

Remarks

In *Le Règne Animal* of Cuvier, H. Milne Edwards (1837b: pl. 24) illustrated *Gecarcinus ruricola* as his representation of *Gecarcinus*, and, on the basis of the title of this work, this can be considered a type designation. Some authors cite the year 1838, but, according to Cowan (1976), plate 24 was produced in March 1837 (see Ng *et al.* 2008: 215).

The genus *Gecarcinus* new status differs from *Hartnollius* n. gen. by many characters, which are listed in Table 1. The level of generality of the distinguishing characters between them is similar to those that differentiate *Gecarcinus* from *Johngarthia*, and their number is even greater.

No gecarcinid has such a globose carapace and small deeply embedded orbits as *Gecarcinus ruricola*. According to Britton *et al.* (1982), during growth an expansion in the lateral carapace dimension provides a small increase in branchial volume but a larger increase in surface area, which presumably facilitates gaseous exchanges with the atmosphere: small individuals (40 mm cw) of *G. ruricola* have approximately the same branchial chamber surface area than *Hartnollius lateralis* n. comb., whereas individuals of greater width have increasingly greater branchial area. If greater respiratory surface and respiratory capacity are desirable for *G. ruricola*, larger individuals will have a selective advantage. As it grows, the carapace swells more and more to accommodate the branchiostegal lung so that the proximal crest of the antero-lateral margin (see Fig. 4A-C) becomes more and more attenuated until it disappears completely, and the orbits become enclosed in the carapace (Figs 2A; 17; 18).

Several species initially assigned to *Gecarcinus* were separated by Türkay (1970: 343), who created for them the subgenus *Johngarthia*, later elevated to generic rank (Türkay 1987). *Johngarthia* Türkay, 1970 includes the type species *Johngarthia planata* (Stimpson, 1860), *J. lagostoma* (H. Milne Edwards, 1837), *J. malpilenis* (Faxon, 1893), *J. weileri* (Sendler, 1912), *J. oceanica* Perger, 2019, and the enigmatic *J. cocoensis* Perger, Vargas & Wall, 2011. The distinctive characters of *Johngarthia* mainly concerned the G1 (short, folded outwards, without a long, narrow horny tube), the merus of mxp3 with a slit-shaped fissure approximately on the inner margin, and the exopodite of mxp3 long, with setae extending beyond the ischium-merus articulation. Larval development also distinguishes *Johngarthia planata* from that of *Hartnollius lateralis* n. comb. (Cabrera 1966; Cuesta *et al.* 2007). It is worth noting that *Johngarthia lagostoma* (see Tavares & Mendonça Jr 2022: fig. 47A, F) shows some resemblance to *G. ruricola* in the globular carapace, recessed antenna, long and obliquely directed merus of mxp3 that reaches almost the front. It is interesting to remind that Tavares (1991) found no synapomorphies to support the monophyly of *Johngarthia*. Colavite *et al.* (2021), studying the morphology of the first zoeal stage of *J. lagostoma*, endemic to the Atlantic oceanic islands of Ascencion, Trindade and Martin Vaz, Fernando de Noronha and the Rocas Atoll, suggested that the uncommon large eyes could be an autapomorphy of the species and again discussed the validity of this genus.

Gecarcinus ruricola (Linnaeus, 1758)

(Figs 1-4; 6; 10A, D; 11A; 16-18; 21; Table 1)

Cancer ruricola Linnaeus, 1758: 626. — Herbst 1783: 119, pl. 3 fig. 36, pl. 4 fig. 37; 1790: 262, pl. 20 fig. 116; 1799: 39, pl. 49 fig. 1. — Fabricius 1798: 339. — Latreille 1817: 17.

Ocypode tourlourou Latreille, 1803: only pl. 44 fig. 2 (see below under *Ocypode tourlourou* Latreille, 1803).

Gecarcinus ruricola – Leach 1815: 322. — H. Milne Edwards 1837a: 26; 1837b: pl. 20, fig. 1, a-c. — Desmarest 1825: 113, pl. 11 (nec 12) fig. 2. — Bosc 1830: 252. — Lamarck 1838: 459. — Desbonne *in* Desbonne & Schramm 1867: 42. — Verrill 1892: 353. — Stebbing 1893: 80-84. — Doflein 1899: 181. — Rathbun 1918: 352-355, fig. 160, pls 117, 118; 1920: 341 [19]; 1924: 19; 1936: 38. — Chace 1940: 53. — Chace & Holthuis 1948: 26. — Hartnoll 1968: 297; 2015: 400, 402, 404, tables 1, 3. — Chace & Hobbs 1969: 194, 200, figs 66, 67h-j. — Bright & Hogue 1972: 20. — Powers 1977: 140. — Keith 1985: 276, fig. 12B. — Mulder & Stam 1987: 1-40. — Britton *et al.* 1982: 207. — Abele & Kim 1986: 62, 661, 663, fig. a, c. — Atkin 2004. — Venable 2004: unnumbered page and photo. — Baine *et al.* 2005: 1-59, figs 1-10. — Hartnoll *et al.* 2006a: 316-325, figs 1-4, tables 1-7. — Hartnoll & Clark 2006: 149-164. — Hartnoll *et al.* 2007: 425-436; 2014: 532, 534, 538, fig. 1A; 2017: 947, 949, table 4. — Lalana *et al.* 2007: 82. — Felder *et al.* 2009: 1088. — Barro *et al.* 2013: 45. — Vaslet *et al.* 2013: 245, annex 3. — Yokoyama 2013 114. — Diez 2014: 83. — Diez & Jover 2015: 16, fig. 7m-p. — Vides *et al.* 2016: fig. 25. — Diez & Soto-Borrero 2016: 79. — Diez & Espinosa 2018: 151. — Questel 2018: 15; 2019: 12 (and photo), 25 (and unnumbered photos), 33. — Guinot *et al.* 2018: 568, 569, 572, 586, 587, fig. 7A-D. — Poupin 2018: 223, fig. 254. — Parasram *et al.* 2021: 457, fig. 9. — Toledano-Carrasco *et al.* 2021: 218, 221, 224, 226, 230, figs 3F, G, 4, 5, tables 1, 3. — Vendeville *et al.* 2022: 193. — Parasram 2023:127, fig. 3.9. — Marin & Tiunov 2023: 96, 117. — Pinheiro *et al.* 2024: 2, 7.

Geocarcinus ruricola – Young 1900: 238, 239.

Gecarcinus (*Gecarcinus*) *ruricola* – Türkay 1970: 336, fig. 1a-f. — Prahl & Manjarrés 1983: 32, fig. 2A; 1984a: 151, 155, 166, figs 1, 2, 3.1; 1984b: 6, 8. — Abele & Kim 1986: 62. — Scelzo & Varela 1988: 36, 49, fig. 4. — Acevedo 1989: 3-14. — Martinez & Bliss 1989: 3. — Ng *et al.* 2008: 215. — Felder *et al.* 2009: 1088.

Nec Ocypode ruricola – Latreille 1803: 35 (= *Cardisoma guanhumi* Latreille *in* Le Peletier, Serville & Guérin, 1828).

Nec *Ocypode ruricola* – Fréminville 1835: 217 (= *Cardisoma guanhumi* Latreille *in* Le Peletier, Serville & Guérin, 1828 fide Türkay 1970).

Nec *Grapsus* (*Gecarcinus*) *ruricola* – De Haan 1850: 30, pl. c, figs below (= *Gecarcoidea lalandii* H. Milne Edwards, 1837).

Nec *Gecarcinus ruricola* – Cano 1889: 101, 227 (= *Gecarcinus nobilii* Perger & Wall, 2014).

Nec *Gecarcinus ruricola* – Nobili 1901: 46 (= *Gecarcinus nobilii* Perger & Wall, 2014).

TYPE MATERIAL. — **Neotype** (by present designation). **Cuba** • ♂ 55.0 × 76.0 mm; in ethanol; de Boury coll. 1914; Bouvier det. as *Gecarcinus ruricola*; M. Türkay vid. VI.1972; MNHN-IU-2017-8392 (= MNHN-B13155).

OTHER MATERIAL EXAMINED. — **Cuba** • 1 ♂ 66.4 × 95 mm; dry; M. Gundlach [coll]; as *Gecarcinus ruricola*; MNHN-IU-2000-10953 (= MNHN-B10953) • 1 ♂ 66.2 × 93.3 mm; dry; M. Gundlach [coll]; as *Gecarcinus ruricola*; MNHN-IU-2000-10955 (= MNHN-B10955) • 1 ♂ 57.7 × 81.4 mm; dry; M. Gundlach [coll]; as *Gecarcinus ruricola*; MNHN-IU-2000-3764 (= MNHN-B3764) • 1 ♂ 61.7 × 91.6 mm (as *Gecarcinus ruricola*; MNHN-IU-2000-3766 (= MNHN-B3766) • 1 ♀ 60.5 × 83.8 mm; dry; as *Gecarcinus ruricola*; MNHN-IU-2000-10754 (= MNHN-B10754) • 1 young ♂ 17.7 × 23.7 mm, same data as neoype; MNHN-IU-2018-5229 (= MNHN-B13155) • 1 ♀ 52.8 × 69.9 mm; in ethanol; M. Chaper, det. *Gecarcinus*; MNHN-IU-2024-6554 • 1 ♂ 71.0 × 53.0 mm; Playa Larga, III.2004; as *Gecarcinus ruricola*; ZMH-K65343 •

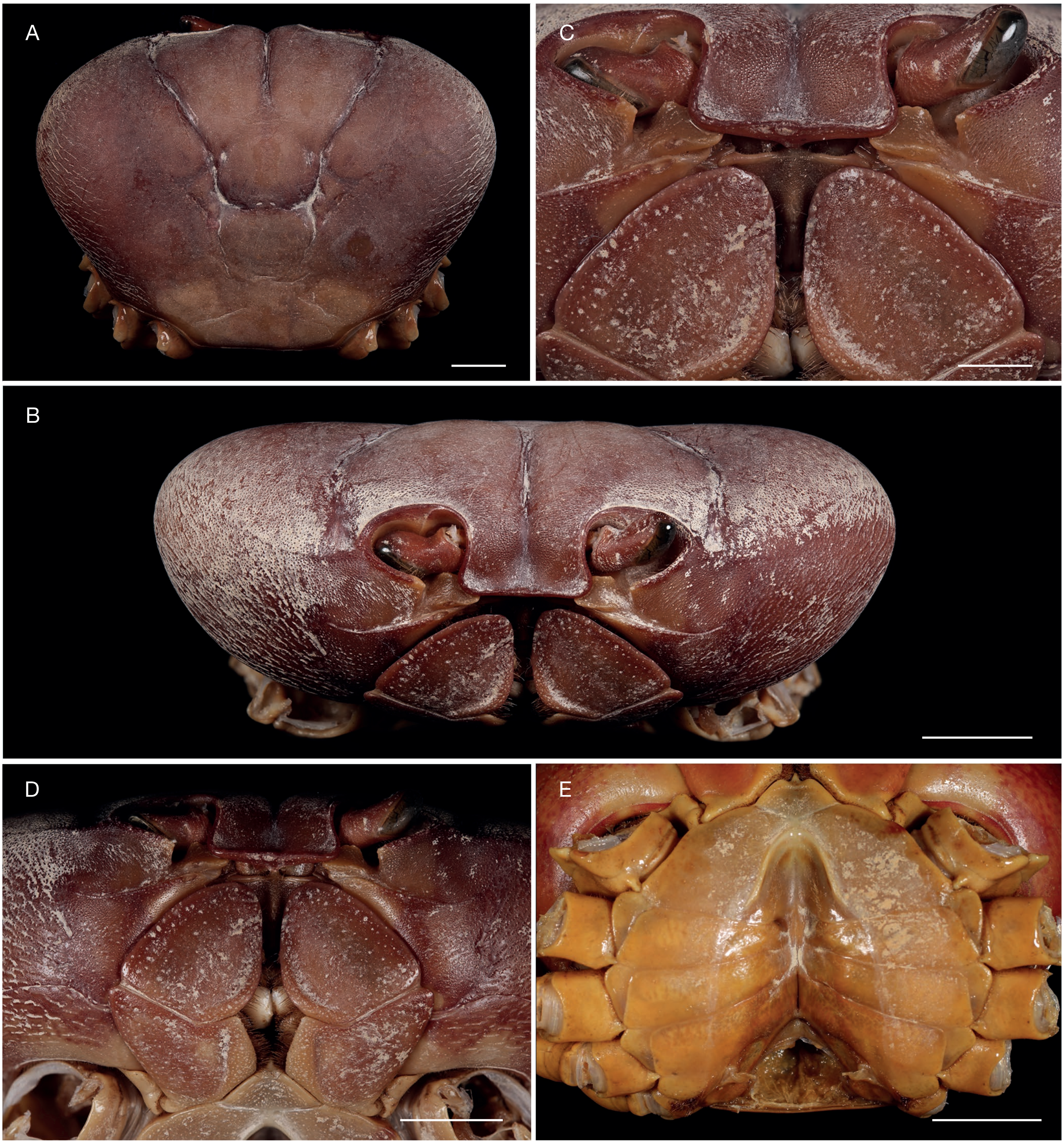

Fig. 2. — *Gecarcinus ruricola* (Linnaeus, 1758): neotype, ♂ 55.0 × 76.0 mm, Cuba, 1914, MNHN-IU-2017-8392 (= MNHN-B13155): **A**, carapace; **B**, frontal view; **C**, front, proepistome, antennae (recessed) and mesial lobe of infraorbital margin; **D**, mxp3; **E**, thoracic sternum. Scale bars: A, B, D, E, 10 mm; C, 5 mm. Credits: MNHN-Soubzmaigne.

1 ♂ 21.2 × 27.0 mm, 3 ♀ 17.9 × 22.2 mm, 44.3 × 59.2 mm, one damaged; off Cape San Antonio, Ensenada de Cajon; 21°52’00”N, 84°57’00”W; *Tomas Barrera Exp.*, Henderson & Bartsch coll.; 22.V.1914; Rathbun det.; R. B. Manning redet.; USNM 48405 • 1 ♂ 51.5 × 71.5 mm, Cabanas, 22°58’32”N, 82°55’00”W; *Tomas Barrera* Exp.; st. 16 (nec depth 4-22 m); Henderson, Brooks & Bartsch coll.; 8/9.VI.1914; USNM 48402 (See Fig. 6H) • 3 ♂ 52.4 × 73.5 mm, 54.0 × 75.0 mm, 55.9 × 75.5 mm; 4 ♀ cl 52.5 mm, 42.7 × 55.9 mm, 40.9 × 54.7 mm, 53.3 × 71.4 mm; P. Bartsch coll.; 1930; R. B. Manning det.; USNM 71242.

Cayman Islands • 1 ♂ 61.2 × 88.0 mm, Cayman Expedition 1938; English Sound, Sta. 31; Coll. & Pres. Oxford University; 11.V.1938; NHM 2024.353. **Little Cayman** • 3 ♂ 56.0 × 78.1 mm, 62.7 × 87.7 mm (yellow morph), 58.2 × 82.6 mm (red morph), 1 ♀ 68.0 × 95.2 mm (red morph); Cayman Expedition 1938, 1938; in bush and plantation; 1952.1.17.4-6; Coll. Oxford University; 11.V.1938;

NHM 2024.353 [1 ♂ 29.3 × 37.0 mm of this sample is *Hartnollius lateralis* n. comb.].
Jamaica • 1 ♂ 56.8 × 80.2 mm; Clydesdale; coll. W. Lynn; 1.VI.1936; alt. 1067 m, Rathbun det.; USNM 72785.
Haiti • 1 ♂ 25.4 × 32.0, 1 ♀ 29.0 × 35.6 mm; Coll. D. F. Weinland, MCZ n°1613, USNM 1513693 (See Fig. 6C).
Near Haiti, Navassa Island (Isle de la Fortune) • 6 ♂ (60.0 × 82,9 mm Cr 63, 55.6 × 76.6 mm Cr 64, 55.9 × 75.9 mm Cr 65, 60.0 × 82.7 mm Cr 66, 55.4 × 77.0 mm Cr 67, 54.0 × 76.2 mm Cr 68; I. Sanderson; 16.XII.1937; det. A. C. Evans; NHM 1967.7.1.80-85. (See Fig. 6A, B).
St Kitts • 1 ♂ (many legs detached) 66.6 × 93.8 mm (red morph); 1912.6.18.1; pres. J. J. Quelch; NHM 1888.26.
Antilles • 1 ♀ 59.8 × 82.2 mm; dry; as *Gecarcinus ruricola*; MNHN-IU-2000-3765 (= MNHN-B3765).
Guadeloupe • 1 ♂ 74.8 × 109.2 mm; dry; as *Gecarcinus ruricola*; MNHN-IU-2000-10876 (= MNHN-B10876) • 1 ♂ 32.7 × 43.4 mm (red morph); Îles des Saintes; KARUBENTHOS 3; Stn IGM4, 15°52.44'N, 61°34.8'W; 28.IX.2024; MNHN-ARBig-LPRig coll.; Parasram det.; MNHN-IU-2024-4640; (see Fig. 6D) • 1 ♀ 41.2 × 54.2 mm, 'red morph'; La Désirade; Parc du Souffleur; KARUBENTHOS 3; Stn AU-EP-09, 16°18'51.0"N, 61°02'55"W, alt. 263 m; dry forest; 10.XI.2024, E. Poirier MNHN-ARBig-LPRig coll.; Parasram det.; MNHN-IU-2024-7258 (See Fig. 6E).
Dominica • 1 ♂ 65.6 × 91.0 mm; near mouth of Layou River, along road at night; H. H. Hobbs Jr coll.; 14.II.1966 and det.; USNM 12693 • 1 ♂ 67.3 × 91.3 mm, 1 ♀ 68.0 × 93.6 mm; on cliff above S. shore of mouth of Layou River; H. H. Hobbs Jr & F. A. Chace coll. 9.III.1964 and det.; USNM 126937 (See Fig. 6F) • 1 ovigerous ♀ 67.2 × 92.5 mm; coll. J. G. Ramage; 1888.26; NHM 1888.26.
Barbados • 1 ♂ 60.0 × 85.4 mm, 1 ♀ 63.2 × 86.6 mm (dark red morphs); Crane Hotel, St. Philip; coastal cliffs; 13°10'25.96"N, 59°44'65.73"W, 28.09.2019; Parasram coll. and det.; BLSZ 059.
Curaçao • 1 ♂ 37.8 × 51.4 mm; Caracas Bay, Hato [Hato caves]; 28.IV.1920; C. van der Horst; USNM 56879.
Colombia, Isla de la Providencia • 4 ♀ 63.4 × 83.9 mm, 66.7 × 89.8 mm, 60.0 × 80.6 mm, 55.2 × 71.5 mm; R/V *Albatross*; S. I. Smith det.; USNM 7343 (See Fig. 6G).
Bahamas • 1 ♀ 59.0 × 81.0 mm; dry, damaged; as *Gecarcinus ruricola*; MNHN-IU-2000-12496 (= MNHN-B12496).

TYPE LOCALITY. — The previous statement of 'America' by Linnaeus (1758) as type locality must be replaced by the place of origin of the neotype, namely Cuba.

DESIGNATION OF A NEOTYPE

In order to fix the taxonomic identity of *Gecarcinus ruricola*, we undertook the necessary steps to trace the type of *Cancer ruricola* Linnaeus, 1758, first by consulting the Catalogue of the 'Linnaean collection' held at Uppsala University, and then by contacting the Linnean Society of London, which provided us with a list of 'Linnaean type specimens', including Crustacea, deposited at that institution (Wheeler 1983). No specimen with this name has been found in these two institutions and therefore no name-bearing type specimen is considered to be extant (ICZN 1999: Article 75.1). In order to define and typify *G. ruricola* objectively by a single specimen, a neotype is designated here. As the neotype must come "as nearly as practicable from the original type locality" (ICZN 1999: Article 75.3.6), in our case from 'America', a Cuban representative (Figs 2; 3A-F) is well suited to be a candidate for the neotype since Linnaeus had received material from various places in America, including this island, for his *Systema Naturae.*

DIAGNOSIS

Like the genus *Gecarcinus* new status, which is represented by the one and only species *G. ruricola*.

REMARKS

According to Hartnoll *et al.* (2006a: table 6), in San Andrès, the species is heterochelic, with no preferential handedness. The larger size of male chelae is small compared to other gecarcinoid species. Growth patterns of the chelae result in modest levels of heterochely and sexual dimorphism. This suggests that both sexes play roles of similar dominance levels during intraspecific interactions. In the material examined, the chelae of male *G. ruricola* are subequal, without marked heterochely and heterodonty (Figs 1A; 3A, B; 4B; 10D; 17; 18), however with exceptions (see Fig. 1B). There appears to be no genetic predisposition for right-handedness in *Gecarcinus ruricola*.

During the night and when disturbed in their burrows during the day, *Hartnollius lateralis* n. comb. and *H. quadratus* n. comb. are known to produce sounds (Klaassen 1973: figs 1-5, and Abele *et al.* 1973: fig. 1, respectively) by friction of the merus of the cheliped against the subhepatic region of the carapace, which bears a number of oblique rows of striae (pars stridens) (Figs 12A; 14A, respectively). However, in the case of *Gecarcinus ruricola*, which has similar striae in the same region (Figs 2B; 4D; 18B), this type of communication does not seem to have been reported.

SIZE

Besides *Gecarcoidea natalis* (Pocock, 1888), from Christmas Island, Indian Ocean, which can exceed 120 mm cw (see Green 1997), *Gecarcinus ruricola* reaches very large sizes, with a modal size of 97-110 mm cw and a maximum recorded of 123 mm cw (Van der Hoeven & Walters 1998; Hartnoll *et al.* 2006a: figs 2, 3). It is one of the largest American gecarcinids, making it a 'museum piece' (Richmond 2003) (Figs 1; 2). The mean carapace width of all measured *Hartnollius lateralis* n. comb. was approximately half that of all measured *G. ruricola*, whereas the mean fronto-orbital distance of *H. lateralis* n. comb. was less than half that of *G. ruricola* (Britton *et al.* 1982: fig. 3), i.e., the carapace of *G. ruricola* lateral to the orbits is proportionately larger than the corresponding area of *H. lateralis* n. comb. The mean size of adult *G. ruricola* is known to differ among the Caribbean Islands: for example, throughout the Grand Cayman both sexes are smaller in terms of body size than other populations in the Caribbean and males are larger than females (see below, *Biology*); by comparison, *H. lateralis* n. comb. shows an increase in mean size from eastern to western localities. *G. ruricola* has by far the most inflated carapace.

COLOUR

Phenotypic plasticity in colour patterns is very often observed in land crabs, and multiple morphs can be recognised in the same species. *Gecarcinus ruricola* is known to exhibit extensive colour polymorphism, with at least four main colour morphs: black, red or purplish, yellow and green, some with subpatterns, as follows. Martinique: carapace and legs intense purplish or dark morph (Fig. 17A); Dominica: black morph

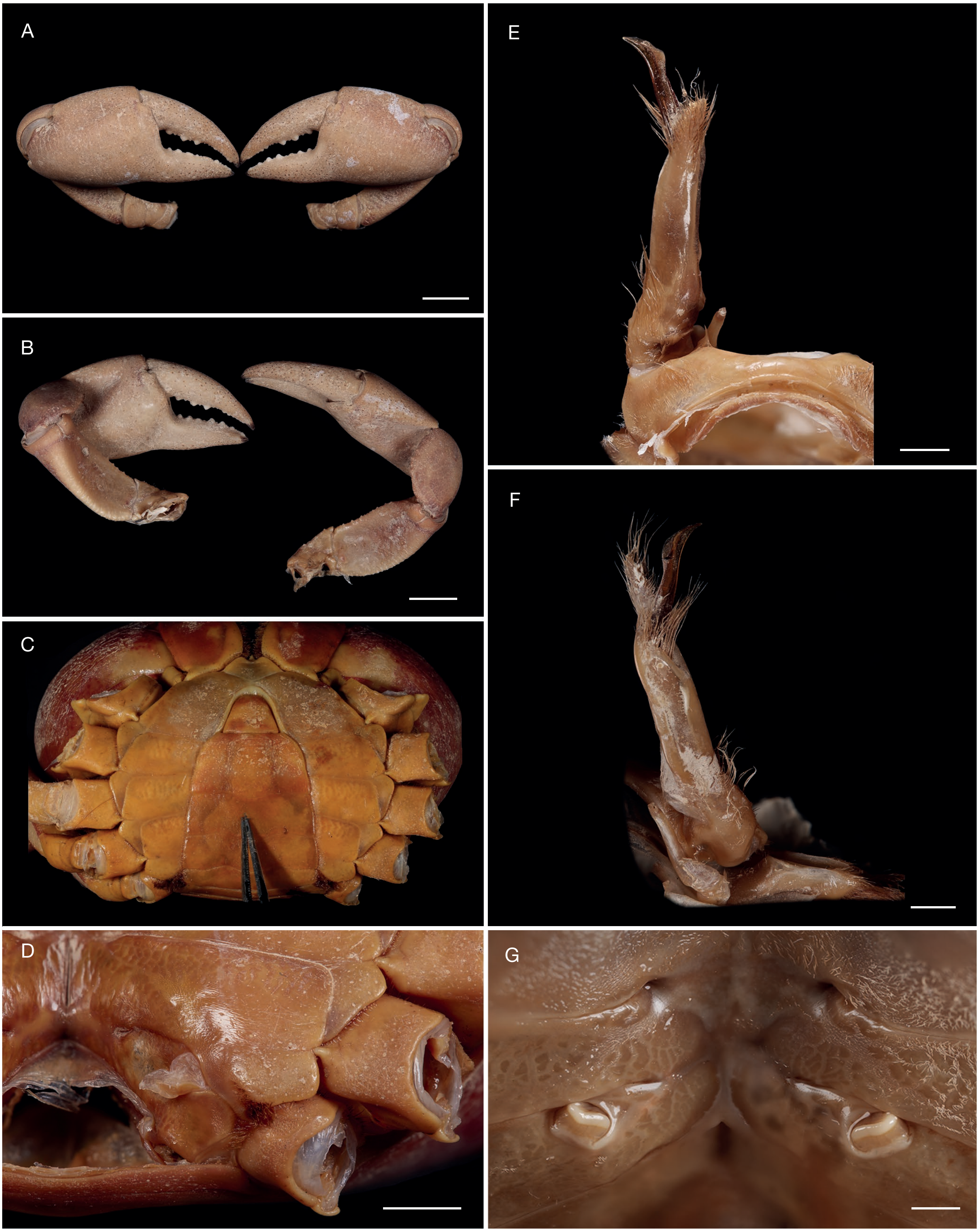

Fig. 3. — *Gecarcinus ruricola* (Linnaeus, 1758): **A**-**F**, neotype, ♂ 55.0 × 76.0 mm, Cuba, MNHN-IU-2017-8392 (= MNHN-B13155): **A**, **B**, chelipeds, external and internal views; **C**, pleon; **D**, penis; **E**, **F**, G1, cephalic and caudal views, and G2; **G**, ♀ 52.8 × 69.9 mm, MNHN-IU-2024-6554: vulvae. Scale bars: A, B, C, 10 mm; D, 5 mm; E, F, G, 2 mm. Credits: MNHN-Soubzmaigne.

that has a rich purple dorsal surface of carapace, with reddish overtones and various spots (Fig. 18H) (Chace & Hobbs 1969), and yellow morph (Fig. 18G); Saint-Barthelemy: a green morph mixed with other colours (Fig. 18A), a red morph (Fig. 18B) also an intense purplish morph or black morph (Fig. 18C); Anguilla: a mixed colour morph (Fig. 18E), a black morph (Fig. 18F) and a yellow morph (Fig. 18D); Grand Cayman: black morph, and subpatterns. The mesial lobe of infraorbital margin is very often, whatever the island and the morph, intensely red (Figs 17; 18). In Puerto Rico, *G. ruricola* has different colours on the carapace, chelae, and legs: some carapaces have varying intensities of purple, from dark to light, blue, and varying intensities of yellow/orange (Rodríguez-Fourquet *et al.* 2025: fig. 6). The Grand Cayman 'black crab' exists in three different colour morphs (Stensmyr *et al.* 2008: fig. 1A, D), but this information must be corroborated because the figure E of the same authors seems to belong to *Hartnollius lateralis* n. comb.

In Cuba, *Gecarcinus ruricola* displays two different patterns: the black and light tan or yellow morphs (Chace 1940: 53). A study of colour polymorphism in the *G. ruricola* from western Cuba, in the Parque Nacional Ciénaga de Zapata (one of best bird watching areas in the world) has identified two different patterns: black and yellow morphs, without any statistically significant difference for the frequency of the yellow colour neither between sexes nor between years; and the relation cheliped-body weight compared between both colours gave similar result (Acevedo 1989: figs 2-4, table 1). A striking but variable red/purplish morph is observed in Cuban *G. ruricola* from La Blanquilla (Scelzo & Varela 1988: fig.4), which can lead to confusion with *Hartnollius lateralis* n. comb. (Fig. 19). A mixed colour morph is also present in Cuba (Fig. 17B).

For *Gecarcinus ruricola* there are no studies focusing on the colour patterns and the significance of the colour diversity. Such a study has been conducted, for example, on *Cardisoma guanhumi* from northeastern Brazil, where the four identified colour patterns could be clearly related to the crab's stage of development (growth size) and sexual maturity, with the smallest individuals being bright orange and the sexually mature adults ranging from brown to blue (Silva *et al.* 2014). It is also possible that colour patterns may change depending on seasonality and the current state of the individual (stress, endogenous rhythms or even temperature variations). They could also be related to osmoregulatory and respiratory physiology, response to desiccation, moult cycle and mating behaviour (Reid *et al.* 1997; Silbiger & Munguia 2008).

In comparison, in *Johngarthia lagostoma* from Trindade Island (Brazil), colouration varies depending on individual size, sex and ecological processes related to differential occupation of available habitats: there are three colour types (black, purple and yellow), with black crabs being exclusive and predominant in the smaller size classes; then, yellow crabs dominate throughout ontogeny, while purple individuals are less frequent. Crabs of all three colour types are present in both sexes, and the frequency of each type are similar in males and females. Black and purple crabs primarily occupy hill areas, whereas yellow crabs predominate throughout the island. Camouflage by background matching appears to be particularly important for small black crabs at recruitment (beach sand) and resident areas (hills vegetation and soil), where individuals exhibit higher colour matching types in both sexes. The frequency of each type, their brightness and colour metrics are similar between beaches and resident areas (hills vegetation and soil), where individuals exhibit higher colour matching (João *et al.* 2023).

Vernacular names

Gecarcinus ruricola is known as the 'black land crab', 'purple land crab', 'red land crab', 'mountain land crab', 'zombie crab', 'Halloween Krabbe', and 'blue crab'. It may be given the surname of 'tourlourou' or 'touloulou' (as in the French Antilles, see Fig. 4A, B), as well as other species of Gecarcinidae, e.g. *Hartnollius lateralis* n. comb. (see below, *Identity of land crabs synonymised with Gecarcinus ruricola or G. lateralis in the literature).*

For the pre-Linnaean nomenclature of gecarcinids, see Holthuis (1959) in his *Crustacea Decapoda of Suriname*. Holthuis (1959: 7) explains that Labat (1724: 47-53) described the species 'Tourlouroux' (*Gecarcinus spec.*), 'Crabes violettes' (= *Gecarcinus spec.*), 'Crabes blanches' (= *Cardisoma guanhumi* Latr.), and that the Suriname species identified by Fermin (1765) as 'Crabes violets', 'Crabes blancs' are not the species referred to by Labat but are *Ucides cordatus* (Linnaeus, 1763) and *Ocypode quadrata* (Fabricius, 1787), respectively. In fact, only *Cardisoma guanhumi* is found in Suriname, and its distribution area extends from Brazil to Bermuda, Bahamas, Southern Florida and the West Indies (Holthuis 1959: 259, pl. 12).

Updated geographical distribution

Gecarcinus ruricola is found without discontinuity throughout much of the Caribbean, only on islands. From the Bahamas and Cuba in the west it extends through the Greater and Lesser Antilles to Barbados in the east, i.e., Jamaica, Hispaniola, Cayman Islands, St. Croix, Saint Martin, Saint-Barthelemy, Saba, Montserrat, Guadeloupe, Martinique, Dominica, Barbados (see Hartnoll 1988a: fig. 2.6). Outlying populations occur on Curaçao, Aruba, Bonaire, Blanquilla, and in the western Caribbean in the Swan Islands off Honduras, Half Moon Caye of the Belize Barrier Reef; and also the Archipelago of San Andrés, Old Providence and Santa Catalina, off the Caribbean coast of Colombia (Powers 1977; Abele & Kim 1986; Hartnoll *et al.* 2007). It is common on some Caribbean islands, but less in others.

There were very few records of *Gecarcinus ruricola* for continental America and, moreover, they have not been confirmed (Hartnoll & Clark 2006). The record from Florida (Rathbun 1918: 355) is only supported by specimens from Loggerhead Key in the Dry Tortugas, where the species was considered rare (Powers 1977; Bliss *et al.* 1978). The location in southeastern Florida by Chace & Hobbs (1969) and Keith (1985) has not been confirmed by other sources, and no specimens or locations are cited (Hartnoll *et al.* 2006a). Our examination of the NMNH material leads to the elimination of *G. ruricola* from continental America. In fact, Rathbun's record from 'Florida' (cited e.g. by Chace & Hobbs 1969;

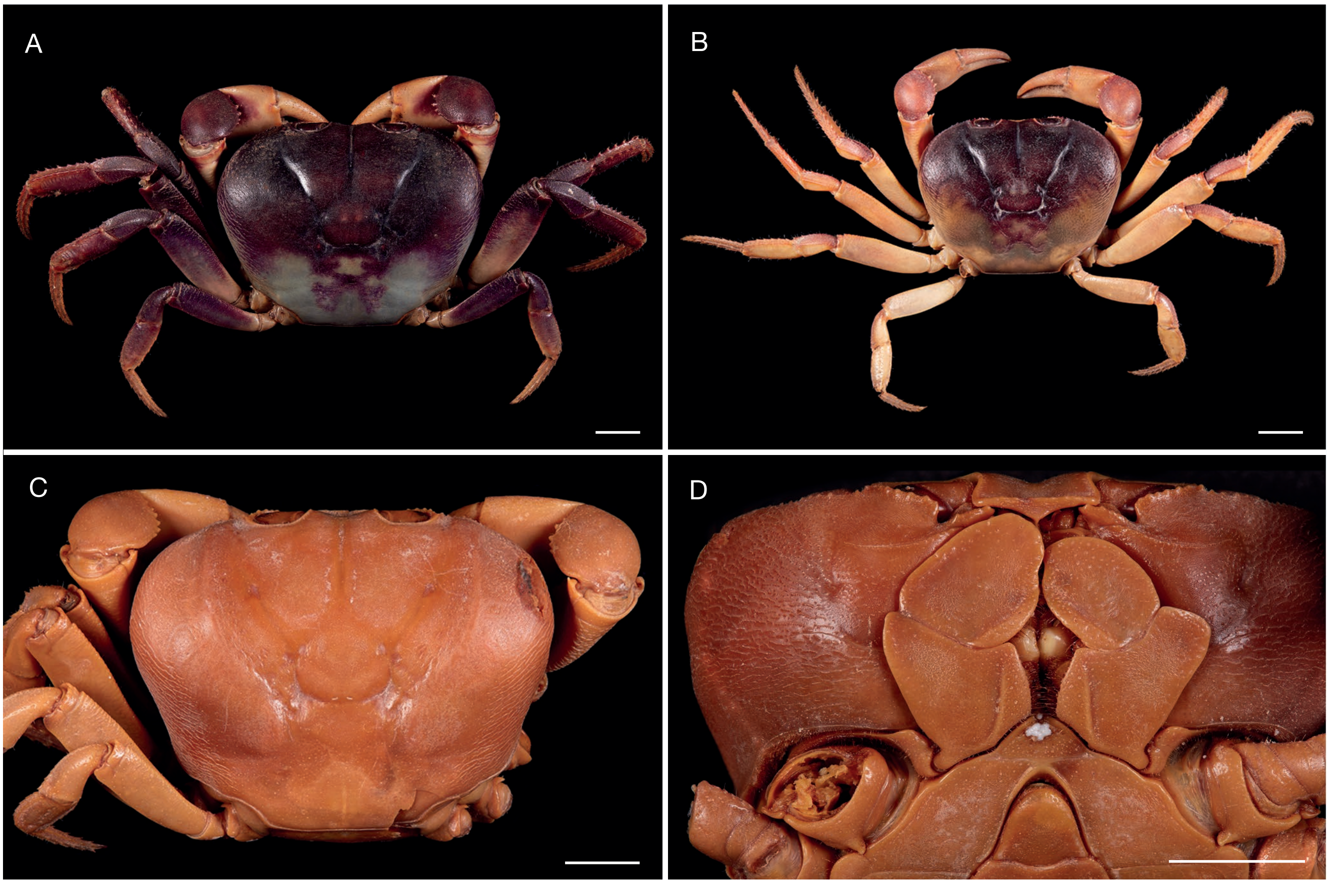

FIG. 4. — *Gecarcinus ruricola* (Linnaeus, 1758). **A**, **B**, typical young adult individuals. **A**, ♀ 41.2 × 54.2, La Désirade; KARUBENTHOS 3, MNHN-IU-2024-7258; **B**, ♂ 32.7 × 43.4 mm, îles des Saintes, KARUBENTHOS 3, MNHN-IU-2024-4640: general dorsal view. **C**, **D**, ♂ 37.8 × 51.4 mm, Curaçao, Caracas Bay, Hato [Hato caves], USNM 56879; **C**, carapace with a short ridge (not well visible here) on each lateral side; **D**, asymmetric mxp3. Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

Keith 1985; Luque 2017) does not apply to *G. ruricola*. The records 'nS Am' and 'E Fla' in Felder *et al.* (2009: 1088) are also erroneous. The two males and two females from the Florida Keys, Loggerhead Key (USNM 71219) (Fig. 5A, B) were misidentified as *G. ruricola* by Rathbun (1918) and are in fact typical *Hartnollius lateralis* n. comb. Similarly, references to 'Nicaragua' mentioned by Chace & Hobbs (1969) and Keith (1985) but not confirmed by other sources, and the absence of citations of other specimens from this location (see Hartnoll *et al.* 2006a) correspond to a misidentification. Our examination of the material (two males) (Fig. 5C, D) from Nicaragua, Greytown (USNM 74612), labelled as *Gecarcinus ruricola* by Rathbun, but later annotated "looks like to me *G. lateralis*" by H. L. Carson, and reidentified as *G. lateralis* by F. H. Barnwell, shows that these crabs are indeed *Hartnollius lateralis* n. comb. Due to the absence of *G. ruricola* in continental America here confirmed, *G. ruricola* would be restricted to the Caribbean Islands and would be an insular species (see Garth 1976 for comments on insular species), which makes previous accounts of its distribution inaccurate.

Note that a crab from Isabel Island, Sinaloa, Mexico, a male 66.0 × 94.0 mm, W. C. Swettt coll. ('red land crab'), 19.III.1933, Rathbun det. (USNM 139315), was misidentified and, according to our examination, is in fact the eastern Pacific land crab *Johngarthia planata* (see Samaniego-Herrera & Bedolla-Guzmán 2012; Perger 2019). The report of *G. ruricola* in the North of Mexico by Leija-Tristán (1985) is most likely *Hartnollius lateralis* n. comb.

The mention of 'Ecuador (Cano, Nobili)' by Rathbun (1910: 612; 1918: 357) regarding the distributional range of *Gecarcinus lateralis* is somewhat confusing because the *Gecarcinus* of Cano (1889: 101, 227) and Nobili (1901: 46), both from Ecuador, are cited by these two authors as *G. ruricola*. This formulation by Rathbun (1910, 1918) is explained by the fact that she attributed these *G. ruricola* specimens from the Pacific coast to *G. lateralis*. The *G. ruricola* of Cano and Nobili were later assigned to *G. quadratus* by Garth (1948: 59). The crab of Nobili (1901) gave its name to *G. nobilii* Perger & Wall, 2014, now *Hartnollius nobilii* n. comb. (see Perger & Wall 2014). Although Perger & Wall (2014) do no mention the *G. ruricola* of Cano (1889: 101, 227) from the same region, Ecuador, it is likely that this specimen also belongs to *Hartnollius nobilii* n. comb.

PHENOTYPIC VARIATIONS

We assembled abundant material of *Gecarcinus ruricola*, a species widespread in many and diverse Caribbean islands, but also reported on the continent, to detect possible intraspecific

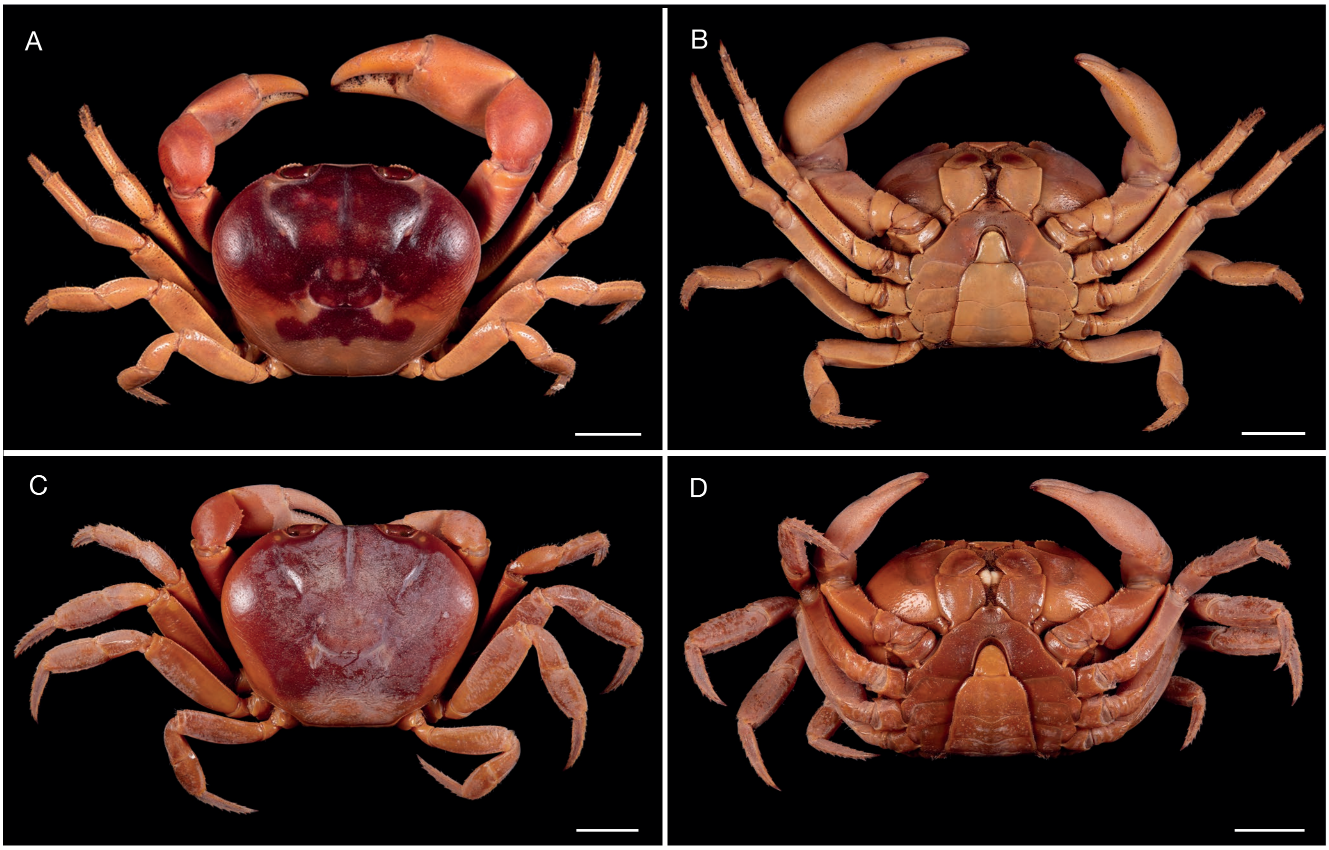

Fig. 5. — Specimens from mainland America identified by Rathbun as *Gecarcinus ruricola* (Linnaeus, 1758), but being in fact *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb. **A**, **B**, ♂ 32.3 × 40.5 mm, Florida, Florida Keys, Loggerhead Key, USNM 71219: **A**, general dorsal view; **B**, ventral view; **C**, **D**, ♂ 32.4 × 44.2 mm, Nicaragua, Greytown, Rathbun det. *Gecarcinus ruricola*; labels by Carson and Barnwell indicating *G. lateralis*, USNM 74612; **C**, general dorsal view; **D**, ventral view. Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

variability or the presence of cryptic species. Since the few previous records of *G. ruricola* from continental America had never been confirmed, it was necessary to review this issue in depth. Our examination has evidenced that the continental species assumed to be *G. ruricola* were in fact *Hartnollius lateralis* n. comb., see above *Updated geographical distribution*; and Figure 5.

The main variation observed concerns the mxp3 (when firmly applied against the buccal wall) and the level reached by the extremity of the sterno-pleonal cavity in relation to the thoracic sternal suture 2/3, which somewhat varies, being either straight or slightly concave (Fig. 6). An extreme condition, with maximum anterior extension of the mxp3 and complete coverage of the buccal cavity, is found in *Gecarcinus ruricola* from Haiti. We examined two lots: one from the NMNH (USNM 1513693, with one male and one female, both small); and another lot from the NHM (NHM 1967.7.1.80-85 with six large males) from the vicinity of Haiti, namely from Navassa Island ('Isle de la Fortune'). These Haitian individuals are characterised by a remarkable feature, that of having their mxp3 reaching the frontal border, and even exceeding it in some, and the meri on each side being entirely joined medially (except at the level of the mandibles), with an irregular latero-internal margin (Fig. 6A-C). The two external maxillipeds form a complete cover to the more internal mouthparts, with only part of the mandibles and some small portions of other maxillipeds being exposed. Therefore, the latero-external margin of the merus is very close to the infraorbital ridge. A character that appears concomitant is the close proximity of the extremity of the sterno-pleonal cavity to the thoracic sternal suture 2/3 (Fig. 6A-C). When compared in all the Haitian specimens we have examined, the mxp3 merus is more or less oval, more or less elongated, and more or less obliquely directed, which demonstrates that this structure is somewhat variable, even among crabs within a population that appears homogeneous. See below under *Gecarcinus depressus* Saussure, 1857.

Considering *Gecarcinus ruricola* from other Caribbean islands, it is clear that the condition of mxp3 is variable. Forward extension and covering of the buccal cavity are observed in crabs from other localities than Haiti, to varying degrees. For example, the small male and female from Guadeloupe collected during Karubenthos 3 Expedition (Fig. 5A, B) show a similar extension of the mxp3 (Fig. 6D, E): the merus reaches the front, and its internal border is slightly concave; each merus joins that of the other side; the extremity of the sternal cavity reaches the sternal suture 2/3. The pattern is the same in *G. ruricola* from Martinique (Fig. 17A). The extension is quite pronounced in a male *G. ruricola* from Dominica (Figs 6F; 18G). In a small male cw 75.9 mm (USNM 2065) and two larger males 60.0 × 85.3 mm, 63.1 × 86.5 mm (BLSZ 059) from Barbados, as well as in a male 66.6 × 93.8 mm (NHM

Fig. 6. — Phenotypic variations of *Gecarcinus ruricola* (Linnaeus, 1758) from various localities: level of mxp3 (resting position) in relation to frontal margin and level of sterno-pleonal cavity's extremity in relation to thoracic sternal suture 2/3: **A**, **B**, Haiti, Navassa Island, NHM 1967.7.1.80-85, CR 66, ♂ 60.0 × 82.7 mm (**A**), CR 64, ♂ 55.6 × 76.6 (**B**); **C**, Haiti, ♂ 25.4 × 32.0 mm, USNM 1513693; **D**, ♂ 32.7 × 43.4 mm, Guadeloupe, îles des Saintes; KARUBENTHOS 3, MNHN-IU-2024-4640; **E**, 1 ♀ 41.2 × 54.2 mm, Guadeloupe, La Désirade, KARUBENTHOS 3, MNHN-IU-2024-7258; **F**, Dominica, near mouth of Layou River, ♂ 65.6 × 91.0 mm, USNM 126937; **G**, Colombia, Providence Island, ♀ 63.4 × 83.9 mm, USNM 7343; **H**, Cuba, Cabanas, ♂ 51.5 × 71.5 mm, USNM 48402, with asymmetric mxp3. Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

1888.26) from St Kitts, the mxp3 are much extended and leave only a very short space between the anterior margin of merus and the front. In a male from Jamaica, the merus reaches the antennules, as in the large male cl 67.0 mm represented by Chace & Hobbs (1969: fig. 66) where the merus covers the epistome and most of the antennular cavities. In specimens of Cayman Islands, the merus reaches either the antennules or only the epistome. On Providencia Island, Colombia, all four females examined have the anterior part of the mxp3 reaching only the epistome but to a variable extent (Fig. 6G). In the material from Cuba, individuals have their mxp3 reaching either the level of the front (Figs 17B) or the antennules or only that of the epistome as in the neotype (Figs 2C-D; 10A); in another specimen (Fig 6H: see right mxp3), the space between the merus and the frontal margin is more or less pronounced.

As these are only occasional and isolated examples, or at least studies involving a far insufficient number of individuals, the above remarks may be biased and may not represent the overall morphology of the external mouthparts in all individuals in the populations of the countries considered. The first male gonopod is known to be the most reliable character for taxonomic decisions (see Toledano-Carrasco 2019: figs 14-19, the numerous figures of *H. lateralis* n. comb. and *H. quadratus* n. comb., as *Gecarcinus*), but, despite careful examination of the G1 in *Gecarcinus ruricola* crabs from various islands, we did not detect any possible variation, at least under a binocular microscope.

The phylogenetic tree based on the mitochondrial genes COI and 16S (Fig. 16), as well as the COI-based genetic distance matrix (Table 3), do not reveal any significant differences between the samples from Cuba and Guadeloupe. We therefore assume that *Gecarcinus ruricola* is a species with intraspecific variability and whose interbreeding populations are reproductively compatible. To corroborate this hypothesis, it would be interesting to include more specimens from different localities in a more in-depth study of the species. It is possible to assume that actually or potentially interbreeding populations are reproductively compatible with other populations The pelagic lifespan of *G. ruricola* is likely to be of 40-50 days and, if water currents are conservatively paced at 1-2 knots, then this would give a potential dispersal range of between 2000 to 4500 km. This potential larval dispersal (see Garth 1976) is sufficiently strong to indicate potential intermixing between Caribbean populations of the species (R. Hartnoll, pers. comm.). We currently have - with material insufficiently representative of a population – no decisive morphological argument in one direction or the other: for example, all Haitian specimens examined from three different lots exhibit a similar morphology of the mxp3 (Fig. 6A-C) but, on the other hand, the specimens from Cuba show a mxp3 merus either extending to the front (Fig. 17B) or reaching only the antennules, or the epistome only (Fig. 6G). Could the low phenotypic disparity observed, which, at this stage, does not, in our opinion, imply taxonomic changes, be related to genetic divergence? The DNA analyses (although limited) of individuals from the Caribbean islands does not demonstrate the existence of cryptic species in a possible *G. ruricola* complex.

BIOLOGY

Gecarcinus ruricola inhabits damp, shaded forest areas or dry upland habitats, retiring into rock crevices or sheltering between tree roots or hiding under fallen trees, sometimes muddy beaches, which distinguishes it from the other three species of *Hartnollius* n. gen. (see Wolcott 1988: fig. 3.1, as *Gecarcinus*). The population biology of *G. ruricola*, studied in the western Caribbean, particularly on two islands of the San Andrés Archipelago, San Andrés and Old Providence/Santa Catalina Islands (Hartnoll *et al.* 2006a), reveals that the 'black land crab' is the most terrestrial of gecarcinids in the Caribbean (some of endemic Jamaican sesarmids are more terrestrial overall). It feeds on fruits, mushrooms and other organic matter from the forest.

In Dominica, *G. ruricola* is found several kilometres inland from the sea, up to 300 m (Chace & Hobbs 1969), and up to 1000 m in Jamaica (Britton *et al.* 1982) and in the San Andrés Archipelago (Hartnoll *et al.* 2006a); it can even live several kilometres inland (Wolcott 1988). *G. ruricola* ('black land crab') is found throughout Grand Cayman (such as *Cardisoma guanhumi*): males reach a larger maximum size than females, both sexes are smaller in terms of body size than other populations in the Caribbean (it may be possible the populations on Grand Cayman reach sexual maturity at an earlier stage and smaller size than other geographic locations), and the reproductive migration season extends over three months on Grand Cayman (Tedford 2018). The lateral regions of the carapace are inflated to accommodate the highly modified respiratory structures.

Its biometric characteristics, distribution and activity have been compared to those of *Hartnollius lateralis* n. comb. by Britton *et al.* (1982, as *Gecarcinus lateralis*). Burrowing is somewhat incidental in *G. ruricola*, whereas *H. lateralis* n. comb. is an active burrower (Wolcott 1988: fig. 3.9) and even moults within its burrow (Weitzman 1963; Bliss 1968; Bliss *et al.* 1978, as *G. lateralis*). *G. ruricola* is frugiforous and mainly nocturnal (Rodríguez-Fourquet *et al.* 2025), except during the breeding migration, whereas *H. lateralis* n. comb. can demonstrate striking diurnal activity, for example in the Cayman Islands forest (Britton *et al.* 1982, as *G. lateralis*) and is mostly herbivorous/omnivorous (Linton & Greenaway 2007: table 3, as *G. lateralis*), sometimes cannibalistic (Wolcott & Wolcott 1984, as *G. lateralis*). Carson (1967), Carson & Wheeler (1967) and Stensmyr *et al.* (2008: fig. 1, as *G. ruricola and G. lateralis*; see also Stensmyr & Hansson 2007, as *G. lateralis*) described the symbiotic relationships of *G. ruricola* (and also *H. lateralis* n. comb.) with drosophilids in the West Indies (see also Bright & Hogue 1972: table 1, as *Gecarcinus*) and in Puerto Rico (Rodríguez-Fourquet *et al.* 2025: fig. 7, as *Gecarcinus ruricola*). Protists have been found in the digestive tract of *H. lateralis* n. comb. (Perger *et al.* 2022).

Gecarcinus ruricola and *Hartnollius lateralis* n. comb. are sympatric in many areas of the Caribbean. Britton *et al.* (1982, as *Gecarcinus lateralis*), who conducted comparative biometric analyses, habitat preferences, activity patterns and other biological data on these two species, highlighted the paucity of literature on *G. ruricola* within its range (in contrast to the extensive literature on *H. lateralis* n. comb.; see under that name), despite it is one of the most conspicuous terrestrial crustaceans, captured and used as food. The increasing presence of human activities in the Caribbean may deprive *G. ruricola* of suitable habitat and thus reduce its numbers.

The study of the reproductive biology of *Gecarcinus ruricola* in the San Andrés Archipelago by Hartnoll *et al.* (2007) provides extensive details on breeding females, annual breeding migration, egg laying (migrating crabs are mostly females with predominance of ovigerous females with the eggs carried under the pleon; some females mate and lay eggs on the landward side, others on the seaward side (see Fig. 21A), migrating females on average are larger than migrating males), fecundity and irregular recruitment. The megalopa of *G. ruricola* is the most terrestrially adapted megalopa described to date for locomotion on land: it is the returning stage from the sea to the terrestrial habitat (Hartnoll & Clark 2006: 162, figs 3-9, table 2). There are sometimes extensive land invasions by megalopae, with pink mass of megalopae crossing the landward side of the coast, a hasty moulting to the first crab and swarming into the forest. But such an invasion is not an annual event. The megalopa is the stage which invades land and normally travels overland some distance before moulting; the migration of berried females to the sea varies in timing and intensity from year to year, with, however, a substantial migration each year (Hartnoll & Clark 2006: 162, fig. 2; Hartnoll *et al.* 2014: 532, fig. 1). A similar land invasion by megalopae occurred in Jamaica in 2006 (Aiken & Pal 2009). And, in Cuba, crabs (red, yellow or black) sometimes emerge by the millions and head towards the sea to deposit their fertilised eggs in the water, mating having previously taken place in underground burrows.

In Puerto Rico, where site fidelity is present (except during migration), only female migration has been observed, meaning that copulation occurs far from the shore and in the forests, which males therefore do not abandon (Rodríguez-Fourquet *et al.* 2025). If this is confirmed, there would be a notable difference with land crabs such as the 'red crab' *Gecarcoidea natalis* (Pocock,1888) on Christmas Island, in which males and females migrate together to the sea and mate there, then the males return to their main residence, while the females remain on the shore to lay their eggs and release them in the sea, before heading towards the forests; a mass recruitment is observed approximately every five years (Hicks 1985; Hicks *et al.*1990).

Role of *Gecarcinus ruricola* and its status as an endangered species

As other gecarcinid land crabs, *Gecarcinus ruricola* is an ecosystem engineer and plays an important role in nutrient recycling and seedling propagation in coastal forests. Given the predicted future decline in precipitation for the Caribbean, the effects of dehydration on feeding preferences of *G. ruricola* were investigated on the Eleuthera Island (Bahamas) by McGaw *et al.* (2019).

Gecarcinus ruricola is a major source of protein and economic subsistence in many countries. It is known to have an extraordinary flavour. It is a popular food item, harvested on many Caribbean islands and offered live in markets (Burggren & McMahon 1988: fig. 3.12B). According to Carson (1974: 3518), "relentlessly hunted down in the populated parts of its range, it remains today principally on small, isolated islands". In Puerto Rico, the species is uncommon, and its harvest is prohibited, suggesting that other factors are affecting the population; *G. ruricola* is classified as vulnerable by Puerto Rico's Department of Natural and Environmental Resources (Rodríguez-Fourquet *et al.* 2025).

In the San Andrés Archipelago, Colombia, on the tiny island of Providence in the southwest Caribbean about 140 miles east of, Bluefields, Nicaragua, *Gecarcinus ruricola*, the 'Cangrejo Negro' or 'black land crab' (Fig. 21) is a cultural symbol of the traditional patrimony, a figure in folklore, and plays an important role within the socio-economic structure of the local demography. Crabs of this species are a major local food source: its extraction and commercialisation is considered the third tier of the economy in Providencia (and also Santa Catalina), because approximately 139 families depend exclusively on black crab commercialisation to survive. Due to indiscriminate and illegal hunting, overexploitation, forest reduction, predators and difficulties in surviving during breeding and migration periods, *G. ruricola* is one of the endangered species of these islands. As a result of the glaring lack of information on *Gecarcinus ruricola*, the Final Report in April 2005 of the *Darwin Initiative for the Survival of Species* launched the project "Sustainable Management of the Black Land Crab, *Gecarcinus ruricola*, Colombia (162/11/015)", which, for example, supported the papers of Hartnoll *et al.* (2006a, 2007) on the biology and reproduction of this species in San Andrés. According to Baine *et al.* (2007), the exploitation of *G. ruricola* in San Andrés for human food is so extensive that the Colombian government has established closed fishing areas, closed seasons, and minimum catch sizes.

The 'Providencia Black Crab Presidium', created to ensure the preservation of a marine and coastal ecosystem and the survival of species that represent an important source of income, is supported by IFAD (International Fund for Agricultural Development) and the European Union, with the collaboration of several strategic local partners (see *Slow Food Foundation for Biodiversity*, *Providencia Black Crab*). On April 1, 2024, the CORALINA Corporation [for the Sustainable Development of the Archipelago of San Andrés, Old Providence and Santa Catalina], "announced to all inhabitants of San Andrés Providencia and Santa Catalina, that from April 1 to July 31, the 'black crab' ban period begins, in accordance with resolutions 156 of 1993 and 1132 of December 30, 2005, for this reason the appropriation, access, capture, possession, extraction, transportation, commercialization or in any other way, the use of the species or derived products is prohibited."

San Andrés natives are known as 'black crabs', and sociologists have coined the term «crab antics» to refer to West Indian cultural behaviours (see *Darwin Initiative for the Survival of Species*, a UK government grants scheme, notably for biodiversity conservation). The 'Crab antics' (i.e., the antics done by the crabs) in San Andrés and Providencia is a metaphor based on the observation of fishermen catching crabs and putting them in an open basket or barrel: the crabs quickly pull down any crab that tries to get out of the basket on its own; if they had cooperated, they could have easily escaped from the basket, but they did not: the lack of cooperation leaves everyone at the bottom of the basket. For a discussion of 'crab antics', see Wilson (1973, 1995, 2017). 'Crab barrel syndrome' (CBS) is similar: no crab can actually get out of the basket, and a person with CBS does not want to see anyone progress except for himself (Uzum & Ozdemir (2020), and 'Crab mentality' or 'crab theory' refers to successful individuals that are seen as a threat by those who want to maintain their position and power, ensuring the collective demise (Tagle 2021).

Gecarcinus ruricola is threatened in the Lesser Antilles by rats (Pascal *et al.* 2004).

PHILATELY

Gecarcinus ruricola is represented on a multitude of postage stamps from West Indies, notably Cuba, and other Caribbean countries (Omori & Holthuis 2000, 2005). The species was featured on two African postage stamps (Tanzanian and Ugandan stamps) for the *International Year of the Ocean* in 1998, under the name 'mountain crab'.

ON THE IDENTITY OF LAND CRABS SYNONYMISED WITH *GECARCINUS RURICOLA* OR *G. LATERALIS* IN THE LITERATURE

Ocypode ruricola *Latreille, 1803*

Latreille (1803: 35 and footnote) described *Ocypode ruricola* with the following features: carapace regularly domed, without edge; dorsal prints short, confused; carpus and palms little ornamented; tarsi with spiny edges; found 'in America between the two Tropics and in their neighbourhoods, perhaps not living further than the neighbouring places of the Line (the Equator)'. Regarded as *Gecarcinus ruricola* by H. Milne Edwards (1837a: 26) and Young (1900: 239, as *Geocarcinus ruricola*), it would be *Cardisoma guanhumi* according to Rathbun (1918: 341); nevertheless, the figures of Latreille (1803: pl. 44 fig. 2), copied from Herbst (1783: pl. 4 fig. 37, as *Cancer ruricola*), represent the true *G. ruricola.* There is no crab labelled *Ocypode ruricola* in the MNHN collection.

Ocypode tourlourou *Latreille, 1803*

In the same paper, Latreille (1803: 36) established *Ocypode tourlourou* from Santo Domingo, for a large species, generally pale yellow, almost whitish, sometimes washed with reddish and presenting the following characters: chelipeds practically unarmed; major cheliped on the right with the fingers bearing a molariform tooth, and a smooth carpus with a small internal tooth; ventral surface with black setae ('poils noirs'); and merus of the legs unidentate. Latreille added that the only figure of Seba [Cancer terrestris] that is suitable for this species is that of t. III, pl. 20, fig. 5 (see Seba 1734-1765). This species, not mentioned by H. Milne Edwards (see 1837a: 26), was considered, without further explanation, to be a true *Gecarcinus ruricola* by Rathbun (1918: 352), Chace & Hobbs (1969: 200) and Türkay (1970: 336) [who does not mention the Latreille's *O. ruricola*]. No crab bearing the name *Ocypode tourlourou* is present in the MNHN collection.

'Tourlourou' is a popular term given during the First World War to infantry soldiers who wore a blue jacket and madder-red trousers. Sailors arriving in the Antilles nicknamed the red crabs 'Tourlourous'. ln French Guyana, 'Tourloulou' denotes any disguised and masked person, alluding to the expression 'Tour le loup', which refers to women wearing a mask and whirling while dancing in ballrooms (Belfort 2013).

Land crabs in Fréminville (1835)

Fréminville (1835: 215) wrote: "Linnaeus was the first to characterize, under the name of *Cancer Ruricola*, the common Tourlouroux of the Antilles; and of all the descriptions that have since been made of this land crab, his is still the best; but nevertheless, his successors, either through negligence or lack of opportunity to observe better, have reported and confused with his *Cancer Ruricola*, two or three distinct species which we will make known below." Fréminville (1835: 215, 216, 217) later wrote: "We are applied particularly to observing land crabs or Tourlouroux and we first noticed that among those understood to this day by naturalists under the names of *Cancer Ruricola*, *Ocypoda Ruricola* and *Gecarcinus Ruricola*, of which they are one and the same species, we could recognise them three distinct ones as Mr. Bosc had already suspected. It is therefore not surprising that the authors differ among themselves in the descriptions they give of the Tourlourou". Fréminville retains the name of *Ocypode Ruricole* for the one of the three species "that is the most common and is the true *Cancer Ruricola* of Linnaeus", and describes its morphology (too vaguely to be identified), its colour pattern and its biology ("lives in the woods and feeds there on leaves, fallen fruits and generally on plant substances"; never carnivorous unlike other gecarcinids; nocturnal; digs burrows; runs with such speed that it seems to glide rather than run, so that it is very difficult to catch, and rushes into the burrow, which serves as its retreat). An Editor's note (p. 213) indicates that it is probably *Cardisoma guanhumi.*

Then, Fréminville (1835) lists four taxa:

1. The *Ocypode Ruricole* or common Tourlourou.
  Ocypoda Ruricola, Fabricius, Bosc.
  Cancer Ruricola Linnaeus.
  Gecarcinus Ruricola, plates from the *Encyclopedia*.

See Bosc (1830: 252): "It is found in America, where it is known as Land Crab. There are probably several species confused under this name".

2. The great Tourlourou. *Ocypoda gigantea* N. [i.e., *Nobis*]

This 'dirty white' crab (see Fréminville 1835: 221) is *Cardisoma guanhumi*, according to an Editor's note (p. 213) and to Chace & Hobbs (1969: 195).

3. The red Tourlourou. *Ocypoda rubra* Fréminville (1835: 222) from Antilles.

According to the Editor's note (p. 213), it seems to be the real *G. ruricola*. It was synonymised with *Gecarcinus ruricola* by Rathbun (1918: 352) without any comment, then by Türkay (1970: 336), Prahl & Manjarrés (1984a: 154), and Ng *et al.* (2008: 215). However, *Ocypode rubra* might not be *Gecarci-*

nus ruricola but could be *G. lateralis* (i.e., *Hartnollius lateralis* n. comb., see below), which is red and digs oblique, complex burrows near the shore. The fact that it "stands as a sentinelle near the opening, and runs very fast" leaves some doubt.

Ocypode agricola *Reichenbach, 1836 (p. 230, 231) (see Reichenbach 1828-1836)*

We attempted to locate the specimens from the Antilles that were used by Reichenbach (1836: 230) to establish *Ocypode agricola*. As was customary at the time, the species was described vaguely and summarily: carapace blood-red; sides raised; margins rounded; orbits round. It lives in holes, is nocturnal, and migrates to the sea and then to land. *O. agricola* was synonymised with *Gecarcinus ruricola* by Rathbun (1918: 352) without any comment, and later by Türkay (1970: 336) and Ng *et al.* (2008: 215). The species is rarely mentioned in the chresonymy of *G. ruricola*, except by some authors such as Chace & Hobbs (1969: 200), Prahl & Manjarrés (1984a: 154), Questel (2019: 26) and Schweitzer *et al.* (2023: 2). With the help of curators and researchers from various German institutions, we learnt that Reichenbach studied in Leipzig and that the remarkable collection of the "Zoologisches Institut Leipzig" is now part (at least) of the Crustacean collection in Dresden. It seems that three specimens in two lots (dry and partly in poor condition) from the Antilles bearing the name '*Gecarcinus ruricola* (Linnaeus, 1758)' and registered «Crustacea - SNSD» were found in the Dresden Collection: but, supposedly purchased later, in 1881, from Flesche, they would probably not be the original Reichenbach's specimens, collected earlier (Andreas Allspach and A. Reimann, pers. comm.). Moreover, if the type of *O. agricola* was included in the Crustacean collection of Dresden, a town destroyed in 1945, it must be considered lost (A. Reimann, pers. comm). Although the crabs listed in the Catalogue of the old Leipzig Collection (started in 1870) are not registered as the syntypes of *Ocypode agricola*, we nevertheless give here some photographs (kindly sent by A. Reimann) of the three specimens from the Antilles (two lots): the mesial lobe of the infraorbital margin just joining front margin in all three specimens (Fig. 7B, E, G) indicates a true *Hartnollius lateralis* n. comb. (Figs 10B; 12B, C; 19); although the anterior margin of mxp3 merus is not notched and is only barely concave, thus not really concordant, it is not distally triangular as in *G. ruricola*: it would be only a variation of *H. lateralis* n. comb.

No specimens of Reichenbach appear to be part of the collection of the Leipzig University (Robert Klesser and Bernhard Detlef, pers. comm.).

Gecarcinus depressus *Saussure, 1857*

Saussure (1857: 305; 1858a: 439, pl. 2 fig. 14, a-c; 1858b: 23, fig. 11) established for two very small specimens from Haiti a new species, *Gecarcinus depressus*, "due to the remarkable configuration of its maxillipeds which seems to indicate a special group within the genus *Gecarcinus*", without any comparison with *G. ruricola*, but with a detailed description, with characters as follows. The mxp3 merus is oval, much less wide than the ischium, does not narrow towards the front and barely narrows towards the back; its anterior margin is subnotched ('subéchancré'), and the dactylus of the legs has four rows of spines. *G. depressus* was synonymised with *G. lateralis* (under its former name, see below under *Harnollius lateralis* n. comb.) by Rathbun (1918: 355) without any comment, then by Chace & Hobbs (1969: 198), Türkay (1970: 337) and most authors. The suggestion by Miers (1886: 218, and footnote, as *Geocarcinus depressus*) that this species might not be distinct from *Gecarcinus lagostoma*, now *Johngarthia lagostoma* (H. Milne Edwards, 1837), cannot be accepted because the mxp3 merus is subnotched on the anterior margin in *G. depressus* (in fact, it appears only very sligthly concave in Saussure's figures), whereas it is clearly notched on the lateral margin in *J. lagostoma* (see Türkay 1970: fig. 5c, as *Gecarcinus* (*Johngarthia*) *lagostoma*). Young (1900: 240, as *Geocarcinus depressus)* provided a description based on Saussure and considered the species valid. In any case, the species *Gecarcinus depressus* deserves close scrutiny.

According to Hollier (2018: 294; see also Hollier & Hollier 2012), two small male syntypes of *Gecarcinus depressus* from Haiti, first dry then transferred into alcohol, are deposited at the MHNG. The two specimens are stored in separate tubes in the same jar, with two typewritten labels indicating that Türkay revised the specimens in 1972 and identified them as *G. lateralis lateralis* (Türkay 1970: 337). But a careful examination of the photographs of these two syntypes (one male 19 × 23 mm, another one damaged), kindly sent by J. Hollier, poses a problem: the two syntypes belong to two different species. Specimen MHNG-ARTO-16403, a male c. 23.1 × 18.7 mm (Fig. 8A-D) is not *G. lateralis* but is quite similar to *G. ruricola* in that the mesial lobe of the infraorbital margin is overlapped by the frontal edge (versus only joined in *G. lateralis*); the mxp3 merus (somewhat asymmetric) is oval and rather close to the front, with an unnotched anterior margin and a barely notched internal margin (versus anterior border emarginated in *G. lateralis*); and the tip of the male sterno-pleonal cavity extends to the thoracic sternal suture 2/3 (versus the two are distant in *G. lateralis*). The small exorbital tooth present (Fig. 5) is also found in our smallest specimens of *G. ruricola* from Haiti (Fig. 6C). These characters are rather those of *G. ruricola.* Although the mxp3 merus of *G. depressus* (Fig. 8C) is not as narrow distally and not as obliquely directed as in our Haitian *G. ruricola* specimens (Fig. 6A-C), even in the smallest examined (Fig. 6C), it remains quite distinct from that of *G. lateralis* (under its former name, see below under *Harnollius lateralis* n. comb. (Figs 10B; 11B; 12A, B). Given the variations observed in the *G. ruricola* examined, it is possible that *G. depressus* is *pro parte* a young *G. ruricola*.

Conversely, specimen MHNG-ARTO-16404, a male *c.* 17.6 × 14.6 mm, with a damaged carapace, has the mesial lobe of the infraorbital margin just joining the frontal margin (Fig. 8E, F); the right mxp3, in place, is smaller, very far from the front; the merus is small, its anterior margin is slightly subnotched whereas its internal margin is slightly bowed; the left mxp3, detached and photographed at higher magnification, shows a clear notch on the anterior margin (Fig. 8F, H). This is the specimen whose Saussure (1858a: 439, pl. 2 fig. 14, a-c; 1858b: 23, fig. 11) depicted the mxp3

Fig. 7. — Crabs from the Antilles in the Catalogue of the old Leipzig Collection identified as *Gecarcinus ruricola* (Linnaeus, 1758), purchased from Felsche [1881], now in the collection of SNSD MTD. Not supposed to be syntypes of *Ocypode agricola* Reichenbach, 1836; it is probably *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb. **A**-**C**, 'specimen 2', ♂, Antilles, SNSD old catalogue No.Crus 1751; No. 274.6: **A**, dorsal view; **B**, frontal view showing mxp3, **C**, ventral view; **D**-**E**, 'specimen 1', Antilles, SNSD old catalogue No.Crus 1751; No. 274.6: **D**, dorsal view; **E**, frontal view showing mxp3; **F**-**H**, ♂, Antilles, SNSD MTK old catalogue Crus 1749; No. 274.4 (nec 274.3, wrong inscription on the specimen): **F**, dorsal view; **G**, frontal view showing mxp3; **H**, ventral view. Credits: André Reimann, SNSD, Dresden.

Fig. 8. — Syntypes of *Gecarcinus depressus* Saussure, 1857, Haiti, at MHNG: **A**-**D**, ♂ *c.* 23.1 × 18.7 mm, MHNG-ARTO-16403: **A**, general dorsal view; **B**, thoracic sternum: **C**, anterior ventral view: merus mxp3 not emarginate on anterior margin, mesial lobe infraorbital margin covered by frontal margin, and extremity of sterno-pleonal cavity at same level as thoracic sternal suture 2/3; **D**, one cheliped and legs (detached). Probably *Gecarcinus ruricola* (Linnaeus, 1758); **E**-**H**, ♂ *c.* 17.6 × 14.6 mm (damaged), MHNG-ARTO-16404; **E**, carapace (damaged), dorsal view; **F**, ventral view; **G**, chelae and legs (detached); **H**, mxp3 (detached), at higher magnification: anterior margin with a small notch. Probably *Hartnollius lateralis* n. comb. Scale bars: A-G, 5 mm, H, 1 mm. Credits: MHNG-Christina Lehmann-Graber.

in the same way on several occasions, and which, in this respect, most resembles *G. lateralis* (under its former name; see under *Hartnollius lateralis* n. comb.), although studied and compared by Saussure on the same page.

If genomic sequencing were to demonstrate the existence of genetically distinct populations in Haiti (simple working hypothesis), the specific name *depressus* could apply. See above, *Phenotypic variations*.

Genus *Hartnollius* n. gen.

(Figs 5, 9; 10B, C, E, F; 11B, C; 12-16; 19; 20; Table 1)

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RESTRICTED CHRESONYMY

All previous mentions of *Gecarcinus* species in the literature that do not refer to *G. ruricola* according to the diagnosis above should be designated as *Hartnollius* n. gen. The list below only contains the references related to *Gecarcinus sensu lato* (unless they concern *G. ruricola*) and/or to one or other of the species reported to it, i.e., *G. lateralis*, *G. quadratus* and *G. nobilii*, which should henceforth be known as *Hartnollius lateralis* n. comb., *H. nobilii* n. comb. and *H. quadratus* n. comb.

The chresonymy presented below in the form of a list has been restricted in view of the numerous taxonomic articles published on Gecarcinidae and also those dealing with the numerous aspects of land crabs (ecological, behavioural, embryological, physiological, biological). We did not take into account the species of *Gecarcinus* attributed to *Johngarthia* before its establishment by Türkay (1970).

Gecarcinus – Stebbing 1893: 79, 80. — Türkay 1973: 84. — Hartnoll *et al.* 2006b: 198. — Tavares & Faria 2010. — Hartnoll 2015: 404. — Luque 2017: 153. — Schweitzer *et al.* 2023: 2.

Geocarcinus and *Geocarcinus lateralis* – Young 1900: 233, 238.

Gecarcinus and *Gecarcinus lateralis* – Rathbun 1901: 14; 1921: 79; 1924: 19; 1936: 388. — Bliss 1968: 357, 359, 360, *et seq.*, figs 2, 6, 7, 9, 10, 12. — Guinot 1979: 123, 136 *et seq.* and p. 214. — Rodríguez 1980: 402, 403, fig. 110, pl. 68. — Britton *et al.* 1982: 207. — Powers & Bliss 1983: 272, 289 *et seq.* — Abele & Kim 1986: 61, 661, 663. — Türkay 1987: 145. — Adamczewska & Morris 2000: 708. — Hartnoll *et al.* 2006b: 203, 211; 2014: 531, 536, 537 and 535. — Guinot *et al.* 2013: 109, 254, 266.

Gecarcinus lateralis – Saussure 1858b: 24. — Desbonne, *in* Desbonne & Schramm 1867: 42. — Verrill 1908: 308. — Chace & Holthuis 1948: 26. — Chace 1956: 159. — Cabrera 1966: 173-187. — Bliss *et al.* 1978: 113-151, figs 6, 7-11, 14-31. — Savazzi 1985: 147-153, figs 1A, 2A, 3A, B, 4, 5A, B. — Abele & Kim 1986: 61, 661, 663. — Scelzo & Varela 1988. — García *et al.* 1998: 27, table 1. — Guinot & Bouchard 1998: 669. — Capistrán-Barradas *et al.* 2003: 323. — Carré 2005: 23. — Vaslet *et al.* 2013: 245, annex 3. — Yokoyama 2013: 114, fig. p. 115. — Questel 2014: 11; 2019: 25, 33, unnumbered figs. — Davie *et al.* 2015a: 61, fig. 71-2.30C. — Poupin 2018: 223; 2024: 138. — Hernández-Aguilera *et al.* 2022: 204.

Gecarcinus quadratus – Stimpson 1857: 29. — Garth 1948: 9, 58, fig. 2. — Hendrickx 1995: 139. — Christy & Wada 2015: fig. 71-8.10.

Gecarcinus and *Gecarcinus quadratus* – Brusca 1980: 297, 302, fig. 20. — Prahl & Manjarrés 1984b: 6.

Gecarcinus lateralis and *G. quadratus* – Türkay 1973: 973, fig. 2, 969. — Powers 1977: 139, 140. — Griffiths *et al.* 2007: 219 *et seq.* — Felder *et al.* 2009: 1088, 1104. — Marin & Tiunov 2023: 113, 117, table 4.

Gecarcinus, *G. lateralis* and *G. quadratus* – Rathbun 1918: 351, 355, 358. — Bright & Hogue 1972: 1, 6, 20, 21, 48. — Prahl & Manjarrés 1984a: 151, 154, 155. — Türkay 1970: 335, key. — Burggren & McMahon 1988: all mentions of *Gecarcinus* species except those concerning *G. ruricola*. — Tavares 1989: 3, 40, 54 and 58; 1991: 213; 2002: 333, fig. 3. — Ng & Guinot 2001: 333. — Cuesta *et al.* 2007: 263. — Ng *et al.* 2008: 215. — Hartnoll *et al.* 2017: 947 and 949.

Gecarcinus lateralis and *G. nobilii* – N. K. Ng *et al.* 2019: 99, fig. 2F.

Gecarcinus, *G. lateralis*, *G. quadratus* and *G. nobilii* – Perger & Wall 2014: 94, 96. — Guinot *et al.* 2018: 550, 561, 568. — Toledano-Carrasco 2016: 28, 32, 37-39, 118, *et seq.*, table 1. — Toledano-Carrasco & Villalobos Hiriart 2018: 67. — Toledano-Carrasco *et al.* 2021: 225, 226, figs 1, 2, 3.

TYPE SPECIES BY PRESENT DESIGNATION. — *Gecarcinus lateralis* Fréminville *in* Guérin, 1832 (see Low *et al.* 2013: 104; N. K. Ng *et al.* 2019: 99).

OTHER INCLUDED SPECIES. — *Gecarcinus quadratus* Saussure, 1853; *G. nobilii* Perger & Wall, 2014.

ETYMOLOGY. — Named in honour of Richard G. Hartnoll, who provided several important and valuable works on the Gecarcinidae, particularly on their biology, and notably on *Gecarcinus ruricola*. Furthermore, and not least, Richard has been, from the beginnings until today, a source of inspiration for the first author, who wishes to express her immense admiration for him. Gender masculine.

DIAGNOSIS

Carapace

Carapace broader than long, flat, with hepatic, subhepatic and branchial regions not markedly inflated, widest part of carapace being more or less in line with antero-lateral angles of mesogastric region. Fronto-orbital distance about half of maximum carapace width in adults. Dorsal surface with shallow grooves: cervical groove terminating anteriorly in a pit near orbital angle; median (or urogastric) groove well-defined but shallow; longitudinal mesogastric groove well-defined but shallow, rising towards frontal margin. Numerous striae along lateral margins of the carapace, used as stridulatory pars stridens. Front short, moderately produced and deflexed, with straight lateral margins and upturned lower margin. Mesial lobe of infraorbital margin angular, just joining front edge, completely exposed. Antero-lateral margins rounded, not delimitated in males; marked by granular margin in females.

Cephalic structures

Antennules very small, folded obliquely. Antennae very short, completely exposed. Orbits typical, outer angle marked. Eyestalks relatively short, curved.

Proepistome, epistome and pterygostome

Proepistome covered by subfrontal plate, thus not visible. Epistome developed, with one median crest and a lateral crest on each side. Buccal cavity rhomboid. Subhepatic and pterygostomial region glabrous, with many striae.

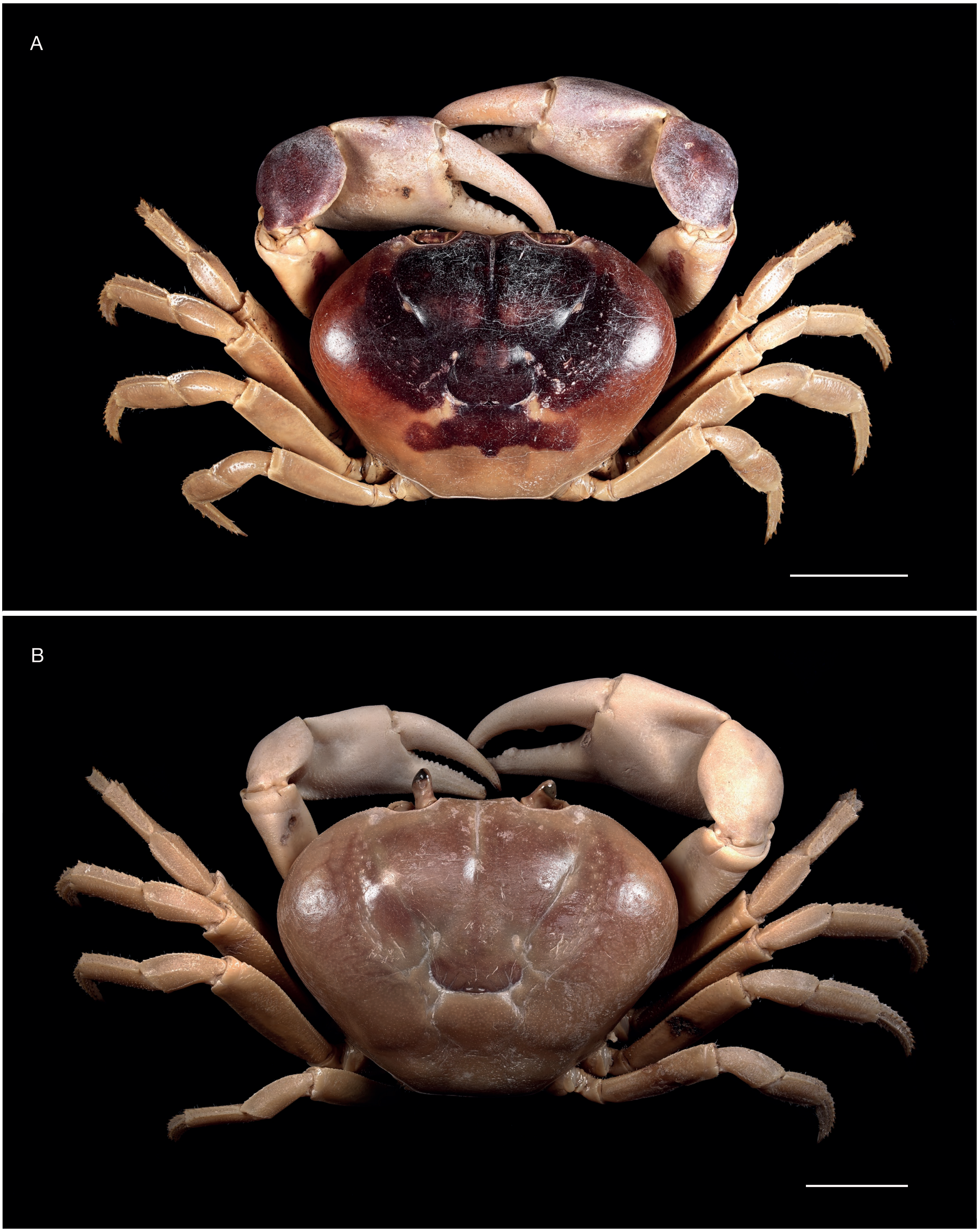

FIG. 9. — *Hartnollius* n. gen., general views: **A**, *H. lateralis* (Fréminville *in* Guérin, 1832) n. comb., ♂ 42.0 × 56.0 mm, Guadeloupe, MNHN-IU-2017-8390 (= MNHN-B24656); **B**, *H. quadratus* (Saussure, 1853) n. comb., ♂ 50.0 × 64.0 mm, Mexico, MNHN-IU-2017-8391 (= MNHN-B20900). Scale bars: 20 mm. Credits: MNHN-Soubzmaigne.

Mxp3

Mxp3 rather small, not reaching epistome (except in *H. quadratus* n. comb.), leaving between them a narrow rhomboid gap, in which mandibles are exposed. Ischium in longitudinal position and merus only slightly obliquely directed, their articulation nearly horizontal. Ischium barely smaller than merus, without longitudinal groove (only a small trace); merus directed slightly obliquely, with anterior margin emarginate but variably, sometimes only slightly, barely concave (*H. quadratus* n. comb.) or with distinct notch; meri of both sides not joining medially (except in *H. quadratus* n. comb.); palp inserted below merus: its first article fused to merus internal surface and with only small portion of last mobile article exposed. Exopod of mxp3 completely concealed, apex not reaching ischium-merus articulation, as narrow suboval plate; without flagellum.

Chelipeds

Male chelipeds massive but not extraordinarily enlarged, very unequal, especially in old males; heterochely and heterodonty usually not or only slightly marked; in rare cases of greatly uneven chelipeds (heterochelic chelae), a more pronounced gap and pronounced heterodonty. No genetic predisposition for right-handedness. Merus smooth (*H. lateralis* n. comb.) or with only small granules on inner lower margin (*H. quadratus* n. comb., *H. nobilii* n. comb.); carpus smooth (*H. lateralis* n. comb., *H. quadratus* n. comb.) or with denticles (*H. nobilii* n. comb.) on inner upper margin; occlusal margins of fingers with small, spaced teeth on both sides. Sexual dimorphism moderate.

Ambulatory legs

P3 moderately spiny. Propodus with unequally developed lateral carinae bearing four rows of weakly developed spines. Dactylus with four rows of small equal spines (*H. lateralis* n. comb., *H. nobilii* n. comb.) or with six rows of small unequal spines (*H. quadratus* n. comb.).

Sterno-pleonal cavity and pleon

Sterno-pleonal cavity moderately setose, short, not close to thoracic sternal suture 2/3, with marked ridge around telson. Male pleon moderately long, with all somites free plus telson; somite 6 with more or less convex lateral margins. Margins of pleon only with fringe of setae.

Thoracic sternum, locking pleonal structures and setal tufts

Thoracic sternum wide, narrowing at level of somite 5, thus restricted at level of P1. Sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed; sternite 2 semi-ovate with convex margins; suture 2/3 present, practically straight or barely concave, in open V-shaped (*H. lateralis* n. comb.); suture 3/4 absent, without lateral trace; sternites 3 + 4 completely fused, with gently concave or nearly straight margins; sutures 4/5 to 7/8 interrupted; sternites 5-7 similarly shaped, sutures well defined; suture 7/8 rather short; sternite 8 not developed medially, totally hidden when pleon is folded; posterior emargination reaching sternite 7 at level of narrow median bridge at level of suture 7/8; another weak median bridge at level of suture 6/7 (*H. lateralis* n. comb., *H. quadratus* n. comb.); deep median line only along sternite 7.

Locking pleonal structure as prominence rather close to suture 4/5, covered by setae; pleonal sockets not delineated, so pleonal locking no longer functional.

Patches of more or less dense hydrophilic setae located along first pleonal somites margins of pleon and at its junction with carapace.

Male gonopore and penis

Male gonopore and penis at level of suture 7/8 emerging rather far from P5 coxo-sternal condyle.

G1 and G2

G1 slightly tapering at its extremity, with unequal setae at its tip; apex short; laterally, a very long, narrow, horny, more or less curved tube, not folded and open all along, and exceeding G1 tip; several horny setae at its base.

G2 very small, without flagellum.

Vulvae

Protruding, oriented nearly horizontally, normally occluded by rigid calcified immobile operculum.

Hartnollius lateralis

(Fréminville *in* Guérin, 1832) n. comb.

(Figs 5; 9A; 10B, E; 11B; 12; 13A, B; 16; 19; Table 1)

Gecarcinus lateralis Fréminville *in* Guérin, 1832 (1829-1837): 7 and caption of pl. 5, fig. 1. — H. Milne Edwards 1837a: 27; Atlas, pl. 18, figs 1-6. — Gerstaecker 1856: 144. — Saussure 1858a: 440. — Desbonne *in* Desbonne & Schramm 1867: 42. — Pocock 1889: 6. — Rathbun 1901: 14; 1910 *pro parte*: 591; 1918 *pro parte*: 355, fig. 161, pls 119, 120 (not material from Ecuador which is likely *H. nobilii* n. comb.); 1920: 19; 1921: 79; 1924: 19; 1933: 95, fig. 91, pl. 18f, 1-3; 1936: 388. — Verril 1908: 308, fig. 2. — Pearse 1916: 554. — Chace & Holthuis 1948: 26. — Bliss *et al.* 1966: 197-212; 1978: 111-152, figs 6, 7-11, 13-31, tables 1, 2. — Bliss 1968: 359, 360, 361, 362, 363, 366, 367, 369, 370, 374, 376 *et seq.*, figs 2, 6, 7, 9, 10, 12, 14, 16-21, tables 2, 3; 1979: 385-41, figs 1-18, table 1. — Chace & Hobbs 1969: 198, figs 65, 67e-g. — Bright & Hogue 1972: 20. — Klaassen 1973: 73-79, figs 5, 6; 1975: 101-174, figs 1-6. — Powers 1977: 139. — Hopkins *et al.* 1979: 192-207. — Rodríguez 1980: 403, fig. 110, pl. 68. — Lemaitre 1981: 261. — Powers & Bliss 1983: 273 *et seq.* — Keith 1985: 274, fig. 12A. — Savazzi 1985: 147-153, figs 1A, 2, 3A, B, 4, 5A, B. — Abele & Kim 1986: 61, 661, 663, fig. b, d. — Scelzo & Varela 1988: 36, 48. — Martinez & Bliss 1989: 1-29. — Hernández-Aguilera *et al.* 1996: 92. — García *et al.* 1998: 27. — Guinot & Bouchard 1998: 669. — Venable 2004: unnumbered page and photo. — Carré 2005: 23. — Schubart *et al.* 2006: 195, table. 1. — Lalana *et al.* 2007: 82. — Ng *et al.* 2008: 215. — Felder *et al.* 2009: 1088. — Yokoyama 2013: 114, fig. p. 115. — Barro *et al.* 2013: 45. — Diez 2014: 83. — Questel 2014: 11; 2018: 15; 2019: 25 (and unnumbered photos), 33. — Hartnoll *et al.* 2014: 535; 2017: 949. — Seike & Curran 2014: 61, 63, 64, 67, 68 figs 2a-c, 3, 4, table 1. — Perger & Wall 2014: 97, figs 2A, B, 4H, I, 5A-C, 6A-C, 7, 8. — Hermoso-Salazar & Arvizu-Coyotzi 2015: 21. — Luque 2017: 153, fig. 3C, D. — Köhnk *et al.* 2017:

2018, fig. 18. — Diez & Espinosa 2018: 151. — Guinot *et al.* 2018: 568, 569. — Poupin 2018: 223; 2024: 138. — N. K. Ng *et al.* 2019: 99, fig. 2F. — Questel 2019: 25, unnumbered photos. — Parasram *et al.* 2021: 466, fig. 8A-D. — Toledano-Carrasco 2016: 37-41; 2019: 16, figs 10A, 11A-D, 2A-J, 13A-I, 14A-N, 16A-N, 20A-F, I-Q. — Toledano-Carrasco *et al.* 2021: 215, 216, 219 *et seq.*, figs 1A, 2A-C, 3A, 4, 5, 7, 8, tables 1, 2, 3. — Vendeville *et al.* 2022: 193. — Hernández-Aguilera *et al.* 2022: 204, pl. 1, fig. F, table 1. — Parasram 2023: 125, fig. 3.8 A, B, C, D.

Ocypoda lateralis – Fréminville 1835: 224.

Gecarcinus (*Gecarcinus*) *lateralis lateralis* – Türkay 1970: 337, fig. 2a-f; 1974: 974, fig. 2a-f. — Willems 1982: 180-201, figs 1-10 (larval development). — Prahl & Manjarrés 1983: 32, fig. 2B; 1984a: 155, 158, 166, figs 3.2, 4; 1984b: 6, 8.

Nec *Gecarcinus lateralis* – Rathbun 1910 *pro parte* (Ecuador): 591 (= *Hartnollius nobilii* (Perger & Wall, 2014) n. comb.).

Nec *Gecarcinus lateralis* – Türkay 1987: 147, fig. 7 (= *Hartnollius nobilii* (Perger & Wall, 2014) n. comb.).

Nec *Geocarcinus lateralis* – Young 1900: 239. (= *Hartnollius quadratus* (Saussure, 1853) n. comb.). — Perger & Wall 2014: 97 (= *Hartnollius quadratus* (Saussure, 1853) n. comb.).

TYPE MATERIAL. — **Neotype** (designation by N. K. Ng *et al.* 2019: fig. 2F). **Guadeloupe** • ♂ 36.7 × 47.2 mm; dry; ; Beaupertuis coll.; as *Gecarcinus lateralis*; MNHN-IU-2000-3758 (= MNHN-B3758).

OTHER MATERIAL EXAMINED — **Guadeloupe** • 1 ♂ (DAMAGED), 1 ♀ 23.9 × 27.6 mm; dry; M. Beaupertuis coll.; as *Gecarcinus lateralis*; MNHN-IU-2000-3757 (= MNHN-B3757) • 22 ♂ 40.5 × 55.7 mm (photo), 40.4× 54.3 mm, 32.8 × 40.7 mm, 32.6 × 41.6 mm, 30.0 × 36.6 mm, 28.0 × 35.0 mm, 25.9 mm, 32.7mm, 24.7 × 30.6 mm, 22.2 × 27.4 mm, 21.4 × 26.0 mm, 21.0 × 26.2 mm, 20.5 × 24.7 mm, 18.5 × 22.6 mm, 15.8 × 18.8 mm, 15.3 × 18.7 mm, 16.7 × 20.6 mm, 16.5 × 20.3 mm, 13.2 × 15.8 mm, 13.0 × 15.7 mm, 12.0 × 14.8 mm, 11.8 × 13.8 mm; 12 ♀: 32.6 × 41.8 mm (photo), 27.5 × 34.2 mm, 27.4 × 35.4 mm, 26.4 × 33.0 mm, 22.4 × 27.7 mm, 20.4 × 25.7 mm, 17.9 × 21.6mm, 17.6 × 21.7 mm, 16.2 × 19.7 mm, 13.4 × 16.4 mm, 13.2 × 16.3 mm; in ethanol; Côte sud de Grande Terre, Anse Vinaigri, Stn 131; Muséum Antilles 1978; 9.VI.1978; as *Gecarcinus lateralis*; MNHN-IU-2017-8390 (= MNHN-B24656) • 1 ♂ 28.2 × 36.3 mm; Îles des Saintes, Terre-de-Haut; KARUBENTHOS 3; Stn IGM1; 15°52.6'N, 61°34.7'W; 8.X.2024; MNHN-ARBig-LPRig coll.; MNHN-IU-2024-5132 • 1 ♀ 29.3 × 35.9 mm; Guadeloupe, Marie-Galante; KARUBENTHOS 3, Stn IGM25, 15°53.3'N, 61°13.3'W; 16.X.2024; MNHN-ARBig-LPRig coll.; MNHN-IU-2024-5551.
Martinique • 1 ♂ 27.8 × 34.6 mm; dry; M. Bélanger; as *Gecarcinus lateralis*; MNHN-IU-2000-10768 (= MNHN-B10768) • 1 ♂ 28.8 × 35.5, 1 ♀ 28.0 × 35.0; dry; M. Bélanger; as *Gecarcinus lateralis*; MNHN-IU-2000-3755 (= MNHN-B3755) • 1 ♂ cl 26.2 ca damaged; dry; as *Gecarcinus lateralis*; MNHN-IU-2000-3756 (= MNHN-B3756).
Cayman Islands, Little Cayman • 1 ♂ 29.0 mm × 37.0 mm, Cayman Expedition, 1938; in bush and plantation; Coll. Oxford University, 1952; 1.17.4-6; det. *Gecarcinus ruricola*; NHM.
Bahamas • 1 ♂ 43.6 × 57.4 mm; dry; as *Gecarcinus ruricola;* MNHN-IU-2000-10933 (= MNHN-B10933).
Panama • 1 ♂ 44.7 × 56.7 mm; Naos Island; Panama Survey; 4.V.1971; C. A. Child, det *Gecarcinus ruricola*; USNM 155253.
Gulf of Mexico, Florida • 2 ♂ 31.0 × 39.9 mm, 32.3 × 40.5 mm, 2 ♀ 38.3 × 47.2 mm, 31.6 × 38.8 mm; Florida Keys; Loggerhead Key, N.End; 30.VII.1926; Rathbun det. *Gecarcinus ruricola*; USNM 71219. (See Fig. 5A, B).
Nicaragua • 2 ♂ 32.4 × 44.2 mm, 31.0 × 40.3 mm, Greytown, Rathbun det. *Gecarcinus ruricola*; label by Carson: "looks like to me *G. lateralis*"; 25.X.1965; Barnwell det. *G. lateralis*, 14VIII.1975; USNM 74612. (See Fig. 5C, D).
French Guiana • 1 specimen 18.0 × 23. mm (damaged); dry; M. Leprieur; as *Gecarcinus lateralis*; MNHN-IU-2000-3754 (= MNHN-B3754).
Mexico • 1 ♂ 43.0 × 55.0 mm; in ethanol; Playa Isla Blanca, Quintana Roo; 21.VII.2018; as *Gecarcinus lateralis;* CNCR 35126.

TYPE LOCALITY. — Guadeloupe (see N. K. Ng *et al.* 2019: 99, 100).

DIAGNOSIS

Carapace

Carapace of smaller size than *Gecarcinus ruricola*, broader than long but proportionally less broad than *G. ruricola*, relatively flat, with hepatic, subhepatic and branchial regions not markedly inflated; widest part of carapace being in line with antero-lateral angles of mesogastric region. Fronto-orbital distance about half or a little less than half of maximum carapace width in adults. Dorsal surface with shallow grooves: cervical groove ending anteriorly in a pit near orbital angle; median (or urogastric) groove and longitudinal mesogastric groove rising towards frontal margin. Numerous striae along lateral margins of the carapace, used as stridulatory pars stridens. Front short, broad, moderately produced and deflexed, widening very little below, its inferior margin being slightly arcuate. Mesial lobe of infraorbital margin angular, just joining front edge and completely exposed. Antero-lateral margins entire, not markedly rounded, joining exorbital angle, with more or less marked junction; marked by granular row in females.

Cephalic structures

Antennules very small, folded obliquely. Antennae very short, completely exposed. Orbits small, with marked angle at anterolateral margin. Eyestalks relatively short, curved.

Proepistome, epistome and pterygostome

Proepistome covered by subfrontal plate. Epistome developed, with one median crest and a lateral crest on each side, setose. Buccal cavity rhomboid. Subhepatic and pterygostomial region glabrous, with many striae.

Mxp3

Mxp3 rather small, not reaching epistome, leaving between them a narrow rhomboid gap, in longitudinal position. Ischium and merus subequal, with their articulation only slightly oblique; ischium barely smaller than merus, without longitudinal groove (only a small trace); merus only slightly directed obliquely, not narrowing anteriorly; anterior margin with slight but distinct emargination, sometimes only concave and with barely marked notch; meri of both sides not joining medially; palp inserted below merus: palp with first article fused to merus internal surface and with mobile distal article barely exposed. Exopod of mxp3 as narrow plate, completely concealed by fringe of thick setae, apex not reaching ischium-merus articulation; without flagellum.

Chelipeds

Male chelipeds massive but not extraordinarily enlarged, very unequal especially in old males, widely gaping; heterochely variable, usually slightly marked; occlusal margins of fingers with small, spaced teeth on both sides; in the rare cases of greatly uneven chelipeds (heterochely), a more pronounced gap and pronounced heterodonty. Merus and carpus of adults without row of granules, entirely smooth or may be with two spiniform granules; young adults with two rows of teeth on merus and spiniform granules on inner margin of carpus. Inner surface of palm of chelae used as stridulatory plectrum by rubbing on pterygostomial striae (pars stridens).

Female chelipeds subequal or nearly so, moderately gaping, therefore sexual dimorphism moderate.

Ambulatory legs

P3 moderately spiny. Propodus with unequally developed lateral carinae bearing four rows of weakly developed spines. Dactylus with four rows of small equal spines.

Sterno-pleonal cavity and pleon

Sterno-pleonal cavity completely glabrous, short, ending far from sternal suture 2/3, with marked ridge around telson. Male pleon moderately long, bell-shaped; with all somites free plus telson; lateral margins with fringe of setae; somite 6 with convex lateral margins, forming lateral shoulder; telson campanulate, narrower than somite 6, with lateral margins slightly marked, tip rounded, relatively narrow.

Female pleon subcircular; telson forming isosceles triangle, as wide as or slightly narrower than posterior margin of somite 6, lateral margins straight, smooth.

Thoracic sternum, locking pleonal structures and setal tufts

Thoracic sternum wide, narrowing at level of somite 5, thus restricted at level of P1; sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed; sternite 2 semi-ovate, with strongly convex margins; suture 2/3 present, practically straight or barely concave and only forming an obtuse angle; suture 3/4 absent, without lateral trace; sternites 3 + 4 completely fused, with concave, obliquely directed margins; sutures 4/5 to 7/8 interrupted; sternites 5-7 similarly shaped, sutures well defined; suture 7/8 rather short; sternite 8 not developed medially, totally hidden when pleon is folded; posterior emargination reaching sternite 7; at level of suture 7/8 only some traces of bridges; deep median line only along sternite 7.

Locking pleonal structure as prominence covered by setae, rather close to suture 4/5; corresponding pleonal sockets not delineated, so pleonal locking no longer functional (Guinot & Bouchard 1998: 660, 685; Köhnk *et al.* 2017: 2212).

Setal tufts of more or less dense hydrophilic setae located along first pleonal somites, margins of pleon and at its junction with carapace.

Male gonopore and penis

Male gonopore and penis at level of suture 7/8 emerging rather far from P5 coxo-sternal condyle.

G1 and G2

G1 slightly tapering at its extremity, apex short, with unequal setae at its end; laterally, a very long, narrow, horny, unfolded and curved tube, open over a long length and exceeding G1 tip; several horny setae at its base.

G2 very small, without flagellum.

Vulvae

Protruding, oriented nearly horizontally, normally occluded by rigid calcified immobile operculum.

Colour

Based on *Gecarcinus lateralis* from Bermuda described by Verrill (1908: 308), Rathbun (1918: 356) wrote: “Commonly the carapace is mostly of a deep reddish brown or plum color; often this color is replaced posteriorly by a wide transverse band of lighter color spotted with yellow; this band extends forward, along each side, becoming narrower and darker, disappearing near the eye-sockets; a pair of small white spots close behind the eye-sockets and another pair in the cardiac region; legs light grayish brown; chelipeds darker and more red; last joint bright orange, underside white.” See also Chace & Hobbs (1969: 198, figs 5A-C, 6A-C, 7, 8, as *G. lateralis*); Parasram *et al.* (2021: fig. 8, as *G. lateralis*) (Fig. 19).

According to Perger & Wall (2014: 105, table 2), the colour of the Pacific *Gecarcinus lateralis* they examined showed little variation (see their figs 5A, 7E-F, 8G, H) and did not approach the range of variability found in *G. lateralis* from the Atlantic coast of Central America, characterised by morphs with transitional forms (see their figs 5B, C, 7A-D, 8A-F). For a detailed study of the colour variation in *G. lateralis* from Bimini, Bahamas, and from the Bermudas, see Martinez & Bliss (1989: figs 1-12, pls 1-3, as *G. lateralis*).

Vernacular names

‘Black land-crab’, ‘common land-crab’ (Rathbun 1918); ‘black-backed land crab‘ in Saint Martin (Yokoyama 2013). Also called ‘Tourloulou’ or ‘Touloulou’, like other species of Gecarcinidae, including *Gecarcinus ruricola*.

Remarks

The authorship of *Gecarcinus lateralis* is traditionally attributed to Fréminville (1835) (e.g. H. Milne Edwards 1837a; Chace & Hobbs 1969; Türkay 1970; Bliss *et al.* 1978; Hartnoll *et al.* 2006a, b; Ng & Guinot 2001; Ng *et al.* 2008; Perger & Wall 2014). Low *et al.* (2013) stated that Guérin (1832 *in* Guérin 1829-1837) should have priority. Fréminville (1835) described *Ocypoda lateralis* from Guadeloupe and its islands (Les Saintes, Marie-Galante, La Désirade), and Martinique in the West Indies, based on specimens he probably collected himself. In the introduction to this paper (1835: 213, footnote), the editor of the volume, namely H. Milne Edwards, indicates about Fréminville’s ‘tourlourou’: “son *Ocypoda lateralis* est une espèce de Gécarcin bien distincte et dont j’ai donné une figure dans mon *Histoire naturelle des Crustacés*. M. Guérin l’a également figurée dans son *Iconographie du règne ani-*

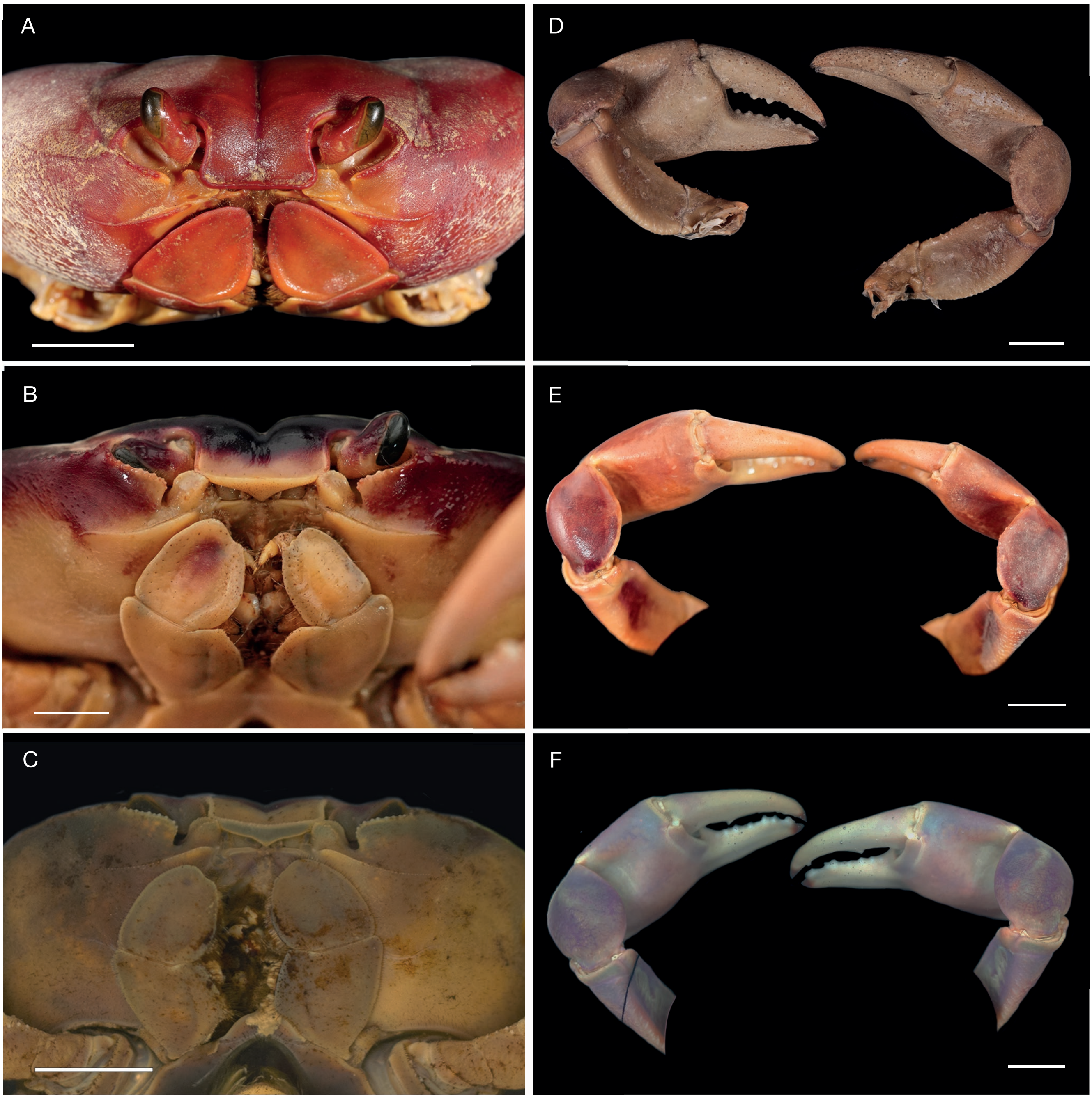

Fig. 10. — **A**-**C**, frontal views, **D**-**F**, chelipeds: **A**, *Gecarcinus ruricola* (Linnaeus, 1758), neotype, ♂ 55.0 × 76.0 mm, Cuba, MNHN-IU-2017-8392 (= MNHN-B13155); **B**, *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., ♂ 43.0 × 55.0 mm, Mexico, CNCR 35126; **C**, *Hartnollius quadratus* (Saussure, 1853) n. comb., ♀ 36.0 × 46.0 mm, Mexico, CNCR 24607; **D**, *Gecarcinus ruricola* (Linnaeus, 1758), neotype, ♂ 55.0 × 76.0 mm, Cuba, MNHN-IU-2017-8392 (= MNHN-B13155): see granules on margins of merus and carpus of chelipeds; **E**, *Hartnollius lateralis* n. comb., ♂ 43.0 × 55.0 mm, Mexico, CNCR 35126: see smooth margins of chelipeds; **F**, *Hartnollius quadratus* (Saussure, 1853) n. comb., ♂ 43.0 × 55.0 mm, Mexico, CNCR 34630: see smooth margins of chelipeds. Scale bars: 10 mm. Credits: A, D, MNHN-Soubzmaigne; B, C, E, F, CNCR-Toledano-Carrasco.

mal.” [“his *Ocypoda lateralis* is a clearly distinct species of ‘Gecarcin’ and to which I have given a figure in my *Histoire naturelle des Crustacés*. M. Guérin has also figured it in his *Iconographie du règne animal*”]. Guérin (1832, *in* Guérin 1829-1837: 7) had previously used the name “*Gecarcinus lateralis* Fréminville” and illustrated what is clearly the same species. It is very likely that Guérin used the same material as Fréminville and that he was aware of the future species by Fréminville. According to the official dates, Guérin’s plate has been published before the description by Fréminville in 1835. According to Low *et al.* (2013), the authorship of *G. lateralis* must be credited to Guérin (1832). But, as Fréminville is solely responsible for the species name in a way satisfying the criteria of availability (Code, Art. 50.1.1), the authorship of *G. lateralis* should be credited to Fréminville *in* Guérin (1832) (see N. K. Ng *et al.* 2019).

As explained by N. K. Ng *et al.* (2019: 100), Türkay (1970), based on erroneous indications given by J. Forest, the curator of Crustacea Collection in the MNHN at the time, regarded as the type series of *Gecarcinus lateralis* material collected by two French naturalists, Beaupertuis and Bélanger, and deposited in this institution. That is why Türkay (1970: 337) selected as lectotype of *Gecarcinus* (*Gecarcinus*) *lateralis* a specimen from Guadeloupe collected by Beaupertuis, MNHN-IU-2000-3758 (= MNHN-B3758). Türkay (1974: 974, 975, fig. 2) then designated as paralectotypes one male and one female from Guadeloupe, MNHN-IU-2000-3757 (= MNHN-B3757), and two males and one female collected by Bélanger from Martinique, MNHN-IU-2000-3755 (= MNHN-B3755), MNHN-IU-2000-3756 (=MNHN-B3756). A colour figure of this lectotype was published by Perger & Wall (2014: fig. 6A-C). However, Beaupertuis' and Bélanger's specimens were probably not collected during this period (i.e., before 1832), these two naturalists having travelled in the Antilles later on, as shown by the entry dates of their material in the CAA (Beaupertuis: 1839 from Guadeloupe; Bélanger: 1859, 1860, 1864 from Martinique), and cannot constitute the original material seen by Guérin (1832). The specimen from Guadeloupe previously referred to, although unsupported, as the lectotype of this species by Türkay (1970), then by Perger & Wall (2014), registered MNHN-IU-2000-3758 (= MNHN-B3758) and eligible for neotype designation, was selected as the neotype of *G. lateralis* by N. K. Ng *et al.* (2019: 99, fig. 2F).

Türkay (1974: 974, fig. 2, as *G. lateralis*) found that the mxp3 showed a high degree of variability in the shape of the merus emargination, and this even in the type series where it may be different in each side.

GEOGRAPHICAL DISTRIBUTION

Hartnollius lateralis n. comb. is distributed along the American Atlantic coast, from Florida to Venezuela and Guiana. Records include Texas (Ray 1967; Britton 1976), and Florida Keys (Bright & Hogue 1972: 21, as *Gecarcinus lateralis;* Hartnoll 1988a: fig. 2.6, as *Gecarcinus lateralis*). In the Caribbean Sea, it is present in Honduras, Swan Islands, Nicaragua, Costa Rica, Panama, Colombia, and in the islands Guadeloupe, Martinique, Puerto Rico, Haiti, Jamaica, Cuba, Bahamas; and also in Bermuda. Toledano-Carrasco *et al.* (2021) assumed that the records from the American Pacific coast by Türkay (1970), Rathbun (1918), Capistrán-Barradas *et al.* (2003), Perger & Wall (2014) and Toledano-Carrasco (2016) were actually *H. quadratus* n. comb. Based on species distribution, the *Gecarcinus quadratus* cited by Rathbun (1910: 591; 1918: 358) from 'Turbo, Colombia' correspond likely to *H. lateralis n. comb.* In Rathbun (1910: 591; 1918: 367), the records 'Bahamas to Guiana; Bermudas' of *Gecarcinus lateralis* correspond well to *H. lateralis* n. comb.; however, the record from Ecuador cited according to the mention of *G. ruricola* by Nobili (1901: 46), later synonymised with *G. lateralis*, corresponds to *Hartnollius nobilii* n. comb. (see Perger & Wall 2014).

The *Gecarcinus ruricola* specimens from mainland America, namely from 'Florida' (USNM 71219) (Fig. 5A, B) (see Rathbun 1918: 355), mentioned by Chace & Hobbs (1969) and Keith (1985), as well as the two males from Nicaragua, Greytown (USNM 74612) (Fig. 5C, D), identified as *G. ruricola* by Rathbun and mentioned by the two same authors but not confirmed by other sources, are in fact *Hartnollius lateralis* n. comb; see above under *G. ruricola*).

Gecarcinus ruricola is partially sympatric with *Hartnollius lateralis* n. comb. in many areas of the Caribbean: namely in the western Atlantic islands, in Lesser Antilles (e.g. Martinique, Guadeloupe, Saint Martin, Saint-Barthelemy), in Greater Antillen (Jamaica, Cuba) and in the Bahamas (Rathbun 1918; Toledano-Carrasco & Villalobos Hiriart 2018).

BIOLOGY

Several important contrasts between *Gecarcinus ruricola* and *Hartnollius lateralis* n. comb. are treated under the first (see above). *H. lateralis* n. comb. is more common than *G. ruricola*, often found 6-9 m above high-tide mark but sometimes up to 1000 m from shore, and is largely herbivorous, but also opportunistic carnivore and cannibal (Wolcott & Wolcott 1984; 1988: fig. 3.3.9; Burggren & McMahon 1988: fig. 3.6).

According to studies on *Hartnollius lateralis* n. comb. carried out by Bliss *et al.* (1978: figs 6, 7-11, 13-31, as *Gecarcinus lateralis*) at Sabal Point, just north of Boca Raton Inlet, Florida, with environmental conditions supporting a dense population of *H. lateralis* n. comb., the crabs can be seen outside of their burrows during the daytime, an unusual behaviour for this species that is typically an active burrower. In eastern Florida, *H. lateralis* n. comb. inhabits wooded areas of dune ridges and back dunes, under logs and leaf litter, and burrows in dry sandy areas; it is primarily nocturnal (Powers 1977: 139). In Martinique, traps to catch the 'touloulou', e.g. '*Z'attrap crab*' or '*bwèt à krab*', are placed over the holes. Observations on the species in Bermuda by Savazzi (1985: figs 1A, 2A, 3A, B, 4, 5A, B, as *Gecarcinus lateralis*; see also Schmalfuss 1978) showed that it excavates permanent tunnels in compacted soil in grass-covered areas or among tree roots and boulders: finely tuberculated terraces on the chelipeds, around the sides of the carapace and on the walking legs, are related to a wedging function (see also Davie *et al.* 2015a: fig.71.2.30C).

In *Hartnollius lateralis* n. comb., moulting and mating can take place inside the burrow, thus far inland. Males defend burrows during breeding migrations (Wolcott 1988: fig. 3.3.10). Ovigerous females must leave their terrestrial burrows and adopt several types of behaviour to reduce the risks (predators, extremes of salinity and wave impact) for both adult females and larvae during migration and spawning, i.e., migrate directly toward the shore (reducing the time to reach the sea, avoiding standing water) to carry their developing egg masses to the surf and release their eggs. Females spawn synchronously; ovigerous females actively release eggs only when they are ripe, preventing premature release (Wolcott & Wolcott 1982, 1988, as *G. lateralis*). Young crabs come up these beaches to live on land. Fertility is very high in land crabs compared to any of soil inhabitants (e.g. berried females of *Hartnollius lateralis* n. comb. carry between 19 000 and 109 000 eggs each (Klaassen 1975, as *Gecarcinus lateralis*; Green *et al.* 1997, as *G. lateralis*), and this high reproductive potential ensures the prosperity of crabs in terrestrial habitats. See Britton *et al.* (1982) for biometric and ecological relationships, including habitat preferences, activity pattern and resource allocation.

During the night and when disturbed in their burrows during the day, *Hartnollius lateralis* n. comb. as well as *H. quadratus* n. comb. are known to produce sounds (Klaassen 1973: figs 1-5; Abele *et al.* 1973: fig. 1, respectively) by friction of the merus of the cheliped against the subhepatic region of the carapace, which bears a number of oblique rows of striae (pars stridens). However, in the case of *Gecarcinus ruricola*, which has similar striae in the same region, this type of communication does not seem to have been reported.

Hartnollius quadratus
(Saussure, 1853) n. comb.
(Figs 9B; 10C, F; 11C; 13C; 14; 16; 20; Table 1)

Gecarcinus quadratus Saussure, 1853: 360, pl. 12 fig. 2. — Stimpson 1857: 29. — Rathbun 1910: 591; 1918, 358, fig. 162, pls 121, 122 (material from 'Turbo, Colombia' corresponds likely to *H. lateralis* n. comb., see below). — Finnegan 1931: 653. — Pesta 1931: 180, pls 5, 6. — Garth 1948: 12, 58, fig. 2. — Bott 1955: 65. — Bright 1966: 190, fig. 4G. — Bright & Hogue 1972: 20. — Powers 1977: 140. — Brusca 1980: 297, 302, fig. 20. — Prahl *et al.* 1984: 29. — Sherman 2002: 67, 70, seq. — Griffiths *et al.* 2007: 219-224, figs 1, 2. — Arzola-González & Flores-Campaña 2008: 45. — Ng *et al.* 2008: 215. — Felder *et al.* 2009: 1004. — Perger & Wall 2014: fig. 6D-F. — Christy & Wada 2015: fig. 71-8.10. — Toledano-Carrasco 2016: 146, 148, 149; 2019: 22, figs 10B, 11E-H, 12K-O, 13J-P, 17A-L, 18A-L, 19A-L, 20G-H, R-X. — Köhnk *et al.* 2017: 2110, fig. 19c, d. — Hartnoll *et al.* 2017: 959. — Toledano-Carrasco & Villalobos Hiriart 2018: 67. — Guinot *et al.* 2018: 568, 569, 567, 589. — N. K. Ng *et al.* 2019: 99, 100. — Toledano-Carrasco *et al.* 2021: 215, 216, 221, 224, 226, 228, 229, 230, 231, figs 1B, 2D-H, 3C, E, 4-6, 8, tables 1-3.

Nec *Gecarcinus* (*Gecarcinus*) *lateralis quadratus* – Türkay 1970: 335, 338, fig. 4. — Prahl 1981: 207: fig. 56.1. — Prahl & Manjarrés 1984a: 155, 166, figs 3, 5.3 (= *Gecarcinus nobilii* Perger & Wall, 2014).

Geocarcinus lateralis – Young 1900: 239 (nec *Gecarcinus lateralis* Fréminville *in* Guérin, 1832).

Gecarcinus lateralis – Perger & Wall 2014: 97 (nec *Gecarcinus lateralis* Fréminville *in* Guérin, 1832).

Nec *Gecarcinus quadratus* – Prahl *et al.* 1990: 29 (= *Gecarcinus nobilii* Perger & Wall, 2014).

TYPE MATERIAL. — **Syntype. Mexico** • 1 ♂ cl 39.7 mm; Mazatlán [M. Verreaux]; ANSP CA3741. Perhaps another one ♂ syntype of which only a small cheliped is preserved.

MATERIAL EXAMINED. — **Mexico** • 1 ♀ 39.4 × 49.7 mm; dry; Oaxaca; rev. M. Türkay VI.1972 det. *Gecarcinus* (*Gecarcinus*) *lateralis*; MNHN-IU-2000-3759 (= MNHN-B3759) • 2 ♀ 40.0 × 51.0 mm, 40.6 × 53.0 mm; dry; MNHN-IU-2000-3761 (= MNHN-B3761); *Gecarcinus quadratus* • 1 ♂ 50.0 × 64.0 mm; in ethanol; Estero El Verde Camacho, Sinaloa; 12.VII.1972, M. Hendrickx det. 1998 *Gecarcinus quadratus*; MNHN-IU-2017-8391 (= MNHN-B20900). **Unknown location** (Gabon?: incorrect location) • 1 ♂ 47.0 × 62.7mm, 1 ♀ 42.4 × 52.7 mm; dry; M. Verreaux; det. *Gecarcinus quadratus*; Türkay Rev. VI.1972 *Gecarcinus lateralis*; MNHN-IU-2000-3762 (= MNHN-B3762).

TYPE LOCALITY. — Mazatlán (Mexico).

DIAGNOSIS

Carapace

Carapace smaller than that of *Gecarcinus ruricola* but larger than that of *Hartnollius lateralis* n. comb., broader than long, relatively flat, with hepatic, subhepatic and branchial regions only slightly inflated; widest part of carapace being in line with antero-lateral angles of mesogastric region. Carapace front about as wide as distance between mesial ends of suborbital cristae. Dorsal surface with shallow grooves: cervical groove terminating anteriorly in a pit near orbital angle; median (or urogastric) groove and longitudinal mesogastric groove rising towards frontal margin. Fronto-orbital distance about half or a little less than one half of maximum carapace width in adults. Front short, broad, moderately produced and deflexed, widening very little below, its inferior margin being slightly arcuate. Numerous striae along lateral margins of the carapace, used as stridulatory pars stridens. Mesial lobe of infraorbital margin angular, just joining front edge and completely exposed. Antero-lateral margins entire, rounded, joining exorbital angle, with more or less marked junction, smooth in males; delineated by granular row in females.

Cephalic structures

Antennules very small, folded obliquely. Antennae very short, completely exposed. Eyestalks relatively short, curved.

Proepistome, epistome and pterygostome

Proepistome covered by subfrontal plate. Epistome developed, with one median crest and a lateral crest on each side, setose. Buccal cavity rhomboid. Subhepatic and pterygostomial region glabrous, with many striae.

Mxp3

Mxp3 rather small, reaching epistome, leaving between them a narrow rhomboid gap, in longitudinal position. Ischium and merus subequal, with their articulation only slightly obliquely directed; ischium barely smaller than merus, without longitudinal groove (only a small trace); merus slightly directed obliquely, anterior margin straight, without distinct emargination, at the very least barely concave, or showing only discontinuity or even having very small notch; meri of both sides practically joining medially; palp inserted below merus: palp with first article fused to merus internal surface and with only small portion of mobile distal article exposed. Exopod of mxp3 as narrow plate, completely concealed by fringe of thick setae, apex not reaching ischium-merus articulation; without flagellum.

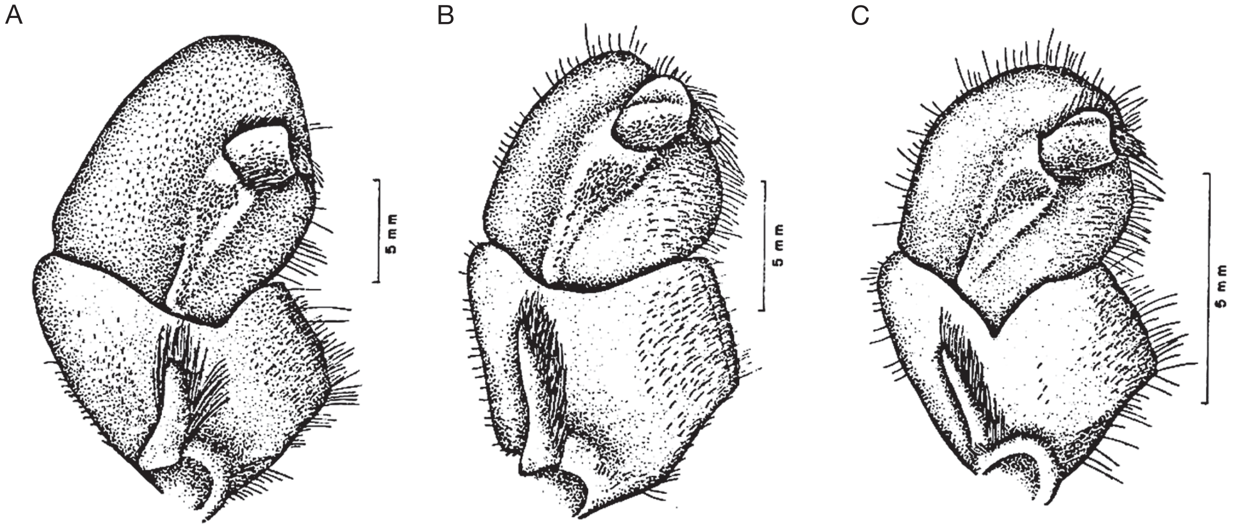

Fig. 11. — Mxp3, internal view, and palp: **A**, *Gecarcinus ruricola* (Linnaeus, 1758), Jamaica, MZUSP 18501 (ex USU-279); **B**, *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., Costa Rica, MZUSP 18509 (ex USU-281); **C**, *H. quadratus* (Saussure, 1853) n. comb., Mexico, MZUSP 18859 (ex AHF) (see Tavares 1989: fig. 14). Courtesy Marcos Tavares.

Chelipeds

Male chelipeds massive but not extraordinarily enlarged, very unequal especially in largest males, not widely gaping; heterochely variable, usually slightly marked; occlusal margins of fingers with small, spaced teeth on both sides; in case of greatly heterochely, pronounced heterodonty. In adults, merus with only small granules and carpus smooth on inner lower margin. Inner surface of palm of chelae used as stridulatory plectrum by rubbing on pterygostomial striae (pars stridens).

Female chelipeds subequal or nearly so, moderately gaping, therefore sexual dimorphism moderate.

Ambulatory legs

P3 moderately spiny. Propodus with unequally developed lateral carinae bearing four rows of weakly developed spines. Dactylus with six rows of small unequal spines, with 5 rows in juveniles.

Sterno-pleonal cavity and pleon

Sterno-pleonal cavity moderately setose, short, not close to sternal suture 2/3, with marked ridge around telson. Male pleon moderately long, bell-shaped; with all somites free plus telson; lateral margins only with fringe of setae; somite 6 with gently convex lateral margins, forming lateral shoulder; telson equilateral triangle-shaped, narrower than posterior margin of somite 6, lateral margins slightly concave.

Female pleon subcircular; telson forming isosceles triangle, as wide as or slightly narrower than posterior margin of somite 6, lateral margins straight, smooth.

Thoracic sternum, locking pleonal structures and setal tufts

Thoracic sternum wide, narrowing at level of somite 5, thus restricted at level of P1; sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed; sternite 2 semi-ovate, with slightly convex margins; suture 2/3 present, practically straight or barely concave and only forming an obtuse angle; suture 3/4 absent, without lateral trace; sternites 3 + 4 completely fused, with concave margin at level of articulation of P1 and convex at junction of mxp3; sutures 4/5 to 7/8 interrupted; sternites 5-7 similarly shaped, sutures well defined; suture 7/8 rather short; sternite 8 not developed medially, totally hidden when pleon is folded; posterior emargination reaching sternite 7; at level of narrow median bridge at level of suture 7/8; deep median line only along sternite 7.

Locking pleonal structure as prominence covered by setae, rather close to suture 4/5; corresponding pleonal sockets not delineated, so pleonal locking no longer functional (see also Köhnk *et al.* 2017: 2112).

Setal tufts of more or less dense hydrophilic setae located along first pleonal somites margins of pleon and at its junction with carapace.

Male gonopore and penis

Male gonopore and penis at level of suture 7/8 emerging rather far from P5 coxo-sternal condyle.

G1 and G2

G1 slightly tapering at its extremity, apex short, with unequal setae at its tip; laterally, a very long, narrow, horny, unfolded, curved tube, open over all along and exceeding G1 tip; several horny setae at its base.

G2 very small, without flagellum.

Vulvae

Protruding, oriented nearly horizontally, normally occluded by rigid calcified immobile operculum.

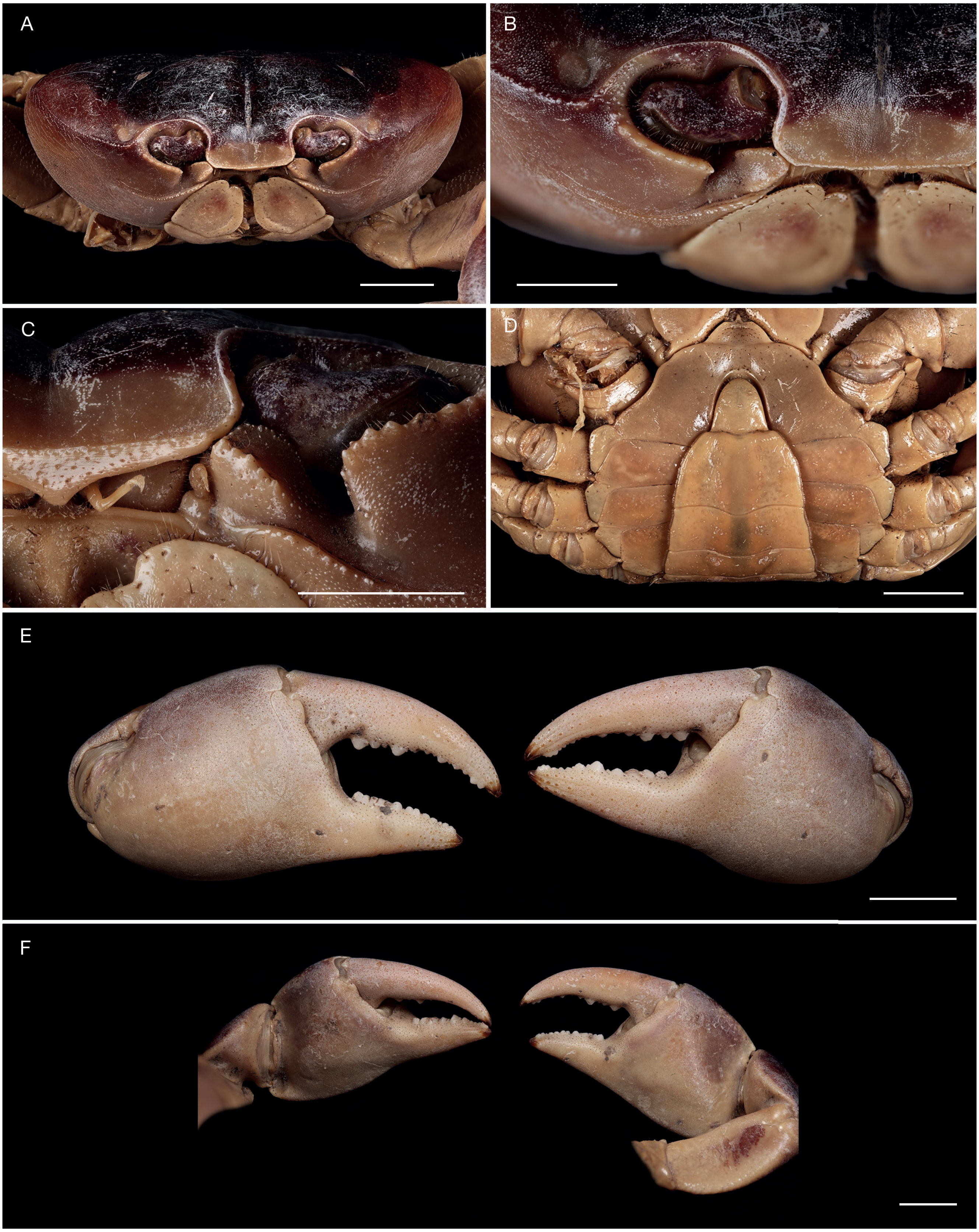

Fig. 12. — *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., ♂ 42.0 × 56.0 mm, Guadeloupe, MNHN-IU-2017-8390 (= MNHN-B24656): **A**, frontal view; **B**, front, orbit, and mesial lobe of infraorbital margin; **C**, front, proepistome (hidden), antenna (exposed) and mesial lobe of infraorbital margin; **D**, thoracic sternum and male pleon; **E**, **F**, external and internal views of chelipeds. Scale bars: A, D, E, F, 10 mm; B, C, 5 mm. Credits: MNHN-Soubzmaigne.

COLOUR

Sex independent colour dimorphism: in males and females, purplish, red, white, with variously coloured spots, intense purple chelipeds and light yellow or orange legs (Fig. 20). For more details, see Perger & Wall (2014: 101, figs 4, 5D) and Toledano-Carrasco (2019: 24, fig. 10B).

REMARKS

According to the original description and figure of *G. quadratus* by Saussure (1853: 360), there is no notch on the anterior margin of the mxp3 merus, so that *Hartnollius quadratus* n. comb. (Fig. 10C) shares with *Gecarcinus ruricola* (Fig. 10A) a slightly similar aspect of this region. In fact, in *H. quadratus* n. comb., the margin is either straight (Rathbun 1918: fig. 162) or discontinuous, and may even have a small notch. The margin of the mxp3 merus of a Mexican male specimen MNHN-IU-2017-8391 (= MNHN-B20900) is asymmetric: straight on one side and very slightly emarginate on the other side (Figs 10C; 14A, B).

Whereas Rathbun (1918: 358) indicated that the type of *Gecarcinus quadratus* was in the 'Geneva Mus.', it was in 'Phil. Acad' according to Stimpson (1857: 29). No specimen is found in the MHNG collection (Hollier 2018). Although not in the list of Spamer & Bogan (1994), according to Boyko (2000: 128) there are parts of one male syntype cl 39.7 mm, from Mazatlán, deposited at the ANSP under the number ANSP CA3741, which contains also a detached male cheliped from perhaps one of two now-lost ANSP specimens.

According to Sherman (2002, as *Gecarcinus quadratus)*, in the Costa Rica's Corcovado National Park, *Hartnollius quadratus* n. comb. lives in fossorial populations, with up to six crabs per square meter in the coastal forest extending about 600 m inland from the Pacific Ocean. *H. quadratus* n. comb. affects plant diversity in a Neotropical continental rain forest by selective seedling consumption. According to Griffiths *et al.* (2007, as *Gecarcinus quadratus*), in the same location it is an engineering species that controls nutrient cycling in tropical forests: during the dry season, the density of land crab burrows decreases with distance from the ocean, so that *H. quadratus* n. comb. is restricted to a narrow coastal zone with a sandy substrate; this distribution could have profound effects on plant community structure.

GEOGRAPHICAL DISTRIBUTION

Hartnollius quadratus n. comb. is found along the American Pacific coast, ranging from the eastern shores of the Gulf of California in Mexico, Nicaragua, Costa Rica (Villegas-Retana & Picado-Masís 2021), Panama (Prahl *et al.* 1984; Hendrickx 1995; Cuesta *et al.* 2007; Perger & Wall 2014; Toledano-Carrasco 2019; Toledano-Carrasco *et al.* 2021). The records of *Gecarcinus quadratus* by Rathbun (1910: 591; 1918: 358) 'Turbo on Atlantic side of Colombia' refer to as *H. lateralis* n. comb. The *H. quadratus* n. comb. from Peru previously reported by Türkay (1970: 338) may belong to *H. nobilii* (see below, under this name). It is important to note that the Pacific *G. lateralis* between the Darien province (Panama) and the Choco dept. (Colombia) may refer to *H. nobilii* n. comb. (Perger & Wall 2014).

FIG. 13. — *Harrtnollius* n. gen.: gonopods and vulvae: **A**, **B**, *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., Guadeloupe, MNHN-IU-2017-8390 (= MNHN-B24656): **A**, ♂ 40.5 × 55.7 mm: G1, G2, caudal view; **B**, ♀ 32.6 × 41.8 mm: vulvae; **C**, *H. quadratus* (Saussure, 1853) n. comb., ♂ 50.0 × 64.0 mm, Mexico, MNHN-IU-2017-8391 (= MNHN-B20900): G1, G2, caudal view. Scale bars: A, C, 2 mm; B, 1 mm. Credits: MNHN-Soubzmaigne.

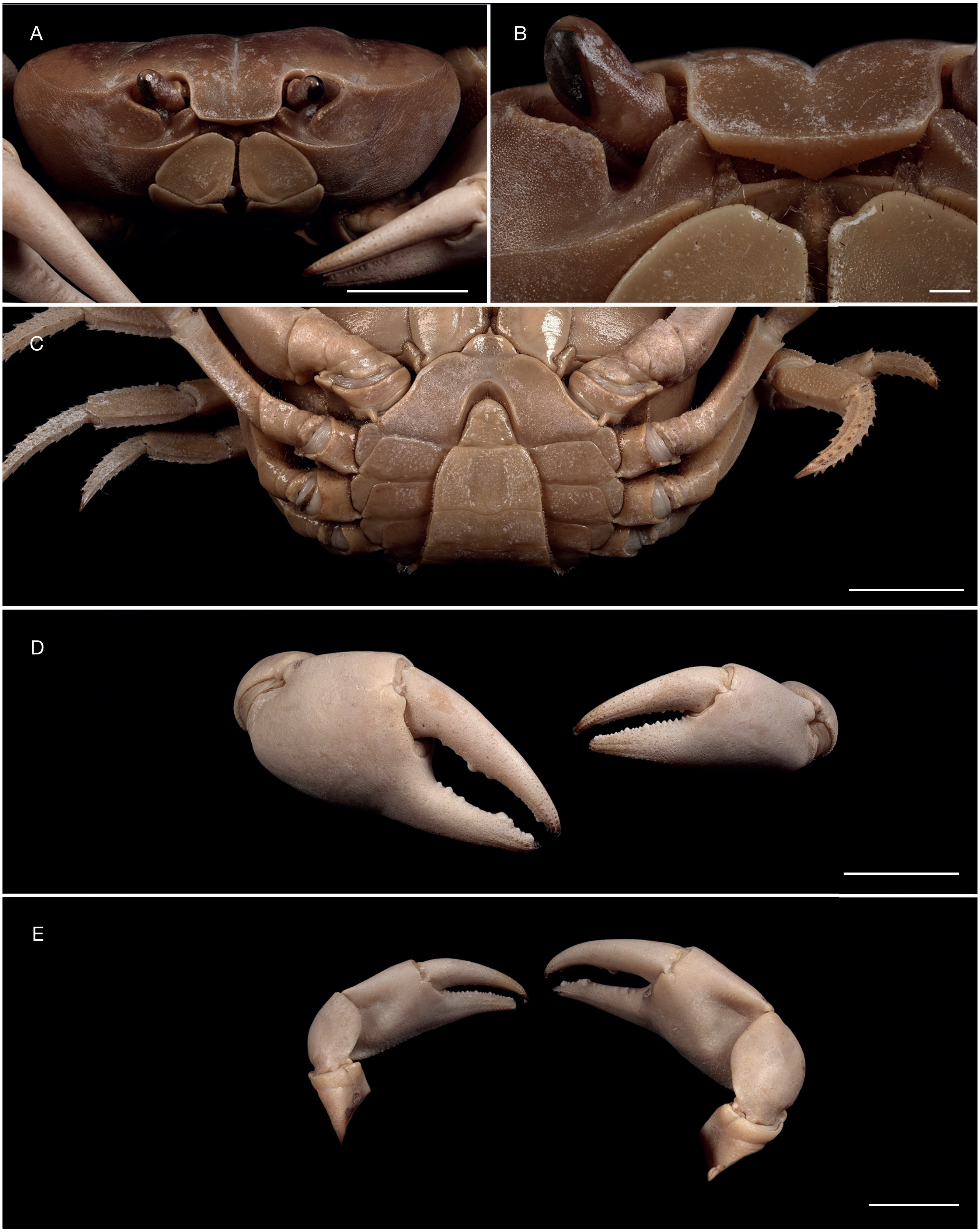

FIG. 14. — *Hartnollius quadratus* (Saussure, 1853) n. comb., ♂ 50.0 × 64.0 mm, Mexico, MNHN-IU-2017-8391 (= MNHN-B20900): **A**, frontal view; **B**, front, proepistome (hidden), antenna (exposed) and mesial lobe of infraorbital margin; **C**, thoracic sternum and male pleon; **D**, **E**, external and internal views of chelipeds. Scale bars: A, C, D, E, 20 mm; B, 2 mm. Credits: MNHN-Soubzmaigne.

Hartnollius nobilii
(Perger & Wall, 2014) n. comb.
(Fig. 15; Table 1)

Gecarcinus ruricola – Nobili 1901: 46 (nec *Cancer ruricola* Linnaeus, 1758).

Gecarcinus (*Gecarcinus*) *lateralis quadratus* – Türkay 1970: 338. — Prahl 1981: 207: fig. 56.1. — Prahl & Manjarrés 1984a: 155, 166, figs 3, 5.3 (nec *Gecarcinus quadratus* Saussure, 1853).

Gecarcinus lateralis – Türkay 1987: 147, fig. 7 (nec *Gecarcinus lateralis* Fréminville *in* Guérin, 1832).

Gecarcinus nobilii Perger & Wall, 2014: 97, fig. 2C-E, 3, 4A-G, 5D. — Toledano-Carrasco 2019: 3, 11, 15. — N. K. Ng *et al.* 2019: 100, fig. 2G. — Toledano-Carrasco *et al.* 2021: 215, 216, 229, 231.

TYPE MATERIAL. — **Paratype. Ecuador** • ♀ 36.6 × 44.3 mm, in ethanol; St Helena, Festa coll. Original label: "*Gecarcinus Festae* Nob. (cotype), Nobili 1901, Muséum Paris", Perger & Wall, 2014 det. *Gecarcinus nobilii*; MNHN-IU-2014-11211 (= MNHN-B12314).

TYPE LOCALITY. — Punta Galera, Ecuador (see Perger & Wall 2014).

DIAGNOSIS

Carapace

Carapace transversely ovate, broader than long, widest in anterior half, relatively flat, with hepatic, subhepatic and branchial regions moderately inflated; widest part of carapace being in line with antero-lateral angles of mesogastric region. Frontal width distinctly wider than distance between the mesial ends of suborbital cristae. Dorsal surface with weakly developed grooves, i.e, cervical, median (or urogastric) and longitudinal mesogastric grooves. Striae along lateral sides of carapace. Front short, broad, moderately produced and deflexed, widening very little below, its inferior margin being slightly arcuate. Mesial lobe of infraorbital margin just joining carapace front edge and completely exposed. Supraorbital margin gently sinuous, with small granules, confluent with anterolateral margin; exorbital tooth weakly developed, tip not over-reaching orbit. Orbital and anterolateral margins marked by row of small granules in males as in females. Anterolateral margins entire, not as rounded, joining exorbital angle, with more or less marked junction.

Cephalic structures

Antennules very small, folded obliquely. Antennae completely exposed. Eyestalks relatively short, curved.

Proepistome, epistome and pterygostome

Proepistome covered by subfrontal plate. Epistome rather developed, with one median crest and a lateral crest on each side. Suborbital, subhepatic and pterygostomial regions sparsely granular laterally.

Mxp3

Mxp3 rather small, not concealing epistome, leaving between them a narrow rhomboid gap, in longitudinal position. Ischium and merus subequal, with their articulation only slightly oblique; ischium without longitudinal groove (only a small trace); anterior margin of merus without distinct emargination, nearly straight, but may be with a slight notch; meri of both sides not joining medially; palp inserted below merus with only distal portion of last mobile article exposed. Exopod of mxp3 as narrow plate, completely concealed by fringe of thick setae, apex not reaching ischium-merus articulation; without flagellum.

Chelipeds

Male chelipeds subequal, widely gaping; heterochely and heterodonty usually not or only slightly marked; occlusal margins of fingers with small, spaced teeth on both sides; in the rare cases of greatly uneven chelipeds (heterochely), a more pronounced gap and pronounced heterodonty. Merus with only small granules on inner lower margin; carpus with denticles on inner upper margin. Female chelipeds subequal or nearly so, moderately gaping, therefore sexual dimorphism moderate.

Ambulatory legs

P3 moderately spiny. Propodus with unequally developed lateral carinae bearing four rows of weakly developed spines. Dactylus with four rows of small equal spines.

Sterno-pleonal cavity and pleon

Sterno-pleonal cavity completely glabrous, short, ending far from sternal suture 2/3, with marked ridge around telson. Male pleon moderately long, bell-shaped; with all somites free plus telson; lateral margins with fringe of setae; somite 6 with convex lateral margins, forming lateral shoulder; telson campanulate, narrower than somite 6, with lateral margins slightly marked, tip rounded, relatively narrow.

Female pleon subcircular; telson forming isosceles triangle, narrower than posterior margin of somite 6, lateral margins straight, smooth.

Thoracic sternum, locking pleonal structures and setal tufts

Thoracic sternum wide, slightly narrowing at level of somite 5; sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed; sternite 2 semi-ovate, with slightly convex margins; suture 2/3 present, practically straight or barely concave and only forming an obtuse angle; suture 3/4 absent, without lateral trace; sternites 3 + 4 completely fused, with obliquely directed margins slightly convex at junction of mxp3, almost straight or gently concave at level of articulation of P1; sutures 4/5 to 7/8 interrupted; sternites 5-7 similarly shaped, sutures well defined; suture 7/8 rather short; sternite 8 not developed medially, totally hidden when pleon is folded; posterior emargination reaching sternite 7.

Male gonopore and penis

Male gonopore and penis at level of suture 7/8 emerging rather far from P5 coxo-sternal condyle.

G1

See Perger & Wall (2014: 101, fig. 2D-E).

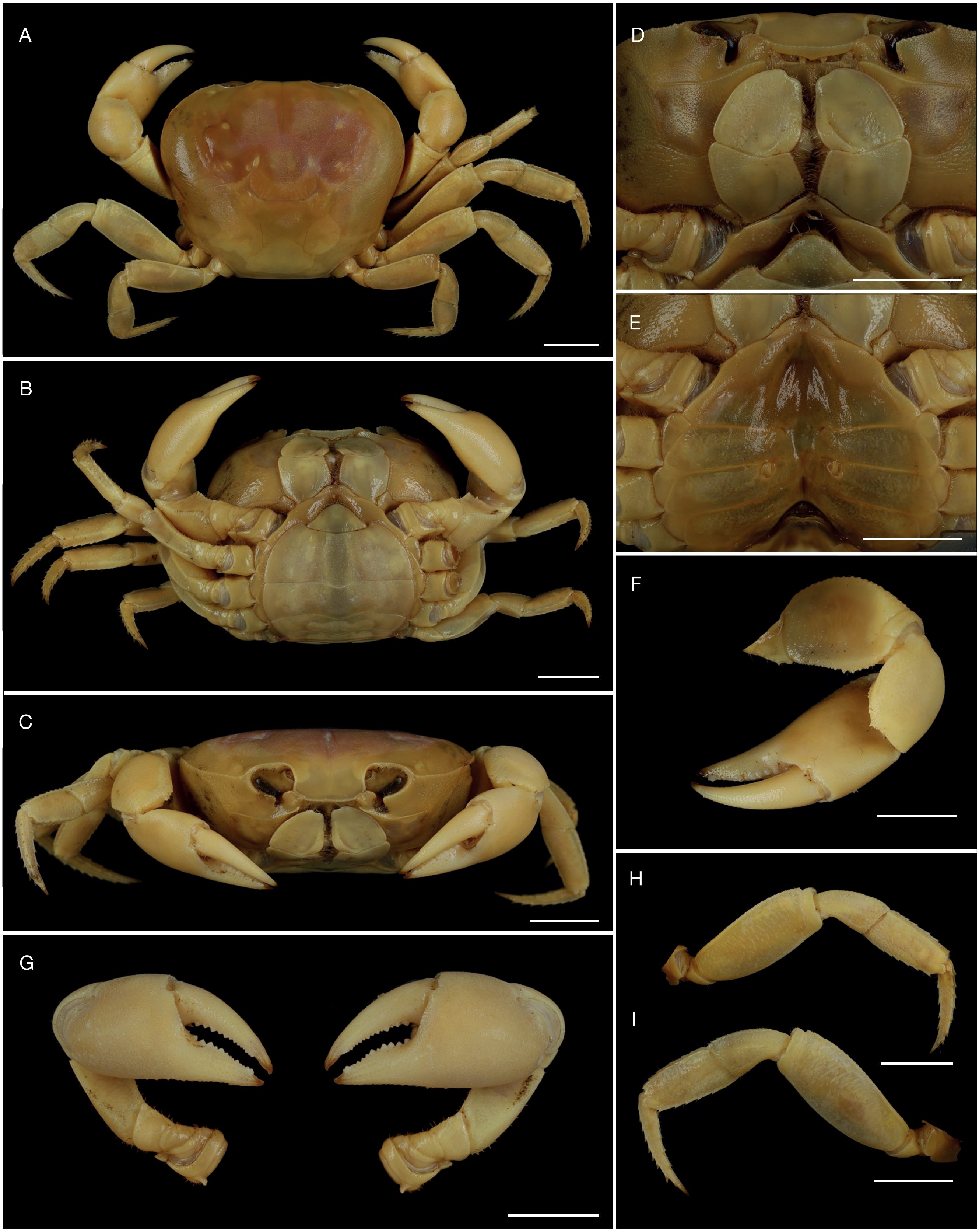

FIG. 15. — *Hartnollius nobilii* (Perger & Wall, 2014) n. comb., paratype, ♀ 36.6 × 44.3 mm, Ecuador, MNHN-IU-2014-11211 (= MNHN-B12314): **A**, dorsal view; **B**, ventral view; **C**, front, orbit, and mesial lobe of infraorbital margin; **D**, front, proepistome (hidden), antenna (exposed), mesial lobe of infraorbital margin, and mxp3; **E**, thoracic sternum, female pleon and vulvae; **F**, left cheliped, internal view; **G**, chelipeds, external view; **H**, right P3; **I**, left P4. Scale bar: 10 mm. Credits: MNHN-Rodríguez Moreno.

Vulvae

Protruding, oriented nearly horizontally, normally occluded by rigid calcified immobile operculum.

COLOUR

Red and white forms in males and females. Light lateral margin on dorsal carapace present, contrasting to dark median pattern, same colour as lateral carapace; some white forms with orange tinge; no orange patch at anterolateral carapace border and at posterior lateral urogastric groove; mesial lobe of infraorbital margin mostly grey; ventro-lateral carapace homogeneously red or white; cheliped palm uniformly red or white (see Perger & Wall 2014: 97, figs 3 with faded colour, 4A-H, 5D, table 2).

REMARKS

The MNHN paratype was collected by Enrico Festa probably during his 1895-1898 trip to Ecuador (*Viaggio del Dr. Enrico Festa nella Republica dell'Ecuador et regioni vicine*), then studied by Nobili, who initially considered it new and dedicated it to Festa under the name "*Gecarcinus festae*" without definitively establishing it. In fact, Nobili never published a description of *Gecarcinus festae*, which is therefore a *nomen nudum*. In 1901, Nobili described *Sesarma festae* and *Uca festae*, and, in the same article, he referred specimens collected in Ecuador to *Gecarcinus ruricola*, a species restricted to the western Atlantic islands (Perger & Wall 2014). The MNHN specimen examined by Nobili and selected as the paratype of the new species *Gecarcinus nobiili*, dedicated to Nobili by Perger & Wall (2014), is shown in their fig. 3D-F and is deposited at the MNHN (Fig. 15). The holotype is preserved at the LACM (see Perger & Wall 2014: 97; N. K. Ng *et al.* 2019: 99).

GEOGRAPHICAL DISTRIBUTION

Ecuador, Colombia and Peru. The specimens of *Gecarcinus* (*Gecarcinus*) *quadratus* from Peru previously reported by Türkay (1970: 338) may belong to *Hartnollius nobilii* n. comb. (see Perger & Wall 2014). The *Gecarcinus ruricola* of Cano (1889: 101, 227) from Ecuador must be also assigned to *H. nobilii* n. comb.

PALAEONTOLOGICAL DATA

Palaeontological analyses can be informative in assessing the continuity of phenotypes over time and geographical areas, but they are limited by the availability of fossils. Practically nothing is known about fossil or subfossil records from *Gecarcinus*. Fossil crab chelae attributed to *Gecarcinus* cf. *ruricola* reported by Donovan & Dixon (1998: 825) from the Pleistocene of Jamaica were later recognised as belonging to a species of *Sesarma* Say, 1817 (see Luque 2017; Luque *et al.* 2017). The Late Holocene remains of *Gecarcinus* sp. reported from Antigua by Pregill *et al.* (1988) would be conspecific with *Hartnollius lateralis* n. comb. (Luque 2017: fig. 1H-J, table 1, as *Gecarcinus lateralis*). A *Gecarcinus* sp. from the late Pleistocene of Bermuda (Crystal Cave) is reported by Luque (2017: table 1). A total of 1400 identifiable Holocene remains of the two co-occurring species *G. ruricola* and *G. lateralis* have been found through field surveys along the northern coast of San Salvador Island and in the Bahamas, with various levels of disarticulation suggesting a low preservation potential (Locatelli 2013: 867, figs 2-7, table 1). Schweitzer *et al.* (2023: 2) report *G. ruricola* from the Holocene in the Caribbean Sea and Mexico. According to Schweitzer *et al.* (2023) records are very few in gecarcinids. According a molecular phylogeny of Thoracotremata by Tsang *et al.* (2022: 5), the family Gecarcinidae (with also the Sesarmidae) originated along with the warm climates during the Late Paleocene and Early Eocene (*c.* 60-50 MYA).

GENETICS

An alignment of 658 base pairs (364 conserved, 139 parsimony-informative and 173 variable) was used for the COI gene and 559 bp (292 conserved, 70 parsimony-informative and 120 variable) for the 16S gene, resulting in a concatenated matrix of 1217 bp (Table 2). Since the trees generated using Bayesian Inference and Maximum Likelihood displayed the same topology, only the BI tree is shown, with the BI and ML support values.

The concatenated tree recovers the two major groups of gecarcinids proposed by Guinot *et al.* (2018), based on the consistency of morphological, larval and genetic data. On the one hand, the clade of crabs with less terrestrial habits (highlighted in purple) formed by the genera *Cardisoma* Latreille, 1828, *Discoplax* A. Milne-Edwards, 1867, and *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018. On the other hand, the clade of gecarcinids with markedly terrestrial habits (highlighted in red) that includes the genera *Gecarcinus*, *Johngarthia* Türkay, 1970 and *Hartnollius* n. gen. (Fig. 16). Focusing on crabs highly adapted to terrestrial life, which are central to this study, *Gecarcinus* is identified as the probable sister taxon to *Hartnollius* n. gen. while in the less terrestrial clade, *Discoplax* and *Tuerkayana* form sister groups, collectively maintaining a close evolutionary relationship with *Cardisoma* (Fig. 16).

Individuals of *Gecarcinus ruricola* from Cuba (ZMH-K65343) and Guadeloupe (MNHN-IU-2024-7258 and MNHN-IU-2024-4640), which morphologically show some differences (position of merus mxp3 in relation to frontal margin, and position of extremity of sterno-pleonal cavity in relation to thoracic sternal suture 2/3), are nested in the same clade with a high branch support (Fig. 16), highlighting that *Gecarcinus ruricola* is a species with some morphological variability across its distribution range.

Pairwise nucleotide divergences for COI with K2P distance (Table 3) indicate a high divergence between *Gecarcinus* and *Hartnollius* n. gen. (on average 9.56 with *H. lateralis* n. comb. and 11.14 with *H. quadratus* n. comb.), values comparable with the divergence between species of different genera such as those of *Hartnollius* n. gen. and *Johngarthia lagostoma* (10.62 with *H. lateralis* n. comb. and 11.40 with *H. quadratus* n. comb.) and *Discoplax longipes* with *Tuerkayana latens* (12.67 %). Notably, the

TABLE 2. — Information on the sequences that were used for the genetic analysis including species name, locality, specimen voucher in their respective collections or museums, GenBank accession number for those cases available, as well as the authors and date of entry into GenBank. In the case of *Gecarcinus* Leach, 1814 and *Hartnollius* n. gen., the label assigned by Toledano-Carrasco *et al.* (2021) is shown instead of GenBank accession number.

Species	**Localities**	**GenBank accession no. 16S/ Authors**	**GenBank accession no. COI / Authors**	**Specimen voucher**
Cardisoma guanhumi	Panama: Bocas Del Toro, Isla Colon, STRI Dock	MK971300.1 / Venera-Ponton *et al.* 2020	MN183871.1/ Venera-Ponton *et al.* 2020	ULLZ13341
Discoplax longipes	New Caledonia: Loyalty I	LC057717.1/ Ng & Shih 2015	LC057721.1 / Ng & Shih 2015	ZRC 2002.51
Discoplax michalis	Guam	LC057719.1/ Ng & Shih 2015	LC057723.1 / Ng & Shih 2015	ZRC 2000.2052-2053
Gecarcinus ruricola	Cuba: Playa Larga	Unpublished (New)	Unpublished (New)	ZMH- K65343
Gecarcinus ruricola	Guadeloupe, Îles des Saintes	Unpublished (New)	Unpublished (New)	MNHN-IU-2024-4640
Gecarcinus ruricola	Guadeloupe, La Désirade	Unpublished (New)	Unpublished (New)	MNHN-IU-2024-7258
Hartnollius lateralis n. comb.	Mexico: Cayo Arcas, Campeche	CACAM M2/Toledano-Carrasco *et al.* 2021	CACAM M2 / Toledano-Carrasco *et al.* 2021	CNCR 34011
Hartnollius lateralis n. comb.	Mexico: Barras de Sontecomapan, Veracruz	BSVER M2/Toledano-Carrasco *et al.* 2021	BSVER M2 / Toledano-Carrasco *et al.* 2021	CNCR 33943
Hartnollius quadratus n. comb.	Mexico: Barra de Boca del Cielo, Chiapas	BCCHI M2/Toledano-Carrasco *et al.* 2021	BCCHI M2 / Toledano-Carrasco *et al.* 2021	CNCR 34630
Hartnollius quadratus n. comb.	Mexico: Punta Mita, Nayarit	PMNAY M1/Toledano-Carrasco *et al.* 2021	PMNAY M1 / Toledano-Carrasco *et al.* 2021	CNCR 33941
Johngarthia lagostoma	No data	KT159744.1/Rodriguez-Rey *et al.* 2016	KM578841.1/ Rodriguez-Rey *et al.* 2016	No data
Tuerkayana magnum	Australia: Christmas Island	AB999608.1/Ng & Shih 2023	AB999628.1/Ng & Shih 2023	ZRC 2012.003
Tuerkayana latens	French Polynesia: Tuamotu	LC057716.1/Ng & Shih 2023	LC057720.1/Ng & Shih 2023	MNHN-IU-2011-5594

TABLE 3. — Genetic distance K2P of Gecarcinidae based on COI gene fragments. The values are given in percentage. The percentage of divergence shown between *Hartnollius* n. gen. with the rest of the genera was based on the averages of the individuals PMNAY M1 and BCCHI M2 for *H. quadratus* (Saussure, 1853) n. comb., and BSVER M2 and CACAM M2 for *H. lateralis* (Fréminville *in* Guérin, 1832) n. comb.

	***Hartnollius quadratus* n. comb.**	***Hartnollius lateralis* n. comb.**	***Gecarcinus ruricola* ZMH-K65343**	***Gecarcinus ruricola* MNHN-IU-2024-7258**	***Gecarcinus ruricola* MNHN-IU-2024-4640**	***Johngarthia lagostoma***	***Cardisoma guanhumi***	***Tuerkayana latens***
Hartnollius quadratus n. comb.	0	–	–	–	–	–	–	–
Hartnollius lateralis n. comb.	5.56	1.32	–	–	–	–	–	–
Gecarcinus ruricola ZMH-K65343	11.14	9.71	–	–	–	–	–	–
Gecarcinus ruricola MNHN-IU-2024-7258	11.14	9.49	0.37	–	–	–	–	–
Gecarcinus ruricola MNHN-IU-2024-4640	11.14	9.49	0.37	0	–	–	–	–
Johngarthia lagostoma	11.40	10.62	10.04	10.04	10.04	–	–	–
Cardisoma guanhumi	20.67	20.65	20.14	20.39	20.39	17.44	–	–
Tuerkayana latens	19.42	18.65	17.63	17.39	17.39	18.94	14.71	–
Discoplax longipes	18.18	17.43	20.41	20.67	20.67	18.49	16.16	12.67

genetic distance between *Gecarcinus* and *Johngarthia* is lower than that between *Gecarcinus* and *Hartnollius* n. gen. (see Table 3), as previously highlighted by Toledano-Carrasco *et al.* (2021). All these findings further support the validity of the new genus.

The average interspecific divergence between *Hartnollius lateralis* n. comb. and *H. quadratus* n. comb. (5.56%) closely matches the 6.1% previously reported by Toledano-Carrasco *et al.* (2021).

Genetic divergence between the two individuals of *Gecarcinus ruricola* (MNHN-IU-2024-7258 and MNHN-IU-2024-4640) from Guadeloupe and the individual from Cuba (ZMH-K65343) is extremely low, almost zero (0.37%).

The genetic distances between individuals of the two subclades of Gecarcinidae are remarkably high, ranging from 17.44% between *Cardisoma guanhumi* and *Johngarthia lagostoma* to 20.58% average between *Discoplax longipes* and *Gecarcinus ruricola* reflecting the high divergence between the two groups.

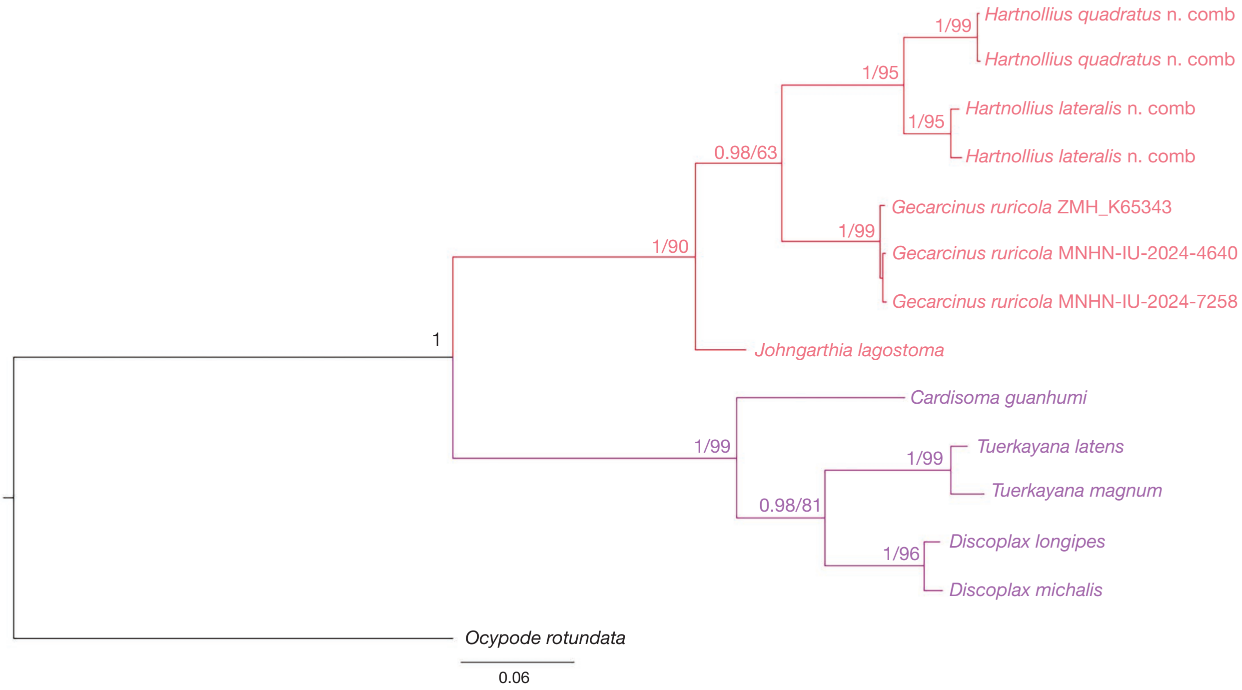

FIG. 16. — Bayesian inference phylogenetic tree of Gecarcinidae based on the concatenation of mitochondrial COI and 16S rRNA gene fragments. Numbers at nodes are support values for BI (posterior probability) and ML (Ultrafast bootstrap). The clade of crabs with less terrestrial habits (*Cardisoma* Latreille, 1828, *Discoplax* A. Milne-Edwards, 1867, and *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018) are highlighted in purple, whereas the clade with markedly terrestrial habits (*Gecarcinus* Leach, 1814, *Hartnollius* n. gen. and *Johngarthia* Türkay, 1970) are highlighted in red. *Ocypode rotundata* Miers, 1882 was included as outgroup.

DISCUSSION

The rationale for a new status for the genus *Gecarcinus* represented by a single member, its type species *G. ruricola*, and for the establishment of *Hartnollius* n. gen. for its three former congeners is not based solely on morphological evidence, which concerns many and diverse traits (see Table 1), including the colour morphs, but also on several biological data, such as the degree of terrestriality both in the adults and megalopa stage (*G. ruricola* is the most terrestrial of the land crabs throughout the Caribbean region), the habitat preferences, the activity patterns, the behaviour, and others features. The widespread presence of *G. ruricola* on almost all Caribbean islands and the proximity of many islands is evidence of a strong potential for dispersal and intermixing between populations. This is all the more likely given the long duration of reproductive life of *G. ruricola* (exceeding 10 years or so, see Hartnoll *et al.* 2007) and the long planktonic life from release of the first zoea to settlement of the megalopa (of the order of up to 60 days). In the small islands of San Andrés and Old Providence (26 and 20 km^2 in area, respectively) and in the even smaller Swan Islands (total area 8 km^2), far from any other island, inhabited by *G. ruricola*, there could be a risk of potential genetic isolation. We have not examined *G. ruricola* from these isolated islands, but the results of Hartnoll *et al.* (2006a, 2007), in addition to the photographs, leave no doubt on the species identity.

The examination of a very abundant material of *Gecarcinus ruricola* demonstrated that it would be a strictly insular species. It also allowed to detect some significant phenotypic variations (position of the mxp3 merus relative to the frontal margin and position of the tip of the sternopleonal cavity relative to the thoracic sternal suture 2/3), but nevertheless insufficient to suspect, at this stage of the morphological study, the possible presence of cryptic species. The molecular analyses based on the COI and 16S genes suggest that these morphological differences, at least between individuals from Cuba and Guadeloupe, are due to intraspecific variability.

The phylogenetic tree (Fig. 16), although including only two species of *Hartnollius* n. gen., *H. lateralis* n. comb. and *H. quadratus* n. comb., supports the monophyly of *Hartnollius* n. gen. with high confidence and shows *Gecarcinus* new status as its sister group. Although this relationship was recovered in both analyses (BI and ML) the branch support was low in the ML tree. On the contrary, the genetic distance shows that *Gecarcinus* has a lower divergence with *Johngarthia* than with *Hartnollius* n. gen. The phylogenetic relationship between *Gecarcinus*, *Hartnollius* and *Johngarthia* requires further study, which is underway by the first two authors.

FIG. 17. — Living *Gecarcinus ruricola* (Linnaeus, 1758): **A**, 'dark land crab' in the field, Martinique, Anse Ceron, forest about 70 m far from the shore, altitude about 4 m; **B**, 'red crab' in the field, Cuba, Bay of Pigs, 22°17'12.28"N, 81°08'18.59"W. Credits: A, F. Lavail (planetedoc.com); B, P. Lindgren (Creative Commons Attribution-Share Alike 4.0).

Fig. 18. — *Gecarcinus ruricola* (Linnaeus, 1758) in the field: different morphs; see the red mesial lobe of infraorbital margin: **A**, **B**, Saint-Barthelemy, St Jean Beach, back-beach vegetation, 27.VI.2015 and 15.VIII.2024, respectively: 'green morph' and 'red morph'; **C**, Saint-Barthelemy, Trace de Colombier, coastal xerophilous forest, 28.VI.2013; 'dark morph'; **D**, Anguilla, Dog Island, flat calcareous islet, xerophilous vegetation, 18.X.2024: 'yellow morph'; **E**, **F**, Anguilla, Prickly Pear East, flat calcareous islet, xerophilous vegetation, 26.III.2018: 'dark morph'; **G**, **H**, Dominica, Cabrits National Park, xerophilous forest, 20.I.2022: 'dark morph' and 'mixed colour morph'. Credits: K. Questel (krl-qtl.odoo.com).

Fig. 19. — *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., living and in the field: **A**, Guadeloupe, Marie-Galante, KARUBENTHOS 3, Stn IGM25, MNHN-IU-2024-5551; **B**, **C**, Guadeloupe, July 2015, on sand; **D**, **E,** Martinique, Anse à Prunes, forest about 65 m far from the shore, altitude about 2 m; **D**, crab bearing a branch; **E**, crab on a tree. Credits: A, L. Corbari-MNHN-ARBig-LPRig; B, C, J. Poupin; D, E, F. Lavail (planetedoc.com).

Fig. 20. — Living *Hartnollius quadratus* (Saussure, 1853) n. comb.: **A**, Mexico, Chiapas, Barra de Boca del Cielo; **B**, ‘Halloween crab’, Costa Rica, Nosara, on a tree, 2006; **C**, Panama, on the beach, 2005; **D**, **E**, Mexico, Chacahua, La Grúa: two views. Credits: A, J. L. Villalobos Hiriart; B, Bhny, Creative Commons Attribution-Share-Alike License 3.0; C, Dozenist, Creative Commons Attribution-Share-Alike License 3.0; D, E, A. López-Velázquez.

Fig. 21. — *Gecarcinus ruricola* (Linnaeus, 1758), the ‘black land crab’, western Caribbean, San Andrés Archipelago, Providence Island: **A**, Fresh Water Bay sector, 2020: after a long annual breeding migration from the damp and shaded forest areas, this ovigerous female, with a large pleon and pleopods bearing ripe eggs, lays its eggs in the sea; **B**, Lighthouse: two females having laid their eggs are setting off again for return migration. Credits: Gabriela Dominguez (MFA/Filmmaker, bluelizardstudio.co).

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We would like to thank our colleagues at other museums who lent us material, which granted to us to increase our knowledge of *G. ruricola* in different parts of its distribution: Paul Clark and Miranda Lowe (NHM) for the loan of specimens from the West Indies; Martha Nizinsky and Adam Stergis (NMNH, Smithsonian Institution) for the loan of a large collection identified as *G. ruricola*; Henri Vallès and Nadeshinie Parasram (UWI) for the loan of two *G.ruricola* from the Barbados. The photographer Aldo López-Velázquez, La Grúa, Chacahua, México, provided us with the photos of *G. quadratus* (now *Hartnollius quadratus* n. comb.). Some of the specimens studied and photographed here come from the expedition "Our Planet reviewed –Guadeloupe's Islands 2024". This survey was organised by the Muséum national d'Histoire naturelle (MNHN) and the Agence régionale de la Biodiversité des Îles de Guadeloupe in cooperation with the Office Français de la Biodiversité (OFB) and the Université des Antilles (UA). We would like to thank the funding partners and technical partners who facilitated the fieldwork: the European Regional Development Fund (FEDER), the Guadeloupe Region, the French Development Agency (AFD), the Guadeloupe National Park, the National Forestry Office (ONF) and the Conservatoire du Littoral (CdL), the Direction de l'Environnement, de l'Aménagement et du Logement (DEAL), the Office de l'Eau, and the local authorities of Les Saintes, Marie-Galante and La Désirade. 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