zoosystema
2026 • 48 • 8

Formal establishment of Gecarcinoidea H. Milne Edwards, 1837 n. stat. (Crustacea, Decapoda, Brachyura), with recognition of two families, Cardisomatidae n. fam. and Gecarcinidae *restrict.*, and new insights on Epigrapsidae Watabe, 2007

Danièle GUINOT
& Paula A. RODRÍGUEZ MORENO

art. 48 (8) — Published on 31 March 2026
www.zoosystema.com

PUBLICATIONS
SCIENTIFIQUES
MUSÉUM NAL HIST NATURELLE

COUVERTURE / *COVER*:
Cardisoma guanhumi Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, Bocas del Toro (Panama). Courtesy A. Anker.

Zoosystema est indexé dans / Zoosystema *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Zoosystema est distribué en version électronique par / Zoosystema *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par / *Articles and nomenclatural novelties published in* Zoosystema *are referenced by:*
- ZooBank® (http://zoobank.org)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / **Zoosystema** *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Geodiversitas***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, **Cryptogamie sous-sections *Algologie*, *Bryologie*, *Mycologie*, *Comptes Rendus Palevol*.**

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

ISSN (imprimé / *print*): 1280-9551/ ISSN (électronique / *electronic*): 1638-9387

Formal establishment of Gecarcinoidea H. Milne Edwards, 1837 n. stat. (Crustacea, Decapoda, Brachyura), with recognition of two families, Cardisomatidae n. fam. and Gecarcinidae *restrict*., and new insights on Epigrapsidae Watabe, 2007

Danièle GUINOT
Institut de Systématique, Évolution, Biodiversité (ISYEB),
Muséum national d'Histoire naturelle, CNRS,
Sorbonne Université, EPHE, Université des Antilles,
case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
daniele.guinot@mnhn.fr (corresponding author)

Paula A. RODRÍGUEZ MORENO
Direction générale déléguée aux Collections,
Muséum national d'Histoire naturelle,
case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
paula.martin-lefevre@mnhn.fr

Submitted on 3 November 2025 | Accepted on 18 December 2025 | Published on 31 March 2026

urn:lsid:zoobank.org:pub:1805F0DB-B51C-4A5E-9EEE-435D4F0E7D06

Guinot D. & Rodríguez Moreno P. A. 2026. — Formal establishment of Gecarcinoidea H. Milne Edwards, 1837 n. stat. (Crustacea, Decapoda, Brachyura), with recognition of two families, Cardisomatidae n. fam. and Gecarcinidae *restrict*., and new insights on Epigrapsidae Watabe, 2007. *Zoosystema* 48 (8): 211-271. https://doi.org/10.5252/zoosystema2026v48a8. http://zoosystema.com/48/8

ABSTRACT

To date, there is no real consensus on the taxonomic status of the family Gecarcinidae H. Milne Edwards, 1837 (land crabs or terrestrial crabs), which is generally considered to comprise seven genera (without including *Epigrapsus* Heller, 1862) and is currently subordinate to the superfamily Grapsoidea MacLeay, 1838. The congruence between adult morphology and larval data allows us to elevate Gecarcinidae to a higher rank and, by providing a diagnosis, to formally establish the Gecarcinoidea H. Milne Edwards, 1837 n. stat. Contrary to the current view, morphology alone, with its unique characters, argues in favour of a superfamily Gecarcinoidea very distinct from the Grapsoidea. Furthermore, the adult morphology and larval data highlight the heterogeneity of Gecarcinoidea n. stat. and, in addition, the existence of separately evolving lineages within it, as documented by Guinot *et al.* (2018). Recent genetic studies have confirmed the diversity of the group, so that, despite unambiguous morphological and biological similarities supporting the Gecarcinoidea n. stat., this group can be divided into two groups of genera sharing a set of characters that allows the relevant criteria for their delimitation to be explicitly recognised. These two groups therefore deserve formal nomina, as follows: Gecarcinidae *restrict.* to encompass the genera *Gecarcinus* Leach, 1814, *Gecarcoidea* H. Milne Edwards, 1837, *Hartnollius* Guinot, Rodríguez Moreno & Toledano-Carrasco, 2025, and *Johngarthia* Türkay, 1970; and Cardisomatidae n. fam. to encompass the genera *Cardisoma* Latreille *in* Le Peletier, Serville & Guérin, 1828, *Discoplax* A. Milne Edwards, 1867 and *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018. The case of the genus *Discoplax*, whose three species all live in caves, often in water, and which are included in the family of terrestrial crabs Gecarcinidae *sensu lato* despite significant morphological differences, is discussed. Cardisomatidae n. fam. forms a group of land crabs that are less terrestrial than Gecarcinidae *restrict.*, and this difference in the degree of terrestriality is reflected in morphological characters that allow them to be differentiated. The morphological study of a series of new characters, practically never used in carcinological taxonomy, namely the female pleon and telson, as well as the female pleopods, provides a new informative dataset for the family-level discrimination of Gecarcinoidea n. stat. The Gecarcinoidea n. stat. becomes a crown group of Thoracotremata Guinot, 1977. Based on morphological, biological, larval, and genetic data, *Epigrapsus* Heller, 1862, generally considered a Gecarcinidae *sensu lato*, though often in an isolated position, and containing only two species, is here split into two genera, namely *Epigrapsus restrict.* and *Grapsodes* Heller, 1865 (which we are reviving), each with a new diagnosis. These two genera share no characters that could link them to either the Cardisomatidae n. fam. or the Gecarcinidae *restrict.*: rather different from each other, each could represent a distinct family within the Grapsoidea *sensu lato*, unless they can be incorporated into other existing families of shore crabs or others groups.

KEY WORDS
Land crabs,
cave crabs,
Grapsodes,
Thoracotremata,
Grapsoidea,
male gonopore,
female pleon,
adaptations,
new family,
new status.

RÉSUMÉ

Définition formelle des Gecarcinoidea H. Milne Edwards, 1837 n. stat. (Crustacea, Decapoda, Brachyura), avec la reconnaissance de deux familles, Cardisomatidae n. fam. et Gecarcinidae restrict.*, et de nouvelles perspectives pour les Epigrapsidae Watabe, 2007.*

À ce jour, il n'existe pas de véritable consensus sur le statut taxonomique de la famille des Gecarcinidae H. Milne Edwards, 1837 (crabes de terre ou crabes terrestres), laquelle est largement considérée comme étant composée de sept genres (sans inclure le genre *Epigrapsus* Heller, 1862), et qui est actuellement subordonnée à la superfamille Grapsoidea MacLeay, 1838. La concordance de la morphologie des adultes et des données larvaires nous permet d'élever les Gecarcinidae à un rang supérieur et, en fournissant une diagnose, d'établir formellement les Gecarcinoidea H. Milne Edwards, 1837 n. stat. Contrairement à l'opinion courante, la morphologie à elle seule, avec ses caractères uniques, plaide en faveur d'une superfamille Gecarcinoidea bien distincte des Grapsoidea. En outre, la morphologie des adultes et les données larvaires mettent en évidence l'hétérogénéité des Gecarcinoidea n. stat., ainsi que l'existence de lignées distinctes au sein de cet ensemble, comme documenté par Guinot *et al.* (2018). Les études génétiques les plus récentes ont confirmé la diversité du groupe. En dépit de similitudes morphologiques et biologiques non ambigües attestant l'unité des Gecarcinoidea n. stat., la superfamille peut donc être divisée en deux groupes de genres qui partagent un ensemble de caractères permettant la reconnaissance explicite de critères pertinents pour leur délimitation. Ces deux groupes méritent donc des dénominations formelles, comme suit : Gecarcinidae *restrict.*, incluant les genres *Gecarcinus* Leach, 1814, *Gecarcoidea* H. Milne Edwards, 1837, *Hartnollius* Guinot, Rodríguez Moreno & Toledano-Carrasco, 2025, et *Johngarthia* Türkay, 1970 ; et Cardisomatidae n. fam., incluant les genres *Cardisoma* Latreille, *in* Le Peletier, Serville & Guérin, 1828, *Discoplax* A. Milne Edwards, 1867 et *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018. Le cas du genre *Discoplax*, dont les trois espèces vivent toutes dans les grottes, souvent dans l'eau, et qui sont incluses dans la famille des crabes terrestres Gecarcinidae *sensu lato* malgré des différences morphologiques significatives, est discuté. Les Cardisomatidae n. fam. forment un groupe de crabes de terre moins terrestres que les Gecarcinidae *restrict.*, et cette différence dans le degré de terrestrialité se traduit par des caractères morphologiques qui permettent de les différencier. L'étude morphologique d'une série de nouveaux caractères, pratiquement jamais utilisés en taxonomie carcinologique, à savoir le pléon et le telson femelles, ainsi que les pléopodes femelles, fournit un nouvel ensemble de données informatif pour la discrimination au niveau familial des Gecarcinoidea n. stat. La superfamille des Gecarcinoidea n. stat. devient un groupe couronne des Thoracotremata Guinot, 1977. En se basant sur les données morphologiques, biologiques, larvaires et génétiques, *Epigrapsus* Heller, 1862, généralement considéré comme un Gecarcinidae *sensu lato*, toutefois souvent dans une position isolée, et contenant seulement deux espèces, est ici scindé en deux genres, à savoir *Epigrapsus restrict.* et *Grapsodes* Heller, 1865 (que nous ressuscitons), chacun avec une nouvelle diagnose. Aucun de ces deux genres ne partage de caractères qui pourraient les relier aux Cardisomatidae n. fam. ou aux Gecarcinidae *restrict.* : bien différent l'un de l'autre, chacun pourrait représenter une famille distincte au sein des Grapsoidea *sensu lato*, à moins que les deux genres puissent être incorporés, ensemble ou séparément, dans d'autres familles existantes de crabes de rivage ou d'autres groupes.

MOTS CLÉS
Crabes de terre,
crabes cavernicoles,
Grapsodes,
Thoracotremata,
Grapsoidea,
orifice mâle,
pléon femelle,
adaptations,
famille nouvelle,
statut nouveau.

INTRODUCTION

While the consensus of the modern taxonomic system has for the most part considered the taxon Gecarcinidae H. Milne Edwards, 1837 (previously with the authorship and date MacLeay, 1838; for the authorship recommended here, see Tavares 1989; Tavares & Mendonça Jr 2022; Guinot *et al.* 2018, Appendix: 602; Guinot *et al.* 2025) to be a family subordinate to the Grapsoidea MacLeay, 1838 [the correct authorship is in fact Grapsoidea H. Milne Edwards, 1837, see Guinot *et al.* 2018, appendix: 602], a superfamily rank Gecarcinoidea within the newly created Thoracotremata Guinot, 1977 had been proposed by Guinot (1977a, b; 1978), though without a diagnosis. This rank was adopted without explanation by Sternberg & Cumberlidge (2001b) in a list of thoracotreme crabs, by the great palaeontologist Glaessner (1980) in his reassessment of Brachyura Pennant, 1777, and by Jamieson & Tudge (2000) in a review of the decapod spermatozoal ultrastructure; its availability has been recently recognised by Sasaki (2019: 12669).

The objective of the present paper is the formal recognition of a higher rank for the Gecarcinidae *sensu lato*, namely Gecarcinoidea H. Milne Edwards, 1837 n. stat., in providing a diagnosis, and of two main subclades that remained unnamed at the time, namely Cardisomatidae n. fam. and Gecarcinidae *restrict.*, by resolving their taxonomic position. The morphological results already highlighted by Guinot *et al.* (2018) were supported by genetic evidence (Toledano-Carrasco *et al.* 2021; Ng & Shih 2023; Z. Wang *et al.* 2023). Seven genera are assigned to the Gecarcinoidea n. stat. The Cardisomatidae n. fam., which corresponds to the first clade of Guinot *et al.* (2018), comprises *Cardisoma* Latreille, *in* Le Peletier, Serville & Guérin, 1828, *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018, and *Discoplax* A. Milne Edwards, 1867 (see *The case of the genus* Discoplax *A. Milne Edwards, 1867*). The Gecarcinidae *restrict.*, which corresponds to the second clade of Guinot *et al.* (2018), comprises *Gecarcinus* Leach, 1814, *Gecarcoidea* H. Milne Edwards, 1837, *Johngarthia* Türkay, 1970, and the recently described genus *Hartnollius* Guinot, Rodríguez Moreno & Toledano-Carrasco, 2025. The current total number of species worldwide is 25 (for comments on *Tuerkayana* aff. *hirtipes* see Guinot *et al.* 2018: 564, 566, and especially p. 603, figs 4F, 5G-I, 6C). The status of *Epigrapsus* Heller, 1862, with two very distinct species whose particular features are so ambiguous that they call into question the taxonomic position of both, is discussed below (see *New insights on the family Epigrapsidae Watabe, 2007*).

The taxonomy of Gecarcinidae *sensu lato* had not been thoroughly revised since the numerous papers of Türkay (1970, 1973a, 1974a, b, 1987; see Sonnewald & Appel 2016), including the description of *Johngarthia* Türkay, 1970, and with the exception of the monograph by Tavares (1989). Their number has increased substantially over the last twenty years, with eight new species recently described (Ng & Guinot 2001; Ng & Shih 2014, 2015, 2023; Ng & Davie 2012; Perger *et al.* 2011; Perger & Wall 2014; Perger 2019). A new generic nomenclature based on morphology, with the creation of one new genus, was proposed by Guinot *et al.* (2018: table 1). Later, based on morphological characters and genetic data, Guinot *et al.* (2025: table 1) showed that the genus *Gecarcinus* was not monophyletic and should be restricted, with *G. ruricola* as type species and sole member, and erected the new genus *Hartnollius* to accommodate *H. lateralis* (Fréminville *in* Guérin, 1832), *H. quadratus* (Saussure, 1853) and *H. nobilii* (Perger & Wall 2014).

Species of Gecarcinidae *sensu lato* are widely distributed in tropical and subtropical regions, where they are abundant and constitute the dominant and archetypal members of the crab fauna inland and on continental sea coasts. In most regions, these crabs are an important food resource and thus are intensively exploited, or considered a potentially valuable food resource as, for example, in Indonesia (Murniati 2023). They play an important ecological role (Green 1997; Sherman 2002; Lindquist *et al.* 2009), particularly in the Caribbean region (Guinot *et al.* 2025), as recently reported in Bahamian society (McGaw *et al.* 2025).

Gecarcinidae *sensu lato*, commonly referred to as 'land crabs' and sometimes as 'semi-terrestrial crabs', are not the only land crabs (see Burggren & McMahon 1988) nor the brachyurans best adapted to life on land (Hartnoll 1988a). They constitute an ancestral marine lineage of brachyuran crabs that have evolved to live primarily on land and are among the marine crabs that successfully invaded the terrestrial environment, with morphological and behavioural characters already documented by H. Milne Edwards (1837) in his *Histoire naturelle des Crustacés*. Although all adult members have attained complete terrestriality, their larval development, which is not abbreviated, takes place in the sea. This contrasts with the primary freshwater crabs, which all live exclusively in freshwater or terrestrial habitats throughout their life cycle and all undergo direct development (Cumberlidge & Ng 2009). According to Wolfe *et al.* (2024), during their evolutionary history, crabs in general left the marine environment at least five and up to 15 times convergently, and returned to the sea from non-marine environments three or four times.

Species of Gecarcinidae *sensu lato* spend their juvenile and adult lives on land (where they can survive miles from the coasts and over 1000 m above sea level), and they only enter the water during the spawning season, although some females, such as those of *Gecarcoidea lalandii* H. Milne Edwards, 1837, clinging to vertical rock faces, drop egg masses into the water without actually entering it (Liu & Jeng 2007). Brooding females hatch their larvae at sea, which, after a typical planktotrophic pelagic life, migrate towards the mainland as megalopae or first crab stages. Larval development makes no concessions to a terrestrial lifestyle, even in the case of species of *Discoplax* that prefers karstic environments and caves, more or less far from the sea, and climbs down from the cliff wall, towards the surf zone (Ng & Guinot 2001). In Gecarcinoidea n. stat., the massive annual migration of male and female reproductive individuals to the ocean, highly synchronised with lunar and seasonal cycles for certain species, followed by their return to land, and the movement of young individuals to terrestrial habitats, is one of the most spectacular features of their adaptation and terrestrialisation

(Johnson 1965; Bliss 1968, 1979; Bliss & Mantel 1968; Bliss *et al.* 1979; Adamczewska & Morris 1996; 2000a; Shokita 1971; Henning 1975; Hicks 1985; Hicks *et al.* 1984, 1990; Wolcott 1988; Morris 2005; Hartnoll & Clark 2006; Hartnoll 2010, 2015; Hartnoll *et al.* 2014; López-Victoria & Werding 2008; Orchard 2012; Rodríguez-Rey *et al.* 2016; Bauer 2018; Cannicci *et al.* 2020; Tavares & Mendonça 2022: fig. 48D; Watson-Zink 2021; Marin & Tiunov 2023).

During the evolutionary transition from sea to land, gecarcinoid crabs develop various physiological and anatomical adaptations to a terrestrial lifestyle related to respiration, reproduction, development, circulation, ion and water balance (Farrelly & Greenaway 1992, 1993; Greenaway 1988, 1999). An essential physiological adaptation for mastering a terrestrial lifestyle includes the need for sensory organs to function in air rather than water, with chemical senses having to be significantly modified from their function in water (Greenaway 1999; Hansson *et al.* 2011). According to Krieger *et al.* (2015), crabs orient themselves very well on land, the vision being the dominating sense in terrestrial Brachyura. The morphological findings and preliminary behavioural observations of these authors suggest that, unlike Anomura MacLeay, 1838, the detection of volatile substances plays only a minor role in the sensory ecology of Brachyura on land, and it is possible that the antennules of brachyurans are only functional in an aquatic environment. With regard to deutocerebral olfaction, mediated by the antennules, the level of terrestrial adaptation has been found to be functional in water and non-functional on land for *Cardisoma armatum*, whereas, presumably for *Gecarcoidea natalis*, it is not functional in water but functional on land (Krieger *et al.* 2015).

Although the monophyly of the Gecarcinidae *sensu lato* is beyond doubt, its homogeneity has long been questioned. H. Milne Edwards (1851; 1853), who subdivided the grapsoid crabs (its tribe Grapsinae) into five groups (agèles), considered the 'Gecarcinacaea' at the same taxonomic level as 'Grapsacaea', 'Varunacaea', 'Cyclograpsacaea', 'Sesarmacaea', and 'Plagusiacaea', namely the traditional grapsoid subfamilies. But, later, the family Gecarcinidae *sensu lato* has been included in the Grapsoidea (as traditionally considered), which comprises families that are mostly almost exclusively marine, sometimes from very deep waters or damp forests (Alcock 1900; Tavares 1989; Martin & Davis 2001; Davie 2002; Ng *et al.* 2008; De Grave *et al.* 2009; Guinot *et al.* 2013; Perger & Wall 2014; Ng & Shih 2014, 2023; Davie *et al.* 2015a, b, c; Krieger *et al.* 2015: fig. 1; Emmerson 2016; Ng 2017; N. K. Ng *et al.* 2019; Perger 2019; C. T. T. Tsang *et al.* 2022; Sun *et al.* 2022; Z. Wang *et al.* 2023; Kobayashi *et al.* 2023; Poore & Ahyong 2023; Wolfe *et al.* 2024; Luque *et al.* 2024). According to Števčić (2005), the Grapsidae MacLeay, 1838 includes a subfamily 'Gecarcininae MacLeay, 1838'. In his numerous articles on land crabs, Türkay (1970, 1973a, b, 1974a, b, 1987) considers them to be Grapsoidea but does not go any further in the discussion.

Based on morphology, Türkay (1987: 145) identified within the family three clearly distinct groups, whose relationships were unclear: the *Cardisoma* group comprising *Cardisoma* and *Discoplax*; the *Gecarcinus* group, comprising *Gecarcinus*, *Johngarthia* and *Gecarcoidea*; and the genus *Epigrapsus* occupying a rather isolated position. In the remarkable cladistic analyses of Tavares (1989: figs 24, 25; 1991: fig. 1), Gecarcinidae *sensu lato* was separated into two groups: (1) *Cardisoma*, with plesiomorphic characters, little modified from the typical facies of Grapsidae, hence a sister group relationship of Gecarcinidae-Grapsidae; and (2) its sister group: *Epigrapsus* + *Gecarcoidea* + *Gecarcinus*, with several synapomorphies concerning the buccal region. The cladogram of Tavares (1991: fig. 1) splitted *Cardisoma* from the group *Epigrapsus* + *Gecarcoidea* + *Gecarcinus*, with the majority of the characters analysed being plesiomorphic in *Cardisoma*; and its sister group presenting several synapomorphies relating to the buccal region. Another cladogenetic event splitted *Epigrapsus* from the group *Gecarcoidea* + *Gecarcinus*, which showed deep modification in the cephalic appendages and the frontal, orbital, suborbital, pterygostomial, and pleonal regions.

A morphology-based cladistic analysis of freshwater crabs by Sternberg *et al.* (1999) found a sister-group relationship of potamoids (with the exception of Trichodactyloidea H. Milne Edwards, 1853) with families of Throracotremata Guinot, 1977, including the Gecarcinidae *sensu lato*. These authors were the first to reveal that potamoid crabs, long recognised as true Heterotremata Guinot, 1977 due to morphology, were more closely associated with thoracotreme crabs than with remaining heterotremes (see also Sternberg & Cumberlidge 2001a, b). Ng *et al.* (2008) shared the same opinion and plead for the recognition of two groups, without a phylogenetically distinct *Epigrapsus*.

Larval characters also highlight the need to split the family Gecarcinidae *sensu lato*, as some authors have long indicated (Willems 1982: tables 2, 3). Cuesta *et al.* (2002) were the first to suggest that the larval morphology of Gecarcinidae *sensu lato* distinguishes them from the rest of the grapsoid families. Zoeal morphology, which presents a mosaic of characters, has made it possible to distinguish two major groups: *Epigrapsus*, *Gecarcinus* and *Gecarcoidea* on the one hand, and *Cardisoma* (as well as *Discoplax*) on the other hand, with the setation of the maxillar endopodite separating the latter group. Furthermore, a series of typical features of their zoeae differentiate them from the zoeae of typical Grapsoidea. According to Cuesta & Anger (2005) and Cuesta *et al.* (2007: tables 5, 6), the zoeal features again support the existence of two major groups with different affinities, either with the Varunidae H. Milne Edwards, 1853 or with the Sesarmidae Dana, 1851. On the basis on overall similarities in zoeal morphology, Cuesta & Anger (2005) suggested affinities between the *Gecarcinus* + *Gecarcoidea* + *Epigrapsus* group and the Varunidae, whereas *Cardisoma* and *Discoplax* shared with the Sesarmidae antennal and pleonal morphologies as well as the setation pattern of the maxillar endopodite. New larval descriptions by Flores *et al.* (2003) and especially by Hartnoll & Clark (2006) confirmed the existence of the same groups, with *Johngarthia* added to the *Gecarcinus* group.

The growing number of studies reconstructing phylogenetic trees from molecular data, combined to varying degrees with morphological data, has intensified the debate and often modified the scheme. Their hypotheses concerning the relationships between families and superfamilies of thoracotreme have sometimes led to different, even contradictory conclusions, but some more recent studies (e.g. Z. Wang *et al.* 2023) are ultimately in perfect agreement with the morphological data (see *Genetic data*).

The identification of two major subclades within the family Gecarcinidae *sensu lato* by Guinot *et al.* (2018) constituted an implicit recognition of a higher rank, but this was not formally stated. Guinot *et al.* (2025), remaining convinced by unique characters of the adult morphology, argued in favour of a suprafamilial status, used 'Gecarcinoidea H. Milne Edwards, 1837' but without providing a diagnosis.

The morphological re-examination of most gecarcinoid genera by Guinot *et al.* (2018), while proposing a new generic nomenclature (albeit retaining a family level for Gecarcinidae *sensu lato*), namely the establishment of the new taxon *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018, led to an unexpected outcome, the need for a reassessment of the group. And, in particular, the profound divergence with previously published data (e.g. Ng *et al.* 2000, 2001; Ng & Guinot 2001; Ng & Davie 2012; Ng & Shih 2014, 2015; Davie *et al.* 2015a, b, c; and subsequent authors) was highlighted. The present paper examines these results and formally proposes to elevate the Gecarcinidae *sensu lato* to the rank of superfamily.

The Gecarcinoidea n. stat. presents two different conditions concerning the position of the sternal gonopore, as documented by Guinot (1979a: 212, fig. 54A-D; see Guinot *et al.* 2013: table 7). *Cardisoma* and *Tuerkayana* (and *Discoplax* to a lesser degree) belong to the Thoracotremata in which the male gonopore opens close to the P5 coxa (but it does not perforate it), and with the penis emerging a short distance from the thoracic sternal suture 7/8 (Fig. 5C, E) (Guinot 1979: fig. 54A-C; Guinot *et al.* 2013: fig. 23A; Guinot *et al.* 2018: fig. 5): the male duct reaches the membrane between the P5 coxa and the thoracic sternum, as shown by our dissections of *Cardisoma* species. According to Shinozaki-Mendes *et al.* (2012: 391-392, fig. 2), dissection of *Cardisoma guanhumi* showed that the ejaculatory duct was located within the endophragmal skeleton and opens at the base of P5. The configuration of *Gecarcinus*, *Gecarcoidea*, *Hartnollius* and *Johngarthia* is quite thoracotreme, with the male gonopore emerging quite far from the P5 coxa, and just below the suture 7/8 (Fig. 5D) (Guinot 1979: fig. 54D; Guinot *et al.* 2018: fig. 7B, C, F, G; Guinot *et al.* 2025: fig. 2E), however without deviating as much as in the Ocypodidae Rafinesque, 1815 and Macrophthalmidae Dana, 1851, for example (Guinot 1979: fig. 53A, B and 53D, respectively).

The congruence of the morphological, larval and genetic data (see below) allows us first to formally establish the superfamily Gecarcinoidea n. stat. by a diagnosis, and then to give life to the families that it comprises, i.e., the Gecarcinidae *restrict.* and the Cardisomatidae n. fam. The Gecarcinoidea n. stat. is thereby separated from the Grapsoidea, a superfamily currently acknowledged as non monophyletic (Chen *et al.* 2018; Zhang *et al.* 2020) and that has been extensively remodeled: it has even proposed to reduce it to the Grapsidae and to the Percnidae Števčić, 2005 (see C. T. T. Tsang *et al.* 2022: figs 3, 4). The diagnosis of Grapsoidea *sensu lato* by Guinot *et al.* (2018) follows the traditional consensus in including many genera, such as in the genetic analysis of Xin *et al.* (2018), of Q. Wang *et al.* (2021: fig. 3) and of Xu *et al.* (2023: fig. 2), whereas that of Liu *et al.* (2019) only distinguishes families. According to Z. Wang *et al.* (2023: fig. 3), paraphyletic Grapsoidea is subdivided in four groups (Grapsoidea 1-4) and also differs from Gecarcinidae *sensu lato* by the unique characteristics of the zoeae.

MATERIAL AND METHODS

Our study is based primarily on the examination of the type species of the gecarcinoid genera and most of their members. The specimens examined are deposited at the Muséum national d'Histoire naturelle (MNHN), Paris, and other international Institutions. Measurements (in millimetres) are of the maximum carapace length (cl) and width (cw), respectively. Terminology follows Davie *et al.* (2015a) and Guinot *et al.* (2018). The thoracic somites are numbered from 1 to 8. The thoracic sternal sutures are designated by the number of the two thoracic sternites involved, and are therefore numbered from 1/2 to 7/8. The description of the thoracic sternum often concerns only the male, although most fundamental characters are generally similar in the modified female thoracic sternum. An interesting character of the group studied is the more or less marked ridge on sternite 4 forming a rim at the extremity of the sterno-pleonal cavity: this ridge generally surrounds and overhangs only the telson. However, in Gecarcinoidea n. stat., it appears in two different ways: either along the telson only or extending partially along the pleonal somite 6.

The chresonymy of genera and species is limited to articles relating to systematics.

ABBREVIATIONS

ICZN	*International Code of Zoological Nomenclature*, sometimes referred to as "Code".

Institutions

AMS	Australian Museum, Sydney;
BLSZ	Barbados Laboratory of Systematic Zoology, Barbados;
MNHN	Muséum national d'Histoire naturelle, Paris;
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo;
NHM	Natural History Museum, formerly British Museum of Natural History (BMNH), London;
NMU	Northern Michigan University, Marquette;
NMNH	National Museum of Natural History (Smithsonian; Arthropoda Collection, USNM), Washington, DC;
USU	Universidade Santa Ursula, Rio de Janeiro;
ZRC	Zoological Reference collection, Lee Kong Chian Natural History Museum, Singapore;
ZMH	Zoologisches Museum Hamburg, Hamburg.

Morphology

♀	female;
♂	male;
G1 and G2	male first and second gonopods;
Mxp1, 2	maxillipeds 1, 2;
Mxp3	maxilliped 3 or external maxillipeds;
PL	female pleopods (PL 2-5);
P1-P5	pereiopods 1-5 (P1 = chelipeds).

Other abbreviations

coll.	collected by;
cl	carapace length;
cw	carapace width;
det.	identified by;
leg.	donated by;
restrict.	from latin *restrictus,* in a restricted sense;
revis.	revised by;
stn	station;
vid.	examined by.

MATERIAL EXAMINED

Cardisoma armatum Herklots, 1851

Benin • 1 ♂ 51.6 × 65.2 mm; Ekp. market; Dr D. Rondelaud coll. and leg.; 1998; Guinot det. 1998; MNHN-IU-2017-11710 (= MNHN-B21986).
Sénégal • 1 ♀ 55.3 × 68.7 mm; "Petite côte de Nianing"; Gruvel coll.; 1907; Bouvier det.; MNHN-IU-2018-5237.

Cardisoma carnifex (Herbst, 1796)

French Polynesia • 1 ♂ 71.2 × 88.0 mm; Society Islands; Tupai Atoll; Exp. SMCB; 13.V.1991; J. Poupin det.; MNHN-IU-2013-14798.
Wallis and Futuna • 1 ♀ 56.5 × 66.3 mm; Wallis I.; WALLIS & FUTUNA Exp., stn 24; 13°20'57"S, 176°13'01"W; 0-1 m; 23.X.2007; Poupin coll.; MNHN-IU-2013-2201.

Cardisoma guanhumi Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828

Guadeloupe • 1 ♂ 56.5 × 68.0 mm; M. Türkay vid. VI.1972; MNHN-IU-2013-14983 (= MNHN-B12270). • 1 ♀ 59.4 × 74.3 mm; Pointe à lambi (Le Moule), herbier à *Thalassia*; Exp. KARUBENTHOS 2012; stn GM15; 16°18'16"N, 61°32'41"W; 1 m; 14.V.2012; MNHN-LPR coll.; Poupin det.; MNHN-IU-2013-4463 • 1 ♂ 35.6 × 43.8 mm, 1 ♀ 28.2 × 35.5; Anse à la Barque; Exp. KARUBENTHOS 2012; stn GM09; 16°5'26"N, 61°46'1"W; 1 m; MNHN-LPR coll.; MNHN-IU-2013-4461 • 1 ♀ 60.0 × 75.6 mm; îles des Saintes, Terre-de-Haut; KARUBENTHOS 3; stn IGM1; 15°52.6'N, 61°34.7'W; 7.X.2024; MNHN-ARBig-LPRig coll.; MNHN-IU-2024-4621.

Discoplax gracilipes Ng & Guinot, 2001

Philippines • paratypes, 2 ♂ 30.9 × 35.6 mm, 40.6 × 46.9 mm; Panglao Island; Bohol; local villagers coll.; 18.XII.2000; MNHN-IU-2014-11218 (= MNHN-B27771). • paratypes, 1 ♂ 26.3 × 29.6 mm, 1 ♀ 19.9 × 22.7 mm; Tawala Cave; Panglao Island; Bohol; L. Liao coll. (not Y. Cai *et al.*, according to Ng & Guinot 2001); 17.XII.2000; MNHN-IU-2014-11217 (= MNHN-B27770) • paratype ♀ 22.1 × 25.7 mm; Panglao Islands; Bohol; Tuala Cave; stn 85-062; T. M. Iliffe coll.; 3.IV.1985; MNHN-IU-2014-11214 (= MNHN-B26950).

Discoplax longipes A. Milne Edwards, 1867

New Caledonia • holotype ♂ 54.0 × 55.0 mm; dry; MNHN-IU-2000-3763 (= MNHN-B3763).
Loyalty Islands • 1 ♀ 32.5 × 36.7 mm; Lifou; Inegoj Cave; 12.VIII.95; Guinot & Ng det. 1999; MNHN-IU-2017-8405 (= MNHN-B26944) • 1 ♂ 32.4 × 37.2 mm, 1 ♀ 32.6 × 37 mm; Loyalty Islands, Lifou, at the back of Inegoj Cave, near the lake, freshwater, at hand; B. Séret coll.; 2.IX.1993; D. Guinot det. 1993; MNHN-IU-2008-11402 (= MNHN-B24815).

Gecarcinus ruricola (Linnaeus, 1758)

Cuba • Neotype (see Guinot *et al.* 2025: 270); ♂ 55.0 × 76.0 mm; de Boury coll. 1914; Bouvier det. *Gecarcinus ruricola*; M. Türkay vid. VI.1972; MNHN-IU-2017-8392 (= MNHN-B13155) • 1 ♂ 66.2 × 93.3 mm; dry; M. Gundlach [coll]; as *Gecarcinus ruricola*; MNHN-IU-2000-10955 (= MNHNB10955) • 1 ♂ 57.7 × 81.4 mm; dry; M. Gundlach [coll]; as Gecarcinus r*uricola*; 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 ovigerous ♀ 52.8 × 69.9 mm; M. Chaper det. *Gecarcinus*; MNHN-IU-2024-6554 • 1 ♂ 71.0 × 53.0 mm; Playa Larga; III.2004; as *Gecarcinus ruricola*; ZMH-K65343 • 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 • 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, stn 31; Coll. & Pres. Oxford University; 11.V.1938; NHM 2024.353.
Little Cayman • 3 ♂ 56.0 × 78.1 mm 2.7 × 87.7 mm (yellow morph), 58.2 × 82.6 mm (red morph), 1 ♀ 68.0 × 95.2 mm (red morph); Cayman Expedition 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*].
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.
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; A. C. Evans det.; NHM 1967.7.1.80-85.
St Kitts • 1 ♂ (many legs detached) 66.6 × 93.8 mm (red morph); 1912.VI.18.1; 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 • 1 ♀ 41.2 × 54.2 mm, 'red morph'; Marie-Galante I.; Capesterre-de-Marie-Galante; KARUBENTHOS 3; Stn MPA-OG-09; 15°57.2'N, 61°13.3'W; alt. 189m; Forêt sèche sur calcaire; 24.X.2024, Gargomini O., Tercerie S., MNHN-ARBig-LPRig coll.; Parasram det.; MNHN-IU-2024-7258.
Dominica • 1 ♂ 65.6 × 91.0 mm; near mouth of Layou River, along road at night; H. H. Hobbs Jr coll. and det.; 14.II.1966; USNM12693 • 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. and det.; 9.III.1964; USNM 126937 • 1 ovigorous ♀ 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.
Bahamas • 1 ♀ 59.0 × 81.0 mm; dry, damaged; as *Gecarcinus ruricola*; MNHN-IU-2000-12496 (= MNHN-B12496).

Gecarcoidea humei (Wood-Mason, 1874); see Ng *et al.* 2008.

Papua New Guinea • 1 ♂ ca 50.0 × 67.4 mm (carapace damaged); N. Borneo, Sabah, Pulau Kalampunian Damit, underneath rock crevices; Laenyanti coll.; 6.V.1987; P. K.L. Ng det. IV 1991; MNHN-IU-2025-8004 (= MNHN B22189, ex ZRC 1987.871).

Gecarcoidea lalandii H. Milne Edwards, 1837

Papua New Guinea • 1 ♂ 52.0 × 73.3 mm; Wonad I., Exp. PAPUA NIUGUINI, stn PM43; 29.XI.2012; MNHN-IU-2013-13254.
Vietnam • 2 ♂ 44.3 × 59.6 mm, 39.0 × 51.7 mm; Golfe de Siam; A. Krempf; coll. 1921 (n° 2.200); E.-L. Bouvier det. *Gecarcoidea lalandei* (sic) = *Pelocarcinus humei* (Wood Mason); MNHN-IU-2017-8404 (= MNHN-B29590).
Papua New Guinea • 1 ♂ 50.5 × 72.0 mm; Wonad Island, night tide, sandy beach and intertidal rocks; Exp. PAPUA NIUGUINI; stn PM43; 5°08'08" S, 145°49'17" E; 0-1m; 29.XI.2012; MNHN-LPR coll.; MNHN-IU-2013-13254 • 1 ♀ 41.0 × 53.9 mm; Yabob village, Gum River, intertidal rocks and logs; Exp. PAPUA NIUGUINI; stn PM08; 5°15'18"S, 145°46'39"E; 0-1m; 12.XI.2012; MNHN-LPR coll.; P. K. L. Ng det.; MNHN-IU-2013-454.

Gecarcoidea natalis (Pockock, 1888)

Christmas Island (Eastern Indian Ocean, Australian Territory) • 1 ♂ 67.3 × 92.6 mm, 1 ♀ 58.2 × 78.7 mm; Hosnie's Spring; RMBR Christmas Island Expedition coll.; 24.I.2010; P. K. L. Ng det. 2010; MNHN-IU-2025-8001 (= ex ZRC 2012.0177).

Hartnollius lateralis (Fréminville *in* Guérin, 1832)

Guadeloupe • neotype (designation by N. K. Ng *et al.* 2019: fig. 2F) ♂ 36.7 × 47.2 mm; dry; Beaupertuis coll.; as *Gecarcinus lateralis*; MNHN-IU-2000-3758 (= MNHN-B3758). • 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 ×32.7 mm, 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 × 21.6 mm, 17.6 × 21.7 mm, 16.2 × 19.7 mm, 13.4 × 16.4 mm, 13.2 × 16.3 mm; 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; Iles 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 mm ca damaged; dry; as *Gecarcinus lateralis*; MNHN-IU-2000-3756 (= MNHN-B3756).
Cayman Islands, Little Cayman • 1 ♂ 29.0 × 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.

Hartnollius nobilii (Perger & Wall, 2014)

Ecuador • paratype ♀ 36.6 × 44.3 mm; 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).

Hartnollius quadratus (Saussure, 1853)

Mexico • syntype ♂ cl 39.7 mm; Mazatlán [M. Verreaux]; ANSP CA3741; Perhaps another ♂ syntype of which only a small cheliped is preserved.
Mexico • 1 ♀ 39.4 × 49.7 mm; dry; Oaxaca; revis. 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) • 1 ♂ 50.0 × 64.0 mm; 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 revis. VI.1972 *Gecarcinus lateralis*; Guinot *et al.* 2025 det. *Gecarcinus quadratus*; MNHN-IU-2000-3762 (= MNHN-B3762).

Johngarthia lagostoma (H. Milne Edwards, 1837)

Southern Atlantic • lectotype (designated by Türkay 1973: 96); ♂ 63.7 × 82.4 mm (measurements by Türkay 63 × 81 mm); coll. Quoy & Gaimard; ?Australasia (inaccurate locality: in fact, Brazil; see N. K. Ng *et al.* 2019; MNHN-IU-2000-3750 (= MNHN-B3750).

Johngarthia oceanica Perger, 2019

Clipperton • 1 ♂ 50.9 × 66.0 mm; South West coast; Centre de Recherches du Service de Santé des Armées, Division de Bio-Ecologie coll.; D. Guinot det. 1969 *Gecarcinus planatus*, M. Türkay VI.1972 revis. *Gecarcinus* (*Johngarthia*) *planata*; MNHN-IU-2011-5165 (= MNHN-B13156) •1 ♂, same data, MNHN-IU-2011-5234 (= MNHN-B13156) • 1 ♀ 54.6 × 69.1 mm; J.-L. Etienne coll.; V.2004; D. Guinot det. 19.V.2005 *Johngarthia planata* • 1 ♀ 54.6 × 69.1 mm; J.-L. Etienne coll.; V.2004; D. Guinot det. 19.V.2005 *Johngarthia planata*; MNHN-IU-2025-8003 (= MNHN-B28823) • 1 ♂ 29.7 × 35.6 mm; Exp. Clipperton 2005; J.-M. Bouchard coll. and det. 2005 *Gecarcinus planatus*; MNHN-IU-2016-10760 (= MNHN-B29848).

Johngarthia planata (Stimpson, 1860)

Baja California • holotype of *Gecarcinus digueti* Bouvier, 1895; ♂ 46.3 × 69.0 mm; coll. M. Diguet; E.-L. Bouvier det. (Original label: "*Gecarcinus planatus* Stimpson, Basse-Californie, M. Diguet (1898), E.-L. Bouvier det."), MNHN-IU-2000-10951 (= MNHN-B10951).

Johngarthia weileri (Sendler, 1912)

Gulf of Guinea • ♂ 54.5 × 71.4 mm, 1 ♀ 32.7 × 40.0 mm; Principe Island, îlot Caroço; *Calypso* 1956 Exp.; stn 87 on land; 26.VI.1956; Forest & Guinot 1966 det. *Gecarcinus lagostoma*; Turkay revis. 1972; MNHN-IU-2018-5230 (= MNHN-B13151).

Tuerkayana magnum (Ng & Shih, 2014)
Indonesia • 1 ♂ 52.8 × 64.9 mm; Java, purchased from dealer; J. C. Y. Lai det. *Discoplax magna* 14.XII.2017; MNHN-IU-2018-5239 (ex ZRC 2017.1393) • 1 ♂ 50.2 × 60.0 mm; same data; MNHN-IU-2018-5240 (ex ZRC 2017.1391).

Tuerkayana rotundum (Quoy & Gaimard, 1824)
Oceania • syntype ♂ 50.0 × 63.0 mm; M. Guérin coll.; Quoy & Gaimard det. *Thelphusa rotunda*; M. Türkay vid. VI.1972 and det. *Cardisoma rotundum*; dry; MNHN-IU-2000-3745 (= MNHN-B3745).
Loyalty Islands • 1 ♀ 32.7 × 40.1 mm, 1 ♀; Caillot 1886; MNHN-IU-2017-11711 (= MNHN-B13141), erroneously cited as MNHN-IU-2013-3740 in Guinot *et al.* 2018: fig. 4G • 1 ♂ 28.5 × 36.0 mm; Lifou Island, Easo Cave; 17 m; Richer de Forges coll. and det. *Discoplax rotundum*; 20.VIII.1993; MNHN-IU-2017-8393 (= MNHN-B24813).

Tuerkayana celeste (Ng & Davie, 2012)
Christmas Island • paratypes 1 ♂ 79.9 × 101.0 mm, 1 ♀ 67.3 × 82.0 mm; stn CI 11; Hosnie's Springs (freshwater); uplifted *Bruguiera* patch; coll. RMBR-CI 2010 Expedition; 24.I.2010; MNHN-IU-2018-5238 (ex ZRC 2012.0015).

Tuerkayana latens Ng & Shih, 2023
French Polynesia • holotype ♂ 42.7 × 52.8 mm; Tuamotu, Niau Atoll; 2006; J. F. Butaud coll. and det. *Discoplax rotunda*; MNHN-IU-2011-5594.

Tuerkayana aff. *hirtipes* (Dana, 1851) See Guinot *et al.* 2018, appendix: 602, 603.
Loyalty Islands • 1 ♂ 61.0 × 79.0 mm; Lifou Island; We Cave; Richer de Forges coll. and det. *Discoplax hirtipes*; 14.VII.1993; MNHN-IU-2017-8397 (= MNHN-B24811).

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
Subection THORACOTREMATA Guinot, 1977

Superfamily Gecarcinoidea H. Milne Edwards, 1837 n. stat.
(Table 1)

Gécarciniens H. Milne Edwards, 1837: 7 in table, 16-27 *pro parte*.

Gecarcinidae MacLeay, 1838: 63, in key.

Geocarcinidae Miers 1886: xiv, 216, 346 219 [invalid emendation of Gecarcinidae], *pro parte*.

Gecarcinoidea Guinot 1977a: 406; 1977b: 1050; 1978: 287. — Glaessner 1980: fig. 22. — Jamieson & Tudge 2000: table 7. — Sternberg & Cumberlidge 2001b: 38. — Guinot *et al.* 2018: 561-570, figs 4-7, 11A, table 1; 2025: 266.

Included families. — Gecarcinidae *restrict.* and Cardisomatidae n. fam. The family Epigrapsidae Watabe, 2007, is not included, see below, *New insights on the family Epigrapsidae Watabe, 2007.*

Superfamilial diagnosis (see Table 1)
Carapace wider than long, widest in anterior half, generally transversally ovate or subquadrate, varying from not inflated to inflated and even vaultlike (Fig. 1). Dorsal surface with regions hardly, weakly or distinctly demarcated. Lateral striae distinct, numerous (Gecarcinidae *restrict.*) or, if present, faint, and more often absent (Cardisomatidae n. fam.). In Cardisomatidae n. fam., presence of a stridulatory apparatus only in *Discoplax*, with granular suborbital crest acting as pars stridens and thickened ridge on cheliped merus acting as plectrum. In Gecarcinidae *restrict.*, subhepatic and pterygostomial striae, one possibly acting as pars stridens (with inner surface of palm of chelae as plectrum): stridulation at least reported in *Hartnollius lateralis* but possible in other genera, which have similar striae. Carapace dorsal surface without grooves or with only a few grooves; cervical groove indistinct, shallow or deep; H-shaped depression; branchial regions more or less swollen, sometimes greatly swollen. Anterolateral margins strongly arched, convex, unarmed or granular, possibly with a single postorbital tooth or notch. Supra- and infraorbital margins not fusing or meeting along their outer edges. Orbits either proportionally very small, or small and deep, compared to carapace size (Figs 2D-F; 3B, C) (Gecarcinidae *restrict.*), or larger, transversally elongated (Figs 2A-C; 3A) (Cardisomatidae n. fam.). Fronto-orbital border more than half width of carapace (Cardisomatidae n. fam.) or half or less than half width of carapace (Gecarcinidae *restrict.*). Front entire, either relatively wide and weakly deflexed (Cardisomatidae n. fam.) or relatively narrow and strongly deflexed (Gecarcinidae *restrict.*). Antennular fossae linear, narrow or higher. Antennulae folded nearly transversally to slightly obliquely. Proepistome either prominently dome-shaped at various extent (Cardisomatidae n. fam.), or small and narrow, covered or not by subfrontal plate (Gecarcinidae *restrict.*). Antennae very small, nearly longitudinal; flagellum bent. Buccal frame either elongate-subquadrate, well delineated laterally, with wide, thick, straight anterior margin joining anterior border of epistome (Figs 2A-C; 3A) (Cardisomatidae n. fam.), or quadrate, subcircular or rhomboid, not delineated laterally, with its anterior border being the anterior limit of epistome (Figs 2D-F; 3B, C) (Gecarcinidae *restrict.*). Epistome with anterior margin either as two concave edges joining medially (Cardisomatidae n. fam.), or linear (Gecarcinidae *restrict.*). Mxp3, when closed, leaving rhomboidal gap, so food can still enter the mouth and be processed by mandibles; ischium and merus typically very wide; merus constricted at the point of its articulation with ischium; palp either articulating at antero-external angle of merus and normal, i.e., with three mobile articles visible externally (Figs 2A-C; 3A) (Cardisomatidae n. fam.), or articulating in middle of anterior border of merus and with first article fused to merus internal surface, the two mobile distal articles being concealed, not visible (Figs 2F; 3C) (*Gecarcinus*, *Hartnollius*), or more or less visible (Figs 2E-F; 3B) (other genera of Gecarcinidae *restrict.*). Mxp3 exopod either exposed and provided witht flagellum (concealed) (Figs 2A, B; 3A; 4A) (Cardisomatidae n. fam.), or conspicuously reduced in size, entirely concealed and without flagellum

TABLE 1. — Morphological differences between Cardisomatidae n. fam. and Gecarcinidae *restrict*.

Morphological characters	**Cardisomatidae n. fam.**	**Gecarcinidae *restrict*.**
Carapace	moderately swollen or marquedly swollen	very swollen to strongly swollen
Lateral striae	if present, faint, and more often absent	distinct, numerous
Fronto-orbital border	more than half width of carapace	half or less than half width of carapace
Front	relatively wide, not much deflexed	relatively narrow, strongly deflexed
Orbits	developed, transversally elongated	small and deep, more or less oblique or sometimes very small and englobed in carapace (*Gecarcinus ruricola*)
Eyestalks	elongated, completely filling orbits (*Cardisoma*, *Tuerkayana*) or not (*Discoplax*)	short, more or less curved
Proepistome	more or less prominently and dome-shaped, variously sized, exposed	very small, not completely covered by subfrontal plate, therefore visible (*Gecarcinus*), or completely covered by subfrontal plate, therefore hardly discernible (*Hartnollius*, *Gecarcoidea, Johngarthia*)
Buccal frame	elongate-subquadrate, well delineated laterally with wide, thick, straight anterior margin	shorter, quadrate, subcircular or rhomboid, not delineated laterally
Epistome: anterior margin	as two concave edges joining medially	linear
Mxp3	long	shorter
Mxp3 palp	normal, with three mobile articles externally visible	with first article fused to merus internal surface and with two mobile distal articles either concealed, not visible (*Gecarcinus*), or more or less visible (other genera)
Mxp3 exopod	exposed, slender, with concealed flagellum	conspicuously reduced to more or less narrow plate, completely concealed; flagellum lost
Pterygostomial area	setose	glabrous
Sterno-pleonal cavity	deep, with developed lateral slopes	less deep, shallow
Ridge (when pleon is well applied)	marked (*Cardisoma*, *Tuerkayana*) or faint (*Discoplax*), running along telson and also extending along distal part of pleonal somite 6	marked, only running along telson
Pleonal locking structures in males	obscure or absent, non-functional	an oblique prominence, marked (*Gecarcoidea*, *Gecarcinus*) to very marked (*Johngarthia*) in middle of sternite 5. A button more or less close to suture 4/5 (*Hartnollius*). Apparatus non-functional
Male gonopore	sternal but emerging very close to P5 coxo-sternal condyle and membrane lining arthrodial cavity	distant from to P5 coxo-sternal condyle, widely sternal
Penis	penis emerging just at origin of suture 7/8, above P5 coxo-sternal condyle (except in *Discoplax*)	penis emerging rather far from P5 coxo-sternal condyle, at level of suture 7/8, thus in a more sternal position
Female pleon	relatively narrow, oval, and, thanks to dense fringe of setae on margins, completely filling thoracic sternum except for episternites; telson small and narrow, reaching more or less sternite 3 and mxp3, leaving only a reduced lateral portion exposed	much wider, discoid, leaving laterally and especially anteriorly a sternal portion exposed, in addtion to the episternites; telson in the shape of a large triangle
Male and female pleons	bordered by thick fringe of setae along margins	bordered by narrow fringe of setae along margins
G1	long, slender, tip reaching sternal suture 4/5 or not quite reaching it	short, thick; calcified part reaching about middle part of sternite 6 (*Gecarcinus, Hartnollius),* slightly behind (*Gecarcoidea*, *Johngarthia*)
Vulvae	vulvae on sternite 6 just below suture 5/6; sternal cover salient, developed (*Cardisoma*), smaller (*Tuerkayana*), or flat (*Discoplax*)	protruding, obliquely directed, normally occluded by rigid calcified immobile operculum
Setal tufts	no tufts of hydrophilic setae along first pleonal somites; setae on posterior margin of sternite 7	setal tufts of hydrophilic setae along first pleonal somites; setae on posterior margin of sternite 7, slightly on P5 coxae
Stridulatory apparatus	absent, except in *Discoplax* with suborbital ridge acting as pars stridens; plectrum on inner margin of cheliped merus	only signalled in *Hartnollius laterali*s: subhepatic and pterygostomial striae as pars stridens; inner surface of palm of chelae used as plectrum; perhaps also functional in other genera of Gecarcinidae, but not documented

(Figs 2E; 3B, C; 4B) (Gecarcinidae *restrict.*). Pterygostomial region either as a broad densely setose area (Figs 2A-C; 3A) (Cardisomatidae n. fam.), or glabrous, naked (Figs 2D, F; 3B, C) (Gecarcinidae *restrict.*). Pereopods 2-5 robust, unarmed (except dactyli); meri and dactyli rather long, with longitudinal setal ridges, often provided with spine-like stiff setae (Cardisomatidae n. fam.), variously armed with teeth and chitinous spines on dactylus (Gecarcinidae *restrict.*). Male pleon consisting of six free somites plus telson, entirely covering space between last pairs of legs; very long, its extremity ending either very close to suture 2/3 and even beyond it, or very slightly away. Male and female pleons bordered by thick fringe of setae along margins (Cardisomatidae n. fam.), or bordered by narrow fringe of setae along margins (Gecarcinidae *restrict.*). Female pleon either narrow, oval, and, thanks its dense fringe of setae on margins, completely filling thoracic sternum except for episternites, and leaving only a reduced lateral portion exposed; telson small and narrow, reaching more or less sternite 3 and mxp3 (Fig. 8) (Cardisomatidae n. fam.); or much wider, discoid, leaving laterally and especially anteriorly a sternal portion exposed in addtion to the episternites; telson in the shape of a large triangle (Fig. 9) (Gecarcinidae *restrict.*) (see *Female pleon and pleopods*). Ridge on sternite 4 from more or less marked to very thick, surrounding telson and also extending partially along pleonal somite 6 (Cardisomatidae n. fam.) or surrounding telson only (Gecarcinidae *restrict.*). Pleonal somite 6 longest. Two main positions of sternal gonopore and penis: (1) in Cardisomatidae n. fam., gonopore very close to P5 coxa (but without perforating it), and penis emerging from gonopore either at a relatively short distance from thoracic sternal suture 7/8 (Figs 5C, E; 7B: *Cardisoma*, *Tuerkayana*) or emerging at a longer distance, far from thoracic sternal suture 7/8, in posteriormost location (*Discoplax*) (see Guinot *et al.* 2018: fig. 5C, 5F, 5I, 5L, 5O: *D. longipes*, *C. guanhumi*, *Tuerkayana* aff. *hirtipes*, *T. celeste* and *T. magnum* respectively); (2) in Gecarcinidae *restrict.*, gonopore quite far from P5 coxa, and penis emerging at a longer distance in more sternal position, just below thoracic sternal suture 7/8 (Figs 5D; 7C, D: *Gecarcoidea*, *Johngarthia*). Median line deep, either along sternites 8 and 7, reappearing sometimes on sternite 6 after median bridge (*Cardisoma*) (Cardisomatidae n. fam.) or along sternite 7, sometimes slightly extending on sternite 6 (*Gecarcoidea*) (Gecarcinidae *restrict.*). Locking structures either obscure, even absent (Cardisomatidae n. fam.) or present in Gecarcinidae *restrict.* as more or less developed sternal prominence or crest, or as a button more or less close to suture 4/5 (*Hartnollius*); but pleonal sockets not delimited, so pleonal locking no longer functional in the two families (Guinot & Bouchard 1998). G1 long, slender, tip reaching thoracic sternal suture 4/5 or not reaching it completely (Figs 5E; 7B) (Cardisomatidae n. fam.) or short, thick calcified part reaching about middle part of sternite 6 (*Gecarcinus*, *Hartnollius*), slightly behind (*Gecarcoidea*, *Johngarthia*) (Figs 5F; 7D) (Gecarcinidae *restrict.*). G2 very small, spatuliform, without flagellum. Vulvae normally occluded by immobile, rigidly shut, calcified operculum (see below, *Vulvae in Gecarcinoidea* n. stat.). No setal tufts of hydrophilic setae along first pleonal somites and setae on posterior margin of sternite 7 (Cardisomatidae n. fam.), or setal tufts of hydrophilic setae along first pleonal somites; setae on posterior margin of sternite 7, slightly on P5 coxae (Gecarcinidae *restrict.*).

REMARKS

There are a series of degrees of terrestrial adaptations among brachyuran crabs, and it is difficult to determine the characteristics of habit and behaviour that make a crab a 'land crab' (Bliss 1968). All species of Gecarcinoidea n. stat., 'land crabs' *par excellence*, reside in the supratidal zone or more often out of water, active in air, generally nocturnal, cryptic and more often in burrows. Species belonging to the 'grade T3' of Hartnoll (1988a: 10; Alexander & Mantel 1969), such as *Cardisoma* species (Cardisomatidae n. fam.) that seem the least tolerant of dry conditions, require regular access to water, either by going to the sea where they immerse themselves or by drawing from other sources or by reaching the groundwater at the bottom of their burrows. Conversely, in Gecarcinidae *restrict.*, species such as *Gecarcinus ruricola* ('grade T4'), do not require to immerse themselves regularly in water, obtaining water through food, by drinking dew or running water or by uptake from damp substrates. All gecarcinoids are entirely dependent on marine water for their pelagic life (spawning and egg release, larval stages). External evidence of their terrestriality is demonstrated by the inflated carapace, which accommodate the branchial region, more strongly modified in species of Gecarcinidae *restrict.* than in Cardisomatidae n. fam.

Family CARDISOMATIDAE n. fam.
(Figs 1A-C; 2A-C; 3A; 4A; 5A, C, E; 6A, B; 7A, B; Table 1)

urn:lsid:zoobank.org:act:96AA0018-1941-4815-9F88-935213756DFD

Cardisomaceen Nauck, 1880: 27, 65. See *Remarks*.

Cardisomidae Ehrhardt, 1968b: 6: *nomen nudum*. See *Remarks*.

First gecarcinid subclade in Guinot *et al.* 2018: 561, table 1.

TYPE GENUS. — *Cardisoma* Latreille, 1828. (Etymology: from *cor*, cœur, and *soma*, body, i.e., heart-shaped body). Gender neuter.

OTHER GENERA INCLUDED. — *Discoplax* A. Milne Edwards, 1867 (see *The case of the genus* Discoplax *A. Milne Edwards, 1867*); *Tuerkayana* Guinot, N. K. Ng & Rodríguez Moreno, 2018.

NOMENCLATURAL AND TAXONOMIC REMARKS

The name *Cardisoma*, ending in *-soma*, a Greek noun transliterated unchanged into Latin, is part of the name (ICZN, Art. 30.1.2). The genitive singular of *soma*, namely, is *somatis*, and the grammatical stem is thus *somat-* (see International Code of Zoological Nomenclature, ICZN 1964: 129), so that the familial name must be based on the entire generic nomen, with the suffix *–tidae*.

The nomen 'Cardisomaceen' used by Nauck (1880: 27, 65), a plural German vernacular noun referring only to the genus *Cardisoma*, is not clearly used as a scientific name to denote a suprageneric taxon: it therefore cannot become a family-group name. The family name 'Cardisomidae' used by Ehhardt (1968b: 6) only once in passing and without including a diagnosis, should be considered a *nomen nudum*.

Guinot *et al.* (2018) have profoundly modified the composition of the gecarcinoid genera: the two species traditionally assigned to *Cardisoma*, *C. hirtipes* Dana, 1851 and *C. rotundum* (Quoy & Gaimard, 1824), have been assigned to *Tuerkayana*, to which have been added *Discoplax celeste* Ng & Davie, 2012 and *D. magna* Ng & Shih, 2014. A new species, from Polynesia, *Tuerkayana latens* Ng & Shih, 2023, has been added (Ng & Shih 2023).

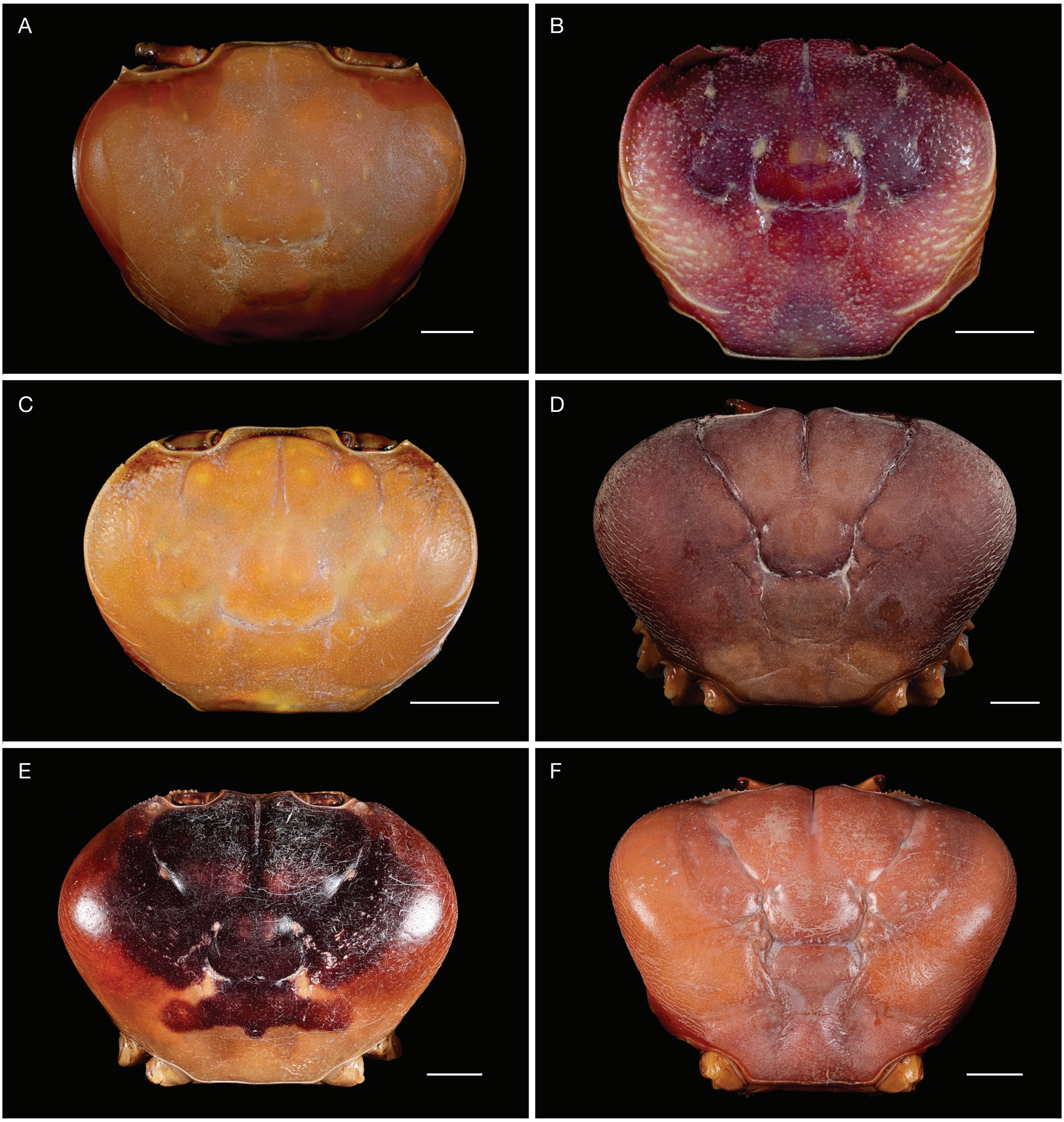

Fig. 1. — Dorsal views of carapace: **A**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♂ 56.5 × 68.0 mm, Antilles, MNHN-IU-2013-14983 (= MNHN-B12270); **B**, *Discoplax longipes* A. Milne Edwards, 1867, ♂ 32.4 × 37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **C**, *Tuerkayana rotundum* (Quoy & Gaimard, 1824), ♀ 32.7 × 40.1 mm, Loyalty Islands, MNHN-IU-2013-3740 (= MNHN-B13141); **D**, *Gecarcinus ruricola* (Linnaeus, 1758), neotype, ♂ 55.0 × 76.0 mm, Cuba, 1914, MNHN-IU-2017-8392 (= MNHN-B13155); **E**, *Hartnollius lateralis* (Fréminville *in* Guérin, 1832), ♂ 42.0 × 56.0 mm, Guadeloupe, MNHN-IU-2017-8390 (= MNHN-B24656); **F**, *Johngarthia weileri* (Sendler, 1912), ♂ 54.5 × 71.4 mm, Gulf of Guinea, Principe Island, MNHN-IU-2018-5230 (= MNHN-B13151). Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

Familial description

Carapace (Fig. 1A-C)

Carapace wider than long, transversally oval, cordate or subquadrate, convex fore and aft, inflated and globulose (*Cardisoma*), or moderately inflated (*Tuerkayana*), or not inflated (*Discoplax*). Dorsal surface with regions weakly or barely demarcated (*Cardisoma*), or clearly marked (*Discoplax*, *Tuerkayana*); grooves more or less marked; posterolateral striae distinct (*Discoplax*), more or less weak (*Tuerkayana*), or absent (*Cardisoma*). Anterolateral borders tumid and strongly arched, distinctly marked or more or less marked, unarmed or with a single small postorbital tooth or notch. Fronto-orbital border more than half the width of carapace. Front relatively wide, not much deflexed; its margin nearly straight (*Cardisoma*, *Discoplax*), or slightly convex (*Tuerkayana*). Subhepatic, subbranchial and posterolateral regions heavily striated (*Discoplax*), or subhepatic and subbranchial areas without striae (*Cardisoma*, *Tuerkayana*). Posterolateral striae absent (*Cardisoma*) or more or less faint but distinct, sometimes disappearing in largest adults (*Tuerkayana*).

Cephalic structures (Figs 2A-C; 3A)
Antennular fossae moderately wide; antennules small, entirely visible. Antenna relatively small, in orbital hiatus. Orbits relatively developed, transversally elongated (*Cardisoma*), either closed laterally by right-angled margin (*Cardisoma*, *Tuerkayana)* or with a wide lateral gap closed by oblique margin (*Discoplax*); exorbital angle marked, with small notch (*Tuerkayana*) or indentation. Eyestalks elongated, entirely filling orbits (*Cardisoma*, *Tuerkayana*) or not (*Discoplax*).

Stridulatory apparatus
Absent, no suborbital ridge (*Cardisoma*, *Tuerkayana*), or present, the suborbital ridge forming the pars stridens; plectrum on inner margin of cheliped merus (*Discoplax*).

Proepistome (Figs 2A-C; 3A)
Proepistome more or less prominently and variously sized dome-shaped (*Cardisoma*), or low and recessed (*Discoplax*, *Tuerkayana*), encircled or not by subfrontal projections.

Buccal frame, epistome, mxp3 and pterygostome (Figs 2A-C; 3A; 4A)
Buccal cavity elongate-subquadrate, delineated laterally, with wide, thick, straight anterior margin joining anterior border of epistome made of two concave edges joining medially. Mxp3 relatively long, gaping, leaving rhomboidal gape when closed; anterior margin of merus emarginate; palp normal, with three mobile articles externally visible; articulating either at antero-external angle of anterior border of merus, or slightly further, so that first article may be partially hidden behind merus (Tavares 1989: figs 3, 12a, *C. guanhumi*). Exopod exposed, slender, and equipped with flagellum, concealed. Broad pterygostomial area densely setose.

Chelipeds
In males, heterochely and heterodonty either strong, increasing at largest sizes, with major chela very stout and fingers markedly gaping; or heterochely moderate, with major chela moderately developed but becoming very stout in large adult males (*Tuerkayana*); or heterochely and heterodonty weak, with male chelipeds only slightly subequal (*Discoplax*).

Ambulatory legs
Variously shaped: relatively robust, short, especially merus and propodus, with small spines and well-developed setae; or long, relatively slender, especially merus and propodus finely spinose (*Discoplax*).

Sterno-pleonal cavity and male pleon (Figs 5A, C, E; 6A, B; 7A, B)
Sterno-pleonal cavity long, its tip fairly close to suture 2/3, deep, very wide (*Discoplax*) or narrower (*Cardisoma*, *Tuerkayana*), with developed lateral slopes; ridge on sternite 4 either marked (e.g. *Cardisoma*, *Tuerkayana*) or faint (*Discoplax*), surrounding telson only or also extending along pleonal somite 6, when pleon is applied against sternal surface. Male pleon with all somites free, plus telson; narrow and triangular (*Cardisoma*, *Tuerkayana*) or distinctly wider (*Discoplax*); somite 6 conspicuously elongated, narrow (*Cardisoma*), shorter and broader (*Tuerkayana*), very short and rounded (*Discoplax*), with oblique (*Cardisoma*) or slightly convex margins (*Discoplax*, *Tuerkayana*). Telson elongated (*Cardisoma*), or short (*Tuerkayana*), or very short, bluntly tipped (*Discoplax*). Male pleon bordered by thick fringe of setae along margins. Absence or strong reduction of hydrophilic setal tufts along first pleonal somites; setae only on posterior margin of sternite 7.

Female pleon (Fig. 8)
Female pleon relatively narrow, oval, with dense fringe of setae on margins, entirely filling thoracic sternum except for the episternites; telson small and narrow, reaching more or less sternite 3 and mxp3, and thus leaving only a reduced sternal part exposed.

Thoracic sternum, locking pleonal structures and setal tufts (Figs 5A, C, E; 6A, B; 7A, B)
Thoracic sternum proportionally wide (*Discoplax*), or narrow; strongly restricted at level of sternite 4 (*Cardisoma*). Sternites 1-2 fused; sternite 1 as small triangular piece at lower level, not separated from sternite 2 by suture; sternite 2 with thick lateral borders, semi-oval, developed or reduced; suture 2/3 present, possibly attenuated medially; suture 3/4 absent, without lateral traces; sternites 3 + 4 completely fused, with more less concave margins, therefore strongly or moderately restricted at level of P1; thoracic sternal sutures 4/5 to 7/8 interrupted; sternites 5-6 similarly shaped, sutures well defined; sternite 7 extending posteriorly near sternal gonopore; suture 7/8 rather short (*Cardisoma*, *Discoplax*), or slightly longer (*Tuerkayana*); sternite 8 rather developed, almost or completely hidden when pleon is folded; posterior emargination reaching sternite 7 at level of very narrow median bridge at suture 7/8; median line deep, either along sternites 8 and 7, interrupted by transverse bridge at level of suture 6/7, and reappearing on sternite 6 (*Cardisoma*); or median line on sternite 8 and extending only on sternite 7 below median bridge, and not extending on sternite 6 (*Discoplax*, *Tuerkayana*).

Locking structures obscure or absent, non-functional.

Male gonopore and penis (Figs 3C, E; 7B)
Male gonopore sternal, very close to P5 coxo-sternal condyle and membrane lining arthrodial cavity; penis emerging from gonopore either at a relatively short distance from thoracic sternal suture 7/8 (*Cardisoma*, *Tuerkayana*) or emerging at a longer distance, far from thoracic sternal suture 7/8, in middle of sternite 8, in posteriormost location (*Discoplax*); narrow

proximal portion of penis concealed under setae of pleonal margins, wedged in small space between P5 coxo-sternal condyle and episternite 7, then followed by thick, sclerotised sheath; ending in large, contorted papilla.

G1 (Figs 5E; 7B)
G1 proportionally long, slender, tip reaching sternal suture 4/5 or not quite reaching it.

Vulvae
Vulvae on sternite 6. Vulva developed, almost oriented vertically, operculum salient, sternal cover all around (*Cardisoma*); vulva very small, operculum moderately salient (*Discoplax*); vulva relatively small, operculum salient, sternal cover obscure (*Tuerkeyana*).

REMARKS (Figs 5C, D; 7B-D)
The male gonopore very close to the P5 coxo-sternal condyle but without perforation of the P5 coxa by the ejaculatory duct (throracotreme configuration), with the penis emerging close to P5 coxa is the most significant character distinguishing the Cardisomatidae n. fam. from the Gecarcinidae *restrict.* The cardisomatid condition represents the most basal condition found in Gecarcinoidea n. stat., whereas the Gecarcinidae *restrict.*, with the male gonopore emerging in a more completely sternal location, represents a more derived thoracotreme condition. In Cardisomatidae n. fam., although the penis is always very close to the P5 coxo-sternal condyle, it emerges either a short distance from the thoracic sternal suture 7/8 (*Cardisoma*, *Tuerkayna*) or further from the P5 coxa, in a posteriormost location (*Discoplax*). Other basal characters of Cardisomatidae n. fam. are the rather developed and horizontal eyes, the configuration of the buccal frame that is well delimited anteriorly and laterally, and the mxp3 with a fully visible palp and typical exopod with flagellum. Sternal locking structures are absent in Cardisomatidae n. fam. but present in Gecarcinidae *restrict.*, however without the complementary pleonal sockets, therefore resulting in a non-functional pleonal locking apparatus.

Within the Cardisomatidae n. fam., *Discoplax* is divergent by a number of characters, see *The case of the genus* Discoplax *A. Milne Edwards, 1867*.

Genus *Cardisoma* Latreille, 1828 *restrict.*

Cardisoma Latreille, 1828: 685.

Cardiosoma Agassiz, 1846 (incorrect spelling for *Cardisoma* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828).

Perigrapsus Heller, 1862 (type species: *Perigrapsus excelsus* Heller, 1862, by monotypy; see Ng *et al.* 2008: 214).

TYPE SPECIES. — *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828.

OTHER SPECIES INCLUDED. — For *Cardisoma*, Berthold (1827: 254, footnote) mentioned two species: *Cancer Guanhumi* of Marcgrave and *Cancer carnifex* of Herbst, names available under Articles 11 and 12 of the Code but suppressed (as nomina oblita) according to Articles 23.9.1 and 23.9.2 of the Code (see Ng *et al.* 2008: 23, 24). *Cardisoma armatum* Herklots, 1851; *C. carnifex* (Herbst, 1796) (see N. K. Ng *et al.* 2019: *C. urvillei* H. Milne Edwards, 1854 (for the date, see Clark 2025) is a junior subjective synonym of the latter); *C. crassum* Smith, 1870.
The two species *Cardisoma hirtipes* Dana, 1851 and *C. rotundum* (Quoy & Gaimard, 1824), traditionally referred to *Cardisoma*, are now members of the genus *Tuerkayana* (Guinot *et al.* 2018).

DIAGNOSIS
Carapace (Figs 1A; 15A-F)
Carapace inflated and thick (Guinot *et al.* 2018: fig. 4A-C, *Cardisoma guanhumi*, *C. carnifex*, *C. armatum*, respectively; Bouchard *et al.* 2013: fig. 12C, *C. carnifex*), reaching up to 130 mm cw in *C. guanhumi* (Türkay 1970; Hartnoll *et al.* 2006). Dorsal surface with regions weakly or hardly demarcated, smooth (Muñoz *et al.* 2025b: fig. 1, *C. armatum*). Fronto-orbital border more than half width of carapace. Front relatively wide, not much deflexed. Anterolateral margin not delimited, unarmed, except for one notch just behind the exorbital angle in *C. guanhumi* (Rathbun 1918: pl. 106, *C. guanhumi*; Türkay 1970: fig. 8a, *C. guanhumi*; Türkay 1973a: fig. 7, *C. armatum*; Türkay 1974a: fig. 11, *C. carnifex*; Tavares 1989: fig. 3, *C. guanhumi*; Bouchard *et al.* 2013: fig. 12C, *C. carnifex*; Rathbun 1918: pl. 108, *C. crassum*; Diez & Capote 2015: fig. 7K, *C. guanhumi*; Toledano-Carrasco 2016: pl. 25A). Subhepatic and subbranchial areas not striated (Guinot *et al.* 2018: fig. 6B, *C. guanhumi*).

Cephalic structures (Fig. 3A)
Antennular fossae linear. Antennule folded obliquely, with short basal article and two flagellae, equipped with numerous aesthetascs, 84 in *C. armatum* (Krieger *et al.* 2015: figs 3B, 4B, 5B). Antenna as in Krieger *et al.* (2015: figs 3, 6B). Orbits developed, transversally elongated, completely filled by eyestalks, closed laterally by right-angled margin (Delfosse 1999: fig. p. 15, *Cardisoma armatum*). Suborbital margin entirely joining exorbital tooth.

Stridulatory apparatus
Absent; no suborbital crest (Guinot *et al.* 2018: fig. 6B, *Cardisoma guanhumi*).

Proepistome (Fig. 3A)
Proepistome wide, prominently dome-shaped (Tavares 1989: fig. 3; Guinot *et al.* 2018: fig. 6B, *Cardisoma guanhumi*).

Buccal frame, epistome, mxp3 and pterygostome (Fig. 3A)
Buccal frame elongate-subquadrate, well circumscribed laterally and anteriorly, with wide, thick, straight anterior margin joining anterior border of epistome as two concave edges joining medially (Kobayashi & Naruse 2023: fig. 6B, *Cardisoma carnifex*). Mxp3 long, filling buccal cavity, leaving between them large rhomboidal gap; palp normal, with three mobile articles entirely exposed. Exopod exposed, slender, with flagellum concealed under merus (Hartnoll 1988b: fig. 2.4.B: Guinot *et al.* 2018: fig. 6b, *C. guanhumi*; Ng & Guinot

2001: fig. 1b and 1c, *C. carnifex*, *C. armatum*, respectively; Ho 2003: fig. p. 28, *C. carnifex*). Pterygostomial area setose, usually narrow.

Chelipeds (Fig. 15D, F)
Male chelipeds with strong heterochely and heterodonty: major chela remarkably stout; fingers elongated, widely gaping, with one main tooth on both prehensile margins; minor chela narrow, long; fingers slightly gaping (Monod 1956: fig. 618, *C. crassum*; Türkay 1970: figs 8a, b and 9b, c, *Cardisoma guanhumi*, *C. crassum*, respectively; Holthuis 1959: pl. 12, *C. guanhumi*; Elegbede *et al.* 2015: fig. 2, *C. guanhumi*; Krieger *et al.* 2015: fig. 2F, *C. armatum*; Ng & Ng 2021: figs 1 and 2-4A, B and 4D, *C. carnifex*, *C. armatum*, *C. crassum*, respectively; Ho 2003: fig. p. 28, *C. carnifex*).

Sterno-pleonal cavity and male pleon (Fig. 5A, C)
Sterno-pleonal cavity deep, moderately wide, ending far from suture 2/3, with developed lateral slopes. Male pleon elongated, may reach sternite 3; somite 6 narrow and conspicuously elongated; ridge on sternite 4 marked, surrounding telson and also extending partially along pleonal somite 6, when pleon is applied against sternal surface (Rathbun 1918: pl. 109, *Cardisoma crassum*; Gmittner & Wotton 1953: fig. 10, *C. guanhumi*; Türkay 1970: fig. 8b, *C. guanhumi*; 1973: figs 8 and 10, *C. carnifex*, *C. armatum*, respectively; Ng & Guinot 2001: fig. 3A and 3C, *C. guanhumi*, *C. armatum*, respectively; Guinot *et al.* 2018: fig. 5D, *C. guanhumi*).

Female pleon (Figs 8A, B)
See below, *Female pleon and pleopods.*

Thoracic sternum, *locking pleonal structures and setal tufts (Fig. 5A, C)*
Thoracic sternum posteriorly inclined, proportionally narrow, especially at level of sternite 4 that is restricted between the P1 (Gmittner & Wotton 1953: fig. 10, *C. guanhumi*; Guinot *et al.* 2018: fig. 5D-F, *C. guanhumi*). Anterior sternites forming proportionally developed plate; sternite 2 semi-oval, bluntly triangular; suture 3/4 absent, without lateral traces; sternite 4 anteriorly narrow and long, with more or less concave margins (Türkay 1970: fig. 8b, *C. guanhumi*; 1973: fig. 8, *C. armatum*; 1974a: fig. 11, *C. carnifex*); ridge on sternite 4 thick, surrounding telson only; a thick bridge at level of suture 6/7 (Ng & Guinot 2001: fig. 3A, *C. carnifex*); suture 7/8 rather short; sternite 8 rather large, developed medially, no visible portion when pleon is folded. Median line on sternites 8, 7 and reappearing on entire sternite 6 in front of median bridge at level of suture 6/7 (Ng & Guinot 2001: fig. 3A, *C. guanhumi*; fig. 3B, *C. carnifex*; fig. 3C, *C. armatum*; Guinot *et al.* 2018: fig. 5D-F, *C. guanhumi*); correspondingly, a median septum at level of sternite 6, higher at level of sternite 7, visible after dissection of *C. carnifex*.

Locking structures absent: no press-button (Guinot 1979: fig. 23F, *C. carnifex*; Guinot & Bouchard 1998: 170; Köhnk *et al.* 2017: fig. 20a, *C. carnifex*; Guinot *et al.* 2018: fig. 5E, *C. guanhumi*); only some remnants of pleonal socket discernible in *C. carnifex* according to Köhnk *et al.* (2017: fig. 20a, b).

Pleon bordered by thick fringe of setae along its margins. Absence or strong reduction of hydrophilic setal tufts in other locations.

Male gonopore and penis (*Fig. 5C)*
Male gonopore close to P5 coxo-sternal condyle but penis emerging at a relatively short distance from thoracic sternal suture 7/8; penis proximally narrow, then more expanded (Guinot 1979: fig. 54A-C; Guinot *et al.* 2013: fig. 23A, *C. carnifex*; Guinot *et al.* 2018: fig. 5F, *C. guanhumi*).

G1
G1 proportionally short, tip just reaching sternal suture 4/5 or slightly beyond (*C. guanhumi*, see Türkay 1970: fig. 8b; Chace & Hobbs 1969: fig. 67a-c; *C. carnifex*, see Türkay 1973a: fig. 4a, b; 1974a: fig. 11; Türkay & Sakai 1976: fig. 4a, b; Tavares 1989: fig. 17a; *C. crassum*, see Türkay 1973a: fig. 5; Ng & Ng 2021: fig. 6A, B and 6D, E and 6F, *C. carnifex*, *C. armatum*, *C. crassum*, respectively).

Vulvae
Vulvae on sternite 6 below suture 5/6; oriented almost vertically; operculum rather developed, salient; sternal cover all around (*C. guanhumi*, *C. crassum*, see Türkay 1970: figs 8E, 9E, respectively; *C. carnifex*, see Türkay 1973a: 9, fig. 11; Türkay & Sakai 1976: fig. 1; C. *guanhumi*, see Souza *et al.* 2013: fig. 1; Souza *et al.* 2017: fig. 1A).

Axial skeleton
C. guanhumi, see Oliveira 2014: fig. 19A, B.

Biology
Most species of Cardisomatidae n. fam. are highly dependent on water. *Cardisoma* species only enter the sea for egg hatching and for planktonic larval life. There are, however, a few exceptions that require regular immersion in seawater: for example, *C. guanhumi* has been observed at some distance off the coast of Florida (Gifford 1962) as has *C. carnifex* in Aldabra Island (Alexander 1976). *Cardisoma guanhumi* and *C. carnifex* regularly immerse themselves in the water of their burrows, about two hours per day in *C. guanhumi* (Gifford 1962; Herreid & Gifford 1963; Camaron 1981); they also drink shallow water in using their chelae with a spooning motion.

The 'blue land crab' *Cardisoma guanhumi* (Fig. 15D-F), which can reach 130 mm cw (see Türkay 1970) and has a longevity of at least 20 years (Burggren & McMahon 1988; Linton & Greenaway 2007; Vogt 2012), is widely distributed in the tropical and subtropical estuarine regions of the western central Atlantic, ranging from southeastern Florida, Central America and Bermuda to Brazil. It generally prefers to live in mangroves and is confined to within 5 km of the sea (e.g. in Jamaica, see Hartnoll 1988b). In southern Florida, crabs use both light and sound receptors to locate food from a distance, reacting immediately to the sight or the sound of the fruit or leaves falling to the ground. This causes them to emerge from their burrows, pick up the fallen items and carry them into their burrows, holding several in each chelipeds and in the mouth (Herreid II 1963). The bluish and white adults (juveniles are pink or orange) of *C. guanhumi*, the species most frequently observed in Dominica (Caribbean Sea), are not always confined to their burrows; they are also found in pools of water in drainage ditches (Chace & Hobbs 1969). A certain degree of site fidelity has been observed in *C. guanhumi* in Porto Rico, at least a return to the same areas as before they departure for mating (Forsee & Albrecht 2012). On Bimini, British Virgin Islands, crabs dig down to the water table to extract water by capillary suction (Bliss 1968: fig. 1). Following an assessment of the genetic diversity (Mitochondrial DNA variation) and population structure across the geographical range of *C. guanhumi*, two genetically distinct groups, based on two predefined populations from the Caribbean, were detected (Gomes *et al.* 2019; Amaral *et al.* 2024). In Costa Rica, *C. guanhumi*, which lives in open fields, forests, mangroves, along rivers banks and constructs deep, multi-chambered burrows, exhibits similar behaviour (Bright 1966: figs 4I, 4J, 7). *C. guanhumi* is also found in Cuba (Diez Garcia 2014), Venezuela (Carmona-Suárez 2011, 2015; Carmona-Suárez & Guerra-Castro 2018) and in Panama (Fig. 15A-F).

In *Cardisoma guanhumi* from northeastern Brazil, the four identified colour patterns are clearly linked to development stage (growth size) and sexual maturity: the smallest individuals are bright orange while sexually mature adults exhibit colours ranging from brown to blue (Silva *et al.* 2014). It is also possible that these colour patterns vary according to the season and the individual's state (stress, endogenous rhythms, or temperature variations). In semi-terrestrial crabs and marine crabs, these colour patterns could also be related to osmoregulatory and respiratory physiology, desiccation, the moult cycle and mating behaviour (Reid *et al.* 1997; Silbiger & Munguia 2008).

According to Oliveira-Neto *et al.* (2008) and Amaral *et al.* (2024), *C. guanhumi* exhibits low genetic differentiation along its coast range in Brazil and does not appear to encounter obstacles to gene flow, thanks to the presence of incomplete oceanographic barriers to the larval transport and dispersal, thus facilitating gene flow along the Brazilian coastline. However, the existence of *C. guanhumi* structured populational stocks has been detected by interpopulation morphological analyses along the northeastern coast of Brazil within a very restricted area of less than 100 km (Duarte *et al.* 2008). The geographical structure of the genetic diversity of *C. guanhumi* was demonstrated by Gomes *et al.* (2019), notably by a high genetic differentiation between the two populations in Florida and Porto Rico, due to oceanic barriers that restrict gene flow between these two regions. In south-central Veracruz, on the Gulf Coast of Mexico (in the Alvarado Lagoon System), the *C. guanhumi* population exhibits high genetic diversity, with significant gene flow between the studied sites, and has expanded during the recent evolutionary past. This suggests that the sizes of crab populations in the lagoon system has not been significantly affected by past exploitation (Rendón-Hernández *et al.* 2021).

A detailed study of *Cardisoma guanhumi* in North Colombia was led by Henning (1975). Today, in Colombia, *C. guanhumi* proliferates in croplands and urban systems at various spatial scales: crab populations are more abundant and composed of larger animals in urban areas and croplands than those in natural habitats, suggesting that human-disturbed systems are stepping stones to extend the geographic range. A long-term reduction in maximum body size, exacerbated by land use changes, likely reflects exploitation regimes consistently targeting larger crabs; and despite its status as a threatened species, the long history of human exploitation combined with livestock farming practices may explain the proliferation *C. guanhhumi* in human-dominated systems, which emphasizes the need to consider conservation in human-dominated systems (Riascos *et al.* 2023).

Cardisoma guanhumi is currently listed as a threatened species by the IUCN in Colombia (Vulnerable; Ardila *et al.* 2002) and in Venezuela (Vulnerable; Carmona-Suárez 2015). In Brazil, the species is classified as 'critically endangered' (SIBBr 2021).

Cardisoma carnifex, found from East Africa and the Red Sea across the Indo-Pacific to the Tuamotu Archipelago, is one of the most common land crabs in the western Indo-Pacific (Holthuis 1977). It typically digs burrows in soils where groundwater is available in the dry season (Bright & Hogue 1972). On Aldabra Island, it inhabits areas where the burrows are generally flooded, at least at high tide (Alexander 1976, 1979). In the three-atoll Tokelau Islands, *C. carnifex* cohabits with *Tuerkayana rotundum* (Yaldwyn & Wodzicki 1979, as *C. rotundum*). It digs burrows near the mangroves in Southern Luzon, Balayan, Batangas (Masagca 2020). Doi *et al.* (2022: figs 1, 2), who observed mating of *C. carnifex* on Iriomote-jima Island, Japan, reported that the males exhibited no courtship behaviour other than drumming on the surface sediment. Larger than the females, males could not enter the female's burrows due to the small size of their entrances and therefore waited for the female to emerge; mating then took place near the female's burrow entrance. After mating, males guarded their mate's burrow and plugged the entrance from the outside, whereas resident crabs sometimes plugged their burrows from the inside. The plugging of the burrow by *C. carnifex* males is similar to the post-copulatory guarding by brachyuran males, which prevents multiple matings in females. A common mating pattern is observed in gecarcinoids, with a hard-female mating and a generally brief courtship. The sperm of *Cardisoma carnifex*, studied by Jamieson *et al.* (1996), does not display the grapsid synapomorphy, namely the loss of the thickened ring.

Cardisoma armatum, the 'tricolour crab', also known as the 'rainbow crab' (in Africa), 'moon crab' or 'patriot crab' (in Nigeria), or 'lagoon land crab', is a tropical species ranging from Senegal to Angola, including the Cape Verde Islands and the Gulf of Guinea (Monod 1956). It is an important fishery resource (Manning & Holthuis 1981). In Ivory Coast, the crab population faces a serious problem of recruitment due to habitat degradation and heavy harvesting pressures, highlighting the need to develop management and protection strategies (Etchian *et al.* 2016).

Cardisoma crassum, the 'blue crab' or 'mouthless crab' (Fig. 15A-C), is a common inhabitant of the mangrove ecosystems of the Panamanian Pacific, from Baja California to Peru; it occurs in Cocos Island, Costa Rica (Gomez 1977) but is absent from Clipperton, Revillagigedo and Malpelo Islands (Perger *et al.* 2011). It constructs burrows that descend to groundwater or burrows in moist soils (Gifford 1962; Herreid & Gifford 1963) and shows higher burrow fidelity during the dry season (Lombardo & Rojas 2022).

Genus *Discoplax* A. Milne Edwards, 1867

Discoplax A. Milne Edwards, 1867: 284.

TYPE SPECIES. — *Discoplax longipes* A. Milne Edwards, 1867.

OTHER SPECIES INCLUDED. — *Discoplax gracilipes* Ng & Guinot, 2001, *pro parte* (not the material of Guam that was added by the first author and is in fact *D. michalis*); *D. michalis* Ng & Shih, 2015. See *The case of the genus* Discoplax *A. Milne Edwards, 1867*.

DIAGNOSIS

Carapace (Fig. 1B)

Carapace more or less rounded, not inflated (Guinot *et al.* 2018: fig. 4D, E; N. K. Ng *et al.* 2019: fig. 2B and 2C, *Discoplax longipes*, *D. gracilipes*, respectively; Kobayashi & Naruse 2023: fig. 1A, *D. gracilipes*), with the maximum recorded size being 61.7-71.9 mm for *D. longipes*. Dorsal surface with regions distinctly marked, covered with granules. Fronto-orbital border more than half width of carapace. Front relatively wide, not much deflexed. Anterolateral margin well delimited, with a marked cleft (in the diagnosis of Gecarcinidae *sensu lato* by Davie *et al.* 2015c: 1117, "anterolateral margins unarmed" must be corrected). Subhepatic and subbranchial areas heavily striated (Ng & Shih 2015: fig. 7A-D and G, H, *D. longipes* and *D. michalis*, respectively; Guinot *et al.* 2018: fig. 6A, *D. longipes*); posterolateral regions with pronounced striae (Ng & Shih 2015: figs 1-3, 6A-C, *D. longipes*; 4A, B, 5, 6D-F, *D. michalis*).

Cephalic structures (Fig. 2A)

Orbits developed but not completely filled by eyestalks, not closed laterally. Suborbital area conspicuously granulated (Ng & Guinot 2001: figs 5B and 9C, *D. longipes*, *D. gracilipes*, respectively; Ng & Shih 2015: figs 4C, 7G, H and 7A, B, *D. michalis*, *D. longipes*, respectively); with suborbital stridulatory crest, see below.

Stridulatory apparatus (Fig. 2A)

Suborbital crest long, forming stridulatory pars stridens consisting of very small, tightly packed granules (Ng & Guinot 2001: figs 5B and 9C, *Discoplax longipes*, *D. gracilipes*, respectively; Ng & Shih 2015: fig. 7A, B and 7G, H, *D. longipes*, *D. michalis*, respectively; Guinot *et al.* 2018: fig. 6A, *D. longipes*; Kobayashi & Naruse 2023: fig. 3A, B, *D. gracilipes*). Plectrum consisting of thickened ridge located on inner margin of P1 merus (Guinot *et al.* 2018: fig. 11A, *D. longipes*), present in both sexes.

Proepistome (Fig. 2A)

Proepistome small, narrow, subquadrate, low, recessed.

Buccal frame, epistome, mxp3 and pterygostome (Fig. 2A)

Buccal frame elongate-subquadrate, circumscribed laterally, with wide, thick, straight anterior margin joining anterior border of epistome as two concave edges joining medially. Mxp3 relatively long, leaving wide rhomboidal gap between them; merus with emargination on anterior border; palp normal, with three mobile articles externally visible. Exopod exposed, with concealed flagellum (Ng & Shih 2015: figs 1C, G, 7A, B and 4D, 7G, H, *Discoplax longipes*, *D. michalis*, respectively). Pterygostomial area setose (Kobayashi & Naruse 2023: fig. 1B).

Chelipeds

Male chelipeds sometimes only slightly subequal; heterochely very weak (Ng & Shih 2015: figs 1A, B, E and 3C, 4A, B, 5, *Discoplax longipes*, *D. michalis*, respectively; Kobayashi & Naruse 2023: figs 2, 3B, *D. gracilipes*).

Ambulatory legs

P2, P3 elongated and slender, especially in *D. gracilipes* (Kobayashi & Naruse 2023: fig. 1), covered with distinct granules and/or striae, appearing very rugose; dorsal margin of merus granular; only lateral margins of propodus and dactylus equipped with short stiff spines or setae (Ng & Shih 2015: fig. 10A, B, G and 10E, F, K, L, *Discoplax longipes*, *D. michalis*, respectively).

Sterno-pleonal cavity and male pleon (Figs *6A; 7A)*

Sterno-pleonal cavity deep, wide. Male pleon very wide (resembling a female pleon), long, reaching almost suture 2/3. Somite 6 very short, particularly broad and rounded, with convex margins; telson short, rounded; ridge on sternite 4 faint, surrounding telson only (Ng & Shih 2015: figs 1D, G, 8A-F and 4D, 9, *D. longipes*, *D. michalis*, respectively; Guinot *et al.* 2018: fig. 5B, *D. longipes*).

Female pleon (Fig. 8D)

Relatively narrow, without strong sexual dimorphic. See below, *Female pleon and pleopods* and *The case of the genus* Discoplax *A. Milne Edwards, 1867*.

Thoracic sternum, locking pleonal structures and setal tufts (Figs 6A; 7A)

Thoracic sternum wide, especially at level of sternite 4 (Ng & Shih 2015: figs 1D, G, 8A-E and 4D, 9, *Discoplax longipes*, *D. michalis*, respectively; Guinot *et al.* 2018: fig. 5A, B, *D. longipes*); sternites 1-3 forming low plate; sternite 1 triangular, separated from sternite 2 by thick ridge anteriorly lined with granules (suture 1/2); sternite 2 very short, flattened, separated from sternite 3 by thin, straight, complete sulcus (suture 2/3); no suture 3/4, without lateral traces; sternite 4 short and wide, with weakly concave lateral margins, thus only weakly restricted between the P1; faint rim delineating margin of sterno-pleonal cavity at level of telson; epister-

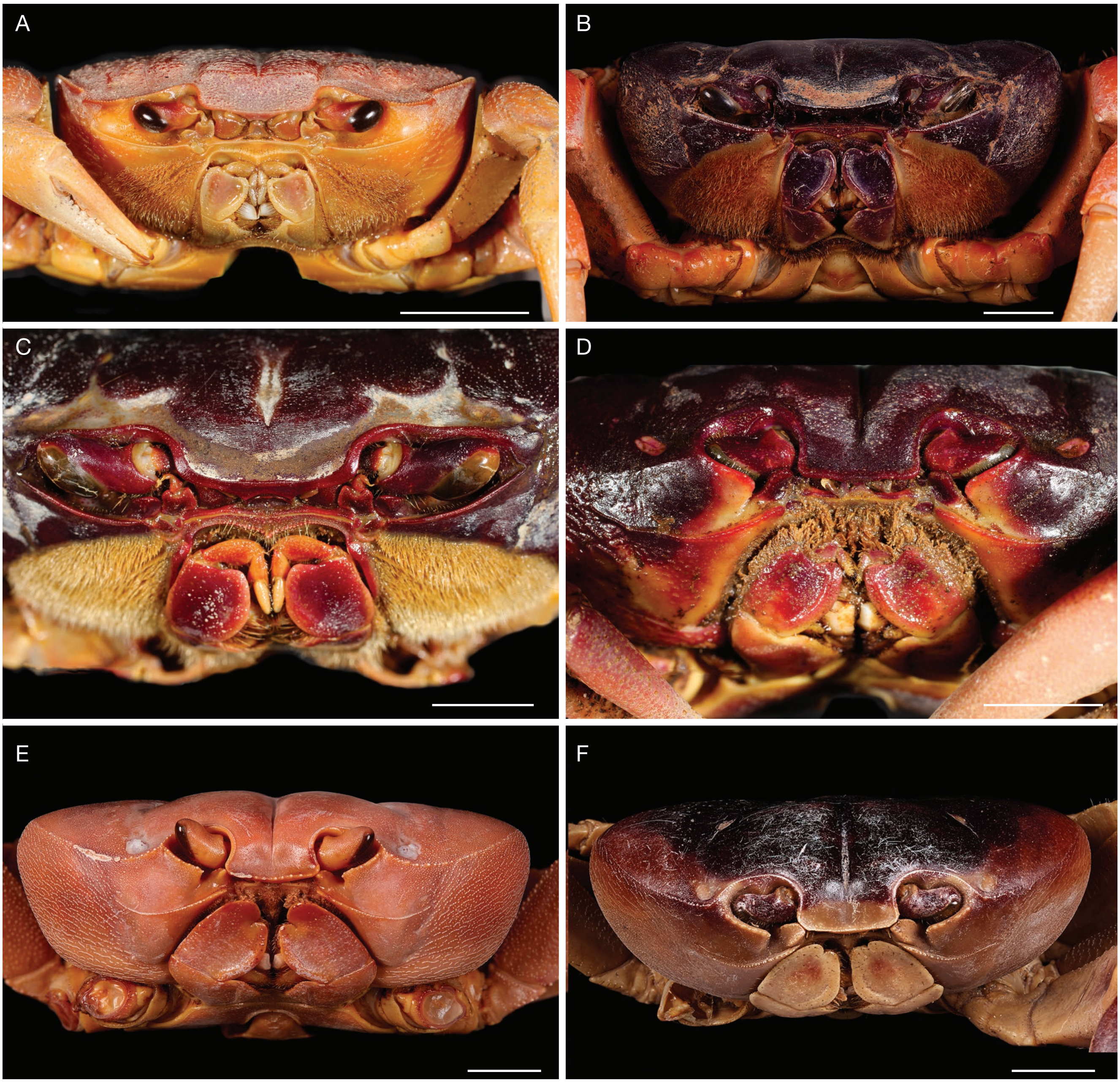

Fig. 2. — Frontal view. **A**, *Discoplax longipes* A. Milne Edwards, 1867, ♂ 32.4 × 37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **B**, *Tuerkayana magnum* (Ng & Shih, 2014), ♂ 52.8 × 64.9 mm, Indonesia, Java, MNHN-IU-2018-5239 (ex ZRC 2017.1393); **C**, *Tuerkayana* aff. *hirtipes* (Dana, 1851), ♂ 61.0 × 79.0 mm, Loyalty Islands, Lifou Island, We cave, MNHN-IU-2017-8397 (= MNHN-B24811); **D**, *Gecarcoidea lalandii* H. Milne Edwards, 1837, ♂ 52.0 × 73.3 mm, Papua New Guinea, MNHN-IU-2013-13254; **E**, *Johngarthia weileri* (Sendler, 1912), ♂ 54.5 × 71.4 mm, Gulf of Guinea, Principe Island, MNHN-IU-2018-5230 (= MNHN-B13151). **F**, *Hartnollius lateralis* (Fréminville *in* Guérin, 1832) n. comb., ♂ 42.0 × 56.0 mm, Guadeloupe, MNHN-IU-2017-8390 (= MNHNB24656). Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

nites 4-6 narrow, longitudinally directed; posterior sternites on same plane as preceding sternites; suture 7/8 rather short (Guinot *et al.* 2018: fig. 5B, C, *D. longipes*); sternite 8 short but developed medially, the posterior emargination being far from reaching sternite 7; no visible portion of sternite 8 when pleon is folded. Median line on sternites 8 and 7, and reappearing on sternite 6 in front of thick and wide median bridge at level of suture 6/7 (Guinot *et al.* 2018: fig. 5B, C, *D. longipes*).

Press buttons on sternite 5 acute, close to suture 4/5, observed in *D. longipes* (Guinot *et al.* 2018: fig. 5B) and *D. gracilipes* (character not mentioned in the description of *D. michalis*), however barely visible due to dense setal cover (a trace in a female *D. longipes* 32.6 × 37.0 mm) (Köhnk *et al.* 2017: fig. 19a); socket on pleonal somite 6 not easily noticeable, except for small cuticular border (Köhnk *et al.* 2017: fig. 19b), thus pleonal locking perhaps no longer functional, at least over certain size.

Pleon bordered by thick fringe of setae along its margins; absence or strong reduction of hydrophilic setal tufts in other locations.

Male gonopore and penis (Fig. 7A)
Male gonopore close to P5 coxo-sternal condyle but penis emerging in middle of sternite 8 thus far from thoracic sternal suture 7/8; penis proximally narrow, then more expanded (Guinot *et al.* 2018: fig. 5C, *D. longipes*).

G1 and G2
G1 proportionally short, stout, almost straight, tip reaching sternal suture 4/5 (Ng & Shih 2015: figs 11, 14A-D, 15A, B, 16A, B and 14E-H, 15C, D, 16C, D, *D. longipes*, *D. michalis*, respectively; Kobayashi & Naruse 2023: figs 4A-D and E, F and G, H, D, *D. gracilipes*, *D. longipes*, *D. michalis*, respectively).

G2 short, spatulate, with pointed tip (see Ng & Shih 2015: fig. 11A, *D. longipes*; Kobayashi & Naruse 2023: 181).

Vulvae
Vulvae small, operculum moderately salient.

BIOLOGY
The genus *Discoplax* is exclusively Indo-Pacific and all species are found in caves.

Discoplax longipes was regarded as 'very rare' by A. Milne Edwards (1867) in New Caledonia, with the holotype simply labelled as from "New Caledonia", without any other indication. The presence of *D. longipes* on the main island of New Caledonia is uncertain. It seems likely that the original specimen on which A. Milne Edwards based his description was actually collected in the nearby Loyalty Islands, where *D. longipes* is not uncommon (Figs 1B; 6A; 7A) (Ng & Guinot 2001: fig. 5; see also Ng & Shih 2015: figs 1, 2). In the Loyalty islands, the caves from which the crabs were collected are completely isolated, without a real communication with the sea (B. Séret, pers. comm.): eggs are laid and incubated in the caves where they live, and the females with ripe eggs migrate to the sea, probably by passing through crevices. According to Ng & Shih (2015), the specimens collected from Fiji and Cook Islands reported by Türkay (1974a) and McLay & Ryan (1990), as well as those from Makatea, Tuamotu and French Polynesia (Poupin 1996; Poupin & Juncker 2010), are probably *D. longipes*. Hypothesis to be verified.

Discoplax gracilipes was previously known only from the Central Philippines, in and around the island of Panglao (a relatively low limestone island with numerous anchialine sinkholes and caves) and in neighbouring islands, Balicasag Island in Bohol, Siquijor (Takeda 2000, as *D.* aff. *longipes*) and in the anchialine environments in Siquijor (Bucol & Alcala 2013: fig. 4). *Discoplax gracilipes* has also been found in Bat Cave, on the eastern side of Samal Islands just south of Davao: in a limestone body, with the entrance at about 100 m away from the sea, the Bat cave appears to connect to the sea because dim light is visible from the water at the innermost part of the cave (Husana *et al.* 2010). *Discoplax gracilipes* was recently collected from an anchialine pool in a cave on Hateruma Island, southern Ryukyu Archipelago, southwestern Japan (Kobayashi & Naruse 2023: fig. 1), which extends the northern limit of the species distributional range by about 1400 km. *D. gracilipes* is characterised by the second and third ambulatory legs markedly elongated, at least 4-5 times carapace length, and, as such, it is best adapted to cave life than *D. longipes.*

D. michalis Ng & Shih, 2015 (Ng & Shih 2015: figs 4, 5, 6E, F, 7G, H, 9, 10E, F, K, L, 14E-H, 15C-H, 16C, D) is a pseudocryptic species only known from limestone caves in Guam.

The morphometrics for the three *Discoplax* species are presented by Kobayashi & Naruse (2023: table 2). See below, *The Case of the genus* Discoplax *A. Milne Edwards, 1867*.

Genus *Tuerkayana*
Guinot, N. K. Ng & Rodríguez Moreno, 2018

Tuerkayana Guinot, N. K. Ng & Rodríguez Moreno, 2018: 564.

TYPE SPECIES. — *Thelphusa rotunda* Quoy & Gaimard, 1824 (see N. K. Ng *et al.* 2019: 101, fig. 3B).

OTHER SPECIES INCLUDED. — *Tuerkayana celeste* (Ng & Davie, 2012); *T. hirtipes* (Dana, 1851); *T. magnum* (Ng & Shih, 2014); *T. latens* Ng & Shih, 2023.
Ng (2017: figs 2, 3) has found the lectotype of *Cardisoma hirtipes* Dana, 1851, a dried male specimen, in the NMNH: it should be considered as the lectotype of *Tuerkayana hirtipes* (see also Ng & Clark 2014, as *Cardisoma hirtipes*).
About *Tuerkayana* aff. *hirtipes*, see Guinot *et al.* 2018 (appendix: 602, 603).

DIAGNOSIS
Carapace (Fig. 1C)
Carapace moderately inflated, convex tranversely and longitudinally (*Tuerkayana rotundum*, *T. hirtipes*, respectively: Ho 2003: figs p. 18 and 29, as *Discoplax rotunda*, *D. hirtipes*; *T. hirtipes*, *T. rotundum* respectively: Fujita 2017b: fig. 5A, as *D. hirtipes*; p. 100, fig. 5b, as *D. rotunda*). Dorsal surface with poorly or well demarcated regions, smooth or granulated along anterolateral borders (Ng & Davie 2012: figs 1, 2, 3A, 4, 5A, B, as *D. celeste*; Ng & Shih 2014: fig. 6A-C, as *D. celeste*; Guinot *et al.* 2018: fig. 4F-I, *Tuerkayana* aff. *hirtipes*, *T. rotundum*, *T. celeste*, *T. magnum*, respectively); posterolateral striae weak but distinct, sometimes disappearing in largest adults (Ng 2017: fig. 2A, as lectotype of *Cardisoma hirtipes*, i.e., lectotype of *T. hirtipes*; Guinot *et al.* 2018: fig. 4F, *T.* aff. *hirtipes*; Ng & Shih 2023: fig. 3A, B, *T. latens*). Fronto-orbital border more than half width of carapace. Front relatively wide, not much deflexed. Anterolateral margin delimited by row of fine granules (Guinot *et al.* 2018: fig. 4H, I, *T. celeste*, *T. magnum*, respectively) or by continuous, long row of distinct granules (Guinot *et al.* 2018: fig. 4G, *T. rotundum*; Ng & Shih 2023: figs 1, 2, 5, *T. rotundum*), or anterolateral margin strongly convex, rounded (Guinot *et al.* 2018: fig. 4F, *T.* aff. *hirtipes*); just behind exorbital angle, a small notch or an indentation with small tooth (Guinot *et al.* 2018: fig. 4G-I, *T. rotundum*, *T. celeste*, *T. magnum*, respectively; Ng 2017: fig. 2A, B, as

lectotype of *Cardisoma hirtipes*, i.e., lectotype of *T. hirtipes*). Subhepatic and subbranchial areas not striated (Ng & Shih 2014: fig. 9A-D, as *Discoplax hirtipes*, *D. celeste*, *D. magna*, respectively).

Cephalic structures (Fig. 2B, C)
Orbits developed, transversally elongated; with lateral gap closed by obliquous margin. Eyestalks elongated, completely filling orbits.

Stridulatory apparatus
Absent; no suborbital crest (Guinot *et al.* 2018: fig. 6C-E, *Tuerkayana* aff. *hirtipes*, *T. celeste*, *T. magnum*, respectively).

Proepistome (Fig. 2B, C)
Proepistome dome-shaped, rather wide but rather low, recessed (*Tuerkayana hirtipes*, see Tavares 1989: fig. 4, as *Cardisoma hirtipes*; Ng & Davie 2012: figs 3B, 5C, as *D. celeste*; Guinot *et al.* 2018: fig. 6C-E, *T.* aff. *hirtipes*, *T. celeste*, *T. magnum*; Ng 2017: fig. 2B, as lectotype of *C. hirtipes*, i.e., lectotype of *T. hirtipes*).

Buccal frame, epistome, mxp3 and pterygostome (Fig. 2B, C)
Buccal frame elongate-subquadrate, circumscribed laterally, with wide, thick, straight anterior margin joining anterior border of epistome; anterior border of epistome as two concave edges joining medially (Kobayashi & Naruse 2023: fig. 6E and 6F, *Tuerkayana hirtipes*, *T. rotundum*, respectively). Mxp3 long; palp normal, with three mobile articles externally visible. Exopod exposed, with concealed flagellum (Ng & Davie 2012: figs 3B, 5C, as *D. celeste*; Ng & Shih 2023: figs 6, 7A and 7C, *T. rotundum*, *T. latens*, respectively). Broad pterygostomial area setose (*T. hirtipes*, *D. celeste*, *D. magna*, see Ng & Shih 2014: fig. 9A, B, and 9C and 9D, as *Discoplax hirtipes*, *D. celeste*, *D. magnum*; *T. latens*, *T. rotundum*, see Ng & Shih 2023: figs 3C, 6, respectively; *T. hirtipes*, see Ho 2003: fig. p. 29).

Chelipeds
Male chelipeds without marked heterochely: major chela moderately developed but becoming very stout in large adult males, fingers elongated (Ng & Davie 2012: figs 1, 3C, 4, 5, as *D. celeste*; Ng & Shih 2014: fig. 6A-C, as *Discoplax celeste*; Fujita 2017a: fig. 1, as *Discoplax rotunda*; Ng 2017: fig. 3A, B, as lectotype of *Cardisoma hirtipes*, i.e., lectotype of *T. hirtipes*), or swollen and with relatively short fingers (Ng & Shih 2023: fig. 9A-C and 9D, *T. rotundum*, *T. latens*, respectively); chela of large adult males of *T. magnum*, not especially enlarged in proportion with long fingers; fingers elongated, partially flattened laterally, sometimes appearing almost blade-like, widely gaping. Pereiopods variously shaped: short, relatively slender, especially merus and propodus (Ng 2017: fig. 3C-H, lectotype of *Cardisoma hirtipes*, i.e., lectotype of *T. hirtipes*) or relatively stout, short, especially merus and propodus (*T. celeste*), or relatively stout, short to slender (*T. magnum*). Chelipeds in females, see Ho (2003: fig. p. 7).

Ambulatory legs
See Ng & Shih 2023: fig. 10A-C, F, G and D, H, *Tuerkayana rotundum* and *T. latens*, respectively.

Sterno-pleonal cavity and male pleon (Figs 5E; 6B; 7B)
Pleon very elongated, reaching sternite 3; somite 6 broad, variously sized and variously shaped, varying from moderately long to very long (Ng & Davie 2012: fig. 6C, D, as *Discoplax celeste*; Ng & Shih 2015: figs 8 and 9, *Discoplax longipes* and *D. michalis*, respectively; Guinot *et al.* 2018: fig. 5G, J and M, *Tuerkeyana* aff. *hirtipes*, *T. celeste*, *T. magnum*, respectively); telson short, bluntly tipped; ridge on sternite 4 marked, surrounding telson and also extending partially along pleonal somite 6 (Ng 2017: fig. 2E, F, lectotype of *Cardisoma hirtipes*, i.e., lectotype of *T. hirtipes*; Guinot *et al.* 2018: fig. 5G, *T.* aff. *hirtipes*; fig. 5J, *T. celeste*; fig. 5M, *T. magum*; Ng & Shih 2023: fig. 8A-E and 8F, *T. rotundum*, *T. latens*, respectively).

Female pleon (Fig. 8C)
See below, *Female pleon and pleopods.*

Thoracic sternum, locking pleonal structures and setal tufts (Figs 5E; 6B; 7B)
Thoracic sternum tilted posteriorly, proportionally wide, especially at level of sternite 4 that is not much restricted between P1 (*Tuerkayana rotundum*, see Türkay 1973a: fig. 14, as *Cardisoma rotundum*; Guinot *et al.* 2018: fig. 5G-I, and J-L, and M-O, *Tuerkeyana* aff. *hirtipes*, *T. celeste*, *T. magnum*, respectively). Sternite 1 small, triangular; sternite 2 broad, dome-shaped; suture 1/2 as more or less arcuate, granulated thick ridge; suture 2/3 complete, straight; no suture 3/4, without lateral traces; sternite 4 proportionally wide and short; ridge on sternite 4 surrounding telson and also extending at various extent along pleonal somite 6; thick, wide bridge at level of suture 6/7 (*Tuerkeyana hirtipes*, see Ng & Guinot 2001: fig. 4C, as *Discoplax hirtipes*); sternite 7 large, developed medially and plunging steeply; suture 7/8 rather short; no visible portion of sternite 8 when pleon is folded. Posterior emargination reaching sternite 7 at level of median bridge on suture 7/8. Median line present on sternite 7, not extending on sternite 6 (Ng 2017: fig. 2D, E, lectotype of *Cardisoma hirtipes*, i.e., lectotype of *T. hirtipes*; Guinot *et al.* 2018: fig. 5H, I, *T.* aff. *hirtipes*; fig. 5K, L, *T. celeste*; fig. 5N, O, *T. magnum*).

Locking pleonal structures absent: no button on setose or glabrous sternite 5; may be a minute button on suture 4/5 for example in holotype male 42.7 × 52.8 mm of *T. latens* (MNHN-IU-2011-5594).

Pleon with thick fringe of long setae along its margins, supplemented by setae on sternites 5 to 8; setae denser at extremity of telson; reduction of hydrophilic setal tufts in other locations.

Male gonopore and penis (Figs 5E; 7B)
Male gonopore close to P5 coxo-sternal condyle but penis emerging at a short distance from thoracic sternal; suture 7/8; penis with narrow proximal portion, continuing by calcified

cylindrical tube, then developing into large papilla, sometimes not exposed due to a short fusion of sternites 7 and 8 (Guinot *et al.* 2018: fig. 5I, *Tuerkeyana* aff. *hirtipes*; fig. 5L, *T. celeste*; fig. 5O, *T. magnum*).

G1 and G2 (Figs 5E; 7B)
Long, slender, tip reaching sternal suture 4/5 or not quite reaching it (*Tuerkeyana rotundum*, *T. hirtipes*, see Türkay & Sakai 1976: figs 5 and 6, as *Cardisoma rotundum*, *C. hirtipes*, respectively; *T. celeste*, see Ng & Davie 2012: fig. 7F-J, as *Discoplax celeste*; *T. hirtipes*, *T. celeste*, *T. magna*, see Ng & Shih 2014: fig. 13A-E and F-J and K-O, as *Discoplax hirtipes*, *D. celeste*, *D. magnum*, respectively; Ng & Shih 2023: fig. 11A-C, E-G, I-K and 11D, H, L, *Tuerkeyana rotundum*, *T. latens*, respectively).

Vulvae
Vulvae on sternite 6 below suture 5/6; practically oriented vertically, seemingly relatively smaller than in *Cardisoma* species; operculum salient; sternal cover all around or obscure (*Tuerkeyana rotundum*, see Türkay 1973a: fig. 12, as *Cardisoma rotundum*; Türkay & Sakai 1976: fig. 3, as *C. rotundum*; *T. hirtipes*, see Türkay 1974a: fig. 13, as *C. hirtipes*; Türkay & Sakai 1976: fig. 2, as *C. hirtipes*).

BIOLOGY
Species of Cardisomatidae n. fam., at least most of them, are highly dependent on water. They are herbiverous crabs (Greenaway & Raghaven 1998) that only emerge in darkness or in wet weather (Gibson-Hill 1947, as *Cardisoma hirtipes*). *Tuerkeyana hirtipes* is confined to wetlands near freshwater, and its burrows reach the water table. *T. hirtipes* and *C. carnifex* are found in karstic beaches in Gunungkidul, in the Special Territory of Yogyakarta in the middle of Java, Indonesia (Hartono *et al.* 2025: table 1, as *C. carnifex* and *Discoplax hirtipes*. *Tuerkeyana celeste*, the 'Blue crab' endemic to Christmas Island, formerly known as *Discoplax celeste*, is an aquatic crab confined to areas of the island where freshwater reaches the surface (Hicks *et al.* 1984, as *Cardisoma hirtipes*). Extensively harvested by local people for consumption in the 1950s, it has been fully protected since 1980 (Hicks *et al.* 1984, as *Cardisoma hirtipes*). For conservation purposes, on Christmas Island *T. celeste* can be considered a single management unit (Turner *et al.* 2013, as *Discoplax celeste*). The live colour of *T. celeste* varies with maturity, but it generally remains homogeneous within each size class: in small individuals, the carapace is invariably brown or purplish-brown, with yellow or orange chelae; when the carapace width reaches 41-51 mm, it remains purplish-brown, but the chelipeds become white; and at a width of 46-52 mm, the carapace and chelipeds are already bluish-white to light blue; larger specimens are always entirely white or blue (Ng & Davie 2012: figs 1, 2A-D, H, as *Discoplax celeste*). There is only one population of *Tuerkeyana celeste* on Christmas Island, this lack of population differentiation probably being explained by oceanic dispersal of the larvae rather than by terrestrial migration.

Tuerkeyana rotundum is less dependent on water. On Aldabra Island, it occurs in rather dry areas (Alexander 1976, as *Cardisoma rotundum*). In Japan, it is observed in the vegetation (Fujita 2017d: 19, fig. 1B). It has been found in an anchialine pool in a cave on Hateruma Island in the southern Ryukyu Archipelago, Japan (Kobayashi & Naruse 2023).

Family GECARCINIDAE H. Milne Edwards, 1837 *restrict.*
(Figs 1D-F; 2D-F; 3B, C; 4B; 5B, D, F;
6C, D; 7C, D; Table 1)

Gécarciniens H. Milne Edwards, 1837: 16, 20, *pro parte*.

Gecarcinidae MacLeay, 1838: 63, *pro parte*.

Geocarcinidae Miers 1886: xiv, 216-219 [invalid emendation of Gecarcinidae], *pro parte*.

Second gecarcinid subclade in Guinot *et al.* 2018: 658.

TYPE GENUS. — *Gecarcinus* Leach, 1814 (Etymology: from *ge*, earth and *carcinus*, crabe).

OTHER GENERA INCLUDED. — *Gecarcoidea* H. Milne Edwards, 1837; *Hartnollius* Guinot, Rodríguez Moreno & Toledano-Carrasco, 2025; *Johngarthia* Türkay, 1970.

FAMILIAL DESCRIPTION
Carapace (*Figs 1D-F; 14A, B)*
Carapace transversally ovate, strongly longitudinally and transversally convex, widest in anterior half. Dorsal surface more or less flat, with certain regions well-delineated, such as gastric and cardiac regions; branchial regions usually greatly swollen, even vaulted-like expanded (*Gecarcinus*); protogastric area and branchial regions becoming conspicuously swollen in large individuals (e.g. *Johngarthia cocoensis*); all grooves similar or certain grooves more pronounced, in particular cervical groove deep or moderately developed, ending anteriorly in a pit near orbital angle; median (or urogastric) groove deep; longitudinal mesogastric groove very deep, rising more or less towards frontal margin. Fronto-orbital border half or less than half width of carapace. Antero-lateral borders rounded, either not well delimitated, with only a marginal line on anterior part not distinctly joining orbital border (*Gecarcinus*, *Gecarcoidea*, *Hartnollius*, and *Johngarthia* pro parte) or lined by 6-16 teeth (*Johngarthia cocoensis*, see Perger *et al.* 2011: figs 2, 3A), more marked in females (Perger *et al.* 2011: fig. 3B). Front long or short, more or less narrow, usually nearly straight or slightly arcuate, variously produced and deflexed.

Cephalic structures (Figs 2D-F; 3B, C)
Antennular fossae narrow (see Tavares 1989: fig. 7, *Gecarcoidea lalandii*). Antennules very small, folded obliquely, hidden under the front. Antenna very small, visible but markedly recessed (*Gecarcinus*) or completely exposed (*Hartnollius*), in orbital hiatus (*Gecarcoidea humei* only) or not (*Gecarcinus*, *Gecarcoidea*, *Hartnollius*, *Johngarthia*). Orbits small and deep,

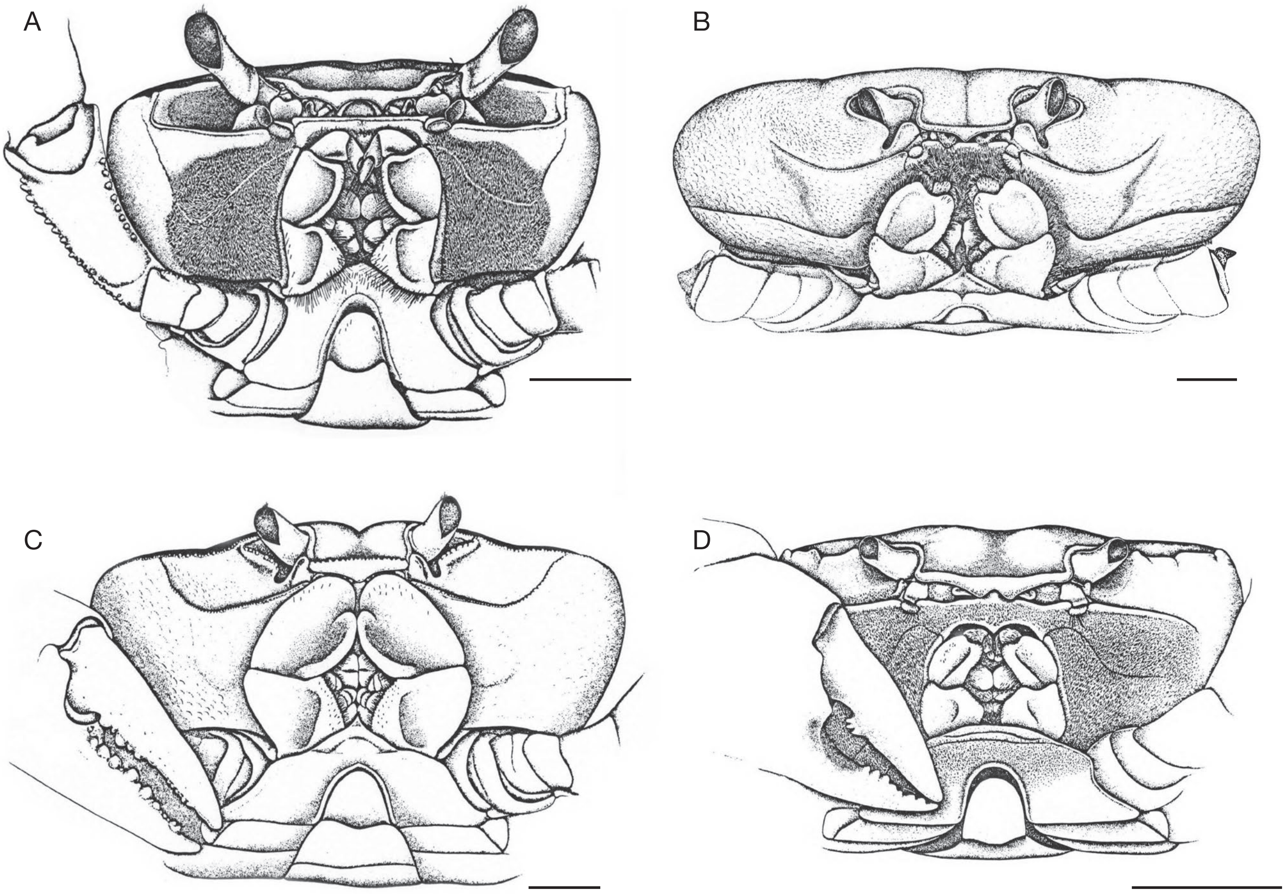

Fig. 3. — Anterior ventral views: **A**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♂, Brazil, Cabo Frio, Tavares det., USU-295; **B**, *Gecarcoidea lalandii* H. Milne Edwards, 1837, ♂, Costa Rica, Bat Island, AMS-P.11710; **C**, *Johngarthia lagostoma* (H. Milne Edwards, 1837), ♂, Trindade Island, Tavares det., MZUSP-9583; **D**, *Grapsodes notatus* Heller, 1865, ♂, Sumatra, Poeloe Babi Island, det. *Epigrapsus notatus*, RMNH-2131. Scale bars: 10 mm. Courtesy Marcos Tavares.

englobed in carapace (*Gecarcinus*) or small and more or less oblique; outer angle usually obtuse and not prominent, or with tooth (*Johngarthia cocoensis*, see Perger *et al.* 2011: figs 2, 3). Eyestalks small, more or less curved.

Stridulatory apparatus

Absent. No suborbital crest acting as pars stridens. Subhepatic and pterygostomial striae acting as pars stridens and inner surface of palm of chelae used as stridulatory plectrum, at least in *Hartnollius* species, probably also in *Gecarcinus* that has similar striae. Not documented in other gecarcinid species.

Proepistome (*Figs 2D-F; 3B, C)*

Proepistome very small, not completely covered by subfrontal plate, thus visible (*Gecarcinus*, see Guinot *et al.* 2025: fig. 2C), or completely covered by subfrontal plate, thus hardly discernible (*Hartnollius*, see Guinot *et al.* 2025: figs 10B, C, 12A-C; *Gecarcoidea*, see Tavares 1989: figs 7, 8; *Johngarthia*, see Tavares 1989: fig. 9, as *Gecarcinus lagostoma*).

Buccal frame, epistome, mxp3 and pterygostome (Figs 2D-F; 3B, C; 4B)

Buccal frame short, quadrate, subcircular or rhomboid, not delineated laterally, with its anterior border being the anterior limit of linear margin of epistome. Mxp3 relatively short, reaching front or antennular fossae (*Gecarcinus*) or just about reaching epistome (*Johngarthia* pro parte) or not reaching epistome (*Hartnollius*), even very far from setose epistome (*Gecarcoidea*, see Tavares 1989: fig. 7), from until leaving gap between lateral borders of buccal frame and exposing epistomial tooth (*Johngarthia cocoensis*); mxp3 leaving between them rhomboidal gap, either proportionally narrow (*Gecarcinus*, *Hartnollius*), or more or less wide (*Gecarcoidea*, *Johngarthia pro parte*), or very wide (e.g. *Johngarthia cocoensis*), in which mandibles are exposed. Ischium and merus either subequal (*Gecarcinus*, *Johngarthia*) or merus shorter than ischium (*Gecarcoidea*). Anterior margin of merus usually emarginate, sometimes deeply fissured, or with V-shaped emargination (*Johngarthia cocoensis*, see Perger *et al.* 2011: fig. 3), or not emarginate (*Gecarcinus*, see Guinot *et al.* 2025: figs 2B-D, 6).

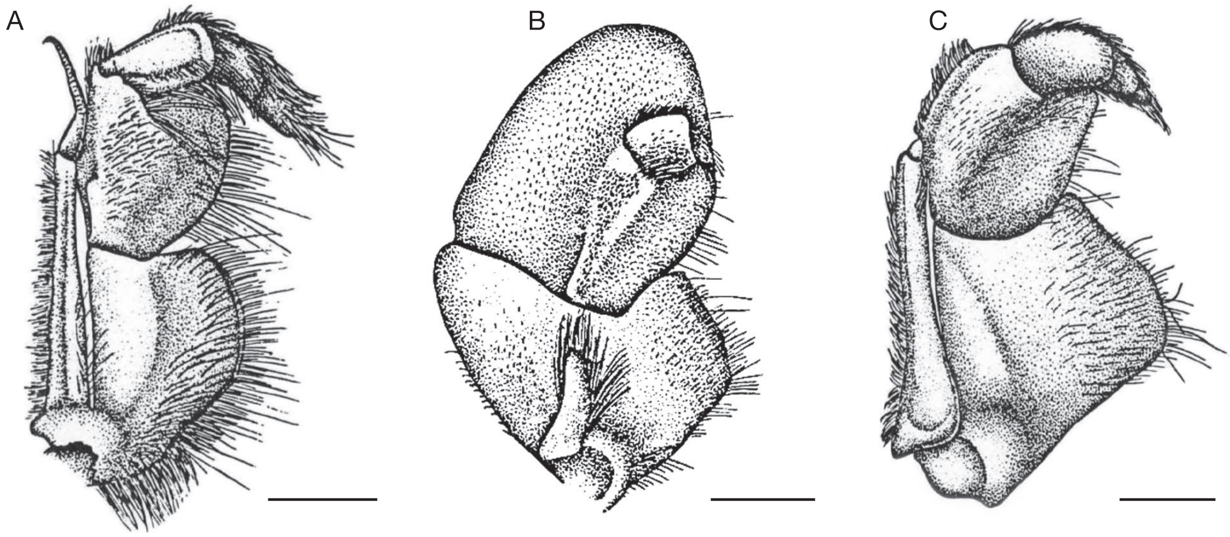

Fig. 4. — Mxp3, internal view, palp and exopod: **A**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♀, Brazil, Niterõi, Lagoa de Itaipu, USU-294; **B**, *Gecarcinus ruricola* (Linnaeus, 1758), Jamaica, Montego Bay, ♂, MZUSP 18501 (ex USU-279); **C**, *Grapsodes notatus* Heller, 1865, ♂, Bismarck Archipelago, New Britain, det. *Epigrapsus notatus*, MHa-K 5715. Scale bars: A, B, 5 mm; C, 1 mm. Courtesy Marcos Tavares.

Palp with first article fused to merus internal surface and with only two distal articles being mobile; palp either completely concealed (*Gecarcinus*), or with last two mobile articles more or less externally visible (other genera); meri of both sides joining medially (*Gecarcinus*, *Johngarthia* pro parte). Exopod completely concealed, as narrow plate, proportionally short or long, its apex reaching or not ischium-merus articulation; without flagellum. Pterygostomial area not setose, glabrous.

Chelipeds
Adult male chelipeds rather massive but not conspicuously enlarged, equal or slightly to moderately subequal, possibly distinctly unequal in large individuals; narrowly gaping; heterochely and heterodonty usually slightly marked or not marked (Fig. 14A, B), more marked in old males (*Hartnollius*).

Sterno-pleonal cavity and male pleon
(Figs 5B, D; 6C, D; 7C, D)
Sterno-pleonal cavity relatively shallow, long, its apex rather close to suture 2/3 (*Gecarcinus*), or short and not close to sternal suture 2/3 (*Hartnollius*, *Gecarcoidea*, *Johngarthia*); ridge on sternite 4 marked, surrounding telson only. Male pleon long, with all somites free plus telson; somite 6 with convex margins (*Hartnollius lateralis*, *Johngarthia cocoensis*); bordered by narrow fringe of setae along margins.

Female pleon (Fig. 9A-E)
Female pleon very wide (narrower only in *Johngarthia*, fig. 9B), discoid, with telson in the form of broad triangle, leaving laterally and further forward, a sternal portion visible in addition to the episternites; bordered by narrow fringe of setae along margins. See below, *Female pleon and pleopods.*

Thoracic sternum, locking pleonal structures and setal tufts
(Figs 5B, D; 6C, D; 7C, D)
Thoracic sternum wide, wider (especially at level of somite 5) in *Gecarcoidea* than in *Gecarcinus* and *Johngarthia.* Sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed; sternite 2 semi-ovate or trapezoidal; suture 2/3 present, straigh or slighly concave (*Hartnollius*) or V-shaped (*Gecarcinus*); suture 3/4 absent, without lateral traces; sternites 3 + 4 completely fused, margins straight more or less sinuous (*Gecarcoidea*, *Johngarthia* pro parte), sligthly convex (*J. cocoensis*, see Perger *et al.* 2011: fig. 4C), obliquely directed (*Gecarcinus*), or concave (*Hartnollius*); 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 along sternite 7 in all genera (Guinot *et al.* 2018: fig. 7B, C; Guinot *et al.* 2025: fig. 3D, *Gecarcinus*), except in *Gecarcoidea lalandii* (Guinot *et al.* 2018: fig. 7F, G), where it slightly extends on sternite 6, and in *G. humei*.

Locking structure as relatively small glabrous prominence (*Gecarcinus*), or as thickened oblique prominence covered by setae (present all along slopes of the cavity) (*Hartnollius lateralis*, *H. quadratus*), or as less prominent crest (*Gecarcoidea lalandii*, *Johngarthia planata*) but pleonal sockets not delineated, so pleonal locking non-functional.

Setal tufts of more or less dense hydrophilic setae located along first somites margins of pleon, at its junction with carapace, on posterior margin of sternite 7, and slightly on P5 coxae (*Hartnollius lateralis*, see Bliss 1963: fig. 20; 1968: fig. 14; 1979: fig. 4, as *Gecarcinus lateralis*).

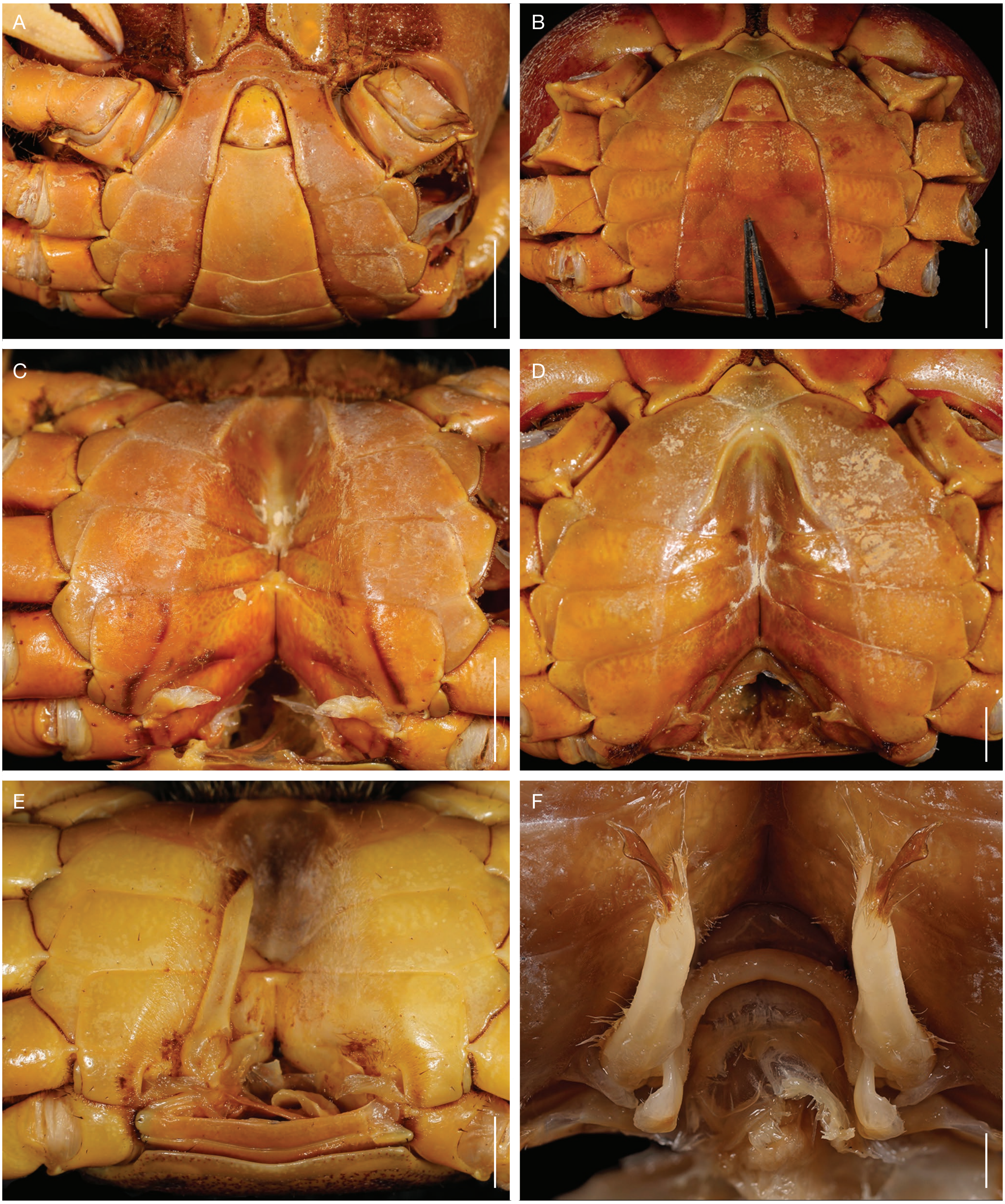

Fig. 5. — Male pleon, thoracic sternum, median line, male gonopore with penis, and gonopods: **A**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♂ 56.5 × 68.0 mm, Guadeloupe, MNHN-IU-2013-14983 (= MNHN-B12270): pleon; **B**, *Gecarcinus ruricola* (Linnaeus, 1758), neotype, ♂ 55.0 × 76.0 mm, MNHN-IU-2017-8392 (= MNHN-B13155): pleon; **C**, *C. guahnumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, MNHN-IU-2013-14983 (= MNHN-B12270): thoracic sternum; **D**, *G. ruricola* (Linnaeus, 1758), neotype, ♂ 55.0 × 76.0 mm, MNHN-IU-2017-8392 (= MNHN-B13155): thoracic sternum; **E**, *Tuerkeyana celeste* (Ng & Davie, 2012), ♂ 44.4 × 52.2 mm, Australia, Christmas Island, det. *Discoplax celeste*, ZRC 2012.0171: gonopods *in situ*; **F**, *Hartnollius quadratus* (Saussure, 1853), ♂ 50.0 × 64.0 mm, Mexico, Estero El Verde, MNHN-IU-2017-8391 (= MNHN-B20900): G1 and G2. Scale bars: A-D, 10 mm; E, 5 mm; F, 2 mm. Credits: MNHN-Soubzmaigne.

Male gonopore and penis (Figs 5D; 7C, D)
Male gonopore widely sternal; penis emerging rather far from P5 coxo-sternal condyle, very close to thoracic sternal suture 7/8 (*Johngarthia planata*, see Guinot 1979: fig. 54D, as *Gecarcinus planatus*; Guinot & Bouchard 1998: fig. 25A, as *Gecarcinus planatus*; *Johngarthia weileri*, see N. K. Ng *et al.* 2007: 246, fig. 4H, as *Gecarcinus weileri*).

G1 and G2 (Figs 5F; 7D)
G1 varying from relatively short to longer and from straight to gently curved. With very long, narrow horny tube, either completely rolled up on itself (Tavares 1989: fig. 18d, *Gecarcinus*; Guinot *et al.* 2025: fig. 3E, F, *Gecarcinus*) or not folded and open all along (Tavares 1989: fig. 18e, as *Gecarcinus lateralis;* Guinot *et al.* 2025: fig. 13A and 13C, *Hartnollius lateralis*, *H. quadratus*, respectively). Pectinate distal part either bent *c.* 75-80° from vertical (Lai *et al.* 2017: fig. 8A, *Gecarcoidea lalandii*) or bent *c.* 45° from vertical (Tavares 1989: fig. 17c, *G. natalis*; Lai *et al.* 2017: fig. 8C and 8B, D, *G. humei*, *G. natalis*, respectively). Caudal process shorter than prominently developed mesial process, with end piece at level of terminal setae (Perger *et al.* 2011: fig. 4A, B, *Johngarthia cocoensis*).

Vulvae
On sternite 5, protruding, more or less close to suture 5/6, normally occluded by rigid calcified, immobile operculum. Slightly obliquely directed (*Gecarcinus*, see Hartnoll 1968; Guinot *et al.* 2025: fig. 3G), or oriented nearly horizontally (Guinot *et al.* 2025: fig 13B, *Hartnollius*). Sternal cover narrow on inner margin (*Gecarcoidea*, *Johngarthia*).

Genus *Gecarcinus* Leach, 1814

Gecarcinus Leach, 1814: 427.

TYPE SPECIES. — *Cancer ruricola* Linnaeus, 1758. Neotype of *Gecarcinus ruricola*, a male from Cuba, MNHN-IU-2017-8392 (= MNHN-B13155), designated by Guinot *et al.* (2018). Monogeneric.

DIAGNOSIS

Carapace (Fig. 1D)
Carapace much broader than long, globular, with hepatic, subhepatic and branchial regions markedly inflated, even vaultlike; widest part of carapace considerably ahead of anterolateral angles of mesogastric region; area lateral to orbits proportionally very large, with fronto-orbital distance in adults about two-fifths carapace width (near half the carapace width in half-grown individuals) (Guinot *et al.* 2025: figs 1, 4A-G). 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 (Guinot *et al.* 2025: figs 1, 2A). Fronto-orbital border half or less than half width of carapace. Front long, proportionally narrow and slightly widening underneath, strongly produced and deflexed, with concave lateral margins and upturned lower margin. Mesial lobe of infraorbital margin elongated, curved around ventrolateral edge of front, covered by front edge (Guinot *et al.* 2025: fig. 2B-D). 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; and so then margins smooth (Guinot *et al.* 2025: figs 1, 2A).

Cephalic structures (Fig. 3C)
Antennules very small, folded obliquely. Antenna very short, visible but markedly recessed. Orbits small and deep, englobed in carapace; outer angle not marked. Eyestalks relatively short, curved (Guinot *et al.* 2025: figs 2B-D, 6).

Proepistome (Fig. 3C)
Proepistome small, not completely covered by triangular median process of subfrontal plate, thus visible. Subhepatic region with many striae; pterygostomial region glabrous, naked (Guinot *et al.* 2025: figs 2B-D, 6).

Buccal frame, epistome, mxp3 and pterygostome (Figs 3C; 4B)
Buccal frame rhomboid to subcircular, not circumscribed laterally, with anterior border being the anterior limit of linear margin of epistome (Guinot *et al.* 2025: fig. 6C). Mxp3 short; when applied well against buccal cavity, with anterior margin of merus reaching only epistome or advancing either to level of antennules or to frontal margin, thus showing phenotypic variations (Guinot *et al.* 2025: fig. 6); leaving between them narrow rhomboid gap, in which mandibles are exposed. Ischium and merus very unequal, their articulation clearly oblique; ischium smaller, merus elongated, both strongly directed obliquely; with marked longitudinal groove. Merus triangular, narrowing anteriorly, with anterior margin entire, not emarginate; meri of both sides more or less joining medially; palp with first article fused to merus internal surface and two mobile distal articles concealed, not visible (Guinot *et al.* 2025: figs 2B-D, 4D, 6). Exopod conspicuously reduced to more or less narrow suboval plate, entirely concealed; apex not reaching ischium-merus articulation, with lateral dense setae; without flagellum (Tavares 1989: fig. 14f; Guinot *et al.* 2025: fig. 11A). Subhepatic region with many striae; pterygostomial region glabrous, naked (Guinot *et al.* 2025: figs 2B-D, 6).

Chelipeds
Adult male chelipeds massive but not extraordinarily enlarged (Guinot *et al.* 2025: figs 1, 3A, B, 4B, *Gecarcinus ruricola*), 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 (Guinot *et al.* 2025: 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 (Guinot *et al.* 2025: 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 (Guinot *et al.* 2025: fig. 1, *Gecarcinus ruricola*).

Sterno-pleonal cavity and male pleon (Fig. 5B, D)
Sterno-pleonal cavity long, its extremity ending either very close to suture 2/3 and even almost exceeding it, or slightly distant; relatively shallow, completely glabrous; ridge on sternite 4 marked, surrounding telson only (Guinot *et al.* 2025: fig. 2E). Male pleon rather long, with all somites free plus telson; margins only with sparse setae; somite 6 with convex margins (Guinot *et al.* 2025: fig. 3C).

Female pleon (Fig. 9A)
See below, *Female pleon and pleopods.*

Thoracic sternum, locking pleonal structures and setal tufts (Fig. 5B, D)
Thoracic sternum wide (especially at level of somite 5); sternite1 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 traces; 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 (Guinot *et al.* 2025: fig. 2E).

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 (Guinot *et al.* 2025: fig. 3C).

Male gonopore and penis (Fig. 5D)
Male gonopore widely sternal and penis emerging rather far from P5 coxo-sternal condyle, just below thoracic sternal suture 7/8 (Guinot *et al.* 2025: fig. 3D).

G1 and G2
G1 relatively short, thick then tapering, 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; horny tube reaching suture 5/6 (Tavares 1989: fig. 18d*;* Guinot *et al.* 2025: fig. 3E, F).

G2 tiny, without flagellum.

Vulvae
Protruding, obliquely directed, normally occluded by a rigid calcified immobile operculum (see Hartnoll 1968; Guinot *et al.* 2025: fig. 3G).

BIOLOGY
For the biology of *Gecarcinus ruricola*, see Guinot *et al.* (2025).

Genus *Gecarcoidea* H. Milne Edwards, 1837

Gecarcoidea H. Milne Edwards, 1837: 25.

Pelocarcinus H. Milne Edwards, 1853: 203 (unnecessary replacement name for *Gecarcoidea* H. Milne Edwards, 1837).

Hylaeocarcinus Wood-Mason, 1874: 187 (type species: *Hylaeocarcinus humei* Wood-Mason, 1874, by monotypy).

Limnocarcinus De Man, 1879: 65 (type species: *Limnocarcinus intermedius* De Man, 1879, by monotypy), see Ng *et al.* 2008.

TYPE SPECIES. — *Gecarcoidea lalandii* H. Milne Edwards, 1837 (see N. K. Ng *et al.* 2019: figs 2H and 3A: *Pelocarcinus cailloti* A. Milne Edwards, 1890 and *P. marchei* A. Milne Edwards, 1890, respectively, both being junior subjective synonyms of *G. lalandii*).

OTHER SPECIES INCLUDED. — *Gecarcoidea humei* (Wood-Mason, 1874); *G. natalis* (Pocock, 1889).

DIAGNOSIS
Carapace
Carapace in adults either transversally subquadrate, with posterolateral margins converging towards posterior carapace margin (*G. humei*), or more or less transversally subovate (*G. lalandii*, see Fujita 2017b: fig. 5D; N. K. Ng *et al.* 2019: fig. 3A, as *Pelocarcinus marchei*; *G. natalis*, see Lai *et al.* 2017: fig. 5I, J). Dorsal surface of adult carapace either with distinct depressed markings on metagastric and urograstric areas (Lai *et al.* 2017: figs 5I, J, 9G, *G. natalis*), or without distinct depressed markings on metagastric and urograstric areas (Fujita 2017b: 102, fig. 5G; Lai *et al.* 2017: figs 5A-F and 9A-F, *G. lalandii*, *G. humei*, respectively). Fronto-orbital border about half or less than half the greatest width of carapace. Front relatively narrow, deflexed (Ho 2003: fig. p. 27, *G. lalandii*). Mesial lobe of infraorbital margin variable: joining or not joining frontal orbital edge, thus leaving or not a gap (Lai *et al.* 2017: fig. 6A-F, all species; Tavares 1989: figs 7, 8, *G. lalandii*; Guinot *et al.* 2018: fig. 7H, *G. lalandii*).

Cephalic structures (Figs 2D; 3B)
Antennular fossae varying from narrow (*G. lalandii*) to wide (*G. humei*). Antennules folded more or less slightly obliquely, with long basal article and two flagellae (*G. natalis*, see Krieger *et al.* 2015: figs 4B, 5B). Antenna (Krieger *et al.* 2015: figs 4B. 6B) with basal article and article 4 exposed, and flagellum directed backwards (*G. lalandii*) or with several articles exposed

and flagellum in orbital hiatus (*G. humei*). Orbits small, deep. Eyestalks short and curved.

Proepistome (Figs 2D; 3B)
Proepistome as small plate inserted under lower frontal margin, completely covered by subfrontal plate, thus hardly visible (all species, see Tavares 1989: figs 7, 8; *G. lalandii*; Lai *et al.* 2017: fig. 6A-F, *G. lalandii*; Guinot *et al.* 2018: fig. 7H, *G. lalandii*).

Buccal frame, epistome, mxp3 and pterygostome (Figs 2D; 3B)
Buccal cavity short, subcircular or rhomboidal, not circumscribed laterally, with its anterior border being the anterior limit of linear anterior margin of epistome (Kobayashi & Naruse 2023: fig. 6A, *G. lalandii*). Mxp3 rather small, short, not reaching epistome by far, leaving between them wide rhomboidal gap. Merus as long as broad (Lai *et al.* 2017: fig. 6A, B, *G. humei*) or longer than broad (Lai *et al.* 2017: fig. 6C, D and 6E, F, *G. lalandii*, *G. natalis*, respectively), with V-shaped emargination (Guinot *et al.* 2018: fig. 7F, *G. lalandii*). Palp inserted in the middle of anterior border of merus; first article fused to merus internal surface; two other mobile articles visible. Exopod conspicuously reduced to more or less narrow and completely concealed plate; as narrow plate not projecting beyond mxp3 ischium-merus articulation; devoid of flagellum (Tavares 1989: figs 7 and 11c, 12c, *G. lalandii*, *G. natalis*, respectively). Subhepatic region with numerous oblique rows of tubercles and striae; pterygostomial area glabrous.

Chelipeds
Heterochely and heterodonty varying from not well marked to more marked (e.g. in *G. natalis*). With a proportion of left-handed individuals, *G. lalandii* is an aggressive predator of dextral and sinistral snails (Sipman 2015).

Ambulatory legs
Ambulatory legs either relatively short, stout (notably P2 and P3), especially with regards to proportions of merus and propodus (Lai *et al.* 2017: fig. 6G, H, *G. humei*), or relatively longer, slender (notably P2 and P3), especially with regards to proportions of merus and propodus (Tavares 1989: fig. 16c, *G. natalis*; Lai *et al.* 2017: fig. 6K, L and 6I, J, *G. natalis* and *G. lalandii*, respectively).

Sterno-pleonal cavity and male pleon (Figs 6C; 7C)
Sterno-pleonal cavity deep, shallow, ending not close from sternal suture 2/3; ridge on sternite 4 marked, surrounding telson only when pleon is applied against sternal surface (Guinot *et al.* 2018: fig. 7F, *G. lalandii*). Male pleon triangular, with all somites free plus telson. Somite 6 broader than long, with lateral margins usually gently convex (Lai *et al.* 2017: fig. 7C, D and 7E, F, *G. lalandii*, *G. natalis*, respectively; Guinot *et al.* 2018: fig. 7E, *G. lalandii*), or distinctly convex (Lai *et al.* 2017: fig. 7A, B, *G. humei*).

Female pleon (Fig. 9E)
See below, *Female pleon and pleopods.*

Thoracic sternum, locking pleonal structures and setal tufts (Figs 6C; 7C)
Thoracic sternum wide (Guinot *et al.* 2018: fig. 7E-G, *G. lalandii*). Sternite 1 as very small narrow tooth, not separated by suture from sternite 2; sternite 2 developed, semi-ovate; suture 2/3 V-shaped; no suture 3/4, no lateral traces; sternites 3 + 4 completely fused, with straight, obliquely directed lateral margins, thus not restricted at level of P1; sternite 8 not developed medially, the triangular posterior emargination reaching sternite 7 at level of thick median bridge at level of suture 7/8; suture 7/8 short. Median line only on sternite 7 with its distal part bumping at level of suture 6/7 into weak median bridge that superficially units both sides of sternal plate (Guinot *et al.* 2018: fig. 7E-G, *G. lalandii*); no portion of sternite 8 dorsally exposed when pleon is folded.

Locking button as large prominence occupying most part of sternite 5 (Guinot *et al.* 2018: fig. 7F, *G. lalandi*), surrounded by setae. No delineated pleonal socket, thus locking system not efficient.

Setal tufts of more or less dense hydrophilic setae located along margins of pleonal somites 1-3, on basal part of sternite 7 and on P5 coxae (*G. lalandii*, see Guinot *et al.* 2018: fig. 7E-G).

Male gonopore and penis (Fig. 7C)
Male gonopore emerging far from P5 coxo-sternal condyle, just below suture 7/8 (Guinot *et al.* 2018: fig. 7G), thus in advanced sternal location.

G1
G1 relatively short and very stout, far from reaching suture 5/6, or proportionately longer and more slender; relatively straight (*G. lalandii*) or more gently curved (*G. humei*, *G. natalis*); with pectinate distal part bent *c.* 75-80° from vertical (Türkay & Sakai 1976: fig. 7a, b; Lai *et al.* 2017: fig. 8A, *Gecarcoidea lalandii*) or bent *c.* 45° from vertical (Tavares 1989: fig. 17c, *G. natalis*; Lai *et al.* 2017: fig. 8C and 8B, D, *G. humei*, *G. natalis*, respectively).

Vulvae
On sternite 6, more or less close to suture 5/6. Protruding, nearly horizontally directed, occluded by rigid calcified immobile operculum. Sternal cover narrow, all around except on inner margin.

BIOLOGY

Gecarcoidea natalis, known as 'Red Land Crab', which exceeds 120 mm cw (Green 1997) and lives for 13 years (Burggren & McMahon 1988; Adamczewska & Morris 2000b; Linton & Greenaway 2007; Vogt 2012), is very abundant on Christmas Island (Indian Ocean). It is found wherever primary rain forest is still intact and where it can excavate a burrow. It retreats there during dry periods and quickly emerges with the arrival of rain. It is mainly her-

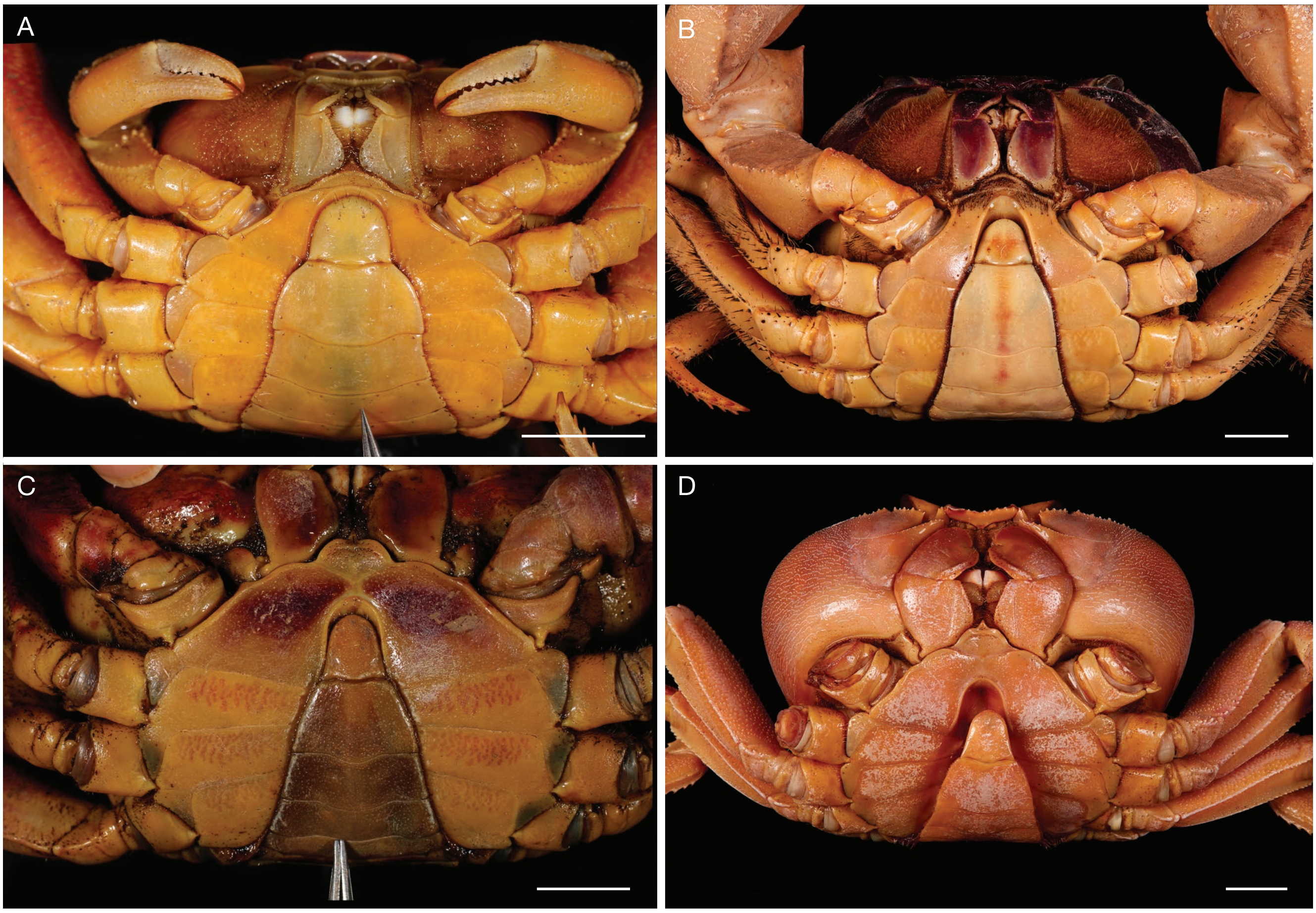

Fig. 6. — Ventral view, with male pleon: **A**, *Discoplax longipes* A. Milne Edwards, 1867, ♂ 32.4 × 37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **B**, *Tuerkayana magnum* (Ng & Shih, 2014), 1 ♂ 52.8 × 64.9 mm, Indonesia, Java, MNHN-IU-2018-5239 (ex ZRC 2017.1393); **C**, *Gecarcoidea lalandii* H. Milne Edwards, 1837, ♂ 52.0 × 73.3 mm, Papua New Guinea, MNHN-IU-2013-13254; **D**, *Johngarthia weileri* (Sendler, 1912), ♂ 54.5 × 71.4 mm, Gulf of Guinea, Principe Island, MNHN-IU-2018-5230 (= MNHN-B13151). Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

bivorous and frugiforous (Greenaway & Raghaven 1998). In the 1990s, the island-wide adult population numbered at least 100 million individuals, and biomass estimates for the species alone far exceeded those of all tropical rainforest fauna combined (Green 1997). The burrows are shallow and do not reach the water table. Red crabs drink by sucking up droplets of stagnant water with the tips of their chelae, using both alternately (Gibson-Hill 1947, as *G. humei natalis*). They accumulate litter around their burrow entrances and create nutrient-rich zones in the soil around these entrances and intermittently plug their burrows throughout the year with leaf mounds or soil (Green 2004a, b). Adult crabs moult in sealed burrows, without access to open water and consume their old exuvia almost immediately (Green 1997). They only enter the sea for egg hatching and larval development. The life cycle of this species, with its annual reproductive migration, is remarkable: eggs are laid and hatch instantly upon contact with water; larval stages (five or six zoeal stages) are spent in the sea; the crabs return to shore as megalopae, with their congregation painting the tideline red; the megalopae transform into young crabs, with millions of 'baby crabs' forming a pink carpet (Hicks *et al.* 1984). This annual breeding migration has been described as one of the ten living wonders of the planet (see Ng & Davie 2012). Massive recruitment is observed in the insular *G. natalis*, but in other gecarcinids recruits are generally few in number and exhibit cryptic behaviour (Pinheiro *et al.* 2024). On Christmas Island, the sympatric *G. natalis* and *Tuerkayana hirtipes* share a similar diet and range: the former shows no preference for different leaf types and feeds chiefly on brown and decaying leaf litter, while *T. hirtipes* prefers green leaves to yellow or brown ones (Greenaway & Raghaven 1998, as *Cardisoma hirtipes*).

In the Marshall Islands, *Gecarcoidea lalandii* occurs in holes in mixed forest and at the edges of plantations (Holthuis 1953). It is generally found where water keeps the soil moist (Bright & Hogue 1972) but it can also be present in higher, drier areas of Palaos Islands (Cameron 1981). In southern Taiwan, *G. lalandii* exhibits unusual larval release behaviour: ovigerous females cling to vertical rock faces and deposit egg masses into the water without actually entering it (Liu & Jeng 2007). This is probably an adaptation to terrestrial life aimed at reducing mortality.

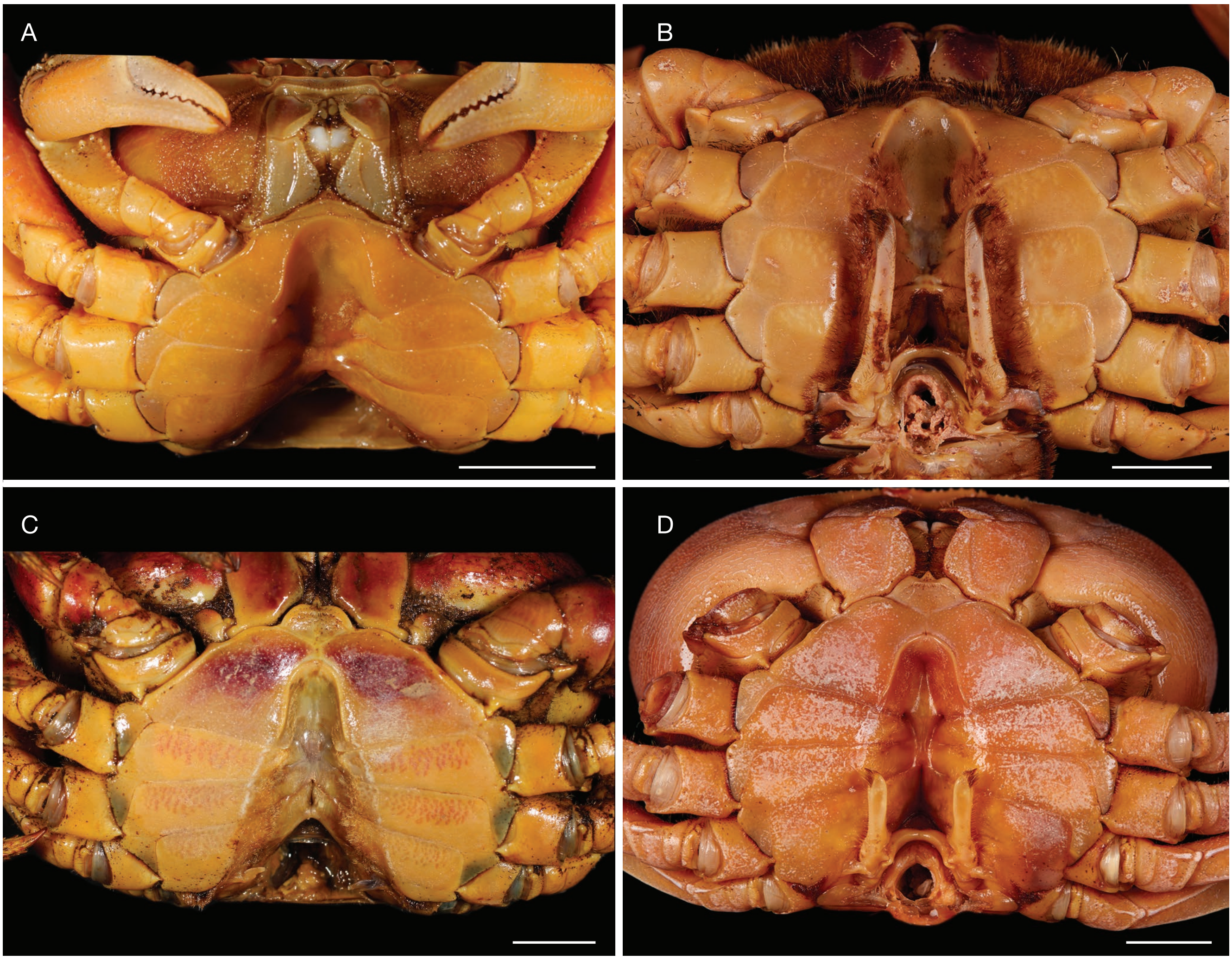

FIG. 7. — Ventral view of males, without pleon: **A**, *Discoplax longipes* A. Milne Edwards, 1867, ♂ 32.4 × 37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **B**, *Tuerkayana magnum* (Ng & Shih, 2014), ♂ 52.8 × 64.9 mm, Indonesia, Java, MNHN-IU-2018-5239 (ex ZRC 2017.1393); **C**, *Gecarcoidea lalandii* H. Milne Edwards, 1837, ♂ 52.0 × 73.3 mm, Papua New Guinea, MNHN-IU-2013-13254; **D**, *Johngarthia weileri* (Sendler, 1912), ♂ 54.5 × 71.4 mm, Gulf of Guinea, Principe Island, MNHN-IU-2018-5230 (= MNHN-B13151). Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

Genus *Hartnollius* Guinot, Rodríguez Moreno & Toledano-Carrasco, 2025

Hartnollius Guinot, Rodríguez Moreno & Toledano-Carrasco, 2025: 284.

TYPE SPECIES. — *Gecarcinus lateralis* (Fréminville *in* Guérin, 1832) (see N. K. Ng *et al.* 2019).

OTHER SPECIES INCLUDED. — *Hartnollius nobilii* (Perger & Wall, 2014) (see N. K. Ng *et al.* 2019); *H. quadratus* (Saussure, 1853). See key of species in Perger & Wall (2014, as *Gecarcinus*).

DIAGNOSIS

Carapace (Figs 1E; 14A, B)

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. Fronto-orbital border half or less than half width of carapace. Front short, narrow, produced and deflexed, with straight lateral margins and upturned lower margin. Mesial lobe of infraorbital margin angular, just joining front edge, completely exposed (*Hartnollius lateralis*, see Toledano-Carrasco 2016: pl. 22, as *Gecarcinus lateralis*). Antero-lateral margins rounded, not delimitated in males; marked by granular margin in females (Guinot *et al.* 2025: figs 9A, 9B, 15A, *H. lateralis*, *H. quadratus*, *H. nobilii*, respectively). Numerous striae along lateral margins of the carapace. Subhepatic striae used as stridulatory pars stridens (see below).

Cephalic structures (Fig. 2F)

Antennules very small, folded obliquely. Antennae very short, completely exposed, visible. Orbits small, with marked outer angle. Eyestalks relatively short, curved (*H. lateralis*, *see* Toledano-Carrasco 2016: pl. 23, as *Gecarcinus lateralis*; Guinot *et al.* 2025: fig. 10B and 10C, *H. lateralis*, *H. quadtatus*, respectively).

Proepistome (Fig. 2F)
Proepistome small, covered by subfrontal plate, thus not visible.

Buccal frame, epistome, mxp3 and pterygostome (Fig. 2F)
Buccal frame short, subcircular to rhomboid, not circumscribed laterally, with its anterior border being the anterior limit of linear anterior margin of epistome. Mxp3 rather small, short, not reaching epistome (except in *H. quadratus*, see Guinot *et al.* 2025: figs 10C, 14A), 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*, see Guinot *et al.* 2025: figs 10C, 14A) or with distinct notch (*H. lateralis*, see Guinot *et al.* 2025: figs 10B, 12A, B; *H. nobilii*, see Guinot *et al.* 2025: fig. 15B-D); meri of both sides not joining medially (except in *H. quadratus*); palp inserted below merus: its first article fused to merus internal surface and only small portion of last mobile article exposed. Mxp3 exopod completely concealed, as narrow, proportionnally short, conspicuously reduced plate, its apex not reaching ischium-merus articulation; without flagellum (*H. lateralis* and *H. quadratus*, see Tavares 1989: figs 13g, 14g and 13e, 14e, as *G. lateralis*, *G. quadratus*, respectively; Guinot *et al.* 2025: fig. 11B and 11C, *H. lateralis*, *H. quadratus*, respectively). Subhepatic area with many striae, pterygostomial areas glabrous, naked.

Chelipeds
Male chelipeds massive but not extraordinarily enlarged, very unequal, especially in old males; heterochely and heterodonty usually not or only slightly marked (Fig. 14A, B); 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)* or with only small granules on inner lower margin (*H. quadratus*, *H. nobilii*); carpus smooth (*H. lateralis*, *H. quadratus*) or with denticles (*H. nobilii*) 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*, *H. nobilii*) or with six rows of small, unequal spines (*H. quadratus*).

Sterno-pleonal cavity and male pleon
Sterno-pleonal cavity shallow, short, not close to thoracic sternal suture 2/3, moderately setose; ridge on sternite 4 marked, surrounding telson only when pleon is applied against sternal surface. Male pleon moderately long, with all somites free plus telson; somite 6 with more or less convex lateral margins; pleonal margins only with fringe of setae (Guinot *et al.* 2025: figs 12D and 14C, *H. lateralis*, *H. quadratus*, respectively).

Female pleon (Fig. 9C, D).
See below, *Female pleon and pleopods.*

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*); 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. Deep median line along sternite 7, apparently slightly extending on proximal region of sternite 6 (Guinot *et al.* 2025: figs 12D and 14C, *H. lateralis*, *H. quadratus*, respectively).

Locking pleonal structure as prominence rather close to suture 4/5, covered by setae; pleonal sockets not delineated, so pleonal locking non-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 close to P5 coxo-sternal condyle, but penis emerging rather far and just below thoracic sternal suture 7/8 (Guinot *et al.* 2025: fig. 13A, *H. lateralis*).

G1 and G2 (Fig. 5F)
G1 short, thick, slightly tapering at 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; apex reaching suture 4/6 or exceeding it (*Hartnollius lateralis* and *H. quadratus*, see Tavares 1989: figs 18e, 19b, as *Gecarcinus lateralis*; fig. 19a, as *G. quadratus; H. lateralis*, *H. quadratus*, see Toledano-Carrasco *et al.* 2021: fig. 3A, B, as *G. lateralis*, *G. quadratus*, respectively; *H. lateralis*, see Toledano-Carrasco 2016: pl. 20, as *G. lateralis*; Guinot *et al.* 2025: fig. 13A and 13C, *H. lateralis*, *H. quadratus*, respectively); several horny setae at its base.

G2 very small, without flagellum (Guinot *et al.* 2025: fig. 13A and 13C, *H. lateralis*, *H. quadratus*, respectively).

Vulvae
Protruding, oriented nearly horizontally, normally occluded by rigid calcified immobile operculum (*H. lateralis*, see Tavares 1989: fig. 18e, as *Gecarcinus lateralis;* Guinot *et al.* 2025: figs 13B and 15E, *H. lateralis*, *H. nobilii*, respectively).

BIOLOGY
For *Hartnollius* species, see Guinot *et al.* (2025).

Genus *Johngarthia* Türkay, 1970

Gecercinus (*Johngarthia*) Türkay, 1970: 343.

Type species. — *Gecarcinus planatus* Stimpson, 1860 (see the neotype of *Johngarthia planata* designated by Perger 2019: 288, fig. 1A-C; see N. K. Ng *et al.* 2019: fig. 2D: *Gecarcinus digueti* Bouvier, 1895, which is a junior subjective synonym of *J. planata*).

Other species included. — *Johngarthia cocoensis* Perger, Vargas & Wall, 2011; *J. lagostoma* (H. Milne Edwards, 1837) (see N. K. Ng *et al.* 2019: fig. 2E, as *Gecarcinus lagostoma*); *J. malpilenis* (Faxon, 1893); *J. oceanica* Perger, 2019; *J. weileri* (Sendler, 1912).
It should be noted that the *Johngarthia lagostoma* of certain authors (e.g. Capart 1951: fig. 80; Forest & Guinot 1966: 94, all as *Gecarcinus*) are in fact *J. weileri* (Manning & Holthuis 1981).

Diagnosis

Carapace (Fig. 1F)
Carapace broader than long, may be transversally ovate, moderately convex, possibly distinctly depressed in frontal and lateral views (*J. oceanica*, see Perger 2019), with hepatic, subhepatic and branchial regions not moderarely inflated or more swollen (*J. lagostoma*, see N. K. Ng *et al.* 2019: fig. 2E, as *Gecarcinus lagostoma*; *J. oceanica*, see Perger 2019). Dorsal surface with marked grooves (*J. weileri*, see Ng *et al.* 2008: fig. 159): median, cervical, urogastric grooves very pronounced; cervical groove more or less terminating anteriorly in a pit near orbital angle; gastric region particularly well defined; median groove or mesogastric groove well-defined, continuing in very deep epigastric longitudinal groove. Gastric, cardiac and intestinal regions well maked. Fronto-orbital border about half or less than half the greatest width of the carapace. Front relatively narrow, much deflexed downwards, ventrolateral edge projecting, more or less straight, lined with mesial lobe of infraorbital margin, narrow, subtriangular, evenly tapering in distal direction or broad, subrectangular, may be curved (*J. lagostoma*, see Tavares 1989, fig. 10, as *Gecarcinus*). Anterolateral margins well marked, may be serrated or lined by more or less granules or sharp teeth (*J. cocoensis*), especially in females. Subhepatic region with many striae.

Cephalic structures (Fig. 2E)
Antennules very small, folded horizontally. Antenna very short, completely exposed. Orbits typical, outer angle marked. Eyestalks relatively short.

Proepistome (Fig. 2E)
Proepistome small, covered by subfrontal plate, hardly or not visible (*J. weileri*, see N. K. Ng *et al.* 2007: fig. 6G, *as Gecarcinus weileri*; *J. lagostoma*, see Tavares & Mendonça Jr 2022: fig. 47A).

Buccal frame, epistome, mxp3 and pterygostome (Fig. 2E)
Buccal cavity rhomboid, not circumscribed laterally, with its anterior border being the anterior limit of linear anterior margin of epistome. Mxp3 short, leaving between them rather wide rhomboid gap, and (when applied well against buccal cavity) anterior margin of merus not reaching epistome (*J. oceanica*, see Perger 2019), or reaching only the epistome, or advancing either to the level of the antennules or to the frontal margin (*J. lagostoma*, see Türkay 1970: fig. 5c, as *Gecarcinus* (*Johngarthia*) *lagostoma*; Tavares 1989: fig. 9, as *Gecarcinus lagostoma*; Perger *et al.* 2011: fig 5D). Merus obliquely directed, with emargination either on inner lateral margin (*J. lagostoma*, see Türkay 1970: fig. 6C; 1973: fig. 18, as *Gecarcinus* (*Johngarthia*) *lagostoma*; Tavares 1989: fig. 9, as *Gecarcinus lagostoma*; Tavares & Mendonça Jr 2022: fig. 47A) or on obliquely directed anterior margin (*J. weileri*, see Türkay 1973a: fig. 17, as *Gecarcinus* (*Johngarthia*) *weileri*; N. K. Ng *et al.* 2007: fig. 7H, as *Gecarcinus weileri*; *J. oceanica*, see Perger 2019: fig. 4C; *J. malpilensis* see Perger *et al.* 2011: figs 5C, 6G-I; *J. cocoensis* Perger *et al.* 2011: fig. 5B; Perger *et al.* 2011: fig. 6D-F; *J. planata*, see Perger *et al.* 2011: fig. 6B, C; Perger 2019: fig. 4A). Meri of both sides more or less joining medially. Palp with first article fused to merus internal surface and with two mobile distal articles either concealed, not visible (*J. lagostoma* and *J. malpilensis*, see Tavares 1989: figs 9, 11d, 13a and 13d, 14d as *Gecarcinus lagostoma*, *G. malpilensis*, respectively) or more or less visible (*J. natalis*, see Tavares 1989: figs 11c, 12c, as *G. natalis*; *J. cocoensis*, see Perger *et al.* 2011: fig. 3; *J. planata* and *J. oceanica*, see Perger 2019: fig. 4A and 4C, respectively). Exopod concealed, as narrow plate either proportionally long, its setae extending beyond ischium-merus joint (*J. lagostoma*, *J. planata*, *J. malpilenis*, see Tavares 1989: fig. 14a-d, as *Gecarcinus lagostoma*, *G. planatus*, *G. malpilenis*, respectively), or short, its setae not extending beyond ischium-merus joint (*J. oceanica*, see Perger 2019); flagellum absent. Pterygostomial areas glabrous, naked.

Chelipeds
Adult male chelipeds usually elongated, not massive, not enlarged, slightly subequal; not gaping; heterochely and heterodonty more usually not marked, or more noticeable in *J. oceanica* (see Perger 2019: 289, figs 1, 2); fingers elongated, their occlusal margins with small, spaced teeth on both sides. Merus with curved internal surface and with marked denticles or teeth on margins; carpus with conspicuous denticles on inner margin. Sexual dimorphism moderate.

Sterno-pleonal cavity and male pleon (Figs 6D; 7D)
Sterno-pleonal cavity long, shallow, completely glabrous; its extremity ending either very close to suture 2/3 and even almost exceeding it, sometimes slightly distant (*J. weileri*, see Türkay 1973a: fig. 16, as *Gecarcinus* (*Johngarthia*) *weileri*); ridge on sternite 4 marked, surrounding telson only when pleon is applied against sternal surface (*J. lagostoma*, see Tavares & Mendonça Jr 2022: fig. 47A). Male pleon rather long, with all somites free plus telson; margins only with sparse setae; somite 6 with convex margins.

Female pleon (Fig. 9B)
See below, *Female pleon and pleopods.*

Thoracic sternum, locking pleonal structures and setal tufts (Figs 6D; 7D)
Thoracic sternum rather wide; sternite 1 as small triangular tooth, not separated by suture from sternite 2, not recessed;

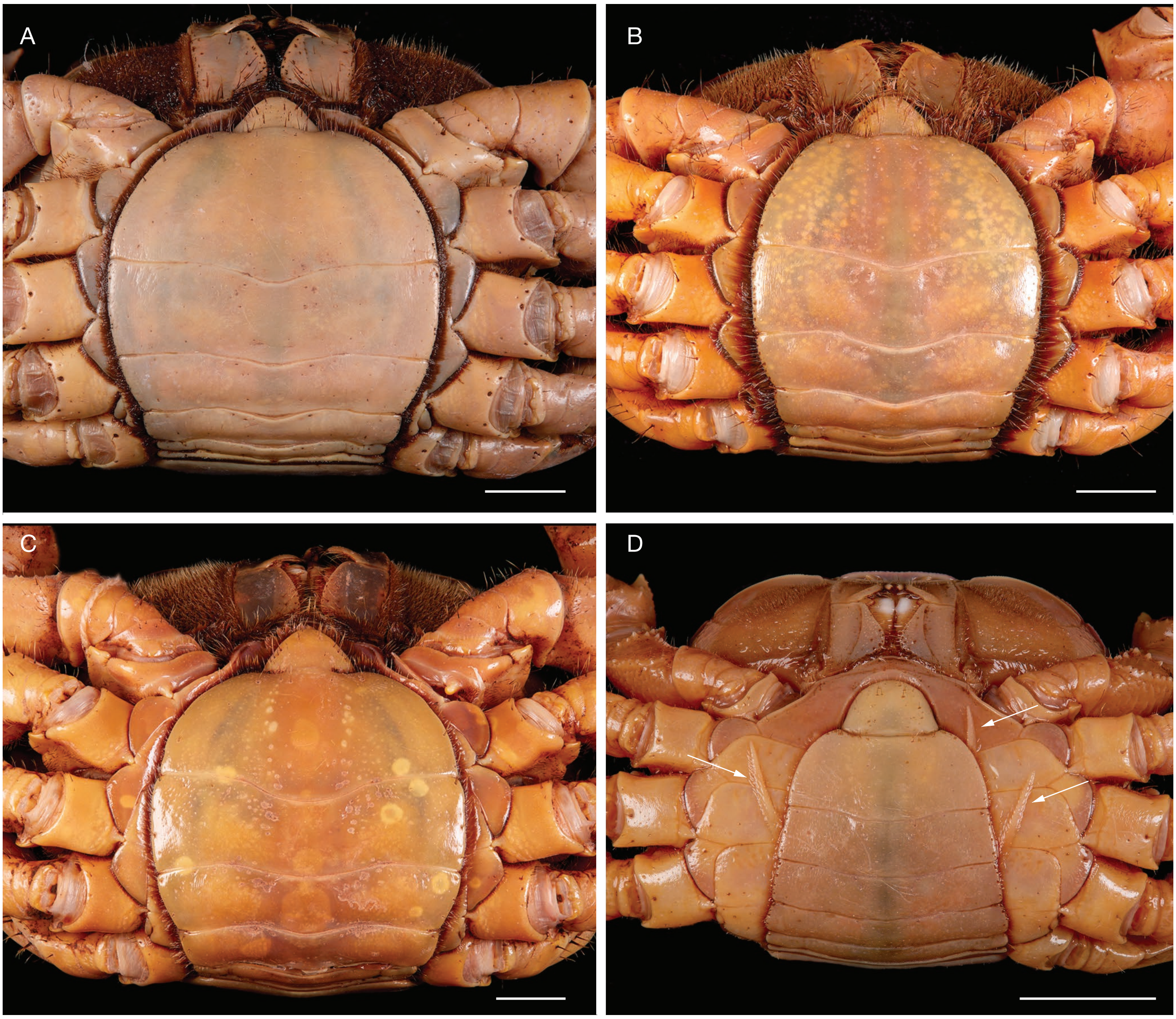

FIG. 8. — Female pleon of Cardisomatidae n. fam.: **A**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♀ 60.0 × 75.6 mm, Guadeloupe, îles des Saintes, MNHN-IU-2024-4621; **B**, *Cardisoma carnifex* (Herbst, 1796), ♀ 56.5 × 66.3 mm, Wallis, MNHN-IU-2013-2201; **C**, *Tuerkayana celeste* (Ng & Davie, 2012), paratype, ♀ 67.3 × 82.0 mm, Christmas Island; Hosnie's Springs, MNHN-IU-2018-5238 (ex ZRC 2012.0015); **D**, *Discoplax longipes* A. Milne Edwards, 1867, ♀ 32.6 × 37 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815), the setose pleopods (see **arrows**) are visible on each side of the pleon. Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

sternite 2 semi-ovate with convex margins; suture 2/3 present, straight or slightly concave; suture 3/4 absent, without lateral traces; sternites 3 + 4 completely fused, with sinuous obliquely directed margins, thus not restricted at level of P1 (*J. malpilensis*, see Türkay 1970, as *Gecarcinus* (*Johngarthia*) *malpilensis*; *J. weileri*, see Türkay 1973a: fig. 16, as *Gecarcinus* (*Johngarthia*) *weileri*); sutures 4/5 to 7/8 interrupted; sutures 4/5 and 6/7 well defined; suture 7/8 rather short; sternites 5 and 6 similarly shaped, sternite 7 narrower and elongated; 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 6/7. Deep median line along sternite 7 and very sligthly extending on basal part of sternite 6.

Locking pleonal structure as rather large prominence about in middle of setose sternite 5 but pleonal sockets not delineated, so locking non-functional (*J. planata*, see Guinot & Bouchard 1998: fig. 25A, B, as *Gecarcinus planatus*).

Setal tufts of more or less dense hydrophilic setae located along second pleonal somite margins and exposed basal part of sternite 7.

Male gonopore and penis (Fig. 7D)

Male gonopore close to P5 coxo-sternal condyle, but penis emerging rather far from P5 coxa, just below thoracic sternal suture 7/8 (*J. oceanica*, see Guinot 1979: fig. 54D, as *Gecarcinus*; *J. planata*, see Guinot & Bouchard 1998: fig. 25A, as *Gecarcinus planatus*; *J. weileri* N. K. Ng *et al.* 2007: fig. 4H, as *Gecarcinus weileri*).

G1 and G2 (Fig. 7D)

G1 short, thick. Mesial process prominently developed, protruding beyond caudal process, endpiece longer than wide, convex, not protruding beyond terminal setae; aperture external, subterminal (*Johngarthia lagostoma*, see Chace & Hobbs 1969: fig. 67d, as *Gecarcinus lagostoma*; Türkay 1970: fig. 5D, as *Gecarcinus* (*Johngarthia*) *lagostoma*; Tavares 1989: figs 17d, 18a, as *Gecarcinus lagostoma*; Tavares & Mendonça Jr 2022: fig. 47G; *J. planata*, see Türkay 1970: fig. 6D as *Gecarcinus* (*Johngarthia*) *planatus*; *J. oceanica*, see Tavares 1989: fig. 18b, as *G. planatus*; *J. malpilensis*, see Tavares 1989: fig. 18c, as *Gecarcinus malpilensis*; *J. cocoensis*, see Perger *et al.* 2011: fig. 4A, B).

G2 tiny, without flagellum.

Vulvae

On sternite 6, more or less close to suture 5/6. Protruding, nearly horizontally directed, occluded by rigid calcified immobile operculum. Sternal cover narrow, all around except on inner margin.

Axial skeleton

Johngarthia lagostoma, see Oliveira 2014: fig. 19C, D.

BIOLOGY

Johngarthia lagostoma (H. Milne Edwards, 1837), which is close to this upper size with a recorded cw of about 100 mm, is endemic to a limited number of oceanic islands in the south Atlantic Ocean. In the central South Atlantic, on Ascension Island, and the Brazilian oceanic islands (Trindade, Martin Vaz, Atol das Rocas, Fernando de Noronha, see Hartnoll *et al.* 2010: fig. 2, upper map) where the species occurs, *Johngarthia lagostoma* is generally restricted to altitudes above 200 m, the only area of the Ascension Island with substantial vegetation. The population comprises several colour morphs: crabs with carapace smaller than 40 mm cw are all dark, and colour variation towards yellow, purple and intermediate morphs appear between 40-50 mm cw. The overall colour distribution of the population is 85% yellow, 5% intermediate, and 10% purple; with the predominance of yellow morphs, possibly an adaptation to reduce heat stress. Males predominate in permanent residential areas located at higher elevations. The intensity of migration varies from year to year and is not obviously related to rainfall. Migrations are dominated by females (on the shore, 80% of crabs are females), and migrants must cross arid and baren lowlands, resulting in significant mortality. A few females mate and lay eggs in upland residential areas; more do so on the migration route, but the majority only after reaching the shore. During the migration season, crabs of both sexes have been found in burrows along the migration routes; these burrows are deserted outside the breeding season. Fecundity averaged 72 000 eggs at 94 mm cw (Hartnoll *et al.* 2010: fig. 2; see also Hartnoll *et al.* 2009). In *Gecarcinus ruricola*, by contrast, a crab of that size would have a calculated fecundity of 199 000 eggs (Hartnoll *et al.* 2007), a disparity that is predominantly accounted for by the larger egg size in *J. lagostoma*.

On Ascension Island, in crabs above about 100 mm cw, around half of the males retained chelae of very similar size and shape, while the other half had strong heterochely in length, and marked differences in chelar morphology; these two morphs occurred in both colour forms, and with either handedness (Hartnoll *et al.* 2017: fig. 1, see also Musick *et al.* 2010).

Johngarthia lagostoma from Trindade Island (Brazil) is well documented. The population is well-established on this island compared to Ascension Island. According to Tavares & Mendonça Jr (2022: figs 46A, 46C, 47A-C), *J. lagostoma* is found from upland habitats up to 600 m altitude. Crabs retreat in their burrows for protection during the heat hours. Many traits, such as the buccal frame entirely covered by the long and broadly operculiform mxp3, with the merus extending anteriorly as far as to cover the antennae and antennules, the reduction of the mxp3 palp and exopod (concealed, and devoid of flagellum), as well as the second and first maxillipeds exopod also devoid of flagellae, limit water loss to a minimum. On Trindade Island, yellow individuals (96.4%) were found predominant, and their chromatic pattern differed from that of other populations (Entringer Jr & Srbek-Araujo 2023). In fact, there are three colour types (black, purple and yellow), with colouration varying according to the individual size, sex and ecological processes related to differential occupation of available habitats (Jão *et al.* 2023). On the same island, *J. lagostoma* recruits inhabit burrows of their congeners that have been abandoned or occupied by adult crabs. Cohabiting recruits reach a maximum size of cw 7.3 mm, after which they are likely to be detected by adults and possibly cannibalised or they leave the burrows naturally (Pinheiro *et al.* 2024).

The male and female reproductive systems of *Johngarthia lagostoma* from Trindade Island (Brazil) described by Mosna *et al.* (2025b: figs 1-6, 8) follow the basic pattern previously described for Thoracotremata. In females, a voluminous seminal receptacle is filled with free spermatozoa; spermatophore plugs and spermatophore packages are absent (Mosna *et al.* 2025a). The average fecundity (mean fecundity 82 938 eggs) recorded for *J. lagostoma* females on Trindade Island closely resembles that of females on Ascension Island (mean fecundity 71 800 eggs) quoted by Hartnoll *et al.* (2010). The male reproductive system (Mosna *et al.* 2025b: fig. 1) exhibits bilateral symmetry with an 'H'-shape. It consists of a pair of testes, located on the upper margin of the cephalothorax and connected to the vasa deferentia, which extend longitudinally over the hepatopancreas, ending at the posterior region of the body. The testis is highly convoluted; the vas deferens is divided into three distinct regions: anterior (a highly convoluted, slender tubular structure), median (long, slightly convoluted), and posterior (appearing as a single slender tube, slightly convoluted and smooth).

On the four Brazilian islands where *Johngarthia lagostoma* is present, mitochondrial DNA sequence analyses of genetic structure and diversity have shown great differentiation indicating that three discrete and significant land crab evolutionary units should be considered, without implying taxonomic changes (Rodríguez-Rey *et al.* 2016). *Johngarthia lagostoma* is

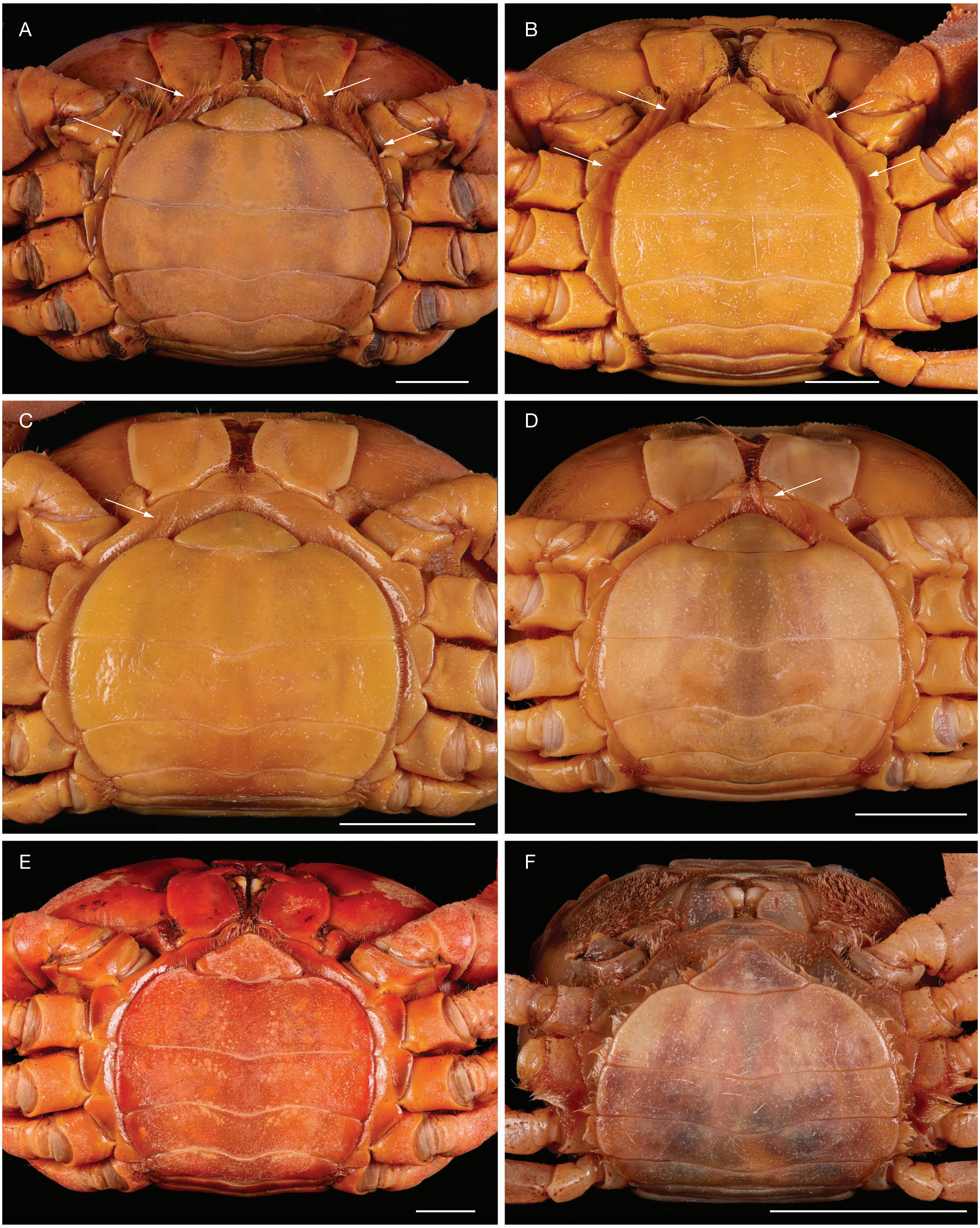

Fig. 9. — Female pleon of Gecarcinidae *restrict*. (**A**-**E**) and of *Grapsodes* Heller, 1865 (**F**): **A**, *Gecarcinus ruricola* (Linnaeus, 1758), ovigerous ♀ 52.8 × 69.9 mm, Cuba, MNHN-IU-2024-6554; **B**, *Johngarthia oceanica* (Perger, 2019), ♀ 54.6 × 69.1 mm, Clipperton, MNHN-IU-2025-8003 (= MNHN-B28823); **C**, *Hartnollius lateralis* (Fréminville *in* Guérin, 1832), ♀ 32.6 × 41.8 mm, Guadeloupe, MNHN-IU-2017-8390 (= MNHN-B24656); **D**, *Hartnollius nobilii* (Perger & Wall, 2014), paratype, ♀ 36.6 × 44.3 mm, Ecuador, St Helena, MNHN-IU-2014-11211 (= MNHN-B12314); **E**, *Gecarcoidea natalis* (Pocock, 1888), ♀ 58.2 × 78.7 mm, Christmas Island, MNHN-IU-2025-8001 (ex ZRC 2012.0177); **F**, *Grapsodes notatus* Heller, 1865, ♀ 18.1 × 21.8 mm, Taiwan, MNHN-IU-2018-5241. In **A**, **B**, the setose pleopods (see **arrows**) are visible on each side of the pleon. Scale bars: 10 mm. Credits: MNHN-Soubzmaigne.

classified as endangered (EN) in Brazilian territory according to IUCN criteria (Mosna *et al.* 2025a).

Johngarthia weileri (Fig. 14C-F) is a terrestrial species from West Africa, largely restricted to the offshore islands of the Gulf of Guinea, but also known from the mainland in Cameroon (Monod 1956; Manning & Holthuis 1981).

Johngarthia malpilensis, considered endemic to Malpelo, an oceanic island of the Colombian Pacific, is distributed all over the main island except in very steep sectors. It shows high mobility, with crabs covering distances over 450 m in a few days on highly irregular surfaces. Omnivorous and opportunistic, it consumes every available resource. On the basis of average density and weight and distribution of crabs, the estimated total biomass of *J. malpilensis* on Malpelo Island is nearly 30 tons. By removing the algal cover and eating, in practice, every type of organism, the Malpelo crab is the major transformer as a recycler of organic matter in the trophic network of the island (López-Victoria & Werding 2008).

The population of *Johngarthia planata* is restricted to inshore islands and the continental mainland coast of the tropical and subtropical Pacific coast of America.

The species *Johngarthia oceanica*, previously confused with *J. planata*, has recently been described for the extensive populations found on the oceanic islands of Clipperton and Socorro (Perger 2019). Studied during the French multidisciplinary scientific CLIPPERTON expedition, from December 2004 to April 2005 (Bouchard & Poupin 2009, as *Gecarcinus planatus*), the population was estimated at 1.25 million individuals, a decrease from 1968 when a previous census had indicated 11 million individuals, a decrease attributed to a reduction of the herbaceous covering on the atoll and perhaps to predation by rats accidentally introduced at the end of the 1990s. Crabs dig many burrows on sandy expanses by the sea. The distribution of the crabs on the atoll is heterogeneous: they are mostly located near the lagoon or in bunches of coconut trees; they make short-range displacements of about 30 m around their burrows, mostly for food that consists of seaweed, vegetation and also carrion. For water intake they rely mostly on food, and specialised hydrophilic setae to extract water from the most humid parts of their burrows. The sex ratio is slightly biased in favor of males, with about eight females for 10 males. Crabs frequently visit the brackish water of the lagoon, also walk along the foam fringe of the strandline and enter the sea water for the pelagic life (Niaussat & Ehrhardt 1968: figs 4-9, as *Gecarcinus planatus*; Ehrhardt 1968a, b; 1973: fig. 2, as *Gecarcinus planatus*).

REMARKS

According to Perger *et al.* (2011: fig. 7), the possible relationship between *Gecarcoidea lalandii* and *Johngarthia cocoensis* is supported by the possibility of long-distance dispersal of larvae from a common ancestor, between the western Pacific and the tropical eastern Pacific region. However, *Gecarcoidea* differs from *Johngarthia* in that the male first gonopod endpiece is significantly wider than long (*G. lalandii*, see Türkay 1974a: fig. 5a, b) and by differences in orbital structures (*G. lalandii*, see Tavares 1989: figs 7, 8).

COMPARISONS BETWEEN CARDISOMATIDAE N. FAM. AND GECARCINIDAE *RESTRICT.*

The Cardisomatidae n. fam. (with its three genera: *Cardisoma*, *Discoplax* and *Tuerkayana*) and Gecarcinidae *restrict.* (with its four genera: *Gecarcinus*, *Gecarcoidea*, *Hartnollius* and *Johngarthia*) are distinguished by a number of morphological characters (Table 1). The most important is the location of the male gonopore. The plesiomorphic condition is presented by the Cardisomatidae n. fam., in which the gonopore is very close to the P5 coxo-sternal condyle and the membrane lining the arthrodial cavity; the penis emerges at a short distance (*Cardisoma*, *Tuerkayana*) or at a greater distance (*Discoplax*) from the P5 coxa and thoracic sternal suture 7/8 (Figs 5C; 7A, B) (*Discoplax longipes*, *Cardisoma guanhumi*, *Tuerkayana* aff. *hirtipes*, *T. celeste* and *T. magnum*, see Guinot *et al.* 2018: fig. 5C, 5F, 5I, 5L, 5O, respectively). The derived condition is presented by the Gecarcinidae *restrict.*, in which the penis emerges far from the P5 coxo-sternal condyle, just below the thoracic sternal suture 7/8 (Figs 5D; 7C, D) (*Gecarcinus ruricola*, see Guinot *et al.* 2025: fig 4K, L; *Johngarthia planata*, see Guinot 1979: fig. 54D, as *G.* (*Johngarthia*) *planatus*; Guinot & Bouchard 1998: fig. 25A, as *G. planatus*; *J. weileri*, see N. K. Ng *et al.* 2007: fig. 4H, as *G. weileri*).

With regard to the emergence of the penis at a relatively short distance from the P5 coxa and relatively far from the thoracic sternal suture 7/8, the condition in Cardisomatidae n. fam. resembles that observed in Grapsidae (at least Grapsinae MacLeay, 1838), which may explain why Gecarcinidae *sensu lato* and Grapsidae are currently grouped together in Grapsoidea by all authors. However, among other dissimilarities, *Grapsus* Lamarck, 1801 differs from *Cardisoma*, *Discoplax* and *Tuerkayana* (Cardisomatidae n. fam.) in that the penis is not basally wedged above the P5 coxo-sternal condyle (*G. tenuicrustatus* (Herbst, 1783), see Guinot 1979: fig. 52A; Karasawa & Kato 2001: fig. 2.19; N. K. Ng *et al.* 2007: fig. 4D; *Grapsus grapsus* (Linnaeus, 1758), see Guinot *et al.* 2013: fig. 23D).

In Cardisomatidae n. fam., locking pleonal structures are obscure, even absent, while they are present in Gecarcinidae *restrict.* as more or less developed sternal prominence or crest, or as a button. But, since the complementary pleonal sockets are not delimitated on somite 6, there is not a functional locking apparatus in the most terrestrial land crabs, *Gecarcinus ruricola.*

Gecarcinid genera are uniform in selected characters (see Table 1), notably: a fronto-orbital border representing half or less than half of the width of the carapace; a front narrow and markedly deflexed; an epistome inserted below the lower margin of the front, and therefore more or less discernible; orbits small and deep; eyestalks short; sterno-pleonal cavity shallow, with ridge on sternite 4 marked, surrounding telson only; G1 short and thick.

An important distinguishing character between the two families is the female pleon. In most Cardisomatidae n. fam. (Fig. 8A-C), it is narrow, bordered by a dense fringe of setae, and covers practically the entire width and length of the thoracic sternum; *Discoplax* (Fig. 8D) is an exception (see

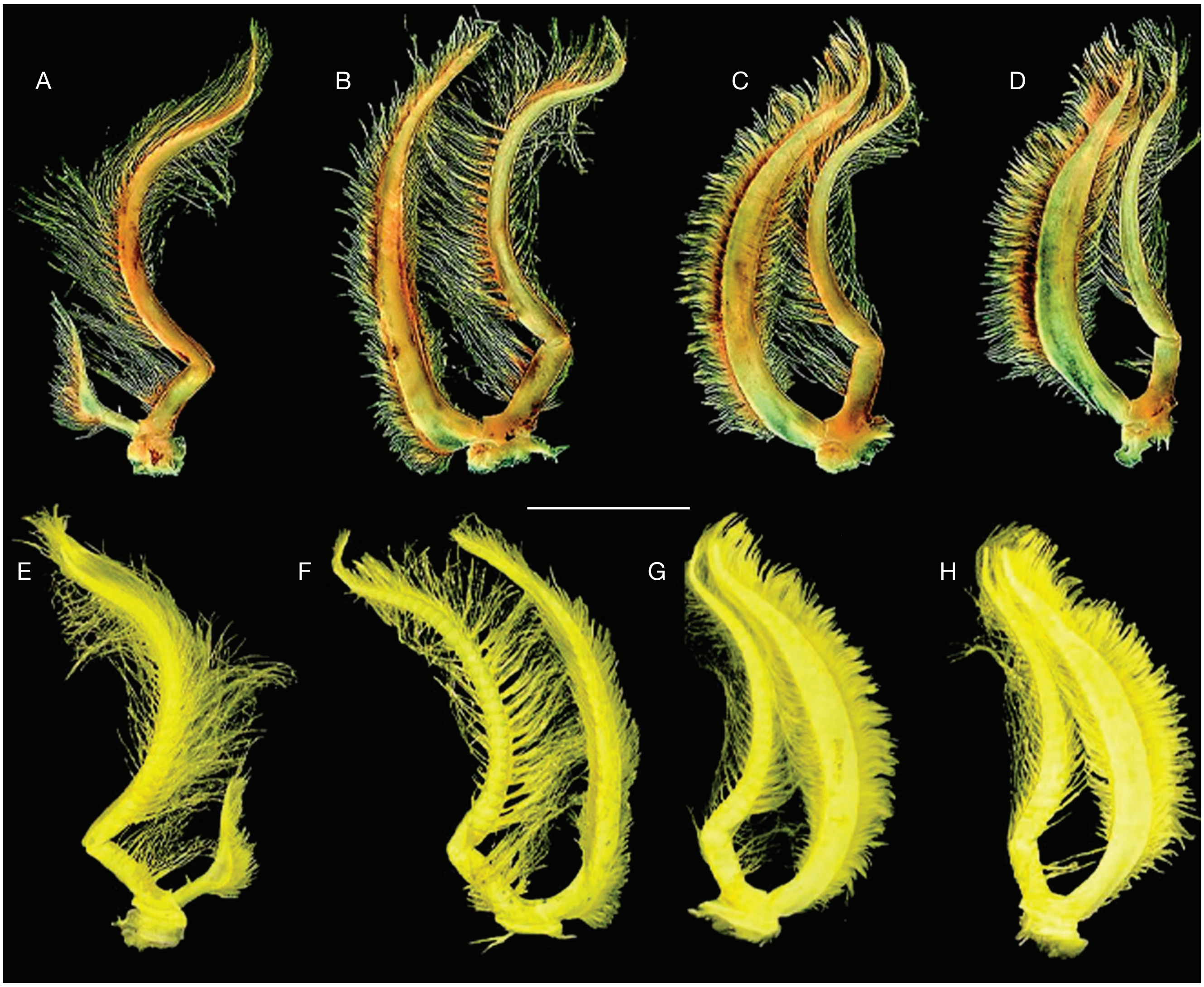

Fig. 10. — Female pleopods of mature *Cardisoma armatum* (Herklots, 1851), ♀ cw 60.4 mm, Liberia (NMU 2008a). Anterior view: **A**, PL 2; **B**, PL 3; **C**, PL 4; **D**, PL 5. Posterior view: **E**, PL 2; **F**, PL 3; **G**, PL 4; **H**, PL 5. Scale bar: 10 mm. (After Cumberlidge *et al.* 2021: fig. 13).

The case of the genus Discoplax *A. Milne Edwards,1867*). In Gecarcinidae *restrict.* (Fig. 9A-E), the female pleon is wider and discoid, bears only a few scattered setae on its margins, and leaves part of the thoracic sternum exposed laterally and especially anteriorly.

Members of Cardisomatidae n. fam. are less modified from the typical brachyuran facies than members of Gecarcinidae *restrict.*, with a plesiomorphy more particularly concerning the buccal region. Cardisomatidae n. fam. has a delimited buccal frame, a developed anterior border of the epistome, a mxp3 with a normal exposed palp and an exposed exopod with a flagellum (Figs 2A-C; 3A; 4A), Conversely, Gecarcinidae *restrict.* has several synapomorphies, namely a short, subcircular or rhomboidal, poorly delimited buccal frame, a linear anterior border of the epistome, a mxp3 palp with the first article fused to the merus internal surface, an exopod conspicuously reduced to a narrow and completely concealed plate, and the loss of its flagellum (Figs 2D-F; 3B, C; 4B). In fact, these disparities in the buccal parts are linked to a different water requirement of Gecarcinidae *restrict.* than in Cardisomatidae n. fam., namely proximity to the sea; deep burrows reaching water level.

The four genera of Gecarcinidae *restrict.*, which constitute the most terrestrial group, with *Gecarcinus ruricola* being the most land-adapted (Hartnoll 1988a, 1988b; Wolcott 1988: fig. 3.1; Richardson & Araujo 2015: fig. 12.2), exhibit several adaptations to reduce water loss: e.g. the buccal frame almost entirely covered by the mxp3 leaving a narrow rhomboid gap (*G. ruricola*, see Guinot *et al.* 2025: figs 2C, D, 6), the reduction of the mxp3 palp and exopod in all genera (Fig. 2B) (and the absence of a flagellum in the exopod of mxp1 and mxp2 in *Johngarthia lagostoma*, see Tavares & Mendonça Jr 2022: fig. 47A-E). This applies not only to adults but also to the post-larval stage, the megalopa that is the landward migration stage of *Gecarcinus ruricola* (Hartnoll *et al.* 2014) and *Johngarthia lagostoma* (Santana *et al.* 2025). The megalopa of *G. ruricola* occupies the most terrestrial habitat, furthest from the sea; thanks to its long locomotion on land, it is the best-adapted terrestrial megalopa described to date. In *Gecarcoidea*, the first crab represents the returning homing stage (Hartnoll & Clark 2006). Other biological aspects show the same divergent trend, with, for example, a longer breeding season in *Cardisoma* species than in other gecarcinoids (Liu & Jeng 2007). In *Gecarcinus ruricola*, migrating crabs are predominantly female, with a predominance of ovigerous females: some females mate and lay eggs on the landward side, others on the seaward side (Hartnoll *et al.* 2007). *Tuerkayana celeste* migrates upstream as a megalopa and only emerges on land as the first crab. In *Gecarcoidea natalis*, males and females migrate to the sea in similar numbers; the courtship and subsequent mating only take place afterwards (Hicks 1985; Hartnoll *et al.* 2010). In *Johngarthia lagostoma*, mating and egg-laying occur at all phases of migration, and the proportion of males migrating towards the sea decreases with distance. In terms of the overall pattern of breeding migrations, *Discoplax longipes*, a cave-dwelling species, represents the opposite end of the spectrum: eggs are laid and incubated in caves where the adults live, and females carrying ripe eggs migrate directly to the sea; no males migrate (see Ng & Guinot 2001).

The phylogenetic tree of Toledano-Carrasco (2019) and in Guinot *et al.* (2025: 298, tables 2, 3, fig. 16) recovered the two major groups of gecarcinoids proposed here, based on the consistency of morphological, larval and genetic data. On the one hand, the clade of crabs with less terrestrial habits (*Cardisoma*, *Discopla*x, and *Tuerkayana*), namely the Cardisomatidae n. fam.; and on the other hand, the clade with distinctly terrestrial habits (*Gecarcinus*, *Johngarthia* and *Hartnollius*), namely the Gecarcinidae *restrict. Gecarcinus* was identified as the probable sister taxon to *Hartnollius* while, within the Cardisomatidae n. fam., *Discopla*x and *Tuerkayana* formed sister groups, collectively maintaining a close evolutionary relationship with *Cardisoma*.

Larval data

The complete larval stage from the first zoeal stage to the megalopa, obtained under laboratory conditions, has been described for three species of *Cardisoma*: *C. guanhumi* by Costlow & Bookhout (1968), *C. carnifex* by Kannupandi *et al.* (1980) (Flores *et al.* 2003 for the first zoeal stages), *C. armatum* by Cuesta & Anger (2005); and for *Tuerkayana hirtipes* by Shokita & Shikatani (1990, as *Cardisoma hirtipes*). For *C. crassum* only the first zoeal stage is known (Vázquez-Lópes *et al.* 2017). Among the Gecarcinidae *restrict.*, larval development is known in *Hartnollius lateralis* (Cabrera 1966, as *Gecarcinus lateralis*; Willems 1982, as *Gecarcinus lateralis lateralis*; Cuesta *et al.* 2007, as *Gecarcinus lateralis*); in *Johngarthia oceanica* (Ehrhardt & Niaussat 1968, as *G. planatus*), and in *J. lagostoma* (Lira *et al.* 2021). It was studied in *Gecarcoidea lalandii* by Cuesta *et al.* (2002) who reviewed the zoeal morphology of the Gecarcinidae *sensu lato*, taking into account all previous descriptions and analysing the relationships. The megalopa of *Gecarcinus ruricola* was described by Hartnoll & Clark (2006). Rice (1980), based solely on the five zoeal stages of *C. guanhumi*, was of the opinion that its characters taken together suggested an evolutionary level for the Gecarcinidae *sensu lato* similar to that of the more basal Grapsidae and Ocypodidae.

Based on the complete larval stages of *Hartnollius lateralis*, Willems (1982, as *Gecarcinus lateralis*) recognised the heterogeneity of the Gecarcinidae *sensu lato*. According to Cuesta *et al.* (2002), the zoeal morphology of the same species, namely the setation of the maxillar endopodite, supports the recognition of two major groups: on the one hand, *Epigrapsus*, *Gecarcinus* and *Gecarcoidea* (our Gecarcinidae *restrict.*, without *Epigrapsus*), and on the other hand *Cardisoma* and *Discoplax* (our Cardisomatidae n. fam.). In a re-evaluation of the gecarcinid larval features, Cuesta *et al.* (2007: tables 5, 6) again distinguished the same two groups: a first group comprising *Cardisoma* and *Discoplax*, characterised by 2, 3 setae on the endopod of the maxilla in zoeae, and in megalopae by the presence of ischial spines on the cheliped (except in *Discoplax*), the absence of setae on the proximal segment of the uropods, and a two-segmented exopod on the mxp3; and a second group comprising *Epigrapsus*, *Gecarcinus*, *Gecarcoidea*, and *Johngarthia*, characterised by setae on the endopod of the maxilla in zoeae, and in the megalopa by the absence of ischial spines on the cheliped, the presence of two setae on the proximal segment of the uropods, and a reduced and unsegmented mxp3 exopod (no data about megalopae of *Epigrapsus* and *Gecarcoidea*). According to Cuesta & Anger (2005) and Cuesta *et al.* (2007: tables 5, 6), zoeal features again support the existence of two major groups. Thanks to the description of the megalopa of *Gecarcinus ruricola*, Hartnoll & Clark (2006: table 2) confirmed the existence of the same two groups: one comprising the *Cardisoma* species and the other with *Gecarcinus*, to which *Johngarthia* was added. According to Lira *et al.* (2021: table 2), *Cardisoma* and *Tuerkayana* differ from *Gecarcinus*, *Gecarcoidea* and *Johngarthia* in their zoeal characters. In conclusion, the larval data corroborate our separation of the Gecarcinoidea n. stat. into two families.

Genetic data

Schubart *et al.* (2000a: fig. 1; 2000b: fig. 1; 2002), who presented the first molecular phylogeny of Grapsoidea based on North American species, recovered a mitochondrial 16S rRNA gene tree with the Gecarcinidae *sensu lato* closely related to the subfamilies Grapsinae, Plagusiinae, Sesarminae, and Varuninae, and 'gave evidence' for a close relationship between grapsid and gecarcinid crabs, even suggesting that Gecarcinidae *sensu lato* evolved within Grapsidae; the monophyly of Gecarcinidae *sensu lato* was not questioned. Subsequent genetic studies by Schubart *et al.* (2006: fig. 1) resolved *Cardisoma* as basal, followed by *Gecarcoidea-Gecarcinus*, but did not support the monophyly of the family, suggesting a paraphyletic taxon. N. K. Ng *et al.* (2007: fig. 8), noting that the orbital structure and the gonopore position were extremely variable, recovered two groups: *Cardisoma* (*C. carnifex*, *C. crassum*) + *Discoplax* (including *D. hirtipes* and *D. rotundum*, now in *Tuerkayana*), and *Gecarcinus* + *Gecarcoidea*. According to Schubart & Cuesta (2010), the phylogenetic status of the Gecarcinidae *sensu lato* as well as the basal relationships among the families of Thoracotremata remain unresolved. However, a combined molecular and larval analysis by Cuesta *et al.* (2002) showed that the status of Gecarcinidae *sensu lato* remained apparently paraphyletic and still unresolved, with *Cardisoma* and *Discoplax* forming a sister group to *Gecarcinus* and *Gecarcoidea*. L. M. Tsang *et al.* (2014: fig. 1; 2018: fig. 2) recognised a *Gecarcoidea* clade (*G. natalis* + *G. lalandii*) and a sister *Tuerkayana* (as *Discoplax) – Cardisoma* clade. Using molecular data from three markers (mitochondrial 12S and 16S rRNAs, and nuclear histone H3), covering a total of 15 thoracotreme families, L. M. Tsang *et al.* (2022: fig. 1) assigned the Gecarcinidae *sensu lato* to the Grapsoidea, confirmed the polyphyly of Grapsoidea, Ocypodoidea Rafinesque, 1815 and Pinnotheroidea (as L. M. Tsang *et al.* 2018: fig. 2), and recognised two gecarcinid clades in the Grapsoidea: a *Gecarcoidea* clade (*G. lalandii* and *G. natalis*) and a *Cardisoma* and *Tuerkayana* (as *Discoplax*) clade. According to Q. Wang *et al.* (2021: fig. 3), *Cardisoma* and *Gecarcoidea* clustered separately, and Gecarcinidae *sensu lato* formed a sister group with Xenograpsidae N. K. Ng, Davie, Schubart & Ng, 2007, Ocypodidae, Dotillidae Stimpson, 1858 and Sesarmidae. The 16S gene trees of Van der Meij & Schubart (2014) recovered two groups: *Cardisoma carnifex* + *Discoplax hirtipes* and *Gecarcinus lateralis* + *Gecarcoidea lalandii*, not clustering together. According to Sun *et al.* (2022), *Epigrapsus* + *Gecarcinus* + *Gecarcoidea* and *Cardisoma* + *Discoplax* + *Tuerkayana* were not recovered clustering together. However, they were recovered by C. T. T. Tsang *et al.* (2022) in a monophyletic Gecarcinidae *sensu lato*, with their deep divergence being able to justify a subfamily status for each (corresponding to what is proposed here, at the familial level). According to these authors, Gecarcinidae and Sesarmidae, two families containing many terrestrial brachyuran species, originated along with the warm climates during the Late Paleocene and Early Eocene (*c.* 60-50 MYA). The ‘Clade V’ (‘New Superfamily 1, unnamed) of C. T. T. Tsang *et al.* (2022: supplementary fig. 1), consists mainly of families with a high degree of terrestrial adaptation, i.e., the Gecarcinidae *sensu lato*, Leptograpsodidae, and Sesarmidae, to which are added two less speciose marine families (Plagusiidae Dana, 1851 and Xenograpsidae) and one freshwater family (Glyptograpsidae Schubart, Cuesta & Felder, 2002). The results of Pan *et al.* (2024) did not support the Clade V of Tsang *et al.* (2022) (Gecarcinidae + Leptograpsodidae + Sesarmidae + Xenograpsidae + Glyptograpsidae), and, instead, they showed that the Plagusiidae + Gecarcinidae and Grapsidae formed a lineage with strong nodal support, while Sesarmidae and Xenograpsidae were more closely related to Varunidae, with moderate nodal support. The morphological characters shared by most members of these families generally include: gaping third maxillipeds, stout male first gonopods with apertures surrounded by stiff setae, and the ability to breathe air in various ways.

Sun *et al.* (2022: figs 1, 3, 5), in a mitogenomic tree, presented all recent hypotheses on relationships within the families and superfamilies of Thoracotremata. The monophyly of Gecarcinidae *sensu lato* was confirmed in the tree obtained by Maximum Likelihood analysis, but with a low support value. However, in the tree derived from Bayesian inference analyses, *Gecarcoidea lalandii* did not cluster with its relatives such as *Cardisoma carnifex* (Herbst, 1796) and was more closely related to the Sesarmidae. Note that genetic results of Kobayashi *et al.* (2023) were similar, with *G. lalandii* not clustering with other gecarcinid species but rather with monophyletic Sesarmidae. These results are not confirmed by morphological characters. Q. Wang *et al.* (2021: 725: fig. 3), who used four genes, tRNAs, rRNAs, PCGs, and control regions (CR) for the Gecarnidae, found that *Cardisoma* (with *C. carnifex* and *C. armatum*) and *Gecarcoidea* (with *G. lalandii* and *G. natalis*) clustered separately, which corresponds to Cardisomatidae n. fam. and Gecarcinidae *restrict.*

The very thorough analysis by Z. Wang *et al.* (2023: fig. 3), who sequenced the complete mitochondrial genomes of four gecarcinoid species and compared them with the existing dataset of 202 mitochondrial genomes of crabs, obtained results that were consistent with the data acquired by our morphological studies. It supported the division of genera established by Guinot *et al.* (2018), namely the two closely related genera *Cardisoma*, and *Tuerkayana*, plus *Discoplax*, with each branch being monophyletic, and highlighted the monophyly of Gecarcinidae *sensu lato*. Their tree showed the close relationship of the three genera that constitute the Cardisomatidae n. fam. The ‘target’ species in the paper of Z. Wang *et al.* (2023: 1) was *Tuerkayana*, i.e., the results in Guinot *et al.* (2018) based on the morphology alone: that is why we particularly appreciate the recognition of the value of taxonomy based on morphological data as evidenced by their sentence on p. 12 “This consequence is consistent with the results of morphological studies, which support *Tuerkayana* as an independent genus”. We agree with the conclusions of Z. Wang *et al.* (2023: 14), who ‘tentatively support the monophyly of Gecarcinoidea’, that, morphologically, species of Gecarcinoidea can be distinguished from other Grapsoidea by the unique characteristics of their zoea larvae (antennal and telson morphology, and setation of the second maxilliped endopod, see Cuesta *et al.* 2002; Ng *et al.* 2008) and that the geographical distribution and unique behaviour of Gecarcinidae and Sesarmidae are not comparable. However, the presence of polyphyly in the N-tree raised the possibility of homology and a close relationship between Gecarcinidae and Sesarmidae. The mitochondrial genome structure of the Gecarcinidae *sensu lato* was found structurally stable, probably on account of common origin or derived from adaptations to a similar terrestrial environment; the figure S10 of Z. Wang *et al.* (2023) showed that all the species in the Gecarcinidae *sensu lato* have the same gene order pattern as the ancestors of Brachyura.

Given the contradictory results of genetic data and often considerable phylogenetic inconsistencies between morphological and phylogenomic data concerning the deep evolution of animals, it should be emphasised that, in the case of Gecarcinidae *sensu lato*, the results obtained from morphology, both larval (several articles by Cuesta *et al.*) and adult (Guinot *et al.*

2018), have prevailed over the latter and have only recently been confirmed by molecular studies. This finding contrasts with the classical view in phylogenomics that genome-scale datasets tend to undermine the credibility of morphological inferences; it effectively challenges the frequent underestimation of traditional taxonomy and the common assumption that genomic data automatically supersede morphological evidence. It should be noted that the numerous and diverse studies on Gecarcinoidea n. stat. and their relatives have provided evidence for a strongly recovered and monophyletic Thoracotremata (L. M. Tsang *et al.* 2008; Chu *et al.* 2015; Chen *et al.* 2018; T. T. Tsang *et al.* 2022; Sun *et al.* 2022; Xu *et al.* 2023; Pan *et al.* 2024).

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. Members of Gecarcinoidea n. stat. are very rare in the fossil record and consist only of remains of the chelae and almost fingers. 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 *H. 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) reported *G. ruricola* from the Holocene in the Caribbean Sea and Mexico. Remains of chelipeds of Pleistocene *Cardisoma guanhumi* were recorded by Schweitzer *et al.* (2008). Luque *et al.* (2018) found remains of chelipeds of *Cardisoma* aff. *crassum* from the Pacific coast of Panama. Fossilised burrows of *Cardisoma guanhumi* have been recorded on Aldabra by Sparacio (2018). Türkay (1978) interpreted fixed fingers from the Pliocene of Costa Rica as potential *Cardisoma guanhumi*. According to the 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).

Johngarthia *versus* Gecarcinus

Several species initially assigned to *Gecarcinus* were separated by Türkay (1970), who created the subgenus *Johngarthia* for them, subsequently elevated to genus rank (Türkay 1987). Tavares (1989, 1991) found no synapomorphies to support the monophyly of *Johngarthia*. Colavite *et al.* (2021), who studied 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 of the first zoea could be an autapomorphy of the species, but ultimately found that this character was actually more widespread within *Johngarthia*. Colavite *et al.* (2021) concluded that no characters of the first zoeal stage could be set forth as diagnostic for this genus to date and again questioned the validity of *Johngarthia* in relation to *Gecarcinus*. Nevertheless, the genus is used by Tavares & Mendonça Jr (2022).

In the phylogenetic tree of Toledano-Carrasco *et al.* (2021) and Guinot *et al.* (2025: tables 2, 3, fig. 16), which indicated a high divergence between *Gecarcinus* and *Hartnollius* (with values comparable to the divergence between species of different genera, such as those of *Discoplax longipes* with *Tuerkayana latens*), the genetic distance between *Gecarcinus* and *Johngarthia* was lower than that between *Gecarcinus* and *Hartnollius.* Morphologically, species of *Johngarthia* also show similarities with *Gecarcinus*, such as the locking pleonal structures in the form of a setose and more or less marked prominence (*Gecarcinus ruricola*, see Guinot *et al.* 2025: fig. 2E; *G. quadratus*, see Köhnk *et al.* 2017: fig. 19c, d; *Johngarthia*, see Guinot & Bouchard 1998: fig. 25A, as *G. planatus*). *Gecarcinus ruricola*, in particular, bears a striking resemblance to *J. lagostoma* in terms of its globular carapace, eyes englobed within the carapace, a recessed antenna, and a mxp3 with a long, obliquely directed merus that reaches almost to the front (*G. ruricola*, see Guinot *et al.* 2025: figs 2d, 6; *J. lagostoma*, see Türkay 1970: fig. 5b, c; Tavares & Mendonça Jr 2022: fig. 47A).

However, there are many distinctive characters between *Johngarthia* and *Gecarcinus*: in the former, the mxp3 merus has a slit-shaped fissure approximately on the inner margin (*J. weileri*, see Fig.2E; *J. lagostoma*, see Tavares 1989: fig. 9, as *Gearcinus lagostoma*; Tavares & Mendonça Jr 2022: fig. 47A-C); the exopod is reduced to a plate fused to the internal face of the ischium, with setae extending beyond the ischium-merus articulation, in *J. weileri* as in *J. lagostoma* (see Tavares & Mendonça Jr 2022: fig. 47B, C); and the G1 is thick, short, and its tip lacks projecting distal setae (*J. lagostoma*, see Tavares 1989: fig. 17d, as *Gecarcinus lagostoma*; Tavares & Mendonça Jr 2022: fig. 47G).

Johngarthia differs from *Gecarcinus* in the adult features already mentioned (Türkay 1970; Perger *et al.* 2011), but also in its larval characters. Cuesta *et al.* (2007) showed that the difference in the mxp3 exopod seen in adults of *Gecarcinus* and *Johngarthia* is also observable in megalopa.

The case of the genus Discoplax *A. Milne Edwards, 1867*

A. Milne Edwards (1867; 1873) considered *Discoplax* to be 'among the grapses', but the genus was very quickly assigned to the Gecarcinidae *sensu lato*. Many authors (Ortmann 1894; Alcock 1900; see also Balss 1934; Türkay 1974b) have regarded *Discoplax* as a junior synonym of *Cardisoma*, and the type species was therefore named *Cardisoma longipes*. But Guinot (1988, 1994) considered *Discoplax* a distinct genus, a position adopted by Türkay (1987), Ng (1998) and Ng *et al.* (2001), as well as by subsequent authors. The inclusion of *Discoplax*, with its three cave-dwelling species, among the land crabs of the family Gecarcinidae *sensu lato* has apparently never been questioned.

Our morphological examination of the three species of *Discoplax*, *D. longipes* (Figs 1B; 2A; 6A; 7A; 8D), *D. gracilipes* and *D. michalis*, clearly highlights the numerous characters that diverge significantly from those of the Gecarcinoidea n. stat. and the Cardisomatidae n. fam. The main differences are the location of the penis (emerging a short distance from the P5 coxa), the slightly sexually dimorphic chelipeds, the morphology of the male and female pleons and their slight sexual dimorphism (Figs 6A; 8D: male and female pleons of *D. longipes*, respectively), the vulvae, the flat carapace with numerous striae, the presence of a stridulatory apparatus (see Table 1 and *Diagnosis of Cardisomatidae n. fam.*). Are these differences related to the cave-dwelling habits of all the species in the genus? Apparently not, since adaptations to cave life usually include long legs (only *D. gracilipes* has very long legs), reduced eyes, light body, and depigmentation, all features absent in *Discoplax*. In *Discoplax longipes*, eggs are laid and incubated in the caves where the adults live, and females carrying ripe eggs migrate directly to the sea; the species does not appear to carry out organised spawning migrations (Türkay 1987).

The type species *Discoplax longipes* is known only from the Loyalty islands, an isolated archipelago of three main islands (Ouvéa, Lifou and Maré) located northeast of the New Caledonian mainland of Grande Terre. The islands are essentially old coral atolls, whose current topography is the result of sea-level fluctuations and erosion. This has led to a karst landscape dotted with numerous caves. Today, many of these caves are flooded and exhibit a wide diversity of sizes, shapes and depths, ranging from a few metres deep to several kilometres in length. The waters in these caves are invariably fresh, although they may be brackish in deeper parts due to seawater percolation through the porous rocks. In Xodre Cave on Lifou Island, where several specimens have been collected by hand, the underground lake is located 400 m from the entrance. The crabs were collected deep in caves, which are sometimes several hundred metres from the sea, therefore completely isolated and without any real communication with the sea (B. Séret, pers. comm.). Despite its normal habitus is *D. longipes* a troglobite?

It should also be noted that there are reasonable doubts regarding the conspecific status of some specimens with *D. longipes* from the Loyalty Islands: for example, of Türkay (1974a, as *Cardisoma longipes*) from many islands in the western Pacific (e.g. Fiji and the Cook Islands), of Yaldwyn (1970, as *Cardisoma longipes*) from Niue, of Sendler (1923) and Poupin & Juncker (2010) from French Polynesia. Even though a Niue specimen clustered with the Loyalty Island material during a molecular analysis performed by Ng & Shih (2015: fig. 17).

The ecology of *D. michalis* in Guam was described in detail by Ng & Guinot (2001: fig. 8A, as *D. longipes*): it is frequently observed in the water, sometimes as deep as two metres; it also shelters in deep crevices and cracks; there is no indication that it digs permanent burrows, and none have been observed. According to Gustav Paulay, who collected a good series of specimens of *D. michalis* (as *D. longipes*) in Guam and Niue, in the central Pacifc, the species is not a true cave crab, but rather a species closely associated with karst environments, using caves whenever possible. In Niue, it is also found in deep crevices outside caves during the day, with locals catching it at night or on full moon nights for food. On this same island, ovigerous female of *D. michalis* reach the sea by using the karst formations, which corresponds to the migration of the females for the reproduction and the release of the eggs into the sea. In Guam, ovigerous specimens have been observed climbing down the karst cliff face from just outside Tumon Bay, and a male specimen was even collected near the University of Guam Marine Biology Laboratory, in areas where no caves are known to exist nearby. Presumably, *D. michalis* is also present in the deep crevices and uneven terrain of the karst forest, emerging out to forage only at night. In summary of all these informations, *D. michalis* may well be a troglophile.

The third species of *Discoplax*, *D. gracilipes*, has been found only in the Philippines, on and around Panglao Island. Located about a kilometre southwest of the island of Bohol, this large and predominantly limestone island has numerous anchialine sinkholes and caves. Specimens of *D. gracilipes* have generally been collected from anchialine pools in water at a depth of one metre, either by hand or using baited traps (Ng & Guinot 2001). Virata Cave, in the southermost part of Panglao, is only about 100 m from the sea, with its entrance opening onto degraded secondary forest. Water is present at the bottom of the deep cave only during the wet season. According the local villagers, *D. gracilipes* hides in the caves during the day but forages near the entrance and nearby forest at night. The gecarcinid *Gecarcoidea lalandii* has also been observed in the cave, but it is also relatively common outside. *D. gracilipes* is regularly caught by the locals for food, especially during the wet season when fishing in the open sea is impossible. These crabs are also more easier to catch when they wander further from the caves in search of food. (Ng & Guinot 2001). It is worth noting that, just outside the cave, *Tuerkayana hirtipes* and *T. rotundum* are also present, even deep inside the caves, according to the locals. These are stygophilic species.

A crucial question arises: are crabs of the genus *Discoplax* that live in caves with specific temperatures and humidity levels truly land crabs, like other species Gecarcinoidea n. stat.? The latter are terrestrial, live on land in regions with high ambient temperatures, and their major challenge is avoiding desiccation (note that some cardisomatids are stygophilic, see above). In the book *Biology of the Land Crabs* (Burggren & McMahon 1988), *Discoplax* is only mentioned as *Cardisoma longipes* in a list and on a map (Hartnoll 1988a: 21, fig. 2.5). The *Discoplax* species do not fit into any of the five grades (T1 to T5) of terrestrial adaptations categorised by Hartnoll (1988a) and, to our knowledge, are not known to possess any of the multiple adaptations that would allow increasing levels of autonomy from the aquatic environment.

It is clear that the karstic and anchialine species of *Discoplax*, which spend part of their time (or even perhaps permanently) in water and part of their time out of water, and which even venture far from caves, are not true terrestrial crabs. Phylogenetically, *Discoplax* belongs to the Gecarcinoidea n. stat. Genetic data (e.g. Ng & Shih 2015; L. M. Tsang *et al.* 2014) do not contradict the relationships between *Discoplax* and Gecarcinidae *sensu lato* and even recognise a *Discoplax-Cardisoma* sister clade (see *Genetic data*). However, from an ecological perspective, *Discoplax* consitutes a unique lineage that did not completely colonise terrestrial habitats. They did not acquire the multiple morphological adaptations for the two lifestyles, i.e., no changes, neither for terrestrial environments nor for life in dark caves. This explains why *Discoplax* is not modified and exhibits significant morphological differences (see Table 1). Brachyuran crabs that have emerged from the sea onto land have several times colonised the semi-terrestrial and terrestrial habitats. In any case, some would have ventured into subterranean habitats. Or is the hypothesis of a secondary return to an aquatic freshwater habitat by these terrestrial crabs more plausible? Determining the appropriate history and transition for *Discoplax* will require further research.

Distinctive characters of Gecarcinoidea n. stat.

Vulvae

In Gecarcinoidea n. stat., the vulva is normally occluded by an immobile, rigidly shut, and calcified operculum (Hartnoll 1968). This immobile operculum "decalcifies for only a short period to allow mating, followed quickly by egg laying" (Hartnoll *et al.* 2010: 89, *Johngarthia lagostoma*). Türkay (1973a: figs 2, 3, 11, 12; 1974a: figs 10, 13) hypothesised that females must actively open the genital duct to copulate: this must therefore be preceded by decalcification. The short period of opercular decalcification allows the operculum to remain mobile for several days, and the timing of copulation and egg-laying by the female, thus signalling the opportunity for mating (see Hartnoll *et al.* 2007). Mating and egg laying are therefore closely linked, with the duration of opercular decalcification probably being short (presumably a few days), as in other thoracotremes (Henmi & Murai 1999). The short duration of the decalcification period determines a short window of opportunity for mating and limits the migratory pattern of males (Hartnoll 2010).

Pleonal attachment

With regard to the locking of the male pleon, the gecarcinoid species, all terrestrial, can have on the thoracic sternite 5 a button, as in *Hartnollius*, or sometimes a quite developed prominence, as in *Gecarcinus ruricola* (Fig. 5D), most often covered with setae. But there is no complementary socket on the pleonal somite 6, making the apparatus non-functional (Guinot & Bouchard 1998: fig. 25A, B). In Cardisomatidae n. fam. (Figs 5C; 7A), the locking structures are obscure or absent. It is curious that crabs such as the gecarcinids that perform long migrations by walking are devoid of an very efficient locking system by button-pression or snap-lock system. The pleon is not fixed, but nevertheless remains applied against the sternal plate in the sterno-pleonal cavity. In Thoracotremata, the lock is very efficient in various groups (e.g. Grapsidae, Plagusiidae, Camptandriidae Stimpson, 1858), but it is reduced, obsolete and non-functional in others (e.g. Sesarmidae, Varunidae), and is even absent completely in the most derived taxa (mainly in Ocypodidae). Conversely, it is worth noting that species of *Epigrapsus sensu lato* (see below), which are less terrestrial in habitat than gecarcinoids, possess a strong and effective locking apparatus (Figs 8F; 9C; 10C).

Female pleon and pleopods

In a remarkable article on primary freshwater crabs, Cumberlidge *et al.* (2021) highlighted the importance of a set of characters that have received little attention from taxonomists and were presumed thought to be uninformative: the female pleon, telson, pleopods, and the egg attachment sites. In mature primary freshwater females (with the exception of Trichodactyloidae H. Milne Edwards, 1853), outside the reproductive period, the pleon almost entirely covers the thoracic sternum, sometimes leaving a small anterior portion exposed (Cumberlidge *et al.* 2021: fig. 4). Depending on the species, juveniles of primary freshwater crabs remain in a brood pouch for a period ranging from 10 days to several weeks (Vogt 2016). The k-selected reproductive strategy (see Pianka 1970) of freshwater crabs involves laying a few large eggs that develop directly into juveniles, which benefit from extensive maternal protection. This contrasts sharply with the r-selected reproductive strategy of most marine crabs characterised by the production of a large number of small-diameter eggs that develop in the sea via a series of pelagic larval stages, and receive no parental care.

A comparative analysis of a female of *Cardisoma armatum* by Cumberlidge *et al.* (2021: 9, fig. 5A) shows that the female pleon, bordered by fringe of setae (such as the male pleon), covers almost the entire thoracic sternum, particularly somite 6, which spans the entire width between coxae of the chelipeds and P2; the telson is small and triangular. In contrast, in the species of two heterotreme families, namely *Doclea ovis* (Fabricius, 1787) (Epialtidae MacLeay, 1838) and *Callinectes sapidus* Rathbun, 1896 (Portunidae Rafinesque, 1815) studied by Cumberlidge *et al.* (2021: fig. 3A, B, respectively), the female pleon covered only a more or less small portion of the thoracic sternum, sometimes only a small part.

Following Cumberlidge *et al.* (2021), we investigated the relationship between the female pleon and the thoracic sternum in Gecarcinoidea n. stat. This character proved to be of great taxonomic importance for differentiating Cardisomatidae n. fam. from Gecarcinidae *restrict.* In Cardisomatidae n. fam. (Fig. 8A-D), the female pleon is relatively narrow, oval, and, thanks to dense fringe of setae on the margins, completely fills the thoracic sternum except for the episternites; the telson, small and narrow, reaches more or less the sternite 3 and the mxp3, leaving only a reduced lateral portion exposed. This arrangement is similar in the cardisomatid species *Cardisoma guanhumi*, *C. carnifex* and *Tuerkayana celeste* (Fig. 8A-C, respectively). However, the genus *Discoplax* (Fig. 8D) is an exception: the narrow female pleon leaves a fairly substantial space between it and the coxae, and the telson only reaches the sternite 4 (see above, *The case of the genus* Discoplax *A. Milne Edwards, 1867*).

In Gecarcinidae *restrict.*, the female pleon is much wider, discoid, with the telson in the shape of a large triangle. It leaves laterally and especially anteriorly a sternal portion exposed, in addtion to the episternites. The arrangement is similar in all gecarcinid species, namely *Gecarcinus ruricola*, *Johngarthia oceanica*, *Hartnollius lateralis*, *H. nobilii* and *Gecarcoidea natalis* (Fig. 9A-E, respectively), as well as in *Gecarcoidea lalandii* (not shown). The narrowest pleon and telson are those of *Johngarthia* (Fig. 9B). In our photographs (Fig. 9A, B, see arrows), the setae that are visible on each side along the margins of the pleon and telson belong to the setose displaced pleopods that protrude anteriorly and laterally, giving the false impression that setae are present on the margins of the pleon, which in fact are only very weakly setose.

The arrangement in Gecarcinoidea n. stat. seems rather similar to that of the primary freshwater crabs of the four families studied by Cumberlidge *et al.* (2021: fig. 4A-D),, where the pleon covers the width of the thoracic sternum (except for the episternites), and leaving or not a small anterior portion exposed.

According to the illustrations of the thoracotreme families by Cumberlidge *et al.* (2021: fig. 5B), in the Grapsidae exemplified by *Goniopsis peli* (Herklots, 1851), somites 1-6 cover the thoracic sternum (taking into account the fringe of setae bordering the pleon as well as the episternites that remain exposed). In contrast, in the Varunidae exemplified by *Eriocheir sinensis* H. Milne Edwards 1853, and in the Sesarmidae exemplified by *Labuanium politum* (De Man, 1888), the pleon is shorter and does not cover the anterior part of the thoracic sternum, thus leaving a sternal portion exposed at the level of the chelipeds and the legs P2 and P3 (Cumberlidge *et al.* 2021: fig. 5D, C, respectively).

In Brachyura, in general, the growth of female pleon shows strong positive allometry before puberty, a marked size increase at puberty, but a reduced positive allometry thereafter (Hartnoll 1974: table 2; 1982). In the Gecarcinoidea n. stat., the characteristic changes in the pleon and pleopods of sexually mature females, described for *Hartnollius lateralis* by Bliss *et al.* (1978, as *Gecarcinus lateralis*) and for *G. guanhumi* by Henning (1975) did "not made clear whether a distinct puberty molt occurs, though the changes in the pleonal width are substantial" (Hartnoll 1988b: 199). Liu & Jeng (2007) found that pleon morphology in *Gecarcoidea lalandii* was not a reliable character to determine the maturity of females. Sexual maturity in female *Cardisoma crassum* (Fig. 15A-C) from Panama ranges about from 49.60 to 56.00 mm cw (Gonzáles 2025); that of *Gecarcoidea natalis* is at about 45 mm cw (Hicks 1985). On Clipperton, *Johngarthia oceanica*, where the mean carapace size is *c.* 45 × 56 mm for males and *c.* 41 × 48 mm for females, the size at maturity of the females is *c.* 16 × 19 mm (Bouchard & Poupin 2009, as *Gecarcinus planatus*). The size of female sexual maturity of *Gecarcinus ruricola* is around 50 mm cw (see Hartnoll *et al.* 2007).

We have examined an ovigerous female of *Gecarcinus ruricola* 52.8 × 69.9 mm, from Cuba (MNHN-IU-2024-6554), carrying tiny eggs: the pleon (Fig. 9A) is not particularly enlarged compared to that of the larger female 60.5 × 83.8 mm, also from Cuba, in dry condition (MNHN-IU-2000-10754 = MNHN-B10754): in the latter, the pleon is significantly wider, however with the same arrangement as in the smaller female and without undergoing any alteration in general shape.

The pleopods of a female *Cardisoma armatum* studied by Cumberlidge *et al.* (2021: fig. 13), all highly setose, are located on somites 2-5 and are composed of an inner exopod (the only one serving as an egg attachment site) and an outer exopod, with the following characters: exopod length of PL 2 markedly reduced, about ¼ that of the corresponding endopod, compared to that of PL 2-5; ischium of PL 2 broad and robust, ending distally in prominent ischial/meral sulcus, and distinctly setose on the external margin; its length remaining constant in PL 2-5 (Cumberlidge *et al.* 2021: 9, fig. 13). The pleopods of all the gecarcinoid females at our disposal that we briefly examined (Fig. 10) seem consistent with those of *C. armatum*, without apparent differences, suggesting that the Gecarcinidae *restrict.* and the Cardisomatidae n. fam. share a similar arrangement.

This pattern is roughly similar to that of the Grapsidae, Sesarmidae, and Varunidae, but there are nevertheless distinctive features related to the respective lengths and shape of the ischia and general setosity (Cumberlidge *et al.* 2021: figs 14-16).

Hydrophilic setae

Among the many attempts to adapt to life on land is the search for a way to escape dessication, a major challenge for crabs that live in regions with high ambient temperatures. Watson-Zink *et al.* (2024) studied in three gecarcinids the osmoregulatory genes that are differentially expressed in the antennal glands and posterior gills in response to desiccation stress. The key structure involved in water storage is the pericardial sac, a paired pouchlike organ that extends far into the branchial chambers, which is globular, e. g. in *Cardisoma guanhumi* and in *Hartnollius lateralis* (Diaz & Rodríguez 1997: fig. 1a-c, and 1d, e, as *Gecarcinus lateralis*). These pericardial sacs are particulary large in land crabs (Hartnoll 1988b: fig. 6.1.A, B). In the Gecarcinidae *restrict.*, the ability to absorb water from the substrate is well developed in *Gecarcoidea natalis* and *H. lateralis*, in which setal tufts extend along the first three pleonal somites and on the P5 coxa to establish a connection with the pericardial sacs (Bliss 1963; 1968: fig. 14A; Greenaway 1988: fig. 7.2.A). In *H. lateralis*, the posterior extension fringed with setae of each pericardial sac terminates near the ventral surface of the crab body, at the thorax/pleon junction, and, at this point, the external ventral hydrophylic setae as well as a contiguous setae-lined channel conduct moisture drops by capillarity to the posterior ventral extension of each pericardial sac (Bliss 1979, as *Gecarcinus lateralis*). In *Gecarcinus ruricola* and *Gecarcoidea lalandii*, the posterior margins of sternites 7 and 8 are lined with dense hydrophilic setae that come into contact with the tufts of setae on P5 coxa and on pleonal somites 2-3 (Figs 5B; 7C). Pericardial sacs are present in other land crabs such as *Cardisoma guanhumi* and *C. carnifex*, where there is a setae-fringed posterior extension of the sac, and, in close proximity, external ventral setae that probably use setal suction to extract water (Greenaway 1988). The external setae serve to collect water from the substrate by capillarity, and, again by capillarity, the setae conduct this water to the posterior extension of the pericardial sacs (Bliss 1963, 1968, 1979).

In Cardisomatidae n. fam., there are no setal tufts of hydrophilic setae along the first pleonal somites, whereas in Gecarcinidae *restrict.* setal tufts of hydrophilic setae are present along the first pleonal somites. In both families, setae are present on the posterior margin of sternite 7, slightly on the P5 coxae in Gecarcinidae *restrict.*

All cardisomatids and gecarcinids lack the Müller's channel, a complex channel to which the setal tufts of Grapsoidea and Ocypodoidea are attached (see Oliveira 2014), but it seems that a Müller's channel exists in Epigrapsidae, at least in *Grapsodes* Heller, 1865 (Fig. 9D, see below).

NEW INSIGHTS ON THE FAMILY EPIGRAPSIDAE WATABE, 2007

A family Epigrapsidae, currently represented only by a single genus and type genus *Epigrapsus* Heller, 1862, was established by Watabe (2007: 55, 56, table IV.1) as the first application case of the Autopoiesis Theory (derived from cognitive neuroscience) to crustacean taxonomy, in the words "The Family Epigrapsidae (new establishment, diagnosis followed Sakai 1976), represented only by the genus *Epigrapsus*, is placed as the morphologically simplest (primitive) potamid taxon". This family name is considered valid because it explicitly refers to the diagnostic characters listed by Sakai (1976: 677 in key), but it seems that it has never been used since. *Epigrapsus* is not a freshwater crab of the family Potamidae Ortmann, 1896, as Watabe (2007) believed.

The genus *Epigrapsus* was traditionally considered to belong to the Gecarcinidae *sensu lato* (Ng *et al.* 1998, 2000; Cuesta *et al.* 2002; Cuesta & Anger 2005; Naruse *et al.* 2018), either in a rather isolated position (Tavares 1991: fig. 1) or forming a third group (Türkay 1987) or regarded as phylogenetically distinct (Ng *et al.* 2008; pers. comm. 2025). The two species assigned to the family Epigrapsidae are semi-terrestrial or intertidal, whereas crabs of the Gecarcinoidea n. stat. are terrestrial, the land crabs by excellence with a very high degree of terrestriality in Gecarcinidae *restrict.*, less marked in Cardisomatidae n. fam. Their larvae live in the sea, while the adults have a terrestrial lifestyle like the gecarcinoids, but, as they live short distance from the shore, they do not undertake long and intense migrations to the sea for reproduce, unlike the gecarcinoids.

The relatively poorly known genus *Epigrapsus* currently comprises two often co-occurring species, both unusual compared to gecarcinoids with respect to their relatively small size and flatter carapaces, their morphology, and, in part, their habits. The taxonomy of the genus and its members has been discussed by Alcock (1900), Tesch (1918), Türkay (1974a, b; 1977), Ng *et al.* (1998, 2000) and Naruse *et al.* (2018). The taxonomy of *E. notatus* has been rather confused, with three junior subjective synonyms. Genetically, C. T. T. Tsang *et al.* (2022) recognised two sister clades, *Epigrapsus* + *Gecarcinus* + *Gecarcoidea* and *Cardisoma* + *Discoplax* + *Tuerkayana. Epigrapsus* was not included in the genetic studies on Gecarcinidae *sensu lato* by Z. Wang *et al.* (2023) or more extensive (Xu *et al.* 2023).

The two species currently assigned to *Epigrapsu*s are *E. politus* Heller, 1862 (type species) and *E. notatus* (Heller, 1865, as *Grapsodes notatus*). Heller (1862, 1865) actually recognised the two species under three different names: *Epigrapsus politus* Heller, 1862 (Heller 1862), with *E. politus* as type species, and *Nectograpsus* Heller, 1865 (Heller 1865) with *N. politus* (Heller 1865: pl. 5, fig. 3) as type species, from Tahiti. The two genera are synonyms because they are based on the same species. On the other hand, Heller (1865: 58) established *Grapsodes* Heller, 1865, with *G. notatus* as type species, from the Nicobar Islands. The binomen *Grapsodes notatus* was used by many authors, and *Grapsodes* was considered either as a genus, e.g. by Alcock (1900) that the adult morphology and Tesch (1918), or as a subgenus of *Epigrapsus* (see Türkay 1974a). Serène (1968), in a checklist, therefore without any explanation, abandoned the binomen *Grapsodes notatus*, and replaced it with *Epigrapsus notatus*. Since then, *notatus* has reverted to its generic name *Epigrapsus.* Türkay (1973b; 1974a) synonymised *Epigrapsus* (*Grapsodes*) *wolfi* Sendler, 1923 and *Epigrapsus* (*Grapsodes*) *notatus punctatus* Sendler, 1923 with *E. notatus* after comparing their types. *Mystacocarcinus crenidens* Hilgendorf, 1888 is also a junior subjective synonym of *E. notatus* (Türkay 1977). A third species, *E. villosus* Ng, 2003, described only from a small male (8.9 × 9.4 mm), from a cave in Guam, was considered a junior synonym of *E. notatus* by Naruse *et al.* (2018), who demonstrated that *E. notatus* undergoes dramatic morphological changes during growth (see also Fujita 2017a: 20, fig. 2). Ng *et al.* (1998: table 1) carefully compared *Epigrapsus politus* with its congener *E. notatus*, both from Taiwan, and listed their distinguishing characters while concluding that the carapace and pleonal shape of *E. notatus* changed considerably with growth, hence a source of confusion for identification.

The MNHN collection contains only one sample of *Epigrapsus politus* from Sumatra (Atjeh), whereas all other specimens, formerly identified as *E. politus* and revised by Türkay in the early 1970s, turn out to be in fact *E. notatus.* The remarks on *Epigrapsus* by Guinot *et al.* (2018: 570), based only on few misidentified specimens are incorrect and should not be fully taken into account. The recent donation from the ZRC of two specimens of *Epigrapsus notatus* from Taiwan allows us to compare the two species and to propose the result of their examination, as part of the present study on Gecarcinoidea n. stat. This yielded a completely unexpected result, even though many researchers (Ng *et al.* 2000, 2008) had clearly listed their numerous and significant differences:

Epigrapsus is not monophyletic, as the differences between the two species are not specific but generic, or even broader. Consequently, we recognise two genera: *Epigrapsus* Heller, 1862, with *E. politus* Heller, 1862 as type species and sole species; and *Grapsodes* Heller, 1865, a valid genus that we are resurrecting with *G. notatus* Heller, 1865 as the type species and sole species.

A new diagnosis of *Epigrapsus restrict.* and of *Grapsodes* is provided, accompanied by a table (Table 2) listing the morphological differences between *Epigrapsus politus* Heller, 1862 and *Grapsodes notatus* Heller, 1865. We have incorporated many of the differences identified by Ng *et al.* (1998: table 1), who examined a large number of specimens of each species and were able to account for variation. Some fundamental characters are added to those previously employed, such as the antennules, antennae, anterior margin of the epistome, and thoracic sternites.

Genus *Epigrapsus* Heller, 1862 *restrict.*

Epigrapsus Heller, 1862: 522. — Alcock 1900: 443. — Tesch 1918: 132 *pro parte*. — Türkay 1974a: 248, *pro parte*. — Ng *et al.* 1998: 71; 2000: 379, *pro parte*. — Fujita 2017a: 22 (only *E. politus*). — Hartnoll *et al.* 2017: 951, *pro parte*. — Naruse *et al.* 2018: 208-216 (only *E. politus*). — Doi *et al.* 2019: 145 *pro parte* (only *E. politus*).

Nectograpsus Heller, 1865: 56.

Type species. — *Epigrapsus politus* Heller, 1962.

Epigrapsus politus Heller, 1862
(Fig. 11; Table 2)

Epigrapsus politus Heller, 1862: 522. — Türkay 1974a: 248, figs 7a, b, 18. — Ng *et al.* 1998: 78, fig. 6; 2000: 379-381. — Cuesta *et al.* 2002: 1675, figs 4A-C, 5A-D, 6A-C. — Fujita 2017a: 22, figs 2, 3; 2017b: 102, fig. 5C. — Hartnoll *et al.* 2017: 942, fig. 5. — Doi *et al.* 2019: 145-157, figs 1-7; 2020: 200-208, figs 1-7.

Nectograpsus politus Heller, 1865: 57, pl. 5 fig. 3, 3a.

Material examined. — **Indonesia** • 1 ♂ 23.0 × 29.1 mm; Sumatra; Atjeh; det. De Man; revis. Türkay *Epîgrapsus politus*; VI.1972; MNHN-IU-2017-10018 (= MNHN-B12585).

Diagnosis

Carapace, transversally ovate**,** not variable**.** Dorsal surface gently convex and swollen; grooves shallow. Anterolateral margins arcuate, with one very low indistinct epibranchial tooth (often absent, thus margin appearing entire); when discernible, separated from exorbital tooth by very small notch. Posterolateral margins distinctly converging towards posterior carapace margin. Fronto-orbital border more than half width of carapace. Front almost entire, not much deflexed, thick. Antennules obliquely folded; basal article well developed and exposed, article 2 obliquely folded, entirely visible. Antenna with basal article (2 + 3) J-shaped, bearing article 4 on short inner side; article 5 well visible; short flagellum bent; no orbital hiatus. Proepistome wide, rectangular, with median process. Orbits delimitated, sheltering most part of podophtalmite. Suborbital ridge thick, tuberculate, possibly acting as pars stridens (inner margin of P1 with ridge, possibly acting as plectrum). Buccal frame elongate-rectangular, delineated laterally. Epistome with anterior margin straight**,** thick, tuberculate. Mxp3 rectangular, distinctly longer than broad, with merus distinctly longer than ischium, leaving distinct rhomboidal median gap when closed; ischium with slight lateral sulcus, bordered by setose ridge; merus with very deep oblique depression all along, bordered by setose ridge; palp inserted near latero-external angle of merus; palp short, with three mobile articles externally visible, first article encroaching on margin of epistome; exopod exposed, slender, with flagellum. Pterygostomial area not setose, possibly with dense velvety setae; subhepatic area sligthly setose. Pereiopods relatively stout and short with merus and dactylus relatively more slender and proportionately longer; anterior margin of rugose squamate to gently serrate; dactylus with scattered spines; surfaces with few or no setae; dactylus with only scattered setae. Chelipeds unequal in males; major chela strongly inflated; in adults, fingers shorter than smooth palm, gaping proximally. Sterno-pleonal cavity shallow, its extremity distant from suture 2/3; ridge on sternite 4 faint, surrounding telson only. Male pleon with all somites free, relatively short; somite 6 wide, with margins straight proximally, convex distally; telson short, bluntly rounded. Thoracic sternum: sternite 1 as a spine in continuity with sternite 2; sternite 2 as large, dome-shaped plate, with convex margins; sternites 3 and 4 fused, with slightly sinuous lateral margins. Median line along sternites 8 and 7. Locking structure only as a small button in anterior third of sternite 5; apparatus non-functional. Male gonopore sternal, distant from P5 coxa; penis emerging distinctly far from suture 7/8, on middle of sternite 8, crossed by sulcus joining P5 coxo-sternal condyle. G1 relatively elongate, stout; distal part almost straight to distinctly bent inwards (towards median longitudinal suture of thoracic sternum). G2 minute, slightly bent. Short setae on P2 and P3 and on P3 and P4 coxae, forming two small setal pouches between P2/P3 and P3/P4.

Geographical distribution

Tahiti (type locality), Tuamotu, Caroline Islands, Bertrand Island (Papua-New Guinea), northern Sumatra, Taiwan, Japan.

Biology

Epigrapsus politus resides in habitats nearer the seacoast and closer to the waterline than does *Grapsodes notatus*, also preferring more rocky/sandy areas than does the latter species. It has few terrestrial adaptations, compared to Gecarcinidae *sensu lato*, and is more vulnerable to overheating and desiccation. Its small size facilitates its cryptic lifestyle. In Japan (Ishigaki Island), it inhabits the supralittoral zone, under small partially embedded stones in sandy areas, covered partially by coastal vegetation (Ng *et al.* 1998; 2000). The species, recently studied on a sandy beach along a small subtropical bay in Japan, on Iriomote-jima Island, was found only above

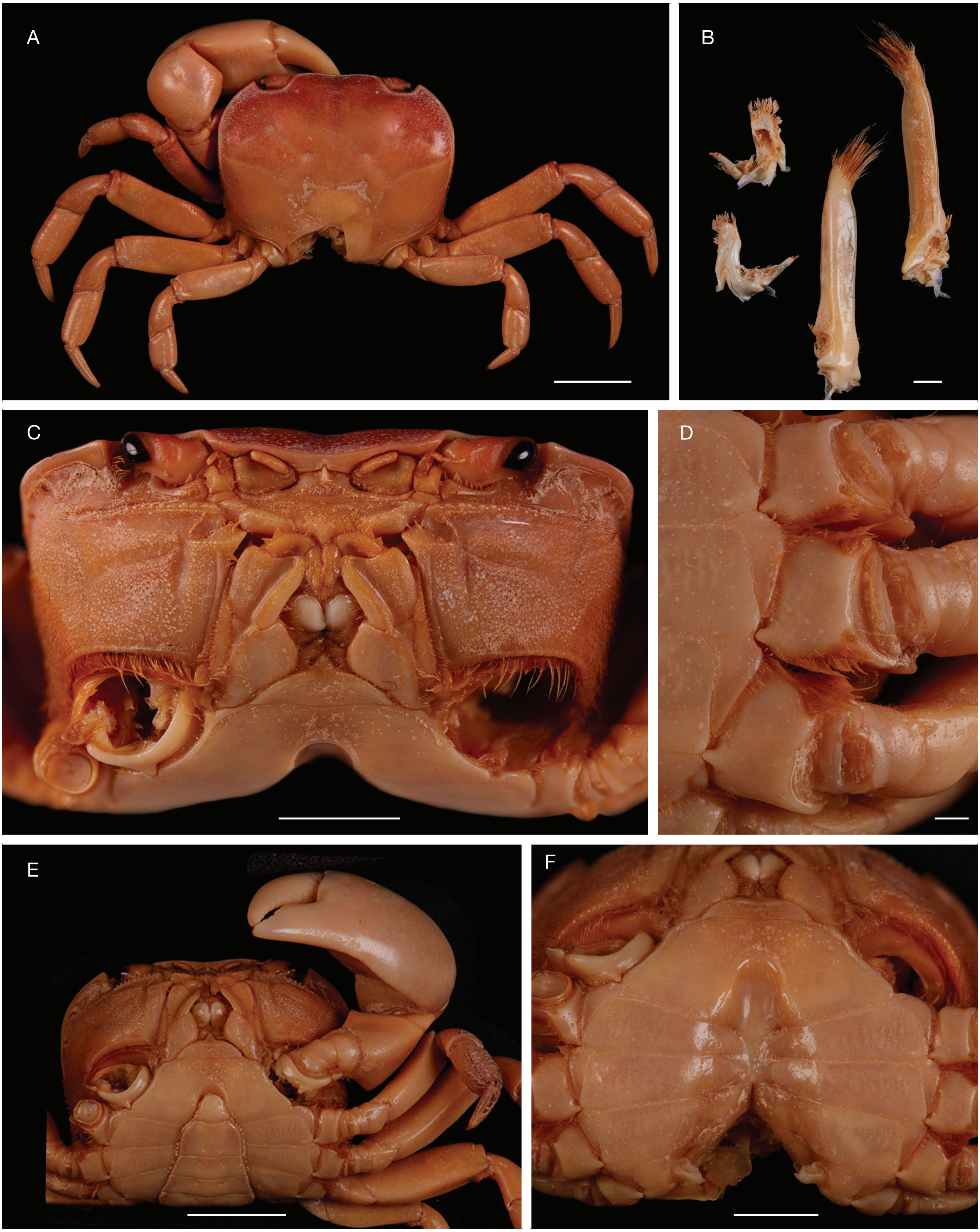

FIG. 11. — *Epigrapsus politus* Heller, 1862, ♂ 23.0 × 29.1 mm, Sumatra, Atjeh, MNHN-IU-2017-10018 (= MNHN-B12585): **A**, dorsal view; **B**, anterior ventral view; **C**, ventral view, with pleon; **D**, G1 and G2; **E**, hydrophilic setal tufts; **F**, thoracic sternum, with penis. Scale bars: A, C, 10 mm; B, F, 5 mm; D, E, 1 mm. Credits: MNHN-Soubzmaigne.

the extreme high water of spring tide, where more cobbles and pebbles were piled by the waves. *E. politus* is characterised by a relative smaller-sized body and smaller size at sexual maturity, compared to that of Gecarcinidae *sensu lato*, by adult males showing progressive polymorphism in chelae, and the proportion of heterochelous males, with the size difference between major and minor chelae increasing with growth (Doi *et al.* 2019). Its reproductive period is shorter and occurs in a cooler season than that of Gecarcinidae *sensu lato* inhabiting the subtropical islands of the northwest Pacific (Doi *et al.* 2020).

According to Ng (pers. comm.), *Epigrapsus politus* is somewhat similar to the species of *Cyclograpsus* H. Milne Edwards, 1837 (Cyclograpsinae H. Milne Edwards, 1853, in Varunidae (in which a new subfamily has recently been recognised, see Muñoz *et al.* 2025a). They share a water-channelling oblique setose ridge on the ischium and merus of the mxp3, and the presence of setal pouches between the coxae of P2/P3 and P3/P4 (Fig. 11E), but can be distinguished, inter alia, by the epistome (Fig. 11B) and the G1 (Fig. 11D), among other features.

Genus *Grapsodes* Heller, 1865

Grapsodes Heller, 1865: 58. — Kingsley 1880: 188, 197. — Alcock 1900: 440 (key p. 441).

Mystacocarcinus Hilgendorf, 1888: 26-29.

Epigrapsus (*Grapsodes*) Sendler, 1923: 27.

Epigrapsus — Tesch 1918: 132 *pro parte*. — Türkay 1974a: 248 *pro parte*. — Ng *et al.* 1998: 71; 2000: 379 *pro parte*. — Fujita 2017a: 20, only. — Hartnoll *et al.* 2017: 939, fig. 3. — Naruse *et al.* 2018: 208 *pro parte.*

Type species. — *Grapsodes notatus* Heller, 1865.

Diagnosis

Carapace squarish to distinctly wider than long, transversally ovate (larger specimens). Females with more quadrate carapaces. Dorsal surface gently convex to strongly convex, with fairly distinct grooves on large specimens; epigastric cristae prominent and sharp in small specimens, weak and rounded in much larger specimens. In males, tufts of short black setae in small and medium-sized individuals, lost in larger individuals, resulting in a glabrous surface. Anterolateral margins gently convex to strongly arcuate (larger specimens); with three teeth: one external orbital tooth and two epibranchial teeth, variously developed and variably arranged, depending on the size. Posterolateral margins subparallel to more or less converging towards posterior carapace margin (larger specimens). Fronto-orbital border more than half width of carapace. Front entire, deflexed, with two developed inner subfrontal lobes; outer lobes shorter. Antennules folded tranversely; basal article exposed, squarish; article 2 small, only partly visible. Antenna with basal article (2 + 3) squarish; article 4 almost invisible; flagellum bent downwards in orbital hiatus. Proepistome small, dome-shaped; encircled by developed inner frontal lobes. Orbit only basally delimitated, sheltering proximal part of podophtalmite; a pointed tooth at inner angle. External orbital tooth acutely triangular, distinctly separated from anterolateral margin by small but distinct cleft; first epibranchial tooth small but distinct; second epibranchial tooth often low or almost undiscernible (more prominent in smaller specimens). Suborbital margin entire, subparallel to frontal margin, not connected to orbit, inner margin with very low tooth, outer edge ending abruptly. Suborbital ridge long, thin, smooth. Epistome with anterior margin formed by thin concave edges joining medially. Buccal cavity relatively short, almost as broad as long and squarish, not delineated laterally. Mxp3 rather short, leaving distinct rhomboidal median gap when closed; ischium and merus with slight short sulcus, without setose ridge; palp inserted near middle of anterior margin of merus; palp short, with three mobile articles visible externally, all included in the buccal cavity; exopod exposed, slender, with vestigial flagellum. Pterygostomial area very setose, subhepatic area not setose. Pereiopods with tufts of setae in youngs and adults, glabrous in larger individuals. Chelipeds subequal in adult males, chela strongly inflated; fingers slightly shorter than smooth palm, both gaping; dactylus with small proximal tooth; fixed finger with distal tooth. Ambulatory legs relatively slender, second and third legs longest. Sterno-pleonal cavity very deep; its extremity not far from suture 2/3; ridge on sternite 4 faint, surrounding telson only. Male pleon with all somites free, long, edged with thin setae; somite 6 with straight margins; telson long, acutely triangular. Thoracic sternum: sternite 1 spine-like at lower level than sternite 2, with scattered short pubescence not obscuring surface; other sternites glabrous; sternite 2 narrower, with straight margins; sternites 3 and 4 fused, with slightly concave lateral margins; sternite 7 without sulcus. Median line along sternites 8 and 7. Locking structure as largely developed and salient rugose prominence, quite close to suture 4/5 and pleonal socket with calcified border, therefore an apparently functional apparatus. Male gonopore sternal, not very distant from P5. Soft and long setae on P3 and P4 coxae, forming a large setal pouch between P3/P4. G1 relatively elongate, slender; distal part almost straight to distinctly bent inwards (towards median line of thoracic sternum) and with numerous long setae; pectinated part spatuliform, subtruncate. G2 very small, bent. Vulva big, rounded, close to suture 5/6, with salient cover and operculum.

Grapsodes notatus (Heller, 1865)
(Figs 3D; 4C; 9C;12; 13; Table 2)

Grapsodes notatus Heller, 1865: 58, pl. 5 fig. 2, 2a.

Mystacocarcinus crenidens Hilgendorf, 1888: 26-29.

Epigrapsus notatus punctatus Sendler, 1923: 28.

Epigrapsus (*Grapsodes*) *wolfi* Sendler, 1923: 28, fig. 3, pl. 21 fig. 4.

Epigrapsus villosus Ng, 2003: 1219-1227, figs 1-3.

Epigrapsus notatus — Tesch 1918: 13, pl. 6 fig. 3. — Türkay 1974a: 251, figs 6a, b, 9, 19 (complete synonymy). — Tavares 1989: figs 5, 6. — Ng *et al.* 1998: 72, figs 1-5. — Cuesta *et al.* 2002: 1680, fig. 7A, B. — Fujita 2017a: 20, fig. 2; 2017c: 336. — Naruse 2005: 220. — Naruse *et al.* 2018: 208-216, figs 1-4.

Epigrapsus politus Guinot *et al.* 2018: 55 (misidentification). — Huet & Poupin 2020: 661-670, fig. 2 (misidentification).

MATERIAL EXAMINED. — **Upolu** • 1 ♂ (dry; damaged); A. Milne Edwards det. *Epigrapsus politus*; erroneously indicated as 'Type' on label; Guinot & Rodríguez Moreno det. *Grapsodes notatus*; MNHN-IU-2000-10869 (= MNHN-B10869).
Taiwan • 1 ♂ 22.7 × 26.9 mm, 1 ♀ 18.1 × 21.8 mm; Hsiang-Chiao-Wan; Checheng; Pingtung County; P. K. L. Ng coll. et det.; X.2012; MNHN-IU-2018-5241 (ex ZRC 2013.0039).
Reunion Island • 1 ♂ 13.7 × 16.2 mm, 1 ♀ 15.3 × 18.7 mm; Manapany-Les-Bains; N. Huet coll.; XI. 2019; N. Huet & J. Poupin det. *Epigrapsus politus* et leg.; XI.2020; Guinot & Rodríguez Moreno redet. *Grapsodes notatus*; MNHN-IU-2013-7280.
Indonesia • 3 ♂ 8.2 × 10.2 mm, 9.1 × 11.2 mm, 10.6 × 13.2 mm, 1 ovigerous ♀ 10.7 × 12.9 mm, 1 ♀ 10.2 × 12.2 mm; Sumatra, Atjeh; De Man det. *Epigrapsus politus*; revis. Türkay VI.1972; Guinot & Rodríguez Moreno redet. *Grapsodes notatus*; MNHN-IU-2017-8252 (= MNHN-B12585).
Polynesia • 1 ♀ 13.5 × 17.2 mm; Hikueru; revis. Türkay VI.1972 *Epigrapsus politus*; Guinot & Rodríguez Moreno redet. *Grapsodes notatus*; MNHN-IU-2013-19845 (= MNHN-B12584).
Hawaiian Islands • 2 ♂ (dry), "iles Sandwich"; A. Milne Edwards det. '*Epigrapsus crassus* manuscrit', thus a *nomen nudum*; Guinot & Rodríguez Moreno det. *Grapsodes notatus*; MNHN-IU-2000-10872 (= MNHN-B10872).

DIAGNOSIS

As for the genus.

REMARK

In *Grapsodes notatus* (Fig. 9F), the female pleon is very wide, as in Gecarcinidae *restrict.*, the telson also, and both leave laterally and more importantly anteriorly a significant sternal space, corresponding to sternite 4. The fringe of setae is moderate, therefore intermediate between the Gecarcinidae *restrict.* and the Cardisomatidae n. fam.

GEOGRAPHICAL DISTRIBUTION

Nicobar Islands (type locality), Talaut Islands (Moluccas), Papua-New Guinea (Bertrand Island), Solomon Islands, Bismarck Archipelago, Admiral Islands, Bonin (= Ogasawara) Islands, Hachijo Islands (Japan), southern Taiwan, Samoa, Tahiti (type locality), Tuamotu, Caroline Islands, northern Sumatra, Reunion Island, Japan, Christmas Island.

BIOLOGY

Grapsodes notatus has totally lost its swimming ability and is a land crab: like members of Gecarcinoidea n. stat., the adults are terrestrial in habit, whereas the larval life takes place in the sea.

Adult *Grapsodes notatus* lead a cryptic life. According to Ng *et al.* (1998, as *Epigrapsus notatus*), the crabs inhabit sheltered forests with numerous limestone rocks. Three gecarcinid species may be found in the same area, namely *Cardisoma hirtipes*, *Turkayana rotundum* and *Gecarcoidea lalandii*. *G. notatus* is found in the supralittoral zone, from vegetated sandy shores to sheltered coastal forests, often under large objects (e.g., rocks, wood, etc.) on soft substrates, or in and around burrows under forest cover. The species is not encountered in open fields and is rarely observed outside the forest, even on rainy nights; crabs emerge from their burrows at night or at daytime just after a rain to scavenge leaves and carry them in their burrows; they do not wander far from their burrows, sometimes foraging during the day; ovigerous females prefer to release their larvae inside surge channels where the effects of wave action are weaker than on the exposed shore (Ng *et al.* 1998; Ho 2003; Liu & Jeng 2005; Shih 2013, as *Epigrapsus notatus*). The migration of ovigerous females to the sea to release larvae can be as short as the distance from the fringe of the coastal forest to the surf, or as long as several hundred metres. The reproductive season is limited to two lunar months in September and October, a relative short time in comparison with gecarcinoid crabs, and the female shows an unusual larval release behaviour: she shakes her whole body laterally very quickly, without any fanning motion of the pleon, a posture which could reduce the chances of being swept away by waves. *Grapsodes notatus* is abundant in Japan, where it lives in the crevices or the rock, not far from the beach, where the freshwater is dropping down (Sakai 1954; Ng *et al.* 2000; Shih 2012; Fujita 2017c, all as *Epigrapsus notatus*).

Grapsodes notatus has been discovered in rather unusual environments (Naruse *et al.* 2018, as *Epigrapsus notatus*): the small male holotype of *Epigrapsus villosus* Ng, 2003 (synonymised with *G. notatus*) came from the entrance of a cave in Guam, situated about 100-200 metres from the shoreline; in northern South China Sea, a young individual has been found under driftwood in the supralittoral zone of Dongsha Island (Shih 2012). In the southern Ryukyus, young and adult forms have been collected from the lower supralittoral zone, under rubble substratum, occasionally splashed with seawater by wave action (Fujita 2017a, as *Epigrapsus notatus*).

The setal pouches of *Grapsodes notatus* (Figs 9F; 12D; 13C), with dense, long tufts of hydrophilic setae, are located at the level of P3/P4 coxae and are attached to the opening of the Müller's channel (situated between P3 and P4): they function to transport water into the branchial chamber. In contrast, in *Epigrapsus politus*, there are two setal pouches between P2/P3 and P3/P4, consisting of short setae. These pouches, which are related to semi-terrestrial life, are found in diverse thoracotremes (Wolcott 1984: fig. 2; Greenaway 1988: fig. 7.2B-D in species of *Geograpsus* Stimpson, 1858; Hartnoll 1988a). Such setal pouches are not found in gecarcinoid land crabs, which are completely terrestrial. Crabs of the family Cardisomatidae n. fam. lack setal tufts (Fig. 5A, C), whereas in Gecarcinidae *restrict.* crabs have tufts of hydrophilic setae but they are located along the margins of the pleon and at its junction with the carapace (Fig. 5B; Table 1)

TABLE 2. — Morphological differences between *Epigrapsus* Heller, 1862 (type species: *E. politus*) and *Grapsodes* Heller, 1865 (type species: *G. notatus* Heller, 1865). Many characters vary considerably with age and size, see Ng *et al.* 1998; Naruse *et al.* 2018.

Morphological characters	***Epigrapsus* Heller, 1862** (monospecific: *E. politus* Heller, 1862)	***Grapsodes* Heller, 1865** (monospecific: *G. notatus* Heller, 1865)
Size	small	large
Carapace	transversely ovate	squarish to distinctly broader than long, transversely ovate (larger specimens)
Dorsal surface of carapace	gently convex and swollen, with shallow grooves	gently to strongly convex, with rather distinct grooves on large specimens
Anterolateral margin	arcuate; one very low epibranchial tooth separated from external orbital tooth by very small notch (often undiscernible or, when absent, margin appearing entire)	gently convex to strongly arcuate (larger specimens); with three teeth: one external orbital tooth and two epibranchial teeth, variously developed and arranged in variable manner
Posterolateral margins	distinctly converging towards posterior carapace margin	subparallel to more or less converging towards posterior carapace margin (larger specimens)
Antennule	obliquely folded; basal article well developed and exposed; article 2 obliquely folded, entirely visible	horizontally folded; basal article squarish, exposed; article 2 small, only partially visible
Antenna	basal article (2+3) J-shaped, bearing article 4 on short inner side; article 5 well visible; short flagellum bent; no orbital hiatus	basal article (2+3) squarish; article 4 almost not visible; flagellum bent down in orbital hiatus
Front	not much deflexed, thick, almost entire	deflexed, with inner and outer subfrontal lobes developed
Orbit	delimitated, sheltering most part of podophtalmite	only basally delimitated, sheltering proximal part of podophtalmite; a pointed tooth at inner angle
Suborbital ridge	thick, tuberculate, possibly acting as pars stridens (inner margin of P1 merus with ridge, possibly acting as plectrum)	longer, thinner, smooth
Proepistome	wide, rectangular, with median process	small, dome-shaped; encircled by developed inner frontal lobes
Buccal frame	elongate-rectangular, delineated laterally	shorter, quadrate, subcircular to rhomboid, not delineated laterally
Epistome: anterior margin	straight, thick, tuberculate	as two concave thin edges joining medially
Mxp3	rectangular, distinctly longer than broad, with merus distinctly longer than ischium	shorter, squarish, as broad as long, with merus barely longer than ischium
Ischium	with slight longitudinal sulcus, bordered by setose ridge	with slight short sulcus; no setose ridge
Merus	with very deep oblique depression all along, bordered by setose ridge	with slight depression; no setose ridge
Palp	inserted near latero-external angle of merus; palp short, with three mobile articles externally visible, first article encroaching on margin of epistome	inserted near middle of anterior margin of merus; palp short, with three mobile articles externally, all included in buccal cavity
Mxp3 exopod	exposed, slender, with flagellum	exposed, slender, with vestigial flagellum
Pterygostomial area	not setose	very setose
Subhepatic area	sligthly setose	not setose
Sterno-pleonal cavity	shallow, its extremity distant from suture 2/3	very deep; its extremity not so distant from suture 2/3
Male pleon	relatively short; somite 6 wide, with margins straight proximally, convex distally	longer; somite 6 long, narrowing distally, trapezoidal, with straight margins
Telson	short, bluntly rounded	long, acutely triangular
Female pleon	not described	wide, leaving laterally and especially anteriorly a sternal portion exposed, in addition to episternites; telson in shape of a large triangle
Thoracic sternum	sternite 1 as a spine in continuity with sternite 2; sternite 2 as a large dome-shaped plate, with convex margins; sternites 3 and 4 fused, with slightly sinuous lateral margins	sternite 1 as a spine in lower level than sternite 2; sternite 2 narrower, with straight margins; sternites 3 and 4 fused, with slightly concave lateral margins
Pleonal locking structure in males	a small button in anterior third of sternite 5; apparatus not functional	a largely developed and salient rugose prominence, rather close to suture 4/5. Apparatus seemingly functional: pleonal socket with calcified border
Male gonopore	sternal, distant from P5	sternal, distant from P5
Penis	emerging distinctly far from suture 7/8, on middle of sternite 8, crossed by sulcus joining P5 coxo-sternal condyle	emerging distinctly far from suture 7/8, on very small sternite 8
G1	relatively short, stout	relatively elongated, slender
Setal pouch	short setae on P2 and P3 and on P3 and P4 coxae, forming two small setal pouches between P2/P3 and P3/P4	soft and long setae on P3 and P4 coxae forming a large setal pouch between P3/P4

FIG. 12. — *Grapsodes notatus* Heller, 1865, ♂ 22.7 × 26.9 mm, Taiwan, MNHN-IU-2018-5241 (ex ZRC 2013.003): **A**, dorsal view; **B**, anterior ventral view; **C**, pouch of hydrophilic setae between P3/P4; **D**, thoracic sternum and G1; **E**, ventral view, with pleon. Scale bars: A, E, 10 mm; B-D, 2 mm. Credits: MNHN-Soubzmaigne.

FIG. 13. — *Grapsodes notatus* Heller, 1865, ♀ 18.1 × 21.8 mm, Taiwan, MNHN-IU-2018-5241: **A**, dorsal view; **B**, ventral view; **C**, thoracic sternum and vulvae. Scale bars: A, B, 10 mm; C, 2 mm. Credits: MNHN-Soubzmaigne.

(Rathbun 1918: figs 163, 165; Greenaway 1988: fig. 7.2.A; Guinot *et al.* 2025). In species of Gecarcinidae *restrict.*, the most terrestrial, water moves from the substrat to the setal tufts, onto the surface of the pericardial sacs and then to the gills. A Müller's channel does not exist in this family nor in Cardisomatidae n. fam. (see above, *Hydrophilic setae in Gecarcinoidea n. stat.*). Instead, in *Grapsodes notatus*, the presence of a coxal setal pouch between P3/P4 (Figs 12D; 13C), indicating the presence of a Müller's channel to which the setae of the pouch are attached, is also present in a location similar to the other semi-terrestrial crabs Grapsoidea and Ocypodoidea (see Oliveira 2014): setal pouches at the level of P3/P4 coxae, in Grapsinae such as *Geograpsus* (see Guinot *et al.* 2018, *Terrestrial adaptation of grapsoids*) or in Ocypodinae Rafinesque, 1815, such as *Ocypode quadrata* (Fabricius, 1787).

Grapsodes notatus as well as *Epigrapsus politus* are not known to stridulate. Yet, there is little doubt that the tuberculated suborbital crest of *E. politus*, not externally connected to the orbit, could act as a pars stridens, and that the ridge on inner margin of P1 merus could represent a plectrum.

REMARKS

The family Epigrapsidae is represented only by *Epigrapsus politus* and is now monogeneric.

The genus *Grapsodes*, which now comprises only *G. notatus*, is therefore monotypic. It is considered here *incertae sedis* within Grapsoidea *sensu lato*. Several morphological characters distinguish *E. politus* and *G. notatus* from the Cardisomatidae n. fam. and the Gecarcinidae *restrict.* (see Tables 1; 2). These taxa should be assigned to the Grapsoidea *sensu lato*.

The identification of *Epigrapsus politus* on the one hand and of *Grapsodes notatus* on the other exceeds the scope of the present article devoted to the Gecarcinoidea n. stat., and only more in-depth studies will enable their position in the appropriate taxonomic unit to be hypothesized.

FIG. 14. — Gecarcinidae *restrict.*, living and in the field: **A**, **B**, *Hartnollius quadratus* (Saussure, 1853), Coiba I., Panama; **C**-**F**, *Johngarthia weileri* (Sendler, 1912), São Tomé I., São Tomé and Principe. Credits: A. Anker.

GENERAL CONCLUSION

The larval morphology of Gecarcinidae *sensu lato* was the first step in distinguishing them from the grapsoid families (Cuesta *et al.* 2002). Taking up the long-standing informal use of the superfamilial rank Gecarcinoidea by the first author, the present article, following the identification of two major subclades within the family Gecarcinidae *sensu lato* by Guinot *et al.* (2018), demonstrates that the adult morphology, with its unique characters, requires a new status, Gecarcinoidea H. Milne Edwards, 1837 n. stat. A diagnosis is provided here. The morphological features outlined above (see Table 1) and the concordance of morphological and larval data allow us to distinguish two gecarcinoid families: the Gecarcinidae *restrict.*, which forms a group with a distinctly terrestrial lifestyle, and the Cardisomatidae n. fam., which forms a group with less terrestrial habits.

Fig. 15. — Cardisomatidae n. fam., living and in the field: **A**-**C**, *Cardisoma crassum* Smith, 1870, Coiba I., Panama; **D**-**F**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828; **D**-**E**, Bocas del Toro, Panama; **F**, Ceará, Brazil. Credits: A-E, A. Anker; F, P.P.G. Pachelle.

We were pleased to confirm the taxonomic value of the female pleon highlighted by Cumberlidge *et al.* (2021), previously considered uninformative, which has proven to be a valid diagnostic character in Gecarcinoidea n. stat.

Relationships within Gecarcinoidea n. stat. can also be examined in terms of their degree of terrestrialisation: the same degree of terrestrialisation is manifested during their landward migration stages, as seen in the megalopae in *Gecarcinus* and *Johngarthia*, with the megalopa of *Gecarcinus* being the best adapted to terrestrial life described to date. Conversely, in the Cardisomatidae n. fam., the *Cardisoma* species and *Tuerkayana celeste* migrate upstream as megalopae and only emerge on land in the first crab stage. The genus *Discoplax* is distinct from the other Gecarcinoidea n. stat., both in its morphology and its more or less cave-dwelling lifestyle. The hypothesis of a specific colonisation of caves could be one explanation for this divergence.

Numerous characters distinguish gecarcinoids from common shore crabs (Grapsoidea), including the configuration of their cephalic appendages, orbits, front and epistome. Gecarcinoidea n. stat. has a higher degree of terrestriality that any Grapsoidea. Species of Gecarcinidae *restrict.* possess hydrophilic setae, an adaptation for absorbing water from the substrate, but lack the Müller's canal present in many grapsoid crabs. Many other characters distinguish Gecarcinoidea n. stat. from the Grapsoidea (acknowledged as non-monophyletic, see Poore & Ahyong 2023).

The genus *Epigrapsus* and *Grapsodes*, which has been relatively little studied and with adults having a semi-terrestrial or intertidal lifestyle, are not included in Gecarcinoidea n. stat. in the present paper. Instead, they appear to be related to families traditionally included in Grapsoidea *sensu lato.* *Epigrapsus* belongs to the Epigrapsidae, if the family remains available, and the position of *Grapsodes* remains uncertain pending further study.

Acknowledgements

We would like to thank our colleagues Peter K. L. Ng and J. C. Mendoza (Lee Kong Chian Natural History Museum, National University of Singapore) for generously providing us with several species, namely *Gecarcoidea natalis*, *Tuerkayana magnum*, *T. celeste* and *Epigrapsus notatus*. We would like to thank our colleagues at other museums who lent us material: Paul Clark and Miranda Lowe (NHM); Martha Nizinsky and Adam Stergis (NMNH, Smithsonian Institution); Henri Vallès and Nadeshinie Parasram (UWI). 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 Région Guadeloupe, the Agence française de Développement (AFD), the Parc national de Guadeloupe, the Office national des Forêts (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. We thank Marcos Tavares (Museu de Zoologia, Universidade de São Paulo) for allowing us to reproduce some sketches of his remarkable master's thesis entitled *Sistemática filogenética dos Gecarcinidae H. Milne Edwards (Gecarcinidae, Brachyura)* and Neil Cumberlidge for the reproduction of one figure (Cumberlidge *et al.* 2021). We thank P. K. L. Ng for bringing the article of Watabe (2007) to our attention. We would like to extend our warmest thanks to Sébastien Soubzmaigne (MNHN, Direction générale déléguée aux Collections) for all the photographs and his valuable assistance with the material. Jean-François Bernardet (Volunteer, MNHN) helped us sort the material and measure the specimens. We are pleased to acknowledge Laure Corbari (Curator of Crustacea collection, MNHN) for giving us access to the collection. Both authors are most grateful to Arthur Anker who generously provided several photographs taken *in situ* and Paulo P. G. Pachelle for two photographs *in situ* of *G. guanhumi*. We would particularly like to thank the editorial staff of *Zoosystema*, Laure Desutter-Grandcolas and Anne Mabille, for their professional and friendly assistance, and in particular for helpful discussion. We would like to express our sincere gratitude to the two referees, in particular Marcos Tavares who, through his considerable involvement, has greatly improved the manuscript with his constructive comments.

REFERENCES

Adamczewska A. M. & Morris S. 1996. — The respiratory gas transport, acid-base state, ion and metabolite status of the Christmas Island Blue Crab, *Cardisoma hirtipes* (Dana) assessed in situ with respect to immersion. *Physiological Zoology* 69 (1): 67-92. https://doi.org/10.1086/physzool.69.1.30164201

Adamczewska A. M. & Morris S. 2000a. — Locomotion, respiratory physiology, and energetics of amphibious and terrestrial crabs. *Physiological and Biochemical Zoology* 73 (6): 706-725. https://doi.org/10.1086/318099

Adamczewska A. M. & Morris S. 2000b. — Ecology and behavior of *Gecarcoidea natalis*, the Christmas Island red crab, during the annual breedin migration. *Biological Bulletin* 200 (3): 305-320. https://doi.org/10.2307/1543512

Alcock A. 1900. —The Brachyura Catometopa, or Grapsoidea. Materials for a carcinological fauna of India. No. 6. *Journal of the Asiatic Society of Bengal*, 69 (II, 3): 279-456. https://doi.org/10.5962/bhl.title.15344

Alexander H. G. L. 1976. — *An ecological study of the terrestrial decapod Crustacea of Aldabra*. Ph. D. thesis, University of London.

Alexander H. G. L. 1979. — A preliminary assessment of the role of the terrestrial decapod crustaceans in the Aldabran ecosystem. *Philosophical Transactions of the Royal Society of London. Series B* Biological Science 286: 241-246. https://doi.org/10.1098/rstb.1979.0031

Alexander H. G. L. & Mantel H. 1968. — Adaptations of crustaceans to land: a summary and analysis of new findings. *American Zoologist* 8: 673-685. https://doi.org/10.1093/icb/8.3.673

Amaral A. C. Z., Cunha B. P., Checon H. H., Godoy A. S. *et al.* 2024. — The high biodiversity of benthic organisms in a coastal ecosystem revealed by an integrative approach. *Biota Neotropica* 24 (2): e20231583. https://doi.org/10.1590/1676-0611-BN-2023-1583

Ardila A., Navas G. & Reyes J. 2002. — *Libro rojo de invertebrados marinos de Colombia*. INVEMAR. Ministerio de Medio Ambiente. La serie de libros rojos de especies amenazadas de Colombia.

Balss H. 1934. — Die Krabben der Reise J. W. HARMS' nach der Christmas-Insel und dem Malaiischen Archipel. *Zoologischer Anzeiger* 106 (10): 225-237.

Bauer R. T. 2018. — Life-cycle and Seasonal Migrations, *in* Wellborn G. & Thiel M. (eds), *The Natural History of the Crustacea*, Volume 5: Life histories. Oxford University Press, New York: 203-229.

Berthold A. A. 1827.— *Latreille's natürliche Familien des Thierreichs. Aus dem Französischen. Mit Anmerkungen und Zusätzen.* Landes-Indstrie-Comptoirs, Weimar [Brachyuren (Brachyures) Brachyura: 252-259].

Bliss D. E. 1963. — The pericardial sacs of terrestrial Brachyura, *in* Whittington H. D. & Rolfe W. D. I. (eds), *Phylogeny and Evolution of Crustacea. Harvard University Museum of Comparative Zoology* Special Publication: 59-78.

Bliss D. E. 1968. — Transition from water to land in decapod crustaceans. *American Zoologist* 8 (3): 355-392. https://www.biodiversitylibrary.org/page/42295206

Bliss D. E. 1979. — From sea to tree: saga of a land crab. *American Zoologist* 19 (2): 385-410. https://doi.org/10.1093/icb/19.2.385

Bliss D. E. & Mantel L. H. 1968. — Adaptations of crustaceans to land: a summary and analysis of new findings. *American Zoologist* 8 (3): 673-685. https://www.jstor.org/stable/3881419

Bliss D. E., Van Montfrans J., Van Montfrans M. & Boyer J. R. 1978. — Behavior and growth of the land crab *Gecarcinus lateralis* (Fréminville) in southern Florida. *Bulletin of the American Museum of Natural History* 160: 111-152. http://hdl.handle.net/2246/563

Bouchard J.-M. & Poupin J. 2009. — Éléments d'écologie et nouveau recensement de la population du crabe terrestre *Gecarcinus planatus* Stimpson,1860 (Decapoda: Brachyura), *in* Charpy L. (coord.), *Clipperton, environnement et biodiversité d'un microcosme océanique*. Muséum national d'Histoire naturelle, Paris; IRD, Marseille, 420 p. (Patrimoines naturels; 68).

Bouchard J.-M., Poupin J., Cleva R., Dumas J. & Dinhut V. 2013. — Land, mangrove and freshwater decapod crustaceans of Mayotte region (Crustacea Decapoda). *Atoll Research Bulletin* 592: 1-69. https://doi.org/10.5479/si.00775630.592

Bright D. B. 1966. — The land crabs of Costa Rica. *Revista de Biologia Tropical* 14 (2): 183-203.

Bright D. B. & Hogue C. L. 1972. — A synopsis of the burrowing land crabs of the world and list of their arthropod symbionts and burrow associates. *Contributions in Science* 220: 1-58. https:/doi.org/10.5962/p.241205

Bucol A. A. & Alcala M. L. R. 2013. — Anchialine crustaceans (Crustacea: Decapoda) from Siquijor Island, Philippines. *Philippine Scientist* 50: 59-72.

Burggren W. W. & Mcmahon B. R. 1988 (eds). — *Biology of the land Crabs*. Cambridge University Press, Cambridge, 479 p.

Cabrera J. A. J. 1966. — Contribuciones carcinologicas. I. El primer estadio zoea en *Gecarcinus lateralis* (Fréminville) (Brachyura Gecarcinidae) procedente de Veracruz, Mexico. *Anales del Instituto de Biologia* 36: 173-187.

Cameron J. N. 1981. — Brief introduction to the land crabs of the Palau Islands: stages in the transition to air breathing. *Journal of Experimental Biology* 218: 1-5.

Cannicci S., Fratini S., Meriggi N., Bacci G., Iannucci A., Mengoni A. & Cavalieri D. 2020. — To the land and beyond: crab microbiomes as a paradigm for the evolution of terrestrialization. *Frontiers in Microbiology* 11: 375372. https://doi.org/10.3389/fmicb.2020.575372

Capart A. 1951. — Crustacés Décapodes Brachyures, *in Expédition océanographique Belge dans les eaux côtières africaines de l'Atlantique Sud (1948-1949). Résultats Scientifiques* 3 (1). Institut Royal des Sciences Naturelles de Belgique, Bruxelles: 11-205.

Carmona-Suárez C. A. 2011. — Present status of Cardisoma *guanhumi* Latreille, 1828 (Crustacea: Brachyura Gecarcinidae) populations in Venezuela. *Interciencia* 36 (12): 908-913.

Carmona-Suárez C. A. 2015. — Cangrejo de tierra, *Cardisoma guanhumi*, *in* Rodriguez J. P., Garcia-Rawlins A. & Rojas-Suarez F. (eds), *Libro Rojo de la Fauna Venezolana* (*Cuarta edición*). Provita y Fundación Empresas Polar. www.especiesamenazadas.org/taxon/arthropoda/crustacea/decapoda/gecarcinidae/cardisoma/cangrejo- de-tierra

Carmona-Suárez C. A. & Guerra-Castro E. J. 2018. — Populations of *Cardisoma guanhumi* Latreille *in* Latreille, Le Peletier, Serville & Guérin, 1828 (Decapoda: Brachyura: Gecarcinidae) in mangrove forests and coastal grasslands in Venezuela. *Journal of Crustacean Biology* 38 (6): 1-9. https:// doi. org/ 10. 1093/jcbiol/ ruy074

Chace F. A. & Hobbs H. H. 1969. — The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. Bredin-Archbold-Smithsonian Biological Survey of Dominica. *United States National Museum Bulletin* 292: 1-258. https://doi.org/10.5479/si.03629236.292.1

Chen J., Xing Y., Yao W., Zhang C., Zhang Z., Jiang G. & Ding Z. 2018. — Characterization of four new mitogenomes from Ocypodoidea & Grapsoidea, and phylomitogenomic insights into thoracotreme evolution. *Gene* 675: 27-35. https://doi.org/10.1016/j.gene.2018.06.088

Chu K. H. C., Schubart C. D., Shih H.-T. & Tsang L. M. 2015. — Genetic diversity and evolution of Brachyura (Chapter 71-13), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & Vaupel Klein J. C. Von (eds), *Treatise on Zoology – Anatomy, Taxonomy, Biology*. Crustacea. Decapoda: Brachyura, 9C-2. Brill, Leiden and Boston: 775-820.

Clark P. F. 2025. — Dating the crustacean text and plates by Henri Milne Edwards and Pierre Hippolyte Lucas in Alcide d'Orbigny's Voyage dans l'Amérique méridionale (1835-1847). *Archives of Natural History* 52 (2): 292-299. https://doi.org/10.3366/anh.2025.0994

Colavite J., Tavares M., Braga De Mendonça Jr. J. & Santana W. 2021. — The first zoeal stage of *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Crustacea: Brachyura: Gecarcinidae), with comments on the validity of the genus. *Thalassas*: *An International Journal of Marine Sciences* 37: 767-773. https://doi.org/10.1007/s41208-021-00343-y

Costlow J. D. & Bookhout C. G. 1968. — The complete larval development of the land crab *Cardisoma guanhumi* Latreille in the laboratory (Brachyura Gecarcinidae). *Crustaceana* Supplementl 2: 259-270.

Cuesta J. A. & Anger K. 2005. — Larval morphology and salinity tolerance of a land crab from West Africa, *Cardisoma armatum* (Brachyura: Grapsoidea: Gecarcinidae). *Journal of Crustacean Biology* 25 (4): 640-654. https://doi.org/10.1651/C-2551.1

Cuesta J. A., Liu H.-C. & Schubart C. D. 2002. — First zoeal stages of *Epigrapsus politus* Heller, *E. notatus* (Heller) and *Gecarcoidea lalandii* H. Milne Edwards, with remarks on zoeal morphology of the Gecarcinidae MacLeay [*sic*] (Crustacea: Brachyura). *Journal of Natural History* 36 (14): 1671-1685.

Cuesta J. A., Garcia-Guerrero M. & Hendrickx M. E. 2007. — The complete larval development of *Johngarthia planatus* (Brachyura: Grapsoidea: Gecarcinidae) described from laboratory reared material, with notes on the affinity of *Gecarcinus* and *Johngarthia*. *Journal of Crustacean Biology* 27 (2): 263-277. https://doi.org/10.1651/C-2642.1

Cumberlidge N. & Ng P. K. L. 2009. — Systematics, evolution, and biogeography of the freshwater crabs, *in* Martin J. W., Crandall K. A. & Felder D. L. (eds), *Crustacean Issues: Advance in Decapod Crustacean Phylogenetics*. CRC Press, Leiden.

Cumberlidge N., Johnson E. C., Leever E. M., Soma J. B., Ahles K. M., Kamanli S. A. & Clark P. F. 2021. — The significance of female dimorphic characters of primary freshwater crabs for the systematics of Eubrachyura (Crustacea: Decapoda: Brachyura). *Journal of Crustacean Biology* 41 (4): 1-27. https://doi.org/10.1093/jcbiol/ruab058

Davie P. J. F. 2002. — Crustacea: Malacostraca. Eucarida (Part 2). Decapoda Anomura, Brachyura, *in* Wells A. & Houston W. W. K. (eds), *Zological Catalogue of Australia*. Vol. 19.3B. CSIRO Publishing, Melbourne: xiv + 641 p.

Davie P. J. F., Guinot D. & Ng P. K. L. 2015a. — Anatomy and functional morphology of Brachyura (Chapter 71-2), *in* Castro

P., Davie P. J. F., Guinot D., Schram F. R. & Vaupel Klein J. C. von (eds), *Treatise on Zoology –Anatomy, Taxonomy, Biology.* Crustacea. Decapoda: Brachyura, 9C-1. Brill, Leiden and Boston: 11-163.

Davie P. J. F., Guinot D. & Ng P. K. L. 2015b. — Phylogeny of Brachyura (Chapter 71-16), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & Vaupel Klein J. C. Von (eds), *Treatise on Zoology –Anatomy, Taxonomy, Biology*. Crustacea. Decapoda: Brachyura, 9C-2. Brill, Leiden and Boston: 921-979.

Davie P. J. F., Guinot D. & Ng P. K. L. 2015c. — Systematics and classification of Brachyura (Chapter 71-18), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & Vaupel Klein J. C. Von (eds), *Treatise on Zoology – Anatomy, Taxonomy, Biology*. Crustacea. Decapoda: Brachyura, 9C-2. Brill, Leiden and Boston: 1049-1130.

De Grave S., Pontcheff N. D., Ahyong S. T., Chan T.-Y., Crandall K. A., Dworschak P. C., Felder D. L., Feldmann R. M., Fransen C. H. J. M., Goulding L. Y. D., Lemaitre R., Low M. E. Y., Martin J. W., Ng P. K. L., Schweitzer C. E., Tan S. H., Tshudy D. & Wetzer R. 2009. — A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology* Supplement 21: 1-109.

Delfosse E. 1999. — Un crabe magnifique : le Tourlourou *Cardisoma armatum* Herklots, 1851(Crustacea Decapoda Gecarcinidae). *Bulletin n° 1 de l'association Phyllie* 15-20.

Diaz H. & Rodríguez G. 1977. — The branchial chamber in terrestrial crabs: a comparative study. *Biological Bulletin* 153: 485-504. https://doi.org/10.2307/1540602

Diez Garcia Y. L. 2014. — Lista actualizada de los cangrejos braquiuros (Decapoda: Brachyura) de Cuba. *Revista de Investigaciones Marinas* 34 (2): 74-93. http://www.cim.uh.cu/rim/

Diez Y. L. & Capote A. J. 2015. — List of marine crabs (Decapoda: Anomura and Brachyura) of shallow littoral of Santiago de Cuba, Cuba. *Check List* 11 (2): 1601. https://doi.org/10.15560/11.2.1601

Doi W., Kato S., Itoh D., Mizutani A. & Kohno H. 2019 — Distribution, size structure, and relative growth of *Epigrapsus politus* (Brachyura: Gecarcinidae) in a subtropical bay in Japan. *Crustacean Research* 48: 145-157.

Doi W., Itoh D., Mizutani A. & Kohno H. 2020. — Reproductive biology of the land crab *Epigrapsus politus* Heller, 1862 (Brachyura: Gecarcinidae) on Iriomote-jima, Japan. *Journal of Crustacean Biology* 40 (2): 200-208. https://doi.org/10.1093/jcbiol/ruaa003

Doi W., Mizutani A. & Kohno H. 2022. — Mating and burrow plugging behavior of *Cardisoma carnifex* on the Iriomote-jima Island in Japan. *Crustacean Research* 51: 137-145. https://doi.org/10.18353/crustacea.51.0_137

Donovan S. K. & Dixon H. L. 1998. — A fossil land crab from the late Quaternary of Jamaica (Decapoda, Brachyura, Gecarcinidae). *Crustaceana* 71: 824-826. https://www.jstor.org/stable/20106057

Duarte C. M., Dennison W. C., Orth R. J. W. & Carruthers T. J. B. 2008. — The charisma of coastal ecosystems: addressing the imbalance. *Estuaries and Coasts J CERF* 31: 233-238. https://doi.org/10.1007/s12237-008-9038-7

Ehrhardt J. P. 1968a. — Recensement en 1968 de la population de *Gecarcinus planatus* Stimpson sur l'atoll de Clipperton. *Rapport particulier n° 40, CRSSA/BIO-ECO*, Paris, 9 p.

Ehrhardt J. P. 1968b. — Expériences de survie à l'immersion du crabe terrestre *Gecarcinus planatus* Stimpson. Centre de Recherche du Service de Santé des Armées, Division de Biologie Générale et Ecologie. Muséum national d'Histoire naturelle: Laboratoire d'études sur les Animaux Irradiés (L.E.R.A.I.) et Centre National de la Recherche Scientifique (CNRS): *Centre de Recherches sur les Zones Arides* 43: 1-8.

Ehrhardt J. P. 1973. — *Le comportement des Gecarcinidae, Brachyoures terrestres d'après les exemplaires de l'île de Clipperton*. Comptes Rendus du quatre-vingt-seizième Congrès des Sociétés Savantes, Toulouse 1971, Section des Sciences, Tome 3, Biologie générale et animale. Paris, Bibliothèque nationale: 437-452.

Ehrhardt J. P. & Niaussat P. 1968. — Les premiers stades du développement larvaire du Brachyoure gecarcinidé *Gecarcinus planatus* Stimpson. *CRSSA/MNHN/CNRS*, n° 44/ BIO-ECO, 9 p., plus Annexes 1 et 2 and bibliographie.

Elegbede I. O., Lawal-Are A. O. & Popoola T. R. 2015. — Size and growth of *Cardiosoma* [sic] *armatum* and *Cardiosoma* [sic] *guanhumi* as ecological parameters for mangrove ecosystem. *Journal of Marine Science: Research & Development* 5: 164. https://doi.org/10.4172/2155-9910.1000164

Emmerson W. D. 2016. — *A Guide to, and checklist for the Decapoda of Namibia, South Africa and Mozambique*. Volume 3. Cambridge Scholars Publishing: 1-711.

Entringer H. Jr & Srbek-Araujo A. C. 2023. — Habitat use, non-breeding groupings and chromatic pattern in *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Decapoda, Gecarcinidae) in Trindade Island, South Atlantic Ocean. *Neotropical Biology and Conservation* 18 (1): 83-95. https://doi.org/10.3897/neotropical.18.e101409. https://www.scielo.br/j/nau/a/44HtqQzcWHrfqvsHDPJ9N6h/?lang=en

Etchian o. A., Dakouri r., Ble c. M., Lawal-are a. E. & Cuesta J. C. 2016. — Some ecological aspects of the gecarcinid land crab, *Cardisoma armatum* Herklots, 1851 (Crustacea, Brachyura, Gecarcinidae) from the estuarine region of the Comoe River, Côte d'Ivoire. *International Journal of Biological and Chemical Sciences* 10 (2): 457-474. https://doi.org/10.4314/ijbcs.v10i2.1

Farrelly C. A. & Greenaway P. 1992. — Morphology and ultrastructure of the gills of terrestrial crabs (Crustacea, Gecarcinidae and Grapsidae): adaptations for air-breathing. *Zoomorphology* 112 (1): 39-49. https://doi.org/10.1007/BF01632993

Farrelly C. A. & Greenaway P. 1993. — Land crabs with smooth lungs: Grapsidae, Gecarcinidae, and Sundathelphusidae ultrastructure and vasculature. *Journal of Morphology* 215 (3): 245-260. https://doi.org/10.1002/jmor.1052150306

Flores V., J. Paula J. & Dray T. 2003. — First zoeal stages of grapsoid crabs (Crustacea: Brachyura) from the East African coast. *Zoological Journal of the Linnean Society* 137: 355-383. https://doi.org/10.1046/j.1096-3642.2003.00054.x

Forest J. & Guinot D. 1966. — Campagne de la Calypso dans la Golfe de Guinée et aux Iles Principe, São Tomé et Annobon (1956). 16. Crustacés Décapodes: Brachyoures, *in Résultats Scientifiques des Campagnes de la Calypso VII. Annales de l'Institut Océanographique*, Paris, *nouvelle série* 44: 23-124.

Forsee R. A. & Albrecht M. 2012. — Population estimation and site fidelity of the land crab *Cardisoma Guanhumi* (Decapoda: Brachyura: Gecarcinidae) on Vieques Island, Puerto Rico. *Journal of Crustacean Biology* 32 (3): 435-442. https://doi.org/10.1163/193724012x626467

Fujita Y. 2017a. — Distributional records of four rare land crabs (Gecarcinidae) in Sakishima Island Group, southern Ryukyus, Japan. *Fauna Ryukyuana* 36: 19-26. [In Japanese, with Abstract and figure captions in English]. http://w3.u-ryukyu.ac.jp/naruse/lab/Fauna_Ryukyuana.html

Fujita Y. 2017b. — Fauna of decapod crustaceans in Minna-jima Island, Miyako Island Group, southern Ryukyu Islands, Japan. *Miyako-shi Sogo Hakubutsukankiyo* 21: 91-110. [in Japanese with English abstract]

Fujita Y. 2017c. — *Epigrapsus notatus* (Heller, 1865), *in* Okinawa Prefecture (ed.), *Threatened Wildlife in Okinawa*, Third Edition (Animals) — Red Data Okinawa — Okinawa Prefecture, Naha, 336 p. [In Japanese].

Fujita Y. 2017d. — New distributional records of two cavernicolous decapods from Yonaguni-jima Island, Yaeyama Island Group, southern Ryukyus, Japan. *Fauna Ryukyuana* 34: 7, 8. [In Japanese]

Gibson-Hill C. A. 1947. — Field notes on terrestrial crabs. *Raffles Bulletin of Zoology* 18: 43-52.

Gifford C. A. 1962. — Some observations on the general biology of the land crab, *Cardisoma guanhumi* (Latreille), in South Florida. *Biological Bulletin* 123 (1): 207-223. https://doi.org/10.2307/1539516

Glaessner M. F. 1980. — New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia* 104 (6): 171-192. https://biostor.org/reference/114219

Gmittner T. E. & Wotton R. M. 1953. — Crabs from the Island of St. Thomas. *Proceedings of the Pennsylvania Academy of Science* 27: 261-272.

Gomez L. D. 1977. — La mosca del cangrejo terrestre *Cardisoma crassum* Smith (Crustacea: Gecarcinidae) en la Isla del Coco, Costa Rica. *Revista de Biología Tropical* 25 (1): 59-63.

Gomes S. O., Souza I. G. B., Santos M. F., Silva G. R., Albrecht M., McKinley A. S., Bentzen P. & Diniz F. M. 2019. — Discovery of novel NGS-mined microsatellite markers and an exploratory analysis of genetic differentiation between two Western Atlantic populations of *Cardisoma guanhumi* Latreille, 1825 (Decapoda: Brachyura: Gecarcinidae). *Journal of Crustacean Biology* 39 (2): 181-18. https://doi.org/10.1093/jcbiol/ruy115

Green P. T. 1997. — Red crabs in rain forest on Christmas Island, Indian Ocean: activity patterns, density and biomass. *Journal of Tropical Ecology* 13 (1): 17-38. https://www.jstor.org/stable/2559891

Green P. T. 2004a. — Field observations of moulting and moult increment in the Red Land Crab, *Gecarcoidea natalis* (Brachyura Gecarcinidae) on Christmas Island (Indian Ocean). *Crustaceana* 77 (1): 125-128.

Green P. T. 2004b. — Burrow dynamics of the Red Land Crab *Gecarcoidea Natalis* (Brachyura, Gecarcinidae) in rain forest on Christmas Island (Indian Ocean). *Journal of Crustacean Biology* 24 (2): 340-349. https://doi.org/10.1651/C-2447

Greenaway P. 1988. — Ion and water balance, *in* Burggren W. W. & McMahon B. R. (eds), *Biology of the land crabs*. Cambridge: Cambridge University Press: 211-248.

Greenaway P. 1999. — Physiological diversity and the colonisation of land, *in* Schram F. R., Vaupel Klein J. C. von (eds), *Proceedings of the fourth international Crustacean congress*, vol. I, Amsterdam, The Netherlands, 20-24 July 1998. Leiden, Brill Academic Publishers: 823-842.

Greenaway P. & Raghaven S. 1998. — Digestive strategies in two species of leaf-eating land crabs (Brachyura: Gecarcinidae) in a rain forest. *Physiological and Biochemical Zoology* 71: 36-44. https://doi.org/10.1086/515882

Guinot D. 1977a. — *Données nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyoures*. Unpulished doctoral thesis, Université Pierre et Marie Curie, 2 vols. i-xv + 1-486 + xvi-xxiv, 56 unnumbered pages, 78 figs, 31 pls, 14 tables.

Guinot D. 1977b. — Proposition pour une nouvelle classification des Crustacés Décapodes Brachyoures. *Comptes Rendus hebdomadaires des séances de l'Academie des Sciences (Paris), sér. D*, 285: 1049-1052.

Guinot D. 1978. — Principes d'une classification évolutive des Crustacés Décapodes Brachyoures. *Bulletin biologique de la France et de la Belgique, nouv. sér.*, 112 (3): 211-292.

Guinot D. 1979. — *Morphologie et phylogenèse des Brachyoures*. Muséum national d'Histoire naturelle, Paris (Mémoires du Muséum national d'Histoire naturelle, Sér. A – Zoologie; 112): 1-354, pls 1-25.

Guinot D. 1985. — Crustacea (chapter restricted to brachyuran decapod Crustacea), *in* Richard G. (ed.), *Fauna and flora. A first compendium of French Polynesia sea-dwellers, volume I French Polynesian coral reefs*, Fifth International Coral Reef Congress, Tahiti: 446-455.

Guinot D. 1988. — Les crabes cavernicoles du monde. *Mémoires de Biospéologie* 15: 3-40.

Guinot D. 1994. — Decapoda Brachyura, *in* Juberthie C. & Decou V. (eds), *Encyclopaedia Biospeologica. Tome 1*. Société de Biospéologie, Moulis (CNRS) and Bucarest (Académie Roumaine): 165-179, figs 1-3, pl. 1.

Guinot D. & Bouchard J.-M. 1998. — Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema* 20 (4): 613-694. https://sciencepress.mnhn.fr/en/periodiques/zoosystema/20/4/evolution-des-systemes-de-maintien-de-l-abdomen-chez-les-brachyoures-crustacea-decapoda-brachyura

Guinot D., Tavares M. & Castro P. 2013. — Significance of sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zootaxa* 3665 (1): 1-414. https://doi.org/10.11646/zootaxa.3665.1.1

Guinot D., Ng N. K. & Rodríguez Moreno P. A. 2018. — Review of grapsoid families for the establishment of a new family for *Leptograpsodes* Montgomery, 1931, and a new genus of Gecarcinidae H. Milne Edwards, 1837 (Crustacea, Decapoda, Brachyura, Grapsoidea MacLeay, 1838). *Zoosystema* 40: 547-604. https://sciencepress.mnhn.fr/en/periodiques/zoosystema/40/26. https://doi.org/10.5252/zoosystema2018v40a26

Guinot D., Rodríguez Moreno P. A. & Toledano-Carrasco I. A. 2025. — The charismatic *Gecarcinus ruricola* (Linnaeus, 1758), type species of *Gecarcinus* Leach, 1814, with a neotype designation and genetic data, and new generic assignment, *Hartnollius* n. gen., for the three remaining species of the genus (Crustacea, Brachyura, Gecarcinidae). *Zoosystema* 47 (16): 261-314. https://doi.org/10.5252/zoosystema2025v47a16. http://zoosystema.com/47/16

Hansson B. S., Harzsch S., Knaden M. & Stensmyr M. C. 2011. — The neural and behavioral basis of chemical communication in terrestrial crustaceans, *in* Breithaupt T. & Thiel M. (eds), *Chemical communication in crustaceans*. New York: Springer: 149-173.

Hartnoll R. G. 1968. — Morphology of the genital ducts in female crabs. *Journal of the Linnean Society* (Zoology) 47: 279-300. https://doi.org/10.1111/j.1096-3642.1968.tb00512.x

Hartnoll R. G. 1974. — Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). *Crustaceana* 27 (2): 131-136. https://www.jstor.org/stable/20102127

Hartnoll R. G. 1982. — Growth, *in* Bliss D. E. & Abele L. G. (eds), *The Biology of Crustacea, vol. 2, Embryology, Morphology and Genetics*. Academic Press, New York: 119-116.

Hartnoll R. G. 1988a. — Evolution, systematics and geographical distribution, *in* Burggren W. W. & McMahon B. R (eds), *Biology of Land Crabs*. Cambridge University Press: 6-54.

Hartnoll R. G. 1988b. — Growth and moulting, *in* Burggren W. W. & McMahon B. R. (eds), *Biology of Land Crabs*. Cambridge University Press: 186-210.

Hartnoll R. G. 2010. — Chastity belts and planktotrophic larvae: constraints on gecarcinid reproductive behaviour, *in* Castro P., Davie P. J. F & Ng P. K.L. (eds), *Studies on Brachyura: a homage to Danièle Guinot*. *Crustaceana Monographs* 11: 153-171.

Hartnoll R. G. 2015. — Postlarval life histories (Chapter 71-7), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & Vaupel Klein J. C. von (eds), *Treatise on Zoology –Anatomy, Taxonomy, Biology*. Crustacea. Decapoda: Brachyura, 9 (C) (I). Brill, Leiden and Boston: 375-416.

Hartnoll R. G. & Clark P. F 2006. — A mass recruitment event in the land crab *Gecarcinus ruricola* (Linnaeus, 1758) (Brachyura: Grapsoidea: Gecarcinidae), and a description of the megalop. *Zoological Journal of the Linnean Society* 146 (2): 149-164. https://doi.org/10.1111/j.1096-3642.2006.00195.x

Hartnoll R. G., Mackintosh T. & Pelembe T. J. 2006. — *Johngarthia lagostoma* (H. Milne Edwards, 1837) on Ascension Island - a very isolated land crab population. *Crustaceana* 79: 197-215. https://www.jstor.org/stable/20107642

Hartnoll R. G., Baine M. S. P., Britton A., Grandas Y., James J., Velasco A. & Richmond M. G. 2007. — Reproduction of the black land crab, *Gecarcinus ruricola*, in the San Andrés Archipelago, western Caribbean. *Journal of Crustacean Biology* 27 (3): 425-436. https://doi.org/10.1651/S-2772.1

Hartnoll R. G., Broderick A. C., Godley B. J. & Saunders K. E. 2009. — Population structure of the land crab *Johngarthia lagostoma* on Ascension Island. *Journal of Crustacean Biology* 29: 57-61. https://doi.org/10.1651/08-2992.1

Hartnoll R. G., Broderick A. C., Godley B. J., Musick S., Pearson M., Stroud S. A. & Saunders K. E. 2010. — Reproductionin the land crab *Johngarthia lagostoma* on Ascension Island. *Journal of Crustacean Biology* 30 (1): 83-92. https://doi.org/10.1651/09-3143.1

Hartnoll R. G., Régnier-McKellar C., Weber N. & Weber S. B. 2014. — Return to the land; the stages of terrestrial recruitment in land crabs. *Crustaceana* 87: 531-539. https://doi.org/10.1163/15685403-00003294

Hartnoll R. G., Weber N., Weber S. B. & Liu H.-C. 2017. — Polymorphism in the chelae of mature males of the land crabs *Johngarthia lagostoma* and *Epigrapsus* spp. *Crustaceana* 90 (7-10): 931-951. https://doi.org/10.1163/15685403-000035

Hartono D. A. N., Ati D. W., Saputra1 E. F., Wicaksono F. R., Pramadaningtyas P. S., Yap C. K. & Setyawan A. D. 2025. — Spatial distribution and diversity of intertidal crustaceans in karstic beaches of southern Java, Indonesia. *Indo Pacific Journal of Ocean Life* 9 (1): 26-35. https://doi.org/10.13057/oceanlife/o090103

Herreid II C. F. 1963. — Observations on the feeding behavior of *Cardisoma guanhumi* (Latreille) in Southern Florida. *Crustaceana* 5: 176-180. https://www.jstor.org/stable/20141018

Herreid II C. F. & Gifford C. A. 1963. —The burrow habitat of the land crab *Cardisoma guanhumi* (Latreille). *Ecology* 44: 773-775. https://doi.org/10.2307/1933027

Heller C. 1862. — Neue Crustaceen gesammelt während der Weltumsegelung der k. k. Fregatte Novara, *Verhandlungen der Kaiserlich-Königlichen zoologisch-botanischen Gesellschaft in Wien* 12: 519-528.

Heller C. 1865.— Crustacean, *in Reise der* österreichischen *Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des commodores B. von Wüllerstorf-Urbair*, Zoologischer Theil, Zweiter Band, 3: 1-280.

Henmi Y. & Murai M. 1999. — Decalcification of vulvar operculum and mating in the ocypodid crab *Ilyoplax pusilla. Journal of Natural History* (London) 247: 133-137. https://doi.org/10.1111/j.1469-7998.1999.tb00201.x

Henning H. G. 1975. — Oekologische, ethologische und sinnesphysiologische Untersuchungen an der Landkrabbe *Cardisoma guanhumi* Latreille (Crustacea, Brachyura). *Forma et Functio* 8: 463-510. https://doi.org/10.1590/1519-6984.01913

Hicks J. 1985. — The breeding behaviour and migrations of the terrestrial crab *Gecarcoidea natalis* (Decapoda: Brachyura). *Australian Journal of Zoology* 33 (2): 127-142. https://doi.org/10.1071/ZO9850127

Hicks J., Rumpff H. & Yorkston H. 1984. — *Christmas Crabs*. Christmas Island Natural History Association, Christmas Island. (first edn).

Hicks J., Rumpff H. & Yorkston H. 1990. — *Christmas Crabs*. Christmas Island Natural History Association, Christmas Island. (2nd edn).

Hilgendorf F. 1888. — Bemerkungen über die Morphologie der Augenhöhle von *Gecarcinus* und über eine neue verwandte Gattung *Mystacocarcinus. Sitzungsbericht der Gesellschaft Naturforschender Freunde zu Berlin* 1888: 26-29.

Ho P.-H. 2003. — *Land crabs of the Kenting National Park*. Kenting National Park Board: 1-47.

Holthuis L. B. 1953. — Enumeration of the decapod and stomatopod Crustacea from Pacific coral islands. International Union of Biological Sciences. International Trust for Zoological Nomenclature, in *Atoll Research Bulletin Bulletin* 24: 1-66.

Holthuis L. B. 1959. — The Crustacea Decapoda of Suriname (Dutch Guiana). *Zoologische Verhandelingen* 44: 1-296, pls 1-16. https://repository.naturalis.nl/pub/317569/ZV1959044001.pdf

Holthuis L. B. 1977. — The Grapsidae, Gecarcinidae and Palicidae (Crustacea Decapoda) of the Red Sea. *Israël Journal of Zoology* 26: 141-192. https://doi.org/10.1080/00212210.1977.10688447

Huet N. & Poupin J. 2020. — First record of *Epigrapsus politus* Heller, 1862 from Réunion Island (Decapoda, Brachyura, Gecarcinidae). *Crustaceana* 93 (6): 661-670. https://doi.org/10.1163/15685403-bja10034

Husana D. E. M., Naruse T. & Kase T. 2010. — A new species of the genus *Karstarma* (Crustacea: Decapoda: Brachyura: Sesarmidae) from anchialine caves in the Philippines. *Raffles Bulletin of Zoology* 58: 51-55.

ICZN, International Commission on Zoological Nomenclature 1964. — *International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology*. London, 175 p.

ICZN, International Commission on Zoological Nomenclature 1999. — *International Code of Zoological Nomenclature.* International Commission of Zoological Nomenclature. Fourth Edition. Adopted by the association with the British Museum (Natural History), London, 338 p.

Jamieson B. G. M. & Tudge C. C. 2000. — Crustacea-Decapoda, *in* Adiyodi K. G. & Adiyodi R. G. (series eds), Jamieson B. G. M. (volume ed.), *Reproductive Biology of Invertebrates*. Volume I, Part C. Progress in Male Gamete Ultrastructureand Phylogeny. John Wiley and Sons. Chichester: 1-95

Jamieson B. G. M., Guinot D. & Richer De Forges B. 1996. — Contrasting spermatozoal ultrastructure in two thoracotreme crabs, *Cardisoma carnifex* (Gecarcinidae) and *Varuna litterata* (Grapsidae) (Crustacea: Brachyura). *Invertebrate Reproduction and Development* 29: 111-126.

Jão M. C., Duarte R. C., Freire A. S. & Pinheiro M. A. A. 2023. — Intraspecific color diversity and camouflage associated with ontogeny in an insular land crab. *Behavioral Ecology and Sociobiology* 77: 120. https://doi.org/10.1007/s00265-023-03394-8

Johnson D. S. 1965. — Land crabs. *Journal of the Malayan Branch of the Royal Asiatic Society* 38: 43-66.

Kannupandi T., Khan S., Thomas M., Sundaramoorthys S. & Natarajan R. 1980. — Larvae of the land crab *Cardisoma carnifex* (Herbst) (Brachyura: Gecarcinidae) reared in the laboratory. *Indian Journal of Marine Sciences* 9: 271-277.

Kingsley J. S. 1880. — Carcinological notes, No. IV. Synopsis of the Grapsidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1880: 187-224.

Karasawa H. & Kato H. 2001. — Decapoda, Isopoda and Stomatopoda, *in* Ikeya N., Hirano H. & Ogasawara K. (eds), The database of Japanese fossil type specimens described during the 20th Century. *Palaeontological Society of Japan*, Special Papers 39: 420-434.

Kobayashi H. & Naruse T. 2023. — A distant record of the cavernicolous land crab, *Discoplax gracilipes* (Crustacea: Decapoda: Gecarcinidae) from Japan. *Species Diversity* 28: 177-187. https://doi.org/10.12782/specdiv.28.177

Kobayashi G., Itoh H. & Nobuyoshi N. 2023. — Molecular phylogeny of thoracotreme crabs including nine newly determined mitochondrial genomes. *Zoological Science* 40: 1-11. https://doi.org/10.2108/zs220063

Köhnk S., Gorb S. N. & Brandis D. 2017. — The morphological and functional variability of pleon-holding mechanisms in selected Eubrachyura (Crustacea: Decapoda). *Journal of Natural History* 51 (35, 36): 2087-2132. https://doi.org/10.1080/00222933.2017.1355076

Krieger J., Braun P., Rivera N. T., Schubart C. D., Müller C. H. G. & Harzsch S. 2015. — Comparative analyses of olfactory systems in terrestrial crabs (Brachyura): evidence for aerial olfaction? *PeerJ*. https://doi.org/10.7717/peerj.1433

Lai J. C. Y., Shih H.-T. & Ng P. K. L. 2017. — The systematics of land crabs of the genus *Gecarcoidea* and recognition of a pseudocryptic species, *G. humei*, from the eastern Indian Ocean

(Crustacea: Decapoda; Gecarcinidae). *Invertebrate Systematics* 31: 406-426. https://doi.org/10.1071/IS16052

Latreille P. A. 1825-1828. — *in* Le Peletier A. L. M., Serville J. G. A & Guérin Méneville F. E. *Histoire naturelle. Entomologie, ou histoire naturelle des Crustacés, des Arachnides et des Insectes. Encyclopédie Méthodique* 10 (2): 681-685.

Leach W. H. 1814. — Custaceology; *in* Brewster D. (ed.), Edinburg Encycloplaedia 7 (2): 385-437.

Lindquist E. S., Krauss K. W., Green P. T., O'Dowd D. J., Sherman P. M. & Smith T. J. 2009. — Land crabs as key drivers in tropical coastal forest recruitment. *Biological Reviews* 84: 203-223. https://doi.org/10.1111/j.1469-185x.2008.00070.x

Linton S. M. & Greenaway P. 2007. — A review of feeding and nutrition of herbivorous land crabs: Adaptations to low quality-plant diets. *Journal of Comparative Physiology* B, 177: 269-286. https://doi.org/10.1007/s00360-006-0138-z

Lira S. M. A., Lima C. D. M., Teixeira I. A. & Schwamborn R. 2021. — The first zoeal stage of the yellow land crab *Johngarthia lagostoma* (Milne Edwards, 1837) (Decapoda: Brachyura: Gecarcinidae). *Zootaxa* 4990 (1): 192-200. https://doi.org/10.11646/zootaxa.4990.1.13

Liu H.-C. & Jeng M.-S. 2005. — Reproduction of *Epigrapsus notatus* (Brachyura: Gecarcinidae). *Taiwan Journal of Crustacean Biology* 25 (1): 135-140. https://doi.org/10.1651/C-2499

Liu H.-C. & Jeng M.-S. 2007. — Some reproductive aspects of *Gecarcoidea lalandii* (Brachyura: Gecarcinidae) in Taiwan. *Zoological Studies* 46: 347-354. http://www.bioone.org/doi/full/10.1651/C-2499

Liu Y., Yang T.-T., Xin Z.-Z., Liu Q.-N., Zhang D.-Z. & Tang B.-P. 2019. — The complete mitochondrial genome sequence of *Metaplax longipes* (Grapsoidea: Varunidae). *Mitochondrial DNA* part B- 4 (1): 1280-1282. https://doi.org/10.1080/23802359.2019.1574626

Locatelli E. R. 2013. — Preservation potential of gecarcinid land crabs (Decapoda, Brachyura, Gecarcinidae) from San Salvador. *Palaios* 28: 867-874. https://doi.org/10.2110/palo.2013.083

Lombardo R. C. 2025. — Size at sexual maturity in *Cardisoma crassum* (Brachyura: Gecarcinidae) from the Gulf of Montijo, Panama. *Revista Ciencias Marinas y Costeras* 17 (2): 107-127. https://doi.org/10.15359/revmar.17-2-6

Lombardo R. C. & Rojas M. 2022. — Burrow fidelity in the bue crab, *Cardisoma crassum* (Smith 1870) (Brachyura: Gecarcinidae) from the Ponuga River, Veraguas, Panama. *Nauplius* 30: e2022033. https://doi.org/10.1590/2358-2936e2022033

López-Victoria M. & Werding B. 2008. — Ecology of the endemic land crab *Johngarthia malpilensis* (Decapoda: Brachyura: Gecarcinidae), a poorly known species from the tropical Eastern Pacific. *Pacific Science* 624: 483-493. https://doi.org/10.2984/1534-6188(2008)62[483:EOTELC]2.0.CO;2

Luque J. 2017. — Fossil hermit and land crabs (Decapoda: Anomura, Brachyura) from the Quaternary of Antigua and Bermuda. *Journal of Crustacean Biology* 37 (2): 151-156. https://doi.org/10.1093jcbiol/rux007

Luque J., Schweitzer C. E., Santana W., Portell R. W., Vega F. J. & Klompmaker A. A. 2017. — Checklist of fossil decapod crustaceans from tropical America. Part I: Anomura and Brachyura. *Nauplius* 25: e2017025 (1-85). https://doi.org/10.1590/2358-2936e2017025

Luque J., Christy J. H., Hendy A. J. W., Rosenberg M. S., Portell R. W., Kerr K. A. & Palmer A. R. 2018. — Quaternary intertidal and supratidal crabs (Decapoda, Brachyura) from tropical America and the systematic affinities of fossil fiddler crabs. *Journal of Systematic Palaeontology* 16 (12), 1037-1055. https://doi.org/10.1080/14772019.2017.1362599

Luque J., Bracken-Grissom H., Ortega-Hernández J. & Wolfe J. 2024. — Fossil calibrations for molecular analyses and divergence time estimation for true crabs (Decapoda: Brachyura). *Palaeontologia Electronica* 27 (2): a38. https://doi.org/10.26879/1332

MacLeay W. S. 1838. — On the Brachyurous Decapod Crustacea brought from the Cape by Dr Smith, in Smith A., *Illustrations of the Annulosa of South Africa; being a Portion of the Objects of Natural History Chiefly Collected during an Expedition into the Interior of South Africa, under the Direction of Dr. Andrew Smith in the Years 1834, 1835, and 1836; Fitted out by 'The Cape of Good Hope Association for Exploring Central Africa', Invertebratae.* Smith, Elder & Co., London: 53-71, pls 2, 3.

Man J. G. de 1879. — On some new or imperfectly known podophthalmous Crustacea of the Leyden Museum. *Notes from the Leyden Museum* 1 (2): 53-73. https://zenodo.org/badge/DOI/10.5281/zenodo.16147039.svg

Manning R. B. & Holthuis L. B. 1981. — West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306: i-xii, 13-379.

Marin I. N. & Tiunov A. V. 2023. — Terrestrial crustaceans (Arthropoda, Crustacea): taxonomic diversity, terrestrial adaptations, and ecological functions. *Zookeys* 1169: 95-162. https://doi.org/10.3897/zookeys.1169.97812

Martin J. W. & Davis G. E. 2001. — An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series* 39: 1-124.

Masagca J. T. 2020. — Freshwater and semi-terrestrial crab fauna of selected areas in Southern Luzon, Philippines. *American Journal of Zoology* 3 (1): 26-34. https://doi.org/10.11648/j.ajz.20200301.15

McGaw I. J., McSweeney M. T., Bigelow W. F., Gaitor K. T., Seamone S. G., O'Shea O. R., Higgs N. D., Brittain C. & Kuenzi M. T. 2025. — Harvesting practices and local ecological knowledge (LEK) of Bahamian Land Crabs: bridging gaps between traditional and scientific knowledge. *Animals* 15: 2941. https://doi.org/10.3390/ani15202941

McLay C. L. & Ryan P. A. 1990. —The terrestrial crabs *Sesarma* (*Sesarmops*) *impressum* and *Geograpsus crinipes* (Brachyura, Grapsidae, Sesarminae) recorded from the Fiji Is. *Journal of the Royal Society of New Zealand* 20 (1): 107-118. https://doi.org/10.1080/03036758.1990.10426735

Miers E. J. 1886. — Report on the Brachyura collected by H.M.S. Challenger during the Years 1873-76. *Report on the Scientific Results of the Voyage of H. M. S. Challenger* 17 (49): i-xlix 1-362, pis 1-29. https://biodiversitylibrary.org/page/49400162

Milne Edwards A. 1867. — Description de quelques espèces nouvelles de Crustacés Brachyoures. *Annales de la Société Entomogique de France* (4) 7: 263-288. https://biostor.org/reference/102346

Milne Edwards A. 1873. — Recherches sur la faune carcinologique de la Nouvelle-Calédonie. *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris* 9: 155-332, pIs 4-18. https://doi.org/10.5962/bhl.title.10410

Milne Edwards H. 1837. — *Histoire Naturelle des Crustacés comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux.* Librairie Encyclopédique de Roret, Paris. vol. 2: 1-531. https://www.biodiversitylibrary.org/page/16093809

Milne Edwards H. 1851. — Observations sur le squelette tégumentaire des Crustacés décapodes, et sur la morphologie de ces animaux. *Annales des Sciences naturelles sér. 3* (Zoologie) 16: 221-291 [1-71], pls 8-11.

Milne Edwards H. 1853. — Mémoire sur la famille des Ocypodiens, suite. *Annales de Sciences Naturelles Ser. 3* Zool. 20: 163-228. https://www.biodiversitylibrary.org/page/35466171

Monod T. 1956. — Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut français d'Afrique Noire* 45: 1-674.

Morris S. 2005. — Respiratory and acid-base responses during migration and to exercise by the terrestrial crab *Discoplax* (*Cardisoma*) *hirtipes*, with regard to season, humidity and behavior. *Journal of Experimental Biology* 208 (22): 4333-4343. https://doi.org/10.1242/jeb.01918

Mosna E. E. D., Oliveira M. A. M., João M. C. A. & Pinheiro M. A. A. 2025a. — Reproductive potential of the endangered land crab, *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Brachyura: Gecarcinidae), from Trindade Island, Brazil. *Nauplius* 33: e20250549. https://doi.org/10.1590/2358-2936e20250549

Mosna E. E. D., Pinheiro M. A. A., João M. C. A., Zara F. J. & Garcia-Bento M. A. 2025b. — Reproductive system of the insular yellow crab *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Brachyura: Gecarcinidae) from production to the storage of seminal fluid. *Journal of the Marine Biological Association of the United Kingdom* 105: e134, 1-16. https://doi.org/10.1017/S0025315425100842

Muñoz I., García-Raso J. E. & Cuesta J. A. 2025a. — A new varunid subfamily (Decapoda, Brachyura, Grapsoidea, Varunidae) for crabs from European and West African waters, with the description of two new genera and two new species. *Ecology and Evolution* 15: e71712. https://doi.org/10.1002/ece3.7171

Muñoz I., García-Raso J. E., Sánchez Chillón B. & Cuesta J. A. 2025b. — Marine crabs from African Waters housed in the Museo Nacional de Ciencias Naturales (MNCN-CSIC) — An opportunity for biogeographic and systematic studies — Part II: Thoracotremata. *Diversity* 17: 689 (1-42). https://doi.org/10.3390/d17100689

Murniati D. C. 2023. — The divesity and distribution of Gecarcinidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura), a potential land crab as a valuable food resource, in Indonesia. *IOP Conf. Series: Earth and Environmental Science* 1275: 012038. https://doi.org/10.1088/1755-1315/1275/1/012038

Musick S., Pearson M., Stroud S. A. & Saunders K. E. 2010. — Reproduction in the land crab *Johngarthia lagostoma* on Ascension Island. *Journal of Crustacean Biology* 30: 83-92. https://www.jstor.org/stable/27753981

Naruse T. 2005. — *Epigrapsus notatus* (Heller, 1865), *in* Okinawa Prefecture (ed.) *Threatened Wildlife in Okinawa, Second Edition (Animals)* – Red Data Okinawa – Okinawa Prefecture, Naha. p. 220. [In Japanese]

Naruse T., Shih H.-T., Fujita Y., Mendoza J. C. E. & Ng P. K. L. 2018. — Size-associated morphological changes in *Epigrapsus notatus* (Heller, 1865) and the taxonomic status of *E. villosus* Ng, 2003 (Crustacea: Decapoda: Brachyura: Gecarcinidae). *Raffles Bulletin of Zoology* 66: 208-216.

Nauck E. 1880. — Das Kaugerüst der Brachyuren. *Zeitschrift* für *wissenschaftliche Zoologie* 34: l-69.

Ng N. K., Davie P. J. F., Schubart C. D. & Ng P. K. L. 2007. — Xenograpsidae, a new family of grapsoid crabs (Crustacea: Brachyura) associated with shallow water hydrothermal vents. *Raffles Bulletin of Zoology* Supplement 16: 233-256.

Ng N. K., Rodríguez Moreno P. A., Naruse T., Guinot D. & Mollaret N. 2019. — Annotated catalogue of brachyuran types (Crustacea, Decapoda, Brachyura) in the Muséum national d'Histoire naturelle, Paris. Part II. Thoracotremata, superfamily Grapsoidea (Gecarcinidae and Grapsidae). *Zoosystema* 41 (7): 91-130. https://doi.org/10.5252/zoosystema2019v41a7. http://zoosystema.com/41/7

Ng P. K. L. 1998. — Crabs, *in* Carpenter K. E. & Niem V. H. (eds), *FAO Species identification guide for fishery purposes. Theliving marine resources ofthe Western Central Pacific. Volume 2. Cephalopods, crustaceans, holothurians and sharks*. Food & Agriculture Org., Rome: 1045-1155.

Ng P. K. L. 2003. — On a new species of *Epigrapsus* (Decapoda, Brachyura, Gecarcinidae) from a cave in Guam. *Crustaceana* 75 (10): 1219-1122. https://doi.org/10.1163/156854002321518153

Ng P. K. L. 2017. — On the extant type material of *Cardisoma hirtipes* Dana, 1851, and *Cardisoma obesum* Dana, 1851 (Crustacea: Brachyura: Gecarcinidae). *Nauplius* 25: e2017019 [p. 1-7]. https://doi.org/10.1590/2358-2936e2017019

Ng P. K. L. & & Clark P. F 2014. —The type of the land crab *Cardisoma hirtipes* Dana, 1851 (Crustacea: Brachyura: Gecarcinidae). *Zootaxa* 3860 (6): 596-599. https://doi.org/10.11646/zootaxa.3860.6.8

Ng P. K. L. & Davie P. J. F 2012. — The blue crab of Christmas Island, *Discoplax celeste*, new species (Crustacea: Decapoda: Brachyura: Gecarcinidae). *Raffles Bulletin of Zoology* 601: 89-100.

Ng P. K. L. & Guinot D. 2001. — On the land crabs of the genus *Discoplax* A. Milne Edwards, 1867 (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new cavernicolous species from the Philippines. *Raffles Bulletin of Zoology* 49 (2): 311-338.

Ng P. K. L. & Ng P. Y. C. 2021. — Land crabs (Crustacea: Brachyura: Gecarcinidae) of Singapore. *Nature in Singapore* 14: e2021001. https://doi.org/10.26107/NIS-2021-0001

Ng P. K. L. & Shih H.-T. 2014. — The systematics of the land crabs of the *Discoplax hirtipes* (Dana, 1851) species-group (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new species from the eastern Indian Ocean. *Raffles Bulletin of Zoology* Supplement 30: 109-135.

Ng P. K. L. & Shih H.-T. 2015. — The land crabs of the *Discoplax longipes* A. Milne Edwards, 1867 species group, with description of a new species from Guam (Crustacea: Decapoda: Brachyura: Gecarcinidae). *Zootaxa* 3980 (3): 379-405. https://doi.org/10.11646/zootaxa.3980.3.3

Ng P. K. L. & Shih H.-T. 2023. — *Tuerkayana latens*, a new species of land crab from French Polynesia, with a discussion on the phylogeny of the genus (Crustacea: Decapoda: Brachyura: Gecarcinidae). *Zoological Studies* 62: 10. https://doi.org/10.6620/ZS.2023.62-10

Ng P. K. L., Guinot D. & Davie P. J. F 2008. — Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology* Supplement 17: 1-286.

Ng P. K. L., Liu H.-C. & Wang C.-H. 1998. — A newly recorded land crab, *Epigrapsus notatus* (Heller, 1865) (Crustacea: Decapoda: Brachyura: Gecarcinidae) from Taiwan. *Journal of Taiwan Museum* 51 (2): 71-82.

Ng P. K. L., Nakasone Y. & Kosuge T. 2000. — Presence of the land crab, *Epigrapsus politus* Heller (Decapoda: Brachyura: Gecarcinidae) in Japan and Christmas Island, with a key to the Japanese Gecarcinidae. *Crustaceana* 73 (3): 379-381. https://doi.org/10.1163/156854000504336

Ng P. K. L., Wang C.-H., Ho P.-H. & Shih H.-T. 2001. — An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series*, Taipei, 11: 1-86.

Niaussat P. & Ehrhardt J. P. 1968. — Quelques aspects de l'éthologie du crabe terrestre *Gecarcinus planatus* Stimpson, de l'atoll de Clipperton. *Rapport particulier, CRSSA CRSSA/MNHN/CNRS, n° 39/BIO-ECO*, 22 p.

Oliveira T. Stauffer de 2014. — *Modificações esqueletais e apendiculares torácicas para captação de* água *do solo em caranguejos semiterrestres (Crustacea: Brachyura: Grapsoidea: Ocypodoidea)*. Museu de Zoologia, Université de São Paulo. Dissertacão Mestrado en Sistemática, Taxonomia Animal, Biodiversidade. São Paulo viii + 116 [In Portuguese] https://doi.org/10.11606/D.38.2014.tde-26112014-202417

Oliveira-Neto J. F. de, Pie M. R., Chammas M. A., Ostrensk A. & Boeger W. A. 2008. — Phylogeography of the blue land crab, *Cardisoma guanhumi* (Decapoda: Gecarcinidae) along the Brazilian coast. *Journal of the Marine Biological Association of the United Kingdom* 88 (07): 1417-1423. https://doi.org/ 10.1017/S0025315408001999

Orchard M. 2012. — *Crabs of Christmas island*. Christmas Island: Christmas Island Natural History Association.

Ortmann A. 1894. — Die Decapoden-Krebse des Strassburger Museums. VIII. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) Ill. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 2. Gruppe: Catometopa. *Zoologische Jahrbucher, Abtheilung fur Systematik, Geographie und Biologie der Theire* 8: 683-772, pl. 23.

Pan D., Sun Y., Shi B., Wang R., Ng P K. L., Guinot D., Cumberlidge N. & Sun H. 2024. — Phylogenomic analysis of brachyuran crabs using transcriptome data reveals possible sources of conflicting phylogenetic relationships within the group. *Molecular Phylogenetics and Evolution* 201: 108201.

Perger R. 2019. — A new species of *Johngarthia* from Clipperton and Socorro Islands in the Eastern Pacific Ocean (Crustacea: Decapoda: Gecarcinidae). *Pacific Science* 73: 285-304.

Perger R. & Wall A. 2014. — The description of a new species of the neotropical land crab genus *Gecarcinus* Leach, 1814 (Crustacea, Decapoda, Brachyura, Gecarcinidae). *ZooKeys* 435: 93-109.

Perger R., Vargas R. & Wall A. 2011. — *Johngarthia cocoensis*, a new species of Gecarcinidae MacLeay, 1838 (Crustacea, Decapoda, Brachyura) from Cocos Island, Costa Rica. *Zootaxa* 2911: 57-68.

Pianka E. R. 1970. — On r- and k- selection. *American Naturalist* 104 (940): 592-597.

Pinheiro M. A. A., Dias-Silva I., Kriegler N., Santana W. & João M. C. A. 2024. — Beneath the surface: co-habitation of recruits of the land crab *Johngarthia lagostoma* and its relevance for conservation on oceanic islands. *Journal of the Marine Biological Association of the United Kingdom* 104: e102 (1-9). https://doi.org/10.1017/S0025315424000869

Poore G. C. B. & Ahyong S. T. 2023. — *Marine Decapod Crustacea*. CSIRO Publishing, Australia: 890 p.

Poupin J. 1996. — Crustacea Decapoda of French Polynesia (Astacidea, Palinuridea, Anomura, Brachyura). *Atoll Research Bulletin* 442: 1-114.

Poupin J. & Juncker M. 2010. — *Guide des Crustacés Décapodes du Pacific sud. A Guide to the Decapod Crustaceans of the South Pacific*. Edition CRISP [Coral Reef Initiatives for the Pacific] et CPS [Secrétariat général de la Communauté du Pacifique], Nouméa, Nouvelle-Calédonie, 320 p.

Pregill G. K., Steadmann D. W., Olson S. L. & Grady F. V. 1988. — Late Holocene fossil Vertebrates from Burma quarry, Antigua, Lesser Antilles. *Smithsonian Contributions to Zoology* 463: 1-27.

Rathbun M. J. 1918. — The grapsoid crabs of America. *United States National Museum Bulletin* 97: 14-6. https://doi.org/10.5479/si.03629236.97.i

Reid D. G., Abello P., Kaiser M. J. & Warman C. G. 1997. — Carapace color, inter-molt duration and the behavioral and physiological ecology of the shore crab *Carcinus maenas*. *Estuarine, Coastal and Shelf Science* 44 (2): 203-211. https://doi.org/10.1006/ecss.1996.0212

Rendón-Hernández J. F., Pérez-Rostro C. I., González-Trujillo R., Arcos-Ortega G. F., Jiménez-Badillo M. de L. & Galindo-Cortes G. 2021. — Genetic diversity of the blue land crab *Cardisoma guanhumi* (Latreille 1825 in the Alvarado Lagoon System in Veracruz, gulf coast of Mexico. *Latin American Journal of Aquatic Research* 49 (1): 136-147.

Riascos J. M., Obonaga L. D. &| Ramos J. 2023. — Is the threatened land crab *Cardisoma guanhumi* conquering human-dominated systems? *Ecology and Evolution* 14: e10737. https://doi.org/10.1002/ece3.10737

Rice A. L. 1980. — Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* 35: 271-424. https://doi.org/10.1111/j.1096-3642.1980.tb00060.x

Richardson A. & Araujo P. B. 2015. — Lifestyles of Terrestrial Crustaceans, *in* Thiel M. & Watling L. (eds), *The Natural History of the Crustacea*, Volume 2: Lifestyles and Feeding Biology. Oxford University Press, New York, USA: 299-337.

Rodríguez-Rey G. T., Hartnoll R. G. & Solé-Cava A. M. 2016. — Genetic structure and diversity of the island-restricted endangered land crab, *Johngarthia lagostoma* (H. Milne Edwards, 1837. *Journal of Experimental Marine Biology and Ecology* 474: 204-209. https://doi.org/10.1016/j.jembe.2015.10.016

Sakai T. 1954. — Further notes on the Brachyuran Crustacea of the Hachijo Island. *Records of oceanographic works in Japan* 2 (1): 192-201.

Sakai T. 1976. — *Crabs of Japan and the Adjacent Seas*. Kodansha Ltd., Tokyo, 773 p., 251 pls.

Santana W., Dias-Silva I., João M. C. A., Tavares M. & Pinheiro M. A. A. 2025. — Application of DNA fingerprint to link megalopas and adults of *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Decapoda, Gecarcinidae) and description and illustration of the megalopa stage. *Marine Biodiversity* 55 (3): id.47. https://doi.org/10.1007/s12526-025-01531-2

Sasaki J. 2019. — *The Species List of Decapoda, Euphausiacea, and Stomatopoda, all of the World*. Local Independent Administrative Agency Hokkaido Research Organization, Resources Management and Enhancement Division, (Dôsôken) Abashiri Fisheries Research Institute, Fisheries Research Department: 1-14644.

Schubart C. D. & Cuesta J. A. 2010. — Phylogenetic relationships of the Plagusiidae Dana, 1851 (Brachyura), with description of a new genus and recognition of Percnidae Števčić, 2005, as an independent family, *in* Castro P., Davie P. J. F. & Ng P. K. L. (eds), *Studies on Brachyura: a homage to Danièle Guinot. Crustaceana Monographs* 11: 279-299. https://doi.org/10.1163/ej.9789004170865.i-366.171

Schubart C. D., Neigel J. E. & Felder D. L. 2000a. — Use of the mitochondrial 16S rRNA gene for phylogenetic and population studies of Crustacea, *in* Vaupel Klein J. C. von & Schram F. R. (eds), *The Biodiversity Crisis and Crustacea*. Vol. 2. *Crustacean Issues* 12: 817-830.

Schubart C. D., Cuesta J. A., Diesel R. & Felder D. L. 2000b. — Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetic Evolution* 15 (2): 179-190. https://doi.org/10.1006/mpev.1999.0754

Schubart C. D., Cuesta J. A. & Felder D. L. 2002. — Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. *Journal of Crustacean Biology* 22 (1): 28-44. https://doi.org/10.1651/0278-0372(2002)022[0028:GANBFF]2.0.CO;2

Schubart C. D., Cannicci M., Vannini M. & Fratini S. 2006. — Molecular phylogeny of grapsoid crabs (Decapoda, Brachyura) and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. *Journal of Zoological Systematics and Evolutionary Research* 44: 193-199. https://doi.org/10.1111/j.1439-0469.2006.00354.x

Schweitzer C. E., Velez-Juarbe J., Martinez M., Hull A. C., Feldmann R. M. & Santos H. 2008. — New Cretaceous and Cenozoic Decapoda (Crustacea: Thalassinidea, Brachyura) from Puerto Rico, United States Territory. *Bulletin of the Mizunami Fossil Museum* 3: 1-15.

Schweitzer C. E., Feldmann R. M. & Karasawa H. 2023. — *Treatise Online, Number 166. Part R, Revised, Volume 1, Chapter 8T21: Systematic Descriptions: Subsection Thoracotremata*. Paleontological Institute, Lawrence, Kansas, USA: 1-25. https://doi.org/10.17161/to.vi.20960

Sendler A. 1923. — Die Decapoden und Stomatopoden der Hanseatischen Südsee-Expedition. *Abhandlungen derSenckenbergischen Naturforschenden Gesellschaft* 38: 21-47.

Serène R. 1968. — *Prodromus for a check list of the non-planctontic marine fauna of South-East Asia. The Brachyura of the Indo-West Pacific Region*. Special Publication. Singapore national Academy of Seience 1: 33-112.

Sherman P. 2002. — Effects of land crabs on seedling densities and distributions in a mainland Neotropical rain forest. *Journal of Tropical Ecology* 18: 67-89. https://doi.org/10.1017/S0266467402002043

Shih H. T. 2012. — *Warrior – The Seashore Crabs of Dongsha Island*. Marine National Park, Kaohsiung, Taiwan, 159 p. [In Chinese]

Shih H. T. 2013. —Introduction of the gecarcinid land crabs of the world. *Taiwan Natural Science* 119: 22-37. [In Chinese]

Shinozaki-Mendes R. A., Silva J. R. F. & Hazin F. H. V. 2012. — Development of male reproductive system of the blue land crab *Cardisoma guanhumi* Latreille, 1828 (Decapoda:

Gecarcinidae). *Acta Zoologica (Stockholm)* 93: 390-399. https://doi.org/10.1111/j.1463-6395.2011.00513.x

Shokita S. 1971. — On the spawning habits of the land crab *Cardisoma hirtipes* Dana from Ishigaki Island, in the Ryukyu Islands. *Biological Magazine of Okinawa* 7: 27-32. [In Japanese].

Shokita S. & Shikatani N. 1990. — Complete larval development of the land-crab, *Cardisoma hirtipes* (Brachyura: Gecarcinidae) reared in the laboratory. *Researches on Crustacea* 18: 1-14.

Silbiger N. & Munguia P. 2008. — Carapace color change in *Uca pugilator* as a response to temperature. *Journal of Experimental Marine Biology and Ecology* 355 (1): 41-46. https://doi.org/10.1016/j.jembe.2007.11.014

Silva C. C., Schwamborn R. & Oliverira J. E. L. 2014. — Population biology and color patterns of the blue land crab, *Cardisoma guanhumi* (Latreille 1828) (Crustacea: Gecarcinidae) in the Northeastern Brazil. *Brazilian Journal of Biology* 77 (4): 949-958. https://doi.org/10.1590/1519-6984.01913

Sipman I. 2015. — Predation by *Gecarcoidea lalandii* (Crustacea, Gecarcinidae) on dextral and sinistral *Amphidromus inversus* (Gastropoda, Pulmonata, Camaenidae). *Vita Malacologica* 13: 57-61.

Sistema de Informação Sobe a Biodiversidade Brasileira (SIBBr) 2021. — *Cardisoma guanhumi* Latreille, 1825. https://ala-bie.sibbr.gov.br/ala-bie/species/232259

Sonnewald M. & Apel M. 2016. — In Remembrance of Michael Türkay (3 April 1948-9 September 2015), a Tower of Strength in the World of Crustaceans. *Journal of Crustacean Biology* 36 (1): 106-117. https://doi.org/10.1163/1937240X-00002400

Souza M. I. 2013. — *Morfologia comparada dos ductos genitais femininos e gonopodos masculinos de caranguejos Eubrachyura (Saint Laurent, 1980): reprodução em caranguejos Eubrachyura*. Doctoral thesis, Universidade Estadual Paulista, Instituto do Biocências de Rio Claro: i-vi + 1-140 p.

Souza L. P., Silva J. R. F., Ogawa C. Y. & Camargo-Mathias M. I. 2013. — Morphology of the female genital ducts of the blue land crab *Cardisoma guanhumi* (Crustacea: Brachyura: Gecarcinidae). *Acta Zoologica* (Stockholm) 94: 300-307. https://doi.org/10.1111/j.1463-6395.2011.00556.x

Souza M. I., Silva J. R. F., Araujo A. M. A. & Camargo-Mathias M. I. 2017. — Comparative morphology of the female genital ducts of seven eubrachyuran crabs (Saint Laurent, 1980). *Acta Zoologica* (Stockholm) 2016: 1-11. https://doi.org/10.1111/azo.1215

Sparacio C. A. 2018. — *Morphometry and indicative meaning of blue land crab (*Cardisoma guanhumi*) burrows.* Master Thesis, Department of Earth and Environmental Science.

Sun S., Jiang W., Yuan Z. & Sha Z. 2022. — Mitogenomes provide insights into the evolution of Thoracotremata (Brachyura: Eubrachyura). *Frontiers in Marine Science* 9: 848203. https://doi.org/10.3389/fmars.2022.848203

Sternberg R. von & Cumberlidge N. 2001a. — On the heterotreme-thoracotreme distinction in the Eubrachyura de Saint Laurent, 1980 (Decapoda: Brachyura). *Crustaceana* 74 (4): 321-338. https://doi.org/10.1163/156854001300104417

Sternberg R. von & Cumberlidge N. 2001b. — Notes on the position of the true freshwater crabs within the Brachyrhynchan Eubrachyura (Crustacea: Decapoda: Brachyura). *Hydrobiologica* 449(1/3): 21-39. https://doi.org/10.1023/A:1017560113027

Sternberg R. von, Cumberlidge N. & Rodríguez G. 1999. — On the marine sister groups of the freshwater crabs (Crustacea: Decapoda: Brachyura). *Journal of Zoological Systematics and Evolution Research* 37: 19-38. https://doi.org/10.1046/j.1439-0469.1999.95092.x

Števčić Z. 2005. — The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica* (*Fauna Croatica*) 14 Supplement 1: 1-159.

Takeda M. 2000. — Two species of crabs from an anchialine cave in Balicasag Island, the Philippines. *Omon Ronso* 50: 59-66.

Tavares M. D. S. 1989. — *Sistemática filogenética dos Gecarcinidae H. Milne Edwards (Gecarcinidae Brachyura).* Dissertação de Mestrado apresentada à Coordenação do Curso de Pós-Graduação em Zoologia da Universidade Federal do Rio de Janeiro. 174 p.

Tavares M. S. 1991. — Cladistic analysis and classification of the Gecarcinidae (Crustacea; Brachyura). *Memoirs of the Queensland Museum* 31: 213. https://doi.org/10.17082/j.2204-1478.31.1991.1991-25

Tavares M. D. S. & Mendonça Jr J. de Braga 2022. — Brachyuran crabs (Crustacea, Decapoda) from the remote oceanic Archipelago Trindade and Martin Vaz, South Atlantic Ocean. *Zootaxa* 5146 (1): 1-129. https://doi.org/10.11646/zootaxa.5146.1.1

Tesch J. J. 1918. —The Decapoda Brachyura of the Siboga Expedition. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga-Expeditie Decapoda Monographs* 39 (c): 1-148, 1-6 pls. https://biostor.org/reference/127779

Toledano-Carrasco I. A. 2016. — *Taxonomía y distribución geográfica de la superfamilia Grapsoidea (Crustacea: Decapoda: Brachyura) del golfo de México y Caribe*. Tesis de Licenciatura, Facultad de Ciencias, Universidad Nacional Autónoma de México. 214 p.

Toledano-Carrasco I. A. 2019. — *Revisión filogenética de las especies de cangrejos semiterrestres pertenecientes al género* Gecarcinus *Leach, 1814 (Brachyura: Grapsoidea: Gecarcinidae) de México*. Tesis de Maestría, Universidad Nacional Autónoma de México, México, 95 p.

Toledano-Carrasco I. A., Villalobos J. L. & Álvarez F. 2021. — A morphological, phylogenetic and phylogeographic reappraisal of the land crabs *Gecarcinus quadratus* De Saussure, 1853, and *G. lateralis* Fréminville *in* Guérin, 1832 (Decapoda: Gecarcinidae). Are they different specie? *Zootaxa* 5048 (2): 215-236. https://doi.org/10.11646/zootaxa.5048.2.4

Tsang L. M., Ahyong S. T., Shih H.-T. & Ng P. K. L. 2018. — Further polyphyly of pinnotheroid crabs: the molecular phylogenetic position of the polychaete-associated Aphanodactylidae. *Invertebrate Systematics* 32: 92-99. https://doi.org/10.1071/IS17038

Tsang C. T. T., Schubart C. D., Chu K. H., Ng P. K. L. & Tsang L. M. 2022. — Molecular phylogeny of Thoracotremata crabs (Decapoda, Brachyura): toward adopting monophyletic superfamilies, invasion history into terrestrial habitats and multiple origins of symbiosis. *Molecular Phylogenetics and Evolution* 1: 107596. https://doi.org/10.1016/j.ympev.2022.107596

Tsang L. M., Ma K. Y., Ahyong S. T., Chan T.-Y. & Chu K. H. 2008. — Phylogeny of Decapoda using two nuclear protein-coding genes: origin and evolution of the Reptantia. *Molecular Phylogenetics and Evolution* 48: 359-368. https://doi.org/10.1016/j.ympev.2008.04.009

Tsang L. M., Schubart C. D., Ahyong S. T., Lai J. C. Y., Au E. Y. C., Chan T.-Y., Ng P. K. L. & Chu K. H. 2014. — Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution* 31 (5): 1173-1187. https://doi.org/10.1093/molbev/msu068

Türkay M. 1970. — Die Gercarcinidae Amerikas. Mit einem Anhang uber *Ucides* Rathbun (Crustacea: Decapoda). *Senckenbergiana biologische* 51: 333-354.

Türkay M. 1973a. — Die Gercarcinidae Afrikas. *Senckenbergiana biologica* 54: 81-103.

Türkay M. 1973b. — Zur synonymie von *Epigrapsus notatus* and *Cardisoma carnifex* (Crustacea: Decapoda). *Senckenbergiana Biologica* 54: 105-110.

Türkay M. 1974a. — Die Gercarcinidae Asiens und Ozeaniens. *Senckenbergiana biologica* 55: 223-259.

Türkay M. 1974b. — Bemerkungen zu einigen Landkrabben (Crustacea, Decapoda). *Bulletin du Muséum national d'Histoire naturelle* (3) 2 (1973): 969-980.

Türkay M. 1977. — Die Identität von *Mystacocarcinus crenidens* and *Perigrapsus excelsus* (Crustacea, Decapoda, Gecarcinidae). *Mitteilungen aus dem Zoologischen Museum in Berlin* 53 (1): 157-159.

Türkay M. 1978. — Die fossilen Gecarcinidae (Crustacea: Decapoda). *Senckenbergiana Lethaea* 59: 29-35.

Türkay M. 1987. — Landkrabben. *Natur und Museum* 117 (5): 143 -150.

Türkay M. & Sakai K. 1976. — Die Gercarcinidae von Japan (Crustacea, Decapoda). *Researches on Crustacea* 7: 11-22.

Turner L. M., Hallas J. P., Smith M. J. & Morris S. 2013. — Phylogeography of the Christmas Island blue crab, *Discoplax celeste* (Decapoda: Gecarcinidae) on Christmas Island, Indian Ocean. *Journal of the Marine Biological Association of the United Kingdom* 93 (3): 703-714. https://doi.org/10.1017/S0025315412000598

Van der Meij S. E. T. & Schubart C. D. 2014. — Monophyly and phylogenetic origin of the gall crab family Cryptochiridae (Decapoda: Brachyura). *Invertebrate Systematics* 28: 491-500. https://doi.org/10.1071/IS13064

Vázquez-Lópes H., Cházaro-Olvera S., Vargas-Télles I. & Molina-Ortega M. G. 2017. — Description of first zoeal stage of *Cardisoma crassum* Smith, 1870 (Crustacea: Decapoda: Gecarcinidae). *Journal of Natural History* 51: 837-842. https://doi.org/10.1080/00222933.2017.1302611

Vogt G. 2012. — Ageing and longevity in the Decapoda (Crustacea): a review. *Zoologischer Anzeiger* 251: 1-25. https://doi.org/10.1016/j.jcz.2011.05.003

Vogt G. 2016. — Direct development and posthatching brood care as key features of the evolution of freshwater Decapoda and challenges for conservation, *in* Kawai T. & Cumberlidge N. (eds), *A global overview of the conservation of freshwater decapod crustaceans.* Springer, Cham, Switzerland: 169-198. https://doi.org/10.1007/978-3-319-42527-6_6

Wang Q., Wang J., Wu Q., Xu X., Wang P. & Wang Z. 2021. — Insights into the evolution of Brachyura (Crustacea: Decapoda) from mitochondrial sequences and gene order rearrangements. *International Journal of Biological Macromolecules* 170: 717-727. https://doi.org/10.1016/j.ijbiomac.2020.12.210

Wang Z., Zheng Y., Zhao X., Xu X., Xu Z. & Cui C. 2023. — Molecular phylogeny and evolution of the *Tuerkayana* (Decapoda: Brachyura: Gecarcinidae) genus based on whole mitochondrial genome sequences. *Biology* 12: 974. https://doi.org/10.3390/biology12070974

Watabe H. 2007. — Metabiology of decapods: construction of axiomatic system of the autopoiesis theory. *Ocean Policy Studies* 5: 31-125.

Watson-Zink V. M. 2021. — Making the grade: physiological adaptations to terrestrial environments in decapod crabs. *Arthropod Structure and Development* 64: 101089. https://doi.org/10.1016/j.asd.2021.101089

Watson-Zink V. M., Grosberg R. K., Lai J. C. Y. & Bay R. A. 2024. — Transcriptomic responses of gecarcinid land crabs to acute and prolonged desiccation stress. *BioRxiv*: 1-28. https://doi.org/10.1101/2024.07.03.601969

Willems K. A. 1982. — Larval development of the land crab *Gecarcinus lateralis lateralis* (Fréminville, 1835) (Brachyura: Gecarcinidae) reared in the laboratory. *Journal of Crustacean Biology* 2 (2): 180-201. https://doi.org/10.2307/1547998

Wolcott T. G. 1984. — Uptake of soil interstitial water: mechanisms and ecological significance in the ghost crab *Ocypode quadrata* and two gecarcinid land crabs. *Physiological Zoology* 57 (1): 161-184. https://doi.org/10.1086/physzool.57.1.30155978

Wolcott T. G. 1988. — Ecology, *in* Burggren W. W. & McMahon B. R (eds) *Biology of Land Crabs*. Cambridge University Press, NY: 55-96. https://doi.org/10.1017/CBO9780511753428

Wolfe J. M., Ballou L., Luque J., Watson-Zink V. M., Ahyong S. T., Barido-Sottani J., Chan T. Y., Chu K. H., Crandall K. A., Daniels S. R., Felder D. L., Mancke H., Martin J. W., Ng P. K. L., Ortega-Hernández J., Palacios Theil E., Pentcheff N. D., Robles R., Thoma B. P., Tsang L. M., Wetzer R., Windsor A. M. & Bracken-Grissom H. D. 2024. — Convergent adaptation of true crabs (Decapoda: Brachyura) to a gradient of terrestrial environments. *Systematic Biology* 73 (2): 247-262. https://doi.org/10.1093/sysbio/syad066

Wood-Mason J. 1874. — On a new genus and species (*Hylaeocarcinus humei*) of land-crabs from the Nicobar Islands. *Annals and Magazine of Natural History*, série 4, volume 14: 187-191.

Xin Z., Liu Y., Tang B., Zhou C. & Liu Q. 2018. — A comprehensive phylogenetic analysis of Grapsoidea crabs (Decapoda: Brachyura) based on mitochondrial cytochrome oxidase subunit 1 (*CO1*) genes. *Turkish Journal of Zoology* 42: 46-52. https://doi.org/10.3906/zoo-1703-46

Xu T., Bravo H. & Van der Meij S. E. T. 2023. — Phylomitogenomics elucidates the evolution of symbiosis in Thoracotremata (Decapoda: Cryptochiridae, Pinnotheridae, Varunidae). *Peer Journal*. https://doi.org/10.1016/10.7717/peerj.16217

Yaldwyn J. C. 1970. — Remarks, *in* Anonymus, *Stamp research leads to discovery*. *Philatelic Bulletin of New Zealand Post Office* 5: 2, 1 fig. Yaldwyn J. C. & Wodzicki K. 1979. — Systematics and ecology of the land crabs (Coenobitidae, Grapsidae and Gecarcinidae) of the Tokelau Islands, Central Pacific. *Atoll Research Bulletin* 235: i-iii, 1-55.

Yaldwyn J. C. & Wodzicki K. 1979. — *Systematics and ecology of the land crabs (Decapoda: Coenobitidae, Grapsidae and Gecarcinidae) of the Tokelau Islands, Central Pacific*. National Museum of New Zealand, Wellington, New Zealand: 1-53.

Zhang Y., Gong L., Lu X., Jiang L. & Zhang X. 2020. — Gene rearrangements in the mitochondrial genome of Chiromantes eulimene (Brachyura: Sesarmidae) and phylogenetic implications for Brachyura. International *Journal of Biological Macromolecules* 162: 704-714. https://doi.org/10.1016/j.ijbiomac.2020.06.196

Submitted on 3 November 2025;
accepted on 18 December 2025;
published on 31 March 2026.