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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)

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Leptograpsodes octodentatus (H. Milne Edwards, 1837), ♂ 51.8 × 68.3 mm, South Australia, MNHN-IU-2013-14993 (ex NMV J55301-1).

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Dedicated to the memory of Michael Türkay (1948-2015)

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ABSTRACT
A new family Leptograpsodidae n. fam. is erected to include an unusual genus of grapsoid crabs, *Leptograpsodes* Montgomery, 1931, represented by a burrowing species from South Australia *L. octodentatus* (H. Milne Edwards, 1837), with setal pouches on the coxae of pereiopods 2 to 4 that are evidence of a high degree of terrestrial adaptation. With nearly 600 extant species, the superfamily Grapsoidea MacLeay, 1838 encompasses a diverse range of morphologies and ecologies. Genetic data question its monophyly, whereas the inter- and intrarelationships of included taxa have not been recently examined through a morphological review using a reliable complex of characters (primarily, proepistome, thoracic sternum, male pleon, male genital region, male gonopore, and penis). The reevalution of the morphological characters of *L. octodentatus* in order to reappraise its proper taxonomical status has afforded us the opportunity to review most of grapsoids and, in particular, the Gecarcinidae H. Milne Edwards, 1837 (see Appendix), Grapsidae MacLeay, 1838, Varunidae H. Milne Edwards, 1853 (especially *Cyclograpsus* H. Milne Edwards, 1837), and Xenograpsidae N. K. Ng, Davie, Schubart & Ng, 2007. The discovery that *Leptograpsodes* shares some characters with Gecarcinidae, especially a stridulatory apparatus similar to that of *Discoplax* A. Milne-Edwards, 1867, a feature not previously recorded in either genus, has revealed the need to re-examine the taxonomy of Gecarcinidae. This resulted in an unexpected outcome. *Discoplax* must be restricted to its three troglobitic species: *D. longipes* A. Milne-Edwards, 1867 (type species), *D. gracilipes* Ng & Guinot, 2001, and *D. michalis* Ng & Shih, 2015. *Cardisoma* Latreille, 1828 *sensu stricto* only accommodates *C. guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828

(type species), *C. armatum* Herklots, 1861, *C. carnifex* (Herbst, 1796), and *C. crassum* Smith, 1870. A new genus, *Tuerkayana* n. gen. is hereby established to include two species previously assigned to *Cardisoma*: *T. rotundum* (Quoy & Gaimard, 1824) n. comb. (type species), *T. hirtipes* (Dana, 1851) n. comb., plus two others previously regarded as *Discoplax*: *T. celeste* (Ng & Davie, 2012) n. comb. and *T. magnum* (Ng & Shih, 2014) n. comb. Compared to Varunidae, *Leptograpsodes* bears a superficial resemblance to *Cyclograpsus* H. Milne Edwards, 1837, a paraphyletic genus that must be restricted to its type species *C. punctatus* H. Milne Edwards, 1837 and only its closest congeners. The validity of the subfamilial taxon Heliceinae Sakai, Türkay & Yang, 2006 is recognised. The putative sister-group relationship of *Leptograpsodes* and *Xenograpsus* supported by molecular analyses of Schubart (2011) and Ip *et al.* (2015) is not confirmed by morphology, even if the two families share some traits. The synapomorphies of *Leptograpsodes* justify its separation from all grapsoid lineages as currently conceived. The use of previously overlooked traits, notably related to the thoracic sternum, proves to represent an optimal support for the brachyuran systematics and phylogeny, and presently to redefine the grapsoid taxonomical categories. The complete fusion of thoracic sternites 3 and 4 without any visible suture, even laterally, is proposed as a synapomorphy of Grapsoidea; this character state could be extented to other Thoracotremata in the future. Species of three genera *Leptograpsodes*, *Discoplax* and *Epigrapsus* are reported to exhibit stridulating structures (suborbital pars stridens and plectrum on inner margin of P1 merus). Some nomenclature issues, notably the authorship of the family-group name Gecarcinidae that is here credited to H. Milne Edwards, 1837, are addressed in the Appendix.

KEY WORDS
Grapsidae,
Varunidae,
Xenograpsidae,
Heliceinae,
Cyclograpsinae,
Cyclograpsus,
Discoplax,
Cardisoma,
thoracic sternum,
new combinations,
new genus,
new family.

RÉSUMÉ
Révision des familles de grapsoïdes en vue de l'établissement d'une nouvelle famille pour Leptograpsodes *Montgomery, 1931, et un nouveau genre de Gecarcinidae H. Milne Edwards, 1837 (Crustacea, Decapoda, Brachyura, Grapsoidea).*
Une famille nouvelle Leptograpsodidae n. fam. est établie pour inclure un genre singulier de crabe grapsoïde, *Leptograpsodes* Montgomery, 1931, représenté par une espèce fouisseuse de terriers dans le sud de l'Australie, *L. octodentatus* (H. Milne Edwards, 1837), qui présente des poches de soies sur la coxa des péréiopodes 2 à 4, signe d'un haut niveau d'adaptation terrestre. Avec près de 600 espèces actuelles, la superfamille des Grapsoidea MacLeay, 1838 englobe un large éventail de morphologies et d'écologies. Les données génétiques mettent en cause sa monophylie, tandis que les relations des taxons inclus n'ont pas été examinées récemment dans le cadre d'un examen morphologique utilisant un complexe fiable de caractères (principalement, proépistome, sternum thoracique, pléon mâle, région génitale mâle, gonopore mâle et pénis). Les caractères morphologiques de *L. octodentatus* ont été réexaminés afin de revoir son statut taxonomique. À cette occasion, la plupart des grapsoïdes ont été révisés, en particulier les Gecarcinidae H. Milne Edwards, 1837 (voir l'Appendice), les Grapsidae MacLeay, 1838, les Varunidae H. Milne Edwards, 1853 (surtout *Cyclograpsus* H. Milne Edwards, 1837), et les Xenograpsidae N. K. Ng, Davie, Schubart & Ng, 2007. La découverte que *Leptograpsodes* partage des caractères en commun avec les Gecarcinidae, notamment un appareil stridulatoire similaire à celui de *Discoplax* A. Milne-Edwards, 1867, un trait n'ayant été rapporté à ce jour chez aucun des deux genres, a montré la nécessité de réexaminer la taxonomie des Gecarcinidae. Il en est ressorti un résultat inattendu. *Discoplax* doit être réduit à ses trois espèces troglobies : *D. longipes* A. Milne-Edwards, 1867 (espèce type), *D. gracilipes* Ng & Guinot, 2001, et *D. michalis* Ng & Shih, 2015. *Cardisoma* Latreille, 1828 *sensu stricto* contient seulement *C. guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828 (espèce type), *C. armatum* Herklots, 1861, *C. carnifex* (Herbst, 1796), et *C. crassum* Smith, 1870. Un genre nouveau, *Tuerkayana* n. gen., est établi pour deux espèces précédemment assignées à *Cardisoma*: *T. rotundum* (Quoy & Gaimard, 1824) n. comb. (espèce type), *T. hirtipes* (Dana, 1851) n. comb., plus deux autres auparavant considérées comme appartenant à *Discoplax*: *T. celeste* (Ng & Davie, 2012) n. comb. et *T. magnum* (Ng & Shih, 2014) n. comb. En ce qui concerne les Varunidae, *Leptograpsodes* offre une ressemblance superficielle avec *Cyclograpsus* H. Milne Edwards, 1837, genre paraphylétique qui doit être restreint à son espèce type *C. punctatus* H. Milne Edwards, 1837 et à ses proches congénères. Le taxon sous-familial Heliceinae Sakai, Türkay & Yang, 2006 est reconnu valide. La relation putative de groupe-frère entre *Leptograpsodes* et *Xenograpsus*, étayée par les analyses moléculaires de Schubart (2011) et Ip *et al.* (2015), n'est pas confirmée par la morphologie, même si les deux familles partagent quelques caractères. Les synapomorphies de *Leptograpsodes* justifient sa séparation de toutes les lignées de grapsoïdes dans leur acception actuelle. Le recours à des caractéristiques auparavant négligées, notamment celles en relation avec le sternum thoracique, s'avère représenter un apport optimal de soutien à la systématique et la phylogénie des Brachyoures et, en l'occurrence, pour mieux définir les catégories taxonomiques de Grapsoidea. La fusion complète des sternites thoraciques 3 et 4, sans aucune suture visible, même latérale, est proposée comme synapomorphie des Grapsoidea ; ce caractère pourrait être étendu à tous les Thoracotremata. Les espèces des trois genres *Leptograpsodes*, *Discoplax* et *Epigrapsus* sont signalées comme ayant des structures de stridulation (pars stridens sous-orbitaire et plectrum sur le bord interne du mérus de P1). Quelques questions de nomenclature, notamment la paternité du nom du niveau famille Gecarcinidae portée ici au crédit d'H. Milne Edwards 1837, sont traitées dans l'Appendice.

MOTS CLÉS
Grapsidae,
Varunidae,
Xenograpsidae,
Heliceinae,
Cyclograpsinae,
Cyclograpsus,
Discoplax,
Cardisoma,
sternum thoracique,
combinaisons nouvelles,
genre nouveau,
famille nouvelle.

INTRODUCTION

During the elaboration of the Annotated Catalogue of brachyuran types of the superfamily Grapsoidea MacLeay, 1838 deposited in the Muséum national d'Histoire naturelle, Paris (N. K. Ng *et al.* in press), we were led to review the case of *Leptograpsodes webbhaysi* Montgomery, 1931 from South Australia, type species of the monotypic genus *Leptograpsodes* Montgomery, 1931. *Leptograpsodes webbhaysi*, promptly placed in synonymy with *Cyclograpsus octodentatus* H. Milne Edwards, 1837 (Balss 1935; Tweedie 1942; Bennett 1964), is currently known as *Leptograpsodes octodentatus* (H. Milne Edwards, 1837), a species widely distributed in southern Australia and known as the "burrowing shore crab" (see *Atlas of Living Australia website*; Taylor & Poore 2011).

While the type material of *L. octodentatus* from the King Island, Tasmania, could not be tracked in the Muséum national d'Histoire naturelle (MNHN) collection, two specimens found in the French institution proved to belong to the type series of *L. webbhaysi*, supposedly lost since its description by Montgomery in 1931 (Bennett 1964), and actually the property of the Western Australian Museum.

Examination of the type material of *Leptograpsodes webbhaysi* (Fig. 2E) has shown the need to retrace the events of this intriguing "depository" in the French museum and to select a neotype for *L. octodentatus*. The morphological features of the species have been recently provided and discussed by Poore (2004, as *L. octodentatus*), in addition to those previously described and figured by Montgomery (1931, as *L. webbhaysi*), Tweedie (1942, as *Brachynotus octodentatus*), George (1962, as *L. octodentatus*), and Griffin (1969, as *L. octodentatus*). However, the features of the thoracic sternum, the potential presence of a pleonal holding mechanism, the precise location of the male gonopore, the condition of the penis and related configurations of thoracic sternites 7 and 8 of *L. octodentatus* remained unknown. On the basis of larval and adult morphology, it turned out that *Leptograpsodes* was alternatively considered to be a sesarmid, a grapsid, a varunid, or it combined a mixture of grapsine and varunine characters (see Remarks, below).

Recent molecular studies contradict the inclusion of *Leptograpsodes octodentatus* within the Grapsidae MacLeay, 1838 or the Varunidae H. Milne Edwards, 1853. According to Schubart (2011: 476), based on sequences of the mitochondrial 16S rRNA gene, there was a high and significant probability for considering *Leptograpsodes* and *Xenograpsus* Takeda & Kurata, 1977 sister genera. So, in case of confirmation, *Leptograpsodes*, with its only known species from southern Australian coastal waters, "may be considered the only extant representative of the lineage that gave rise to the colonisation of shallow water hydrothermal vents". It should, however, be noted that the 2011 Schubart's study did not include any varunid, except for *Varuna litterata* (Fabricius, 1798) that was treated as outgroup. The multilocus approach used by Ip *et al.* (2015) has shown that the monophyly of the family Grapsidae was highly supported only when *Leptograpsodes octodentatus* was excluded and suggested as well a putative sister-group relationship to *Xenograpsus testudinatus* N. K. Ng, Huang & Ho, 2000, even its transfer into the family Xenograpsidae N. K. Ng, Davie, Schubart & Ng, 2007. In the same way, this work suffered from not including any varunid except for *Eriocheir sinensis* H. Milne Edwards, 1853 used as outgroup. Ip *et al.* (2015: 224) and Davie *et al.* (2015b: 958) recommended a thorough reexamination of the entire morphology of *Leptograpsodes*, notably of its gonopodal and sternal features. Deploring incongruences between the currently adopted classification of the Grapsidae and their molecular phylogenetics, Schubart (2011) and Ip *et al.* (2015) suggested evaluation of the true position of *Leptograpsodes* by more extensive genetic evidence in increasing taxa sampling that matched with the diversity of thoracotreme crabs. The xenograpsid affinities of *Leptograpsodes* have posed us the major challenge of estimating in this particular case to what extent genetic trees are sufficiently resolved at higher taxonomic levels to be consistent with results based on traditional taxonomy.

This situation required to reevalute the morphological characters of *Leptograpsodes* and compare them to other grapsoids, in order to reappraise its taxonomical status within the Grapsoidea: Gecarcinidae H. Milne Edwards, 1837, Grapsidae, Varunidae (especially with *Cyclograpsus* H. Milne Edwards, 1837), and Xenograpsidae, preceded by a brief revision of a representative number of these grapsoid families. Guinot (1978, 1979) initially proposed a new taxonomic system in which the former grapsid subfamilies should be raised to family level within the Grapsoidea. The present review appeared to be justified, in addition to the list of adult morphological characters applied to distinguish six thoracotreme families by N. K. Ng in her thesis (2006: 693, table 7) and the analysis of the relationships amongst main grapsoid families by N. K. Ng *et al.* (2007: fig. 4).

Accordingly to our investigations, the morphological reappraisal of *Leptograpsodes*, a genus that presently remains monotypic, shows that it is distinct from all grapsoid genera that we have examined. A major difficulty for its affiliation consists in the fact that a set of consistent diagnostic morphological characters is lacking, despite that Grapsoidea being "among the most studied groups in brachyuran phylogenetic analyses due to their high diversity and ecological importance" (Chu *et al.* 2015: 797). With nearly 600 extant species, the superfamily Grapsoidea encompasses an extremely diverse range of morphologies and ecologies. Our thorough morphological reappraisal does not pretend to be a complete revision of grapsoid taxonomy but tries to introduce new criteria, in addition to those upon which is based the traditional taxonomy, not clearly supported by synapomorphies (Guinot 1978, 1979; Guinot *et al.* 2013). The use of a more reliable complex of characters as additional tool for our revision (proepistome, thoracic sternum, its relationships with the male pleon, male genital region, male gonopore and penis) could reveal the validity, accuracy and consistency of parallel diagnoses that currently define the high-ranked grapsoid taxa and Brachyura in general. For example, that

the basal antennal article is immobile and locked against the inner orbital tooth laterally is "apparently a unique apomorphy" of Grapsoidea (N. K. Ng *et al.* 2007: 250) must be corrected to "basal antennal article mobile or immobile" (as done by Davie *et al.* 2015c: 1117) since it is completely movable in *Eriocheir* De Haan, 1835, *Cyrtograpsus* Dana, 1851, at a less degree in *Sesarma* Say, 1817. Consequently, in addition to the recent comments and figures provided by Poore (2004), the morphology of *Leptograpsodes* has been completed by additional data, and a comparison with other grapsoids has been fully reassessed. The question then arose of identifying the grapsoid family or subfamily that may accommodate *Leptograpsodes*. The available evidence from adult morphology does support the present recognition of a new family, Leptograpsodidae n. fam. The phylogenetic relationships with other grapsoid lineages are discussed. The value of morphological features, previously overlooked, notably related to the thoracic sternum, that represent an optimal support for the systematics and phylogeny of Brachyura in general, is also discussed.

MATERIAL AND METHODS

Our study was predominantly based on the type genera of most currently accepted grapsoid families or subfamilies and on the type species of all currently accepted genera, especially in genera supposed to be paraphyletic.

Measurements are provided in millimetres and reported as carapace length (cl) × carapace width (cw) respectively, taken at its maximum (including teeth or spines if present). The following abbreviations are used in the text: G1, first male pleopod, or first gonopod; G2, second male pleopod, or second gonopod; mxp1-mxp3, first to third maxillipeds; P1-P5, first to fifth pereopods (P1 as chelipeds; P2-P5 corresponding to ambulatory legs 1-4). The thoracic somites are numbered from 1 to 8. The thoracic sternal sutures are referred to by the number of the two thoracic sternites that they involve, and thus are numbered from 1/2 to 7/8. The description of the thoracic sternum only concerns the male, even though most of the fundamental characters are generally similar in the modified female sternum.

Abbreviations

ICZN	*International Code of Zoological Nomenclature*, here referred to as "*Code*";
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	Natural History Museum, previously British Museum (Natural History), London;
NMV	Museum Victoria, Melbourne, Victoria, Australia;
TMAG	Tasmanian Museum and Art Gallery, Hobart, Tasmania;
USNM	National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C;
WAM	Western Australian Museum, Welshpool, Australia;
ZRC	Zoological Reference Collection, Lee Kong Chian Natural History Museum (previously Raffles Museum of Biodiversity Research), National University of Singapore.

Comparative material

Superfamily Grapsoidea MacLeay, 1838
Family Gecarcinidae H. Milne Edwards, 1837
(for the authorship, see Appendix)

Cardisoma armatum Herklots, 1861, 1 ♂ 51.6 × 65.2 mm, Benin, Ouémé, Ekpè market, Dr D. Rondelaud coll. and leg. 1998, Guinot det. 1998, MNHN-IU-2017-11710 (= MNHN-B21986).

Cardisoma carnifex (Herbst, 1796), 1 ♂ 71.2 × 88.0 mm, French Polynesia, Society Islands, Tupai Atoll, Exp. SMCB, J. Poupin det., 13.V.1991, MNHN-IU-2013-14798.

Cardisoma guanhumi Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, 1 ♂ 56.5 × 68.0 mm, Antilles, M. Türkay vid., VI.1972, MNHN-IU-2013-14983 (= MNHN-B12270).

Discoplax gracilipes Ng & Guinot, 2001, paratypes, 2 ♂ 30.9 × 35.6 mm, 40.6 × 46.9 mm, Panglao Island, Bohol, Philippines, local villagers coll., 18.XII.2000, MNHN-IU-2014-11218 (= MNHN-B27771); paratypes, 2 ♂ 15.5 × 17.7 × mm, 26.3 × 29.6 mm, 1 ♀ 19.9 × 22.7 mm, Panglao Island, Bohol, Tawala Cave, in pools near entrance, coll. L. Liao *et al.*, 17.XII.2000, MNHN-IU-2014-11217 (= MNHN-B27770); paratype, 1 ♂ 15.5 × 17.7 mm, Panglao Islands, Bohol, Calingoob Cave, station 85-067, coll. T. M. Iliffe, 6.IV.1985, MNHN-IU-2014-11215 (= MNHN-B26951); paratype, 1 ♂ 15.8 × 18.0 mm, Panglao Islands, Bohol, Underpass Cave, station 85-077, T. M. Iliffe coll., MNHN-IU-2014-11216 (= MNHN-B26952); paratype, 1 ♀ 22.1 × 25.7 mm, Panglao Islands, Bohol, Tuala Cave, station 85-062, coll. T. M. Iliffe, 3.IV.1985, MNHN-IU-2014-11214 (= MNHN-B26950).

Discoplax longipes A. Milne-Edwards, 1867, holotype, ♂ 54.0 × 55.0 mm, New Caledonia, dry, MNHN-IU-2000-3763 (= MNHN-B3763) (see N. K. Ng *et al.* in press: fig. 2C); 1 ♂ 36.0 × 44.0 mm, New Caledonia, MNHN-IU-2017-10001 (= MNHN-B17134); 1 ♂ 61.7 × 71.9 mm, 1 ♀, Loyalty Islands, Ouvea Atoll, Cong-Ouloup Cave, coll. J.-P. Guillerm, 26.IX.1987, MNHN-IU-2017-10002 (= MNHN-B20150); 1 ♂ 32.4 × 37.2 mm, 1 ♀ 32.6 × 37 mm, Loyalty Islands, Lifou, Inegoj Cave, B. Séret coll., 2.IX.1993, D. Guinot det. 1993, MNHN-IU-2008-11402 (= MNHN-B24815); 1 ♀ 32.5 × 36.7 mm, 1 ♀, Loyalty Islands, Lifou, Inegoj Cave, 12.VIII.95, Guinot & Ng det. 1999, MNHN-IU-2017-8405 (= MNHN-B26944).

Gecarcinus lateralis Fréminville *in* Guérin, 1832, type, ♂ 36.7 × 47.2 mm, Guadeloupe, coll. Beaupertuis, dry, MNHN-IU-2000-3758 (= MNHN-B3758) (see N. K. Ng *et al.* in press: fig. 2F); 1 ♂ 42.0 × 56.0 mm, Guadeloupe, Grande Terre, Anse Vinaigri, Exp. Museum Antilles 1978, stn 13, 09.VI.1978, MNHN-IU-2017-8390 (= MNHN-B24656).

Gecarcinus quadratus Saussure, 1853, 1 ♂ 50.0 × 64.0 mm, Mexico, Estero El Verde Camacho, Sinaloa, 12.VII.1972, M. Hendrickx det., MNHN-IU-2017-8391 (= MNHN-B20900).

Gecarcinus ruricola (Linnaeus, 1758), 1 ♂ 55.0 × 76.0 mm, Cuba, de Boury coll. 1914, Bouvier det., M. Türkay vid., VI-1972, MNHN-IU-2017-8392 (= MNHN-B13155).

Gecarcoidea lalandii H. Milne Edwards, 1837, 1 ♂ 44.8 × 59.4 mm, Golfe de Siam, A. Krempff 1921, MNHN-IU-2017-8404 (= MNHN-B29590); 1 ♂ 52.0 × 73.3 mm, Papua New Guinea, Wonad I., Exp. PAPUA NIUGUINI, stn PM43, 29.XI.2012, MNHN-IU-2013-13254. (See Lai *et al.* 2017; N. K. Ng *et al.* in press).

Johngarthia lagostoma (H. Milne Edwards, 1837), lectotype, ♂ 63.7 × 82.4 mm, southern Atlantic, coll. Quoy & Gaimard, MNHN-IU-2000-3750 (= MNHN-B3750). The originally cited locality "Australasia" is inaccurate (see Türkay 1973; Tavares 1989; N. K. Ng *et al.* in press: fig. 2E).

Johngarthia planata (Stimpson, 1860), 1 ♂ 29.7 × 35.6 mm, Clipperton, Exp. CLIPPERTON 2005, J.-M. Bouchard coll. and det. 2005, MNHN-IU-2016-10760 (= MNHN-B29848); holotype of *Gecarcinus digueti* Bouvier, 1895, ♂ 46.3 × 69.0 mm, Baja California, coll. M. Diguet, E.-L. Bouvier det., MNHN-IU-2000-10951 (= MNHN-B10951). (See N. K. Ng *et al.* in press: fig. 2D).

Tuerkayana celeste (Ng & Davie, 2012) n. comb., 1 ♂ 44.4 × 52.2 mm, Australia, Christmas Island, Hosnie's Springs, coll. CI 2010 Expedition, 24.I.2010, det. *Discoplax celeste* (ZRC 2012.0171).

Tuerkayana aff. *hirtipes* (Dana, 1851) n. comb., 1 ♂ 61.0 × 79.0 mm, Loyalty Islands, Lifou Island, We cave, Richer de Forges coll. and det. *Discoplax hirtipes*, 14.VII.1993, MNHN-IU-2017-8397 (= MNHN-B24811). See Appendix, "Nomenclatural and taxonomical status of some species" *Gecarcinus hirtipes* Lamarck, 1818".

Tuerkayana magnum (Ng & Shih, 2014) n. comb., 1 ♂ 49.0 × 58.7 mm, Indonesia, Java, Cilacap, from dealer, coll. J. C. Y. Lai, 16.II.2017, det. *Discoplax magna* (ZRC 2017.0252); 1 ♀ 55.5 × 65 mm, Australia, Christmas Island, stn. C1-16, along road towards Dolly Beach, P. K. L. Ng coll., 23.I.2010 (ZRC 2012.0003). (The measurements do not correspond to those given by Ng & Shih (2014: 129) for the sample with same data and same registration number).

Tuerkayana rotundum (Quoy & Gaimard, 1824) n. comb., syntype ♂ 50.0 × 63.0 mm, Oceania, M. Guérin, Quoy & Gaimard det. *Thelphusa rotunda*, M. Türkay vid., VI.1972 and det. *Cardisoma rotundum*, dry, MNHN-IU-2000-3745 (= MNHN-B3745) (see N. K. Ng *et al.* in press: fig. 3B); 1 ♂ 28.5 × 36.0 mm, Lifou Island, Easo Cave, 17 m depth, B. Richer de Forges coll. and det., 20.VIII.1993, MNHN-IU-2017-8393 (= MNHN-B24813); 1 ♂ 36.0 × 44.0 mm, New Caledonia, abundant in AQUACAL breeding tanks of Saint Vincent Bay, MNHN-IU-2017-8396 (= MNHN-B17134); 1 ♂ 28.0 × 26.3 mm, Lifou Island, on the ground, coll. B. Richer de Forges, 18.IV.1993, MNHN-IU-2017-8395 (= MNHN-B24809); 1 ♀ 32.7 × 40.1 mm, Loyalty Islands, Caillot 1886, MNHN-IU-2017-11711 (= MNHN-B13141).

Epigrapsus notatus (Heller, 1865), 1 ♂ 25.3 × 30.0 mm, Taiwan, Hsiang Chiaowan, P. K. L. Ng coll., X.2012 (ZRC 2013.0039).

Epigrapsus politus Heller, 1862, 1 ♂ 10.6 × 13.0 mm, Indonesia, Sumatra, Atjeh, De Man det, M. Türkay vid. VI.1972, MNHN-IU-2017-10018 (= MNHN-B12585).

Family Glyptograpsidae Schubart, Cuesta & Felder, 2002

Glyptograpsus jamaicensis (Benedict, 1892), 1 ♂ 32.8 × 37.4 mm Jamaica, Portland, Reach fall, M. Schuh coll., 27.VI.1992, in deep pools beneath falls, MNHN-IU-2017-8401 (= MNHN-B27715).

Family Grapsidae MacLeay, 1838

Geograpsus crinipes (Dana, 1851), 1 ♂, 46.5 × 53.6 mm, French Polynesia, Tuamotu, Taiaro Atoll, Exp. SMCB, J. Poupin det., 12-20.II.1994, MNHN- IU-2013-14997 (= MNHN-B30304).

Geograpsus grayi (H. Milne Edwards, 1853), type, ♀ 34.1 × 42.1 mm, Australia, dry, MNHN-IU-2000-3421 (= MNHN-B3421) (see N. K. Ng *et al.* in press: fig. 3H); 1 ♂ 27.6 × 31.9 mm, NUK 111, no other data, MNHN-IU-2013-14989.

Goniopsis cruentata (Latreille, 1803), ♂ 40.9 × 49.8 mm, Martinique, coll. M. Plée, dry, MNHN-IU-2000-3407 (= MNHN-B3407) (see N. K. Ng *et al.* in press: fig. 3D); 1 ♂ 42.6 × 50.8 mm, 1 ♀, Rio de Janeiro, Pinheiros I., Drach coll. 1948, MNHN-IU-2013-14998.

Grapsus grapsus Lamarck, 1801, 1 ♂ 23.8 × 26.9 mm, Antilles, Guadeloupe, Grande Terre, Exp. Muséum Antilles, Stn 8, 06.VI.1978, MNHN-IU-2013-10764 (= MNHN-B24641).

Grapsus fourmanoiri Crosnier, 1965, syntype, ♂ 23.2 × 26.6 mm, Madagascar, MNHN-IU-2014-11212 (= MNHN-B11531) (see N. K. Ng *et al.* in press).

Leptograpsus variegatus (Fabricius, 1793), 1 ♂ 42.0 × 44.2 mm, South Western Australia, Albany District, entry 11-1921, ex South Australian Museum, MNHN-IU-2013-15000; 1 ♂ 41.4 × 46.8 mm, Lord Howe Island, Thetis Exp. 1898, entry 11.1921, ex South Australian Museum, MNHN-IU-2016-10763.

Metopograpsus latifrons (White, 1847), 1 ♂ 31.2 × 35.3 mm, Batavia, coll. M. Meder, holotype of *Metopograpsus maculatus* H. Milne Edwards, 1853, dry, MNHN-IU-2000-3554 (= MNHN-B3554).

Metopograpsus messor (Forsskål, 1775), 1 ♂ 13.0 × 18.0 mm, 2 ♀, Madagascar, Maromandia, R. Decary, MNHN-IU-2017-10009 (= MNHN-B12877).

Metopograpsus oceanicus (H. Jacquinot *in* Hombron & H. Jacquinot, 1846), lectotype, ♂ 32.5 × 38.1 mm, Poulo Han (= Hon Island, Papua New Guinea), coll. Hombron & Jacquinot, dry, MNHN-IU-2000-10992 (= MNHN-B10992) (see Castro 2011; N. K. Ng *et al.* in press: fig. 4D); 1 ♂ 22.3 × 28.8 mm, Dar es Salaam, Hartnoll coll. and det., MNHN-IU-2013-14996 (= MNHN-B12878).

Metopograpsus thukuhar (Owen, 1839), 1 ♂ 24.0 × 29.0 mm, French Polynesia, Rapa I., Exp. RAPA 2002, 08.XI.2002, Poupin det. 2003, MNHN-IU- 2017-10008 (= MNHN-B30076).

Pachygrapsus crassipes Randall, 1840, 1 ♂ 27.2 × 30.6 mm, California (USA), Pacific Grove, MNHN-IU-2013-14986 (= MNHN-B12892).

Planes minutus (Linnaeus, 1758), 1 ♂ 10.9 × 11.1 mm, Sargasso Sea, Ladmirault coll., MNHN-IU-2013-14999.

Family Percnidae Števčić, 2005

Percnon abbreviatum (Dana, 1851), 1 ♀ 11.3 × 14.6 mm, Clipperton I., Exp. CLIPPERTON, St. 3, 08.I.2005, MNHN-IU-2017-10017 (= MNHN-B30390).

Percnon affine (H. Milne Edwards, 1853), 1 ♂ 36.0 ×30.0 mm, French Polynesia, Moorea, M. Monteforte coll., Crosnier det. 1985, MNHN-IU-2017-10016 (= MNHN-B12788).

Percnon gibbesi (H. Milne Edwards, 1853), 1 ♂ 30.0 × 27.0 mm, Senegal, T. de Rochebrune coll., MNHN-IU-2017-10010 (= MNHN-B13203); 1 ♂ 19 × 18 mm, Guadeloupe, Petite Terre, 26.V.2012, KARUBENTHOS 2012, stn GR49, MNHN-IU-2013-6664.

Percnon guinotae Crosnier, 1965, 1 ovig. ♀ 38.3 × 33.6 mm, Madagascar, Tulear, MNHN-IU-2017-10014 (= MNHN-B27975); 1 ♂ 23 × 21 mm, N.W. coast of Madagascar, Ambatoloaka beach, Plante coll., 1.7.1965, Crosnier det., MNHN-IU-2017-10015 (= MNHN-B16019).

Percnon planissimum (Herbst, 1804), 1 ♂ 22.8 × 24.4 mm, South Madagascar, Cape Ranavalona, Exp. ATIMO VATAE, 28.IV.2010, st. TM03, MNHN-IU-2010-2291; 1 ♂ 29.7 × 27.7 mm, Réunion Island, St Leu, exp. REUNION 2008, det. J. Poupin, IV.2008, MNHN-IU-2010-19798 (= MNHN-B24534).

Family Plagusiidae Dana, 1851

Davusia glabra (Dana, 1852), 1 ♂ 31.0 × 33.0 mm, 1 ♀ 26.0 × 28.5 mm, Australia, Maroubra Bay, near Sydney, det. *Plagusia glabra*, MNHN-IU-2017-10013 (= MNHN-B11690).

Guinusia chabrus (Linnaeus, 1758), 1 ♂ 69.3 × 78.9 mm, 1 ♀ 74.0 × 81.0 mm, southern Indian Ocean, New Amsterdam I., G. Duhamel coll., MNHN-IU-2017-8290 (= MNHN-B7211).

Guinusia dentipes (De Haan, 1835), 1 ♂ 29.0 × 32.0 mm, Japan, Boucard coll., Bouvier det. 1899 det. *Plagusia dentipes*, MNHN-IU-2017-10012 (= MNHN-B11692); 2 ♀, Japan, Frank, det. *Plagusia dentipes*, MNHN-IU- 2014-23142 (= MNHN-B11691).

Plagusia squamosa (Herbst, 1790), 1 ♂ 43.6 × 46.3 mm, Marquesas Islands, Nuku Hiva, Exp. PAKAIHI I TE MOANA, Stn MQ5-M, 12.I.2012, MNHN-IU-2011-8947.

Family Sesarmidae Dana, 1851

Aratus pisonii (H. Milne Edwards, 1837), 1 ♂ 22.3 × 23.6 mm, Brazil, near Rio de Janeiro, Guaratiba mangrove, M. Tavares coll. and det., MNHN-IU-2013-1491 (= MNHN-B24512).

Chiromantes dehaani (H. Milne Edwards, 1853), 1 ♂ 32.0 × 36.0 mm, Japan, near Tokyo, J. Harmand, Bouvier det., MNHN-IU-2017-10007 (= MNHN-B16234).

Neosarmatium fourmanoiri Serène, 1973, holotype, ♂ 32.0 × 38.0 mm, New Caledonia, Coll. R. Serène, 4.IX.1971, MNHN-IU-2014-23310 (= MNHN-B10459).

Neosarmatium meinerti (De Man, 1887), 1 ♂ 30.1 × 35.5 mm, Madagascar, south of Tulear, Sarodrano mangrove, MNHN-IU-2016-10756.

Selatium elongatum (A. Milne-Edwards, 1869), 1 ♂ 37.0 × 35.9 mm, Madagascar, Nosy Be, A. Crosnier coll and det. 1972, MNHN-IU-2016-10757 (= MNHN-B16244).

Sesarma reticulatum Say, 1817, 1 ♂ 22.1 × 27.0 mm, 1 ♀, New Jersey (USA), J. J. Smith coll., entry 3-1899, Mus. Yale Coll. 3-99, MNHN-IU-2017-8399 (= MNHN-B25784).

Karstama ultrapes (Ng, Guinot & Iliffe, 1994), holotype, ♂ 22.8 × 28.6 mm, Mbetibula Cave, Florida Islands, Nggela Pile Island, Solomon Islands, coll. T. M. Iliffe & S. Sarbu, 15.VIII.1988, Ng *et al.* det. *Sesarmoides ultrapes*, MNHN-IU-13898 (= MNHN-B24796).

Family Varunidae H. Milne Edwards, 1853
Subfamily Cyclograpsinae H. Milne Edwards, 1853

Cyclograpsus punctatus H. Milne Edwards, 1837, syntypes, 2 ♂ 27.9 × 34.1 mm, 29.0 × 37.5 mm, 1 ♀ 20.9 × 25.8 mm, Indian Ocean, M. Reynaud coll., dry. The ♂ 27.9 × 34.1 mm is hereby chosen as lectotype, MNHN-IU-2000-3368 (= MNHN-B3368); the other ♂, MNHN-IU-2000-1116 (= MNHN-B3368) and the ♀, MNHN-IU-2000-3372

(= MNHN-B3372) are paralectotypes (See Appendix, Type material of *Cyclograpsus punctatus* H. Milne Edwards, 1837 (Cyclograpsinae); 1 ♂ 24.9 × 30.8 mm, South Australia, Kangaroo Island, Shoal Bay, MNHN-IU-2013-14994 (= MNHN-B12561).

Cyclograpsus granulosus H. Milne Edwards, 1853, lectotype, ♀ 18.1 × 22.8 mm, Van Diemen (Tasmanie), MM. Quoy & Gaimard coll., J. Forest det. 1963 (see Campbell & Griffin 1966: 153), dry, MNHN-IU-2000-3361 (= MNHN-B3361).

Cyclograpsus henshawi Rathbun, 1902, ♂ 12.5 × 15.7 mm, Hawaii, MNHN-IU-2016-10759 (= MNHN-B12564).

Subfamily Gaeticinae Davie & N. K. Ng, 2007

Gaetice depressus (De Haan, 1835), 1 ♂ 15.7 × 18.0 mm, China, Amoy, C. F. Wang coll.1925, MNHN-IU-2013-14990 (= MNHN-B12089).

Subfamily Heliceinae
Sakai, Türkay & Yang, 2006

Helice tridens (De Haan, 1835), 1 ♂ 28.7 × 34.2 mm, Japan, Frank coll., entry 175-1895, A. Milne-Edwards det., MNHN-IU-2016-10762 (= MNHN-B12098).

Chasmagnathus convexus (De Haan, 1835), 1 ♂ 35.9 × 50.5 mm, dry, China, Hainan, L. T. Chang coll. VI.1924, Türkay det. 1983, MNHN-IU-2000-1117 (= MNHN-B3906).

Subfamily Thalassograpsinae
Davie & N. K. Ng, 2007

Thalassograpsus harpax (Hilgendorf, 1892), 2 ♂ 8.1 × 9.3 mm, 5.3 × 5.7 mm, Scattered Islands, Juan de Nova, BIORECIE 3, 2013, stn 6, J. Poupin det., MNHN-IU-2013-16120.

Subfamily Varuninae
H. Milne Edwards, 1853

Varuna litterata (Fabricius, 1798), 1 ♂ 49.5 × 57.0 mm, Madagascar, Grandidier coll., Balss det., MNHN-IU-2013-14987.

Other Varunidae
(to be assigned to existing subfamilies
or to new taxonomical categories)

Austrohelice crassa (Dana, 1851), 2 ♂ 17.8 × 21.2 mm, 15.4 × 17.3 mm, New Zealand, Otago, A. Crosnier det. 1993, MNHN-IU-2017-8403 (= MNHN-B24890).

Cyrtograpsus angulatus Dana, 1851, 1 ♂ 23.6 × 27.1 mm, Brazil, Rio Grande, Exp. CALYPSO-South America, stn HV184, 09.I.1962, stn 184, MNHN-IU-2017-8402.

Eriocheir japonica (De Haan, 1835), 1 ♂ 30.8 × 39.4 mm, Japan, Frank coll., entry 175-1895, A. Milne-Edwards det., MNHN-IU-2013-14985 (= MNHN-B12579).

Eriocheir sinensis H. Milne Edwards, 1853, 1 ♂ 57.0 × 62.2 mm, France, Paris, River Seine, X.1938, André coll., MNHN-IU-2013-14984 (= MNHN-B12575).

Helograpsus haswellianus (Whitelegge, 1890), 1 ♂ 14.2 × 17.6 mm, Australia near Sydney, Parramatta River, entry 11-1921, ex South Australian Museum (gift), MNHN-IU-2016-10761 (= MNHN-B12515).

Hemigrapsus penicillatus (De Haan, 1835), 1 ♂ 13.4 × 14.0 mm, Japan, entry 58-1897, MNHN-IU-2017-11709 (= MNHN-B12838).

Metaplax distincta H. Milne Edwards, 1852, syntype, 1 ♂ 10.2 × 13.8 mm, Bombay, P. Roux coll., dry, MNHN-IU-2000-10970 (= MNHN-B10970).

Paragrapsus gaimardii (H. Milne Edwards, 1837), 1 ♂ 21.6 × 23.6 mm, Nouvelle Hollande (Australia), dry, MNHN-IU-2000-3588 (= MNHN-B3588).

Platyeriocheir formosa (Chan, Hung & Yu, 1995), paratype, 1 ♂ 54.0 × 57.0 mm, Taiwan, Nan-Ao River, 30.IX.1991, M.S. Huang coll., MNHN-IU-2008-11250 (= MNHN-B22733).

Pseudograpsus albus Stimpson, 1858, 1 ♂ 11.0 × 12.2 mm, French Polynesia, Raivavae Island, RAPA 2002, 16.IV.2002, J. Poupin coll. and det., MNHN-IU-2017-8289 (= MNHN-B30672).

Family Xenograpsidae
N. K. Ng, Davie, Schubart & Ng, 2007

Xenograpsus testudinatus N. K. Ng, Huang & Ho, 2000, 1 ♂ 21.8 × 23.8 mm, NE Coast of Taiwan, off Taschi, exp. TAIWAN 2001, Stn CP81, P. Bouchet, Richer & Chan coll., 08.V.2001,, MNHN-IU-2013-14995 (= MNHN-B30314).

Superfamily Ocypodoidea Rafinesque, 1815
Family Heloeciidae H. Milne Edwards, 1852

Heloecius cordiformis (H. Milne Edwards, 1837), 1 ♂ 15.0 × 23.0 mm, Australia, South West Rocks, lagoon, entry 11-1921, MNHN-IU-2017-8394 (= MNHN-B21489).

HISTORICAL ACCOUNT ON THE MATERIAL OF *LEPTOGRAPSODES WEBHAYSI* MONTGOMERY, 1931 AND STATUS OF THE SPECIES

The genus *Leptograpsodes*, established for *Leptograpsodes webhaysi* by Montgomery (1931: 452, pl. 25, fig. 5, pl. 28, fig. 1a, b), was based on two female specimens collected from the Abrolhos Islands, Western Australia. According to Montgomery (1931: 452, 453), these two type specimens were "sent by post to the Paris Museum for comparison with the specimen believed to be the type of *Brachynotus octodentatus* (Milne-Edwards, 1837)" (*Cyclograpsus octodentatus* H. Milne Edwards, 1837 in its original combination), but they were "unfortunately lost in transit". The description of the genus and species as new taxa (*Leptograpsodes webhaysi*) was therefore made "from notes already taken and not in the presence of the specimen itself". Montgomery (1931) added: "Through the very kind consent of Professor Chas. Gravier [*sic* for Charles Gravier, who was director of the MNHN Laboratory "Vers et Crustacés" from 1917 to 1937], however, it has been possible to re-examine the type of Milne-Edwards's species; the Abrolhos specimens are very closely allied to this [*C. octodentatus*], but differ in certain small particulars. A full description is given, so that it may serve as a redescription of Milne-Edwards's species, except in the points of difference noted."

According to Davie (2002: 215) the British Museum of Natural History could be the "probable depository institution" of the two female syntypes of *Leptograpsodes webhaysi*, but a check in this institution has made known that Montgomery's material was not there (Paul F. Clark, pers. comm.). In fact, the two specimens of Montgomery (1931) had not been lost by Post Office transmission during their transit to France but had finally reached MNHN. These two syntypes from Abrolhos Islands, with original data and measurements similar to those provided by Montgomery (1931), have been recently found in the MNHN collection during the preparation of the "Annotated catalogue of brachyuran types (Crustacea, Decapoda, Brachyura) in the Muséum national d'Histoire naturelle, Paris. Part II" (N. K. Ng *et al.* in press). After our study, this material has been returned to its institution of origin, the Western Australian Museum.

In establishing *Leptograpsodes webhaysi* as a species distinct from *Cyclograpsus octodentatus*, Montgomery (1931: pl. 28, fig. 1a-c) seemingly based the decision mainly on the rather large female 27.0 × 34.0 mm here figured (Fig. 2E). Some listed points of difference between the two species are only due to age variation, various traits, such as those related to the development of the two pits on the dorsal surface of carapace, much more developed in large individuals (see below *Variations with sex and age*). Balss (1935: 142, under *Brachynotus octodentatus*) and Tweedie (1942: 16, under *B. octodentatus*) regarded these differences as too slight to justify specific separation, and both considered *L. webhaysi* almost certainly identical to *Cyclograpsus octodentatus*. Furthermore, the distinguishing characters warranted generic distinction for George (1962) and Griffin (1969; 1971) who adopted the binomen *Leptograpsodes octodentatus*. Their conclusions were followed by other carcinologists, so the 'burrowing shore crab' of southern and southwestern Australia (Griffin 1969: figs 8, 9, table 3) is currently known as *Leptograpsodes octodentatus* (H. Milne Edwards, 1837).

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
Subsection THORACOTREMATA Guinot, 1977
Superfamily GRAPSOIDEA MacLeay, 1838

Family LEPTOGRAPSODIDAE n. fam.

urn:lsid:zoobank.org:act:242B3728-D8CF-4B9E-AE1A-2DE5183BDA3B

TYPE GENUS. — *Leptograpsodes* Montgomery, 1931, by original designation. Gender masculine.

DIAGNOSIS. — Carapace broader than long, with strongly convex lateral margins. Anterolateral margin with prominent exorbital tooth followed by three small teeth decreasing in size posteriorly. Postero-lateral regions with striae. Dorsal surface with pair of oblique lateral grooves and a transverse groove. Front rather wide, deflexed; anterior margin straight. Antennules transversely folded. Antenna: basal article very broad, immobile, with strong lateral expansion and smaller mesial. Proepistome forming broad triangle deeply inserted in lower frontal margin. Eyestalks short. Orbit bounded externally by tooth. Internal suborbital spine moderately large. Suborbital margin sunken, faint; suborbital ridge more dominant, finely but clearly granulated, extending laterally below and beyond orbit. Subhepatic, pterygostomial and subbranchial regions covered by pubescence lacking reticulate pattern. Mxp3 with wide rhomboidal gap; merus trapezoid, not auriculate; no setose crest on ischium and merus; exopodite with flagellum. Apertures of efferent channels moderately sized. At small size, male chelipeds subequal, fingers of major chelae not gaping; strongly unequal at larger size, with much enlarged major chela and fingers gaping. Walking legs rather stout and short, flattened, without setae or black, stiff bristles; pouches of dense tufts of hydrophilic setae at basis of P2-P4 coxae. Thoracic sternum very wide, especially at level of sternite 7, only weakly inclined posteriorly; sternite 1 triangular; sternite 2 rather high, dome-shaped; suture 1/2 as complete, convex ridge; suture 2/3 complete; no trace of sternal suture 3/4, even laterally; lateral margins of sternite 4 deeply hollowed; sternite 3 + 4 wide, rather short; sutures 4/5-7/8 interrupted; at level of suture 6/7 a thick triangular bridge; episternite 7 delimited anteriorly by incomplete sulcus; posterior emargination wide, markedly semicircular, reaching sternite 7; sternite 8 not developed and unexposed medially, only visible laterally; a very small portion discernible when pleon is folded. Suture 7/8 short, lateral. Median line only on sternite 7. Sterno-pleonal cavity wide, not deeply hollowed, with marked rim at level of telson. Pleon with six somites free plus telson. Male gonopore sternal but close to, seemingly joined to, P5 coxa but in posteriormost location in relation to suture 7/8. Penis emerging just above P5 coxo-sternal condyle. Pleonal-locking mechanism effective: a pair of two prominent buttons on sternite 5; on pleonal somite 6 deep socket defined by strongly calcified border; locking buttons present in adult females, but lost at largest size. G1 long, reaching suture 4/5, quite slender, weakly curved outwards distally; lateral surface sparsely setose; medial surface with numerous setae; moderately dense tuft of setae at tip almost concealing short, blunt, horny tip. G2 very small. Vulva in middle of sternite 6, very small, occluded by operculum.

Genus *Leptograpsodes* Montgomery, 1931

Cyclograpsus H. Milne Edwards, 1837: *pro parte* (only *C. octodentatus* p. 80).

Leptograpsodes Montgomery, 1931: 452; George 1962: 71; Bennett 1964: 81; Griffin 1969: 325; 1971: 598; Sternberg & Cumberlidge 1998: 125, 129, 130, 131, 134, figs 3, 5, table 3; Cuesta & Schubart 1999: 163; Schubart *et al.* 2001: 41; Davie 2002: 215; Poore 2004: 506; N. K. Ng 2006: 39; Ng *et al.* 2008: 217; De Grave *et al.* 2009: 44; Cuesta *et al.* 2011: 226; Schubart 2011: 473, 476; Ip *et al.* 2015: 217, 223; Davie *et al.* 2015b: 958.

TYPE SPECIES. — *Cyclograpsus octodentatus* H. Milne Edwards, 1837 by original designation. (senior synonym of *Leptograpsodes webbhaysi* Montgomery, 1931).

GENUS MONOTYPIC. — Gender masculine.

DESCRIPTION

Carapace

Carapace broader than long, sub-hexagonal, with strongly convex lateral margins. One prominent tooth immediately behind orbital angle, and three weak teeth decreasing in size posteriorly, last obsolete. Dorsal surface not swollen, glabrous, markedly granulated on anterior part; two pairs of postfrontal lobes; a trace of oblique groove from first antero-lateral tooth; a pair of deep oblique lateral grooves about at level of second antero-lateral teeth, not reaching deep transverse groove; several striated ridges close to postero-lateral margins; a pair of two characteristics deep pits on each protogastric region.

Front rather wide, deflexed; anterior margin straight. Antennules transversely placed in deep fossae beneath the front. Antenna: basal article very broad, immobile, with a strong external expansion and a smaller internal, the fourth article being inserted in the concavity. Proepistome (interantennular septum) forming a broad triangle deeply inserted in lower frontal margin. Orbit bounded externally by pyramidal tooth that is the most anterior of the antero-lateral border. Supraorbital margins without trace of cleft. Eyestalks short. Suborbital spine three-sided, moderately large. Suborbital margin sunken (not dorsally visible), very faint, finely granulose, continuous from near base of marked orbital spine to near inner limit of orbit; suborbital ridge much more dominant, consisting of small, coalescent granules, extending laterally below and beyond orbit. Presence of stridulatory apparatus (also in females): pars stridens formed by cristiform suborbital ridge rubbing on P1 merus (plectrum). Epistomial margin coarsely granulated. Pterygostome with simple lateral groove, without supplementary groove. Subhepatic, pterygostomial and subbranchial regions covered by thick pubescence lacking distinct reticulate pattern.

Thoracopods

Mxp3 widely gaping, showing a rhomboidal gap between them; ischium much longer than merus and bearing fringe of hairs on both medial and lateral sides; merus trapezoid, not auriculate, narrower proximally than distally, with a not hairy sulcus, bordered by raised ridge that forms the entire internal margin; ischium with smaller ridge. Exopodite normal, not swollen or enlarged: narrow, slender and tapering, fringed with hairs, bearing flagellum.

Male chelipeds long, unequal, smooth, major chela becoming very robust at large size; coxa with small tufts of hydrophilic setae. Merus: at internal surface a whitish, smooth crest acting as the plectrum of the stridulatory apparatus, lost at largest sizes. Carpus with several teeth on inner margin. Palm smooth on outer surface, sparsely tuberculate on inner surface, without hairs on both surfaces. Fingers elongate, narrow, meeting subdistally and forming very narrow spoon at corneous tip, without brush of setae; fixed finger srongly bent downwards, with faint ridge; both occluding margins with rather strong teeth, grouped into strong lobe near base of fixed finger. Female chelipeds equal, narrower, fingers straighter, slightly gaping when closed; chela smooth on both surfaces.

Walking legs rather stout, flattened, P2 and P3 the longest and stoutest. No dense mat of setae on surface of articles and no fringes of setae for swimming ability; merus with transvese striations, without spines on posterior border; propodi with only very few and short spine-like setae; dactyli slender, long, slightly curved, with sparse short, black spine-like setae. Pouches of dense tufts of hydrophilic setae on P2-P4 coxae, thicker and longer on P3, P4.

Pleon

Male pleon with six free somites, widest at middle of laterally convex third somite; following somites narrowing uniformly to distal edge of sixth; somite 6 short, wide. Telson markedly narrower than somite 6.

Thoracic sternum

Thoracic sternum much widened; sternite 1 small, triangular, setiferous, visible between mxp3; sternite 2 rather high, dome-shaped; suture 1/2 convex, as complete, thickened ridge; suture 2/3 complete, thin but conspicuous, underlined by a row of dense setae; no suture 3/4, no trace, even lateral, of entire fusion of sternites 3, 4; sternite 4 short, with deeply hollowed lateral margin; sternite 3 + 4 wide, rather short, covered by dense short setae; on sternite 4 margin of the sterno-pleonal cavity marked by rim at level of telson; sutures 4/5, 5/6 interrupted; suture 6/7 interrupted but, at this level, a transverse ridge forming a thick triangular bridge superficially uniting the two halves of the sternal plate and extending forward to become the bottom of the sterno-pleonal cavity; suture 7/8 interrupted, much shorter than preceding sutures; episternites 4-6 vertically expanded, entirely delimited; sternite 7 much widened; episternite 7 horizontally expanded, delimited anteriorly by an incomplete sulcus; posterior emargination wide, concave, semicircular, reaching sternite 7; sternite 8 unexposed medially, only developed laterally, completely recovered by pleon when closed except for a very small proximal portion close to the P5 coxo-sternal condyle. Median line only on sternite 7, bumping into median bridge. Sterno-pleonal cavity wide, not deeply hollowed, only weakly inclined posteriorly.

Male gonopore and penis
Male gonopore sternal but very close to, seemingly joined to, the P5 coxa but in posteriormost location in relation to suture 7/8. Penis emerging just above P5 coxo-sternal condyle, and formed by cylindrical proximal portion passing between episternite 7 and sternite 8; in large male 51.8 × 68.3 mm as in the smaller male neotype 17.3 × 20.6 mm, when pleon is folded, penis has a small proximal portion (with different colouration) that is exposed, continues as a calcified cylindrical tube and then develops into a large papilla; a very small proximal part of sternite 8 is also exposed, these portions being covered at smallest size (but not visible in male 12.8 × 15.4 mm).

Pleonal-locking mechanism
Pleonal-locking mechanism effective: males with pair of two prominent, acute buttons on sternite 5, rather close to suture 4/5, not covered by gonopods situated more internally within sterno-pleonal cavity; on pleonal somite 6 deep socket posteriorly and defined by strongly calcified, V-shaped border. Locking buttons still present in adult females, at least in specimen measuring 17.1 × 20.6 mm, but then lost.

Gonopods
G1 long, reaching suture 4/5, quite slender, weakly curved outwards distally; sternal surface with moderatly long groove towards medial surface ending in distal flap; lateral surface sparsely setose; medial surface with numerous setae extending from base to tip; a moderately dense tuft of setae at the tip almost concealing short, blunt, horny tip and flap on sternal surface (Fig. 1F). G2 very small.

Vulvae
Vulva in middle of sternite 6, very small, occluded by operculum.

Leptograpsodes octodentatus
(H. Milne Edwards, 1837)
(Figs 1-3)

Cyclograpsus octodentatus H. Milne Edwards, 1837: 80. — Lucas 1840: 71.

Heterograpsus octodentatus – H. Milne Edwards 1853: 160 [194]. — Kingsley 1880: 209. — Haswell 1882: 101.

Brachynotus octodentatus – Tesch 1918: 106 (in key and footnote). — Hale 1924: 69; 1927a: 182, fig. 183; 1927b: 312. — Balss 1935: 142. — Tweedie 1942: 16, fig. 2. — Guiler 1952: 40 (list). — Bennett 1964: 81.

Grapsus inornatus Hess, 1865: 148, pl. 6, fig. 11. — Haswell 1882: 98. — see De Man 1887: 699.

Leptograpsodes webhaysi Montgomery, 1931: 452, pI. 25, fig. 5, pI. 28, fig. 1, la, 1b.

Leptograpsodes octodentatus – George 1962: 71-74, unnumbered figs. — Griffin 1969: 325, figs 1, 2a-c, 3a, 8, 9, table 3; 1971: 598, 603, figs 1-3, 5, tables 2, 3, 5-12. — Davie 2002: 215. — Poore 2004: 297, 503, 506, figs 161b, f, 162d, e, pl. 29d. — Ng *et al.* 2008: 217. — Schubart 2011: 473, 476, fig. 1, table 1. — Ip *et al.* 2015: 221, 223, fig. 2, table 1.

Material examined. — *Leptograpsodes octodentatus* (H. Milne Edwards, 1837): neotype (by present designation), ♂ 17.3 × 20.6 mm, Australia, Tasmania, King Island, coll. D. Alexander, 13.IV.1965 (TMAG G1033); 1 ♂ 12.8 × 15.4 mm, 1 ♀ 17.1 × 20.6 mm, Australia, Tasmania, King Island, Cape Wickham, above high tide level, in freshwater, coll. D. Hird, XII.1996 (TMAG G3854); 1 ♂ 51.8 × 68.3 mm (left-handed), Australia, South Australia, Blue Lagoon at Cactus Beach via Penong, 32°04'20"S, 132°59'24"E, coll. Brian V. Timms, 10.X.2006, by hand, G. Poore det. 2006 (ex NMV J55301-1, as exchange), MNHN-IU-2013-14993; 1 ovigerous ♀ 27.0 × 34.0 mm, South Australia, Australian Mus., entry 1912, *Heterograpsus octodentatus* Edw., Bouvier typ. comp., MNHN-IU-2013-14992 (= MNHN-B12530).
Leptograpsodes webhaysi Montgomery, 1931: syntype, ovigerous ♀ 27.0 × 34.0 mm, Abrolhos, Western Australia, WAM C71736, with several pereipods detached or partially missing; syntype ♀ 16.0 × 20.0 mm, Long Island, Abrolhos, WAM C71737, with several pereiopods missing.

Type Locality. — Australia, Tasmania, King Island.

Description
As for the genus.

Selection of a neotype
The type material of *Cyclograpsus octodentatus* H. Milne Edwards (1837: 80), described without any indication of sex and size, from the King Island in the Bass Strait, between southeast Australia and Tasmania (curiously, the species is indicated as from unknown locality by H. Milne Edwards himself [1853: 160] then by Kingsley [1880: 209]), could not be tracked at the MNHN. It was still deposited in the MNHN collection around 1930 since it was examined by Charles Gravier for comparison with *Leptograpsodes webhaysi.* Griffin (1969: 325) indicated it could be deposited in the MNHN and Davie (2002: 217) wrote "type status unknown MNHP*", thus a probable MNHN depository. But, despite an extensive investigation, it must be today assessed as lost, and therefore the fixation of a neotype is made here (ICZN, art. 72.4.5).

An ovigerous female 28.0 × 35.0 mm, in very good condition, labelled "*Heterograpsus octodentatus* Edw., South Australia, Australian Mus. 1912, Bouvier typ. comp.", MNHN-IU-2013-14992 (= MNHN-B12530), was compared to the type of *Cyclograpsus octodentatus c.* 1930 by E.-L. Bouvier (director of the chair of Entomology in the MNHN from 1917 to 1931), who has perhaps helped Gravier to list the differences from *Leptograpsodes webhaysi* asked by Montgomery (1931: 453). Although this female could be eligible to be the name-bearing type of the species, it was preferable to choose a male, originating from the type locality. Consequently, a male 17.3 × 20.6 mm from King Island (TMAG G1033) is selected here as neotype of *L. octodentatus* (Fig. 2A-D): despite its small size, it has fully developed gonopods and fulfils all the specific characteristics.

Colour
Carapace olivaceous, mottled or spotted with dark brown (Hale 1927a: fig. 183; Tweedie 1942: 18); mottled with black, dark blue or purple and yellow (George 1962: 72, unnumbered fig.). Underside of the body, chelipeds and legs usually much

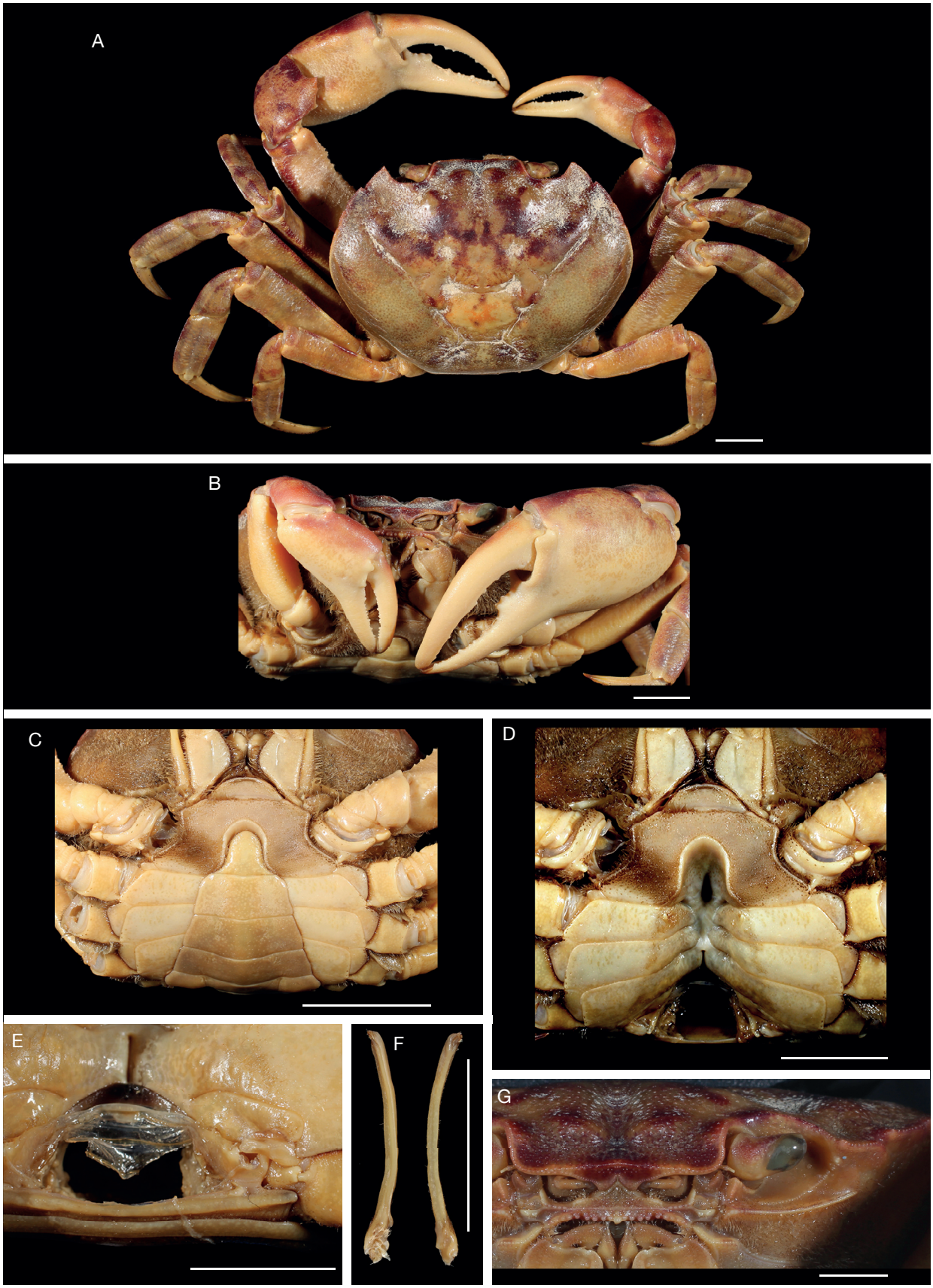

FIG. 1. — *Leptograpsodes octodentatus* (H. Milne Edwards, 1837), ♂ 51.8 × 68.3 mm, South Australia, MNHN-IU-2013-14993 (ex NMV J55301-1): **A**, carapace, dorsal surface; **B**, chelipeds; **C**, thoracic sternum with pleon (setal tufts visible); **D**, thoracic sternum without pleon; **E**, genital area with male gonopore and penis; **F**, G1, two views; **G**, front, orbit, antenna (with articles 1-4 and flagellum) and suborbital ridge as pars stridens. Scale bars: 10 mm.

paler than carapace, with the mottling on the dorsal surface of the chelipeds and legs sometimes bright red (Griffin 1969). In ethanol, carapace dirty yellow mottled with red in patches, and discontinuous rings of a similar dull red on merus, carpus, and propodus of the legs (Montgomery 1931: 454, pl. 25, fig. 5, as *Leptograpsodes webbhaysi*) (see Fig. 2E). Carapace dark brown to purple, with extensive yellow mottling; chelipeds bright red on upper surfaces (Fig. 1A, B) (Poore 2004: colour fig. pl. 29, fig. f).

Variations with sex and age

There is a large difference in size among the specimens we examined. According to George (1962) sexual maturity is reached at a carapace breadth of about 25.0 mm, and large adult males may reach a size of 76.0 mm; a size of more than 70.0 mm is cited by Tweedie (1942) and by Poore (2004). Large-sized adult males (Fig. 1A, B) develop huge, heterochelous and heterodontous chelae, with curved and irregularly toothed fingers, whereas smaller adult males (Fig. 2A, B) and females have more reduced, homochelous and homodontous chelipeds, with straight, regularly toothed fingers. George (1962), who examined a total of 84 specimens of *L. octodentatus* (50 males, 34 females, carapace width 10-70 mm) throughout its geographical range, concluded that the ridges around the orbits, the prominence of the pits on the dorsal surface of the carapace, the dentition and shape of the fingers, and ornamentation of the carpus of the cheliped were subject to significant variation with either age or sex, sometimes both. According to Griffin (1969) examination of the Tasmanian material at hand fully supported George's conclusion. Thus, since the characters listed by Montgomery (1931) as differential characters with respect to *Cyclograpsus octodentatus* are precisely those that are subject to significant variation, they did not support taxonomic separation of eastern and western populations.

Although we have not examined a broad sampling panel of specimens, we agree with the preceding authors and share the assertion of George (1962) that the ridges on the branchial regions become less prominent with increasing overall size. In old cave-dwelling males, the clothing of anterior thoracic sternum and pterygostomial areas has exceedingly dense geniculate setae, resembling brown fur. The genital region is similarly organised in the small male neotype 17.3 × 20.6 mm and in the large male 51.8 × 68.3 mm (Figs 1E; 3A-C): in both the cylindrical portion of penis (differently coloured) and a small proximal part of sternite 8 are exposed over a short distance when the pleon is closed, whereas these portions are covered and not visible at smallest size, for example in the male measuring 12.8 × 15.4 mm.

For the age-related variations of the stridulatory apparatus, see below *Stridulatory structures in grapsoids.*

Geographical distribution and ecology

Leptograpsodes octodentatus is restricted to southern and southwestern Australia as far north as the Abrolhos Islands, and quite widely distributed around Tasmania. It is a large supratidal crab, on rocky parts, found in rock-crevices; it burrows on the beach, sometimes far from the sea (Hale 1927a: fig. 184). It may be found under debris and stones on estuarine areas, in brackish waters (Hale 1927a), even near freshwater streams; adults were never found immersed in the sea (George 1962: 72, fig. p. 74), or only rarely entering the sea (Hale 1927a). The crab is highly resistant to desiccation; old males live singly in burrow. From field observations on the coasts of Tasmania and laboratory experiments (Griffin 1971: figs 1-3, 5, tables 2, 3, 5-12), *L. octodentatus* is known to occur on cliffs and platforms at some localities but more often on fully to semi-exposed boulder; to be also found at some localities on the north of Tasmania at the tops of cliffs burrowing in the earth; to show a tendency to move out of freshwater and remain out of water, being found at all areas located in freshwater seepages, always at a higher level than the 'high tide' level of the sea or saltlake (George 1962). *Leptograpsodes octodentatus* shows a high degree of terrestrial adaptation: it gets water through tufts of hydrophilic setae located on pouches of P2-P4 coxae, to a lesser extent between P1/P2 coxae (Figs 1C, D; 2B) (see *Terrestrial adaptations of grapsoids*).

Remarks

The status of the monotypic genus *Leptograpsodes* has been controversial. On the basis of its morphology, it has been alternatively regarded as a member of several distinct families or subfamilies: Grapsidae (Montgomery 1931; Balss 1935, as *Brachynotus octodentatus*; George 1962; Griffin 1969; 1971; Cuesta & Schubart 1999; Davie 2002; Poore 2004; N. K. Ng 2006: 39; Ng *et al.* 2008; Pinheiro *et al.* 2016); Varuninae by Tweedie (1942: 16, as *Brachynotus octodentatus*), who simultaneously assigned *Cyclograpsu*s H. Milne Edwards, 1837 to Sesarminae, such as Campbell & Griffin (1966: 139) and Haswell (1882). According to Bennett (1964: 81) *Leptograpsodes* was a synonym of *Brachynotus* De Haan, 1833 in the Varuninae, whereas Griffin (1969: 327) pointed out its strong similarities to the Australian varunines, and Griffin (1971: 327) stated that it was an exception among grapsines in possessing only fourteen gills. *Brachynotus*, assigned to Varuninae, is now restricted to the western Atlantic and Mediterranean Sea (Schubart *et al.* 2002).

In the cladistic analysis by Sternberg & Cumberlidge (1998: 125,129, 130, 131, 134, figs 3, 5, table 3), where Sesarminae was recovered as paraphyletic, *Leptograpsodes* was recognised "morphologically quite distant from the other varunines", nesting apart, and was placed in a non-varunine clade, whereas *Cyclograpsus* nested among varunine genera; *Leptograpsodes* was found more properly allied with the Gecarcinidae, Grapsidae, and Sesarmidae rather than to Varunidae (as Varuninae). So far, the morphological generic differences between *Leptograpsodes* and the varunine *Cyclograpsus* were essentially established by Poore (2004, key: 506).

According to Schubart (2011), in excluding *Leptograpsodes* Grapsidae became a relatively small and monophyletic assemblage, a homogeneous family in terms of adult morphology (Banerjee 1960; Crosnier 1965 as Grapsinae; Guinot 1979 as Grapsinae; Sternberg & Cumberlidge 1998; Schubart *et al.* 2002; Poore 2004; N. K. Ng *et al.* 2007), of larval features

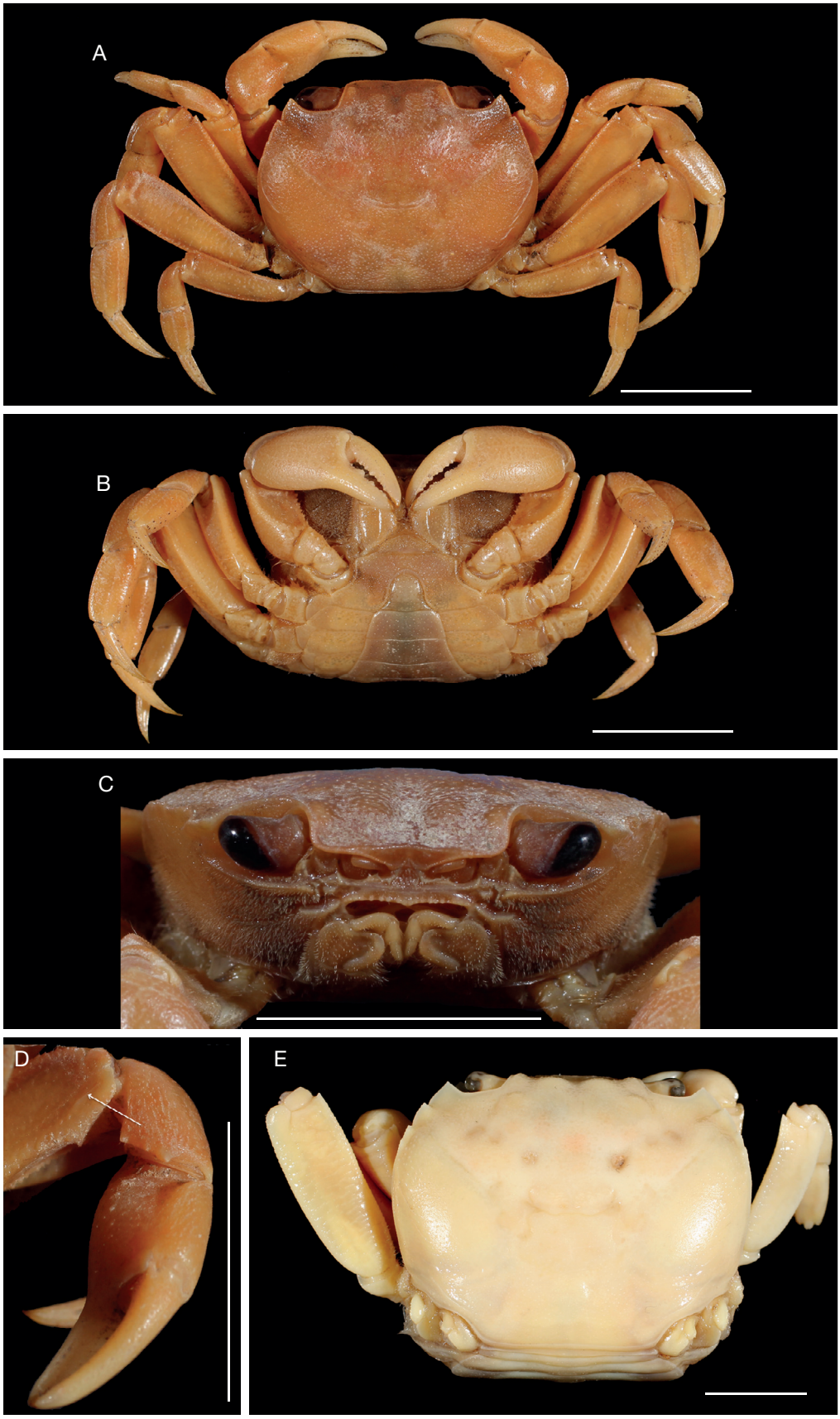

Fig. 2. — *Leptograpsodes octodentatus* (H. Milne Edwards, 1837): **A**-**D**, neotype, ♂ 17.3 × 20.6 mm, Australia, Tasmania, King Island, TMAG G1033: **A**, dorsal view; **B**, ventral view; **C**, frontal view, with suborbital ridge as pars stridens; **D**, close-up view of plectrum as whitish ridge on P1 merus (see arrow); **E**, syntype of *L. webhaysi* Montgomery, 1931, ovigerous ♀ 27.0 × 34.0 mm, Abrolhos, WAM C71736. Scale bars: 10 mm.

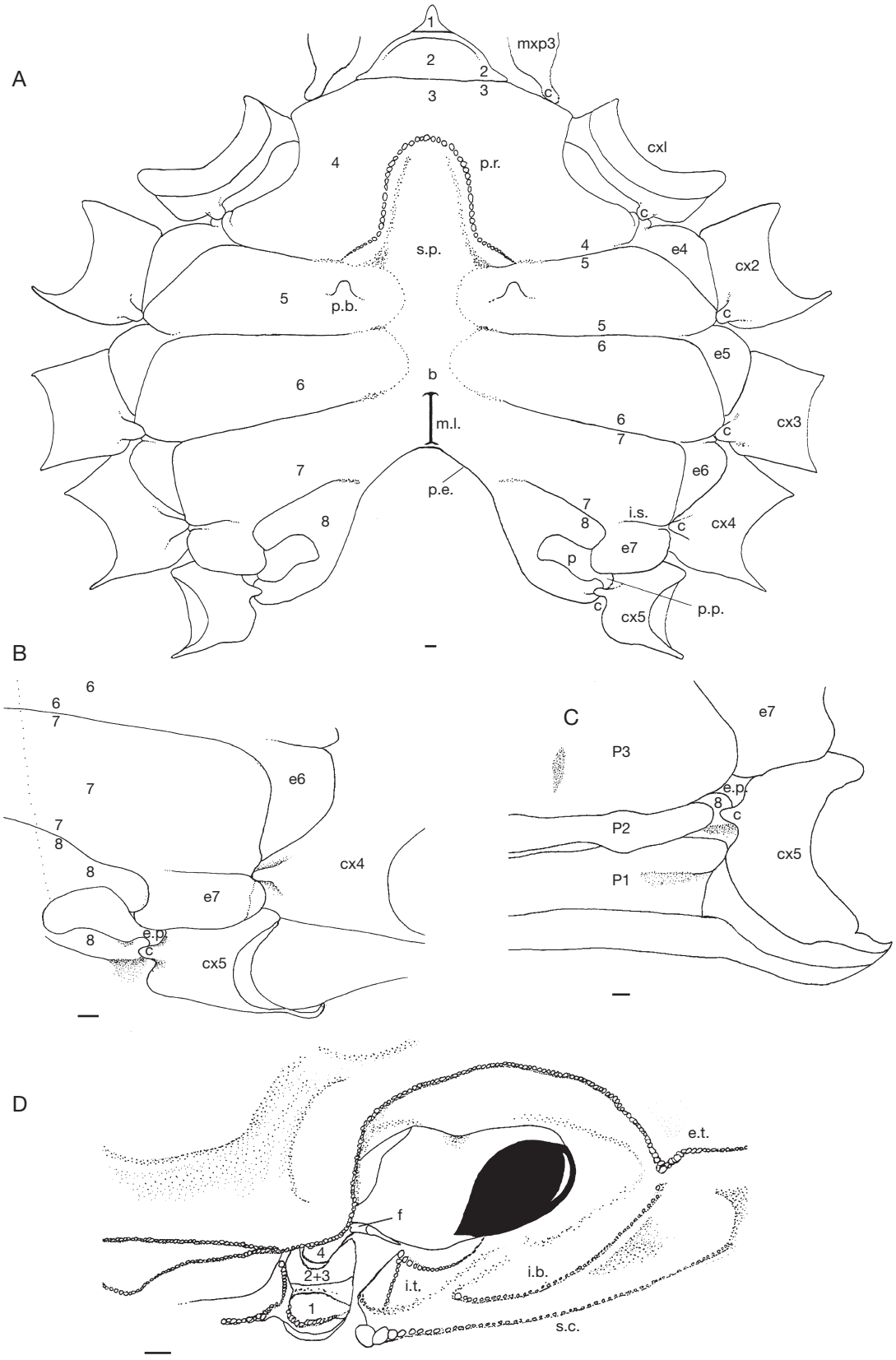

FIG. 3. — *Leptograpsodes octodentatus* (H. Milne Edwards, 1837), ♂ 51.8×68.3 mm, South Australia, MNHN-IU-2013-14993 (ex NMV J55301-1): **A**, thoracic sternum (note sternite 8 not developed medially, only exposed laterally); **B**, genital area with male gonopore and penis; **C**, posterior part of thoracic sternum with pleon; **D**, front and orbit. Abbreviations: **b**, bridge; **b.p.**, press-button; **c**, coxo-sternal condyle; **cx1-5**, P1-P5 coxae; **e.p.**, exposed proximal portion of penis; **e.t.**, extraorbital tooth; **e4-e7**, episternites 4-7; **i.b.**, suborbital border; **i.s.**, incomplete sulcus; **i.t.**, suborbital tooth; **m.l.**, median line; **mxp3**; third maxilliped; **P1**, **P2**, **P3**, pleonal somites 1-3; **p**, penis; **p.e.**, posterior emargination; **p.p.**, proximal portion of penis; **p.r.**, pleonal rim; **s.c.**, stridulating crest; **s.p.**, sterno-pleonal cavity; **1-8**, thoracic sternites 1-8; **1/2-7/8**, thoracic sternal sutures 1/2-7/8. Scale bars: 10 mm.

(Cuesta & Schubart 1999; Cuesta *et al.* 2011 but without data for *Leptograpsodes*), and of molecular data (Schubart *et al.* 2000b, 2002; Schubart & Cuesta 2010). From the analysis of genetic sequences from all grapsid genera and 80% of the known grapsid species, the overall topology of the phylogenetic tree by Ip *et al.* (2015) provided similar results: the monophyly of Grapsidae was supported only when *Leptograpsodes octodentatus* was excluded but did not strongly reject the topology with *L. octodentatus* included in the family; *Leptograpsodes* was placed within the clade of the outgroup, next to *Xenograpsus testudinatus*. Information on the larval development of *L. octodentatus* that is still lacking (see Cuesta & Schubart 1999; Cuesta *et al.* 2011) would be crucial for a complete understanding of the phylogenetic relationships of Leptograpsodidae n. fam.

Our present re-appraisal shows that *Leptograpodes* can be referred to the Grapsoidea, but its comparison with the main evolutionary lineages recognised in this superfamily (gecarcinids, glyptograpsids, grapsids, percnids, plagusiids, varunids, sesarmids, xenograpsids), demonstrates it requires a separate family recognition.

Family Gecarcinidae H. Milne Edwards, 1837

Included genera. — *Cardisoma* Latreille, 1828; *Discoplax* A. Milne-Edwards, 1867; *Epigrapsus* Heller, 1862; *Gecarcinus* Leach, 1814; *Gecarcoidea* H. Milne Edwards, 1837; *Johngarthia* Türkay, 1970; *Tuerkayana* n. gen.

Remarks

Leptograpsodes was never considered related to Gecarcinidae H. Milne Edwards, 1837 (for the authorship, see Appendix), and therefore a comparative analysis with its members is fully justified. First and foremost, a clarification about this family must be done.

Gecarcinidae is currently represented by five genera with large-sized species: *Cardisoma*, *Discoplax*, *Gecarcoidea*, *Gecarcinus*, and *Johngarthia*, which deserve the title of "land crabs", although all of them have to return to the sea for larval release through a migration of reproductive individuals (Hartnoll 2010; Hartnoll *et al.* 2014; Rodríguez-Rey *et al.* 2016; Bauer 2018) and although their larval development shows no concession to a terrestrial lifestyle, even in the case of species preferring karst and cave environments. A sixth genus, *Epigrapsus*, with two small-sized species having a cryptic life, deviates from all gecarcinids.

Today, based on morphological characters that are too often ignored and/or overlooked (see below), the reexamination of all gecarcinids reveals a deep discrepancy from some of the recently published data, especially by Türkay (1987), Ng *et al.* (2000, 2001), Ng & Guinot (2001), Ng & Davie (2012), Ng & Shih (2014, 2015), and many subsequent authors. The changes that we hereby propose are related to their generic nomenclature (see Table 1), whereas the specific identifications accompanied by a remarkable iconography constitute points of agreement, but only partially, however. Change in the taxonomic status of several species will have important consequences, especially for the endemic fauna of Christmas Island, a unique marine biodiversity hotspot: its vulnerable gecarcinid population, worldwide known by its extraordinary migrations, plays an important ecological role in the terrestrial ecosystem and requires a conservation strategy (Hicks *et al.* 1990; Paulay & Starmer 2011; Beeton *et al.* 2010; Turner *et al.* 2011, 2013; Bauer 2018).

The current classification of Gecarcinidae does not reflect the existence of the two main subclades supported by the congruence of morphological, larval and genetic data abovementioned. Establishment of two subfamilies is strongly required but would not be appropriate in the present paper in respect of the project announced in Ng *et al.* (2008: 214): "Davie & Ng, in prep.".

First gecarcinid subclade

Included genera. — *Cardisoma* Latreille, 1828; *Discoplax* A. Milne-Edwards, 1867; *Tuerkayana* n. gen.

Remarks

The sytematics of a part of Gecarcinidae is so complicated that a preliminary account is necessary. The family, extensively studied by Türkay (1970, 1973, 1974a, b) and largely accepted during many years, has been substantially modified over the last twenty years. A new reappraisal again seems to be required.

Discoplax, for a long time monotypic and regarded as distinct from *Cardisoma*, was subsequently and until recently considered a junior synonym of *Cardisoma* (Ortmann 1894; Alcock 1900; Türkay 1974a; Ng 1998; Cuesta & Anger 2005) or a subgenus of *Cardisoma* (Tavares 1991; Cuesta *et al.* 2002), a large genus including *C. guanhumi* (type species), *C. carnifex*, *C. hirtipes*, *C. rotundum*, plus *C. longipes* described as *Discoplax* by A. Milne-Edwards (1867) from New Caledonia but actually from Loyalty Islands (Richer de Forges & Ng 2006; N. K. Ng *et al.* in press). In papers dealing with the cavernicolous fauna, Guinot (1985, 1988, 1994), likewise previously (1979) recognised *Discoplax* distinct from *Cardisoma*, without further elaboration. Without explanation and in contradiction with his previous views, Türkay (1987: 145) added to *Discoplax* two taxa traditionnally (including himself) considered members of *Cardisoma*, *C. hirtipes* and *C. rotundum*. This position statement was provided in a small, general paper on land crabs, without affording justification. If the genus *Cardisoma* remained unchanged in Ng (1998) the unsubstantiated view was accepted and that was the starting point of a confusion that has compounded over time. P. K. L. Ng with Nakasone & Kosuge (Ng *et al.* 2000: 379) wrote: "We follow Türkay (1987) in using the genus *Discoplax* A. Milne-Edwards, 1873, for three species (*C. hirtipes*, *C. rotundum*, and *C. longipes*) previously placed in *Cardisoma*". P. K. L. Ng with Wang, Ho & Shi (Ng *et al.* 2001) followed Türkay (1987) for the generic placement of *C. hirtipes* and *C. rotundum* in *Discoplax*. This approach was subsequently adopted by other authors (Ng & Guinot 2001; Ng *et al.* 2008; Ng & Shih 2014, 2015; Davie *et al.* 2015a, and many others).

KEY TO GENERA *CARDISOMA* LATREILLE, 1828, *DISCOPLAX* A. MILNE-EDWARDS, 1867 AND *TUERKAYANA* N. GEN.

1. Orbit with a large lateral gap closed by an obliquous margin; suborbital ridge, forming a pars stridens; plectrum on the inner margin of cheliped merus. Subhepatic, subbranchial and posterolateral regions heavily striated. Median line on sternites 8 and 7 ..... *Discoplax* A. Milne-Edwards, 1867
— Orbit closed laterally by right-angled margin; no suborbital ridge, no stridulatory apparatus. Subhepatic and subbranchial areas without striae. Posterolateral striae either absent or faint and lost at largest size 2

2. Proepistome prominently dome-shaped. No posterolateral striae; anterolateral margin not delimited, unarmed. Sternite 4 wide and short. Pleonal somite 6 narrow and conspicuously elongated; telson elongated. Median line on sternites 8, 7 and 6 ..... *Cardisoma* Latreille, 1828
— Proepistome dome-shaped wide but low. Weak but distinct posterolateral striae, may disappear in largest adults. Sternite 4 wide and short. Pleonal somite 6 broad and short; telson short, bluntly tipped. Median line on sternites 8 and 7 ..... *Tuerkayana* n. gen.

In describing a new long-legged *Discoplax* species, *D. gracilipes*, closely associated with karst environments, Ng & Guinot (2001: 312, 317) used correct arguments to distinguish *Discoplax* (*D. longipes*, *D. gracilipes*) as a valid genus, but erroneously concluded that the differences observed on the thoracic sternum were not sufficiently significant to "warrant the removal of *D. hirtipes* and *D. rotunda* into a separate genus from *D. longipes* and *D. gracilipes*". As a result, the formerly known *Cardisoma* species *C. hirtipes* and *C. rotundum* were excluded from their previous genus and assigned to *Discoplax*, without acknowledging the important differences between the two genera. So, *Discoplax* became allocated with four species: on the one hand, *D. longipes* and *D. gracilipes* that are cavernicolous with adaptive features as the flat body and long legs but without reduced eyes or other constructive adaptations; on the other hand, *D. hirtipes* and *D. rotunda*, terrestrial species with lifestyles similar to those of other land crabs.

The discovery about at the same time of three new remarkable gecarcinids provided the opportunity to Ng & Shih (2014, 2015) to revisit the taxonomy of *Discoplax* and publish two papers intended to study the molecular relationships between the members of the "*D. hirtipes* species-group" (Ng & Shih 2014: 109). After the description by Ng & Davie (2012) of the famous "blue crab" *D. celeste* endemic to Chritmas Island, two new species were established: *D. magna*, a fully terrestrial species from Christmas Island and the eastern Indian Ocean (Ng & Shih 2014: figs 4, 6D-H, 7, 8, 9D, 11D-K, 12J-L, 13K-O); and *D. michalis*, a crab that lives in limestone caves, occasionally in adjacent limestone cliffs and beach (Ng & Shih 2015: 388, figs 4, 5, 6E, F; 7G, H; 9; 10E, F, K, L; 14E-H; 15C-H; 16C, D), at first cited as *D. longipes* by Ng & Guinot (2001: 317, figs 2A; 4A; 6-8; 12A; 13). Inheriting a difficult taxonomical situation, Ng & Shih (2014, 2015) examined a considerable material of land crabs, provided an abundant illustration and rectified numerous specific misidentifications, for example showing that Türkay's (1974a: 233) records of "*Cardisoma hirtipes*" actually included three species: the true *hirtipes* from numerous localities, *celeste* from Christmas Island, and *magna* (see Ng & Shih 2014: 123). According to Ng & Shih (2015: 128) the "*D. hirtipes*" of Ng & Guinot (2001) likewise covered two species, their "*D. magna*" and what they considered to be the true *hirtipes.* Ng & Shih (2015: 125) stated that, among other examples, the *C. hirtipes* of Hicks *et al.* (1990) was actually "*D. celeste*". After an initial study of the population structure of "*Discoplax hirtipes*" on Christmas Island by Turner *et al.* (2011), these authors were compelled to change its name as "*Discoplax celeste*" in a second paper dealing with its phylogeography (Turner *et al.* 2013).

Although the phylogenetic tree of combined markers by Ng & Shih (2014: fig. 14, 2015: fig. 17) strongly supported *Discoplax* as monophyletic, Ng & Shih (2014, 2015) were finally compelled to recognise two groups, two major lineages: a "*Discoplax hirtipes* species-group" including *D. hirtipes* and *D. celeste*, to which was added *D. magna*; and a "*Discoplax longipes* species-group" including *D. longipes*, *D. gracilipes*, and *D. rotunda*, to which was added the pseudocryptic cave-dwelling species from Guam, *D. michalis*. The genetic data, with *C. carnifex* and *C. armatum* as outgroup, were not considered conflicting with the used taxonomy, i.e., the inclusion of all these species in a unique genus, *Discoplax*.

Today we assume that the two closely related species *Cardisoma hirtipes*, considered "one of the best known land crabs in the Indo-West Pacific" (Ng & Shih 2014: 109), and *C. rotundum* have been inaccurately assigned to *Discoplax*. The first difficulty to overcome is determining whether or not these two species can be reallocated to *Cardisoma* alongside its type species *C. guanhumi* or does the group *hirtipes* + *rotundum* require a special status apart from the typical *Cardisoma*?

TAXONOMIC PROPOSAL

For all that, as our investigations stand at present, it turns out that the genus *Discoplax* of the above-mentioned authors covers in fact two quite distinct groups. As a result (see Table 1):

1) The genus *Discoplax sensu sricto* (type species: *D. longipes*) is admittedly a valid genus but only when restricted to its right members: besides *D. gracilipes*, it also likely contains *D. michalis* (not examined). Consequently, the first major group of Ng & Shih (2014), their "*Discoplax longipes* species-group, also called "long-legged group", including the cave species *D. longipes*, *D. gracilipes* and *D. michalis*, corresponds to our restricted *Discoplax*, i.e., cleared of *D. hirtipes* and *D. rotunda*. The distinctive characters that we use to differentiate *Discoplax* are not related to the troglobitic habits of its species.

2) *Cardisoma* in its traditional acceptance proved to be heterogeneous and thus required to be split into two groups.

Cardisoma sensu stricto is here restricted to its type species *C. guanhumi* and additionally only includes *C. armatum*, *C. carnifex* and *C. crassum* Smith, 1870.

3) A new genus *Tuerkayana* n. gen. is hereby erected for the remaining *Cardisoma*; it corresponds to the second group of Ng & Shih (2015), the "*Discoplax hirtipes* species-group" accommodating *D. hirtipes*, *D. rotunda*, *D. celeste* and *D. magna*, all herein excluded from *Discoplax*. The type species is *T. rotundum* n. comb.

One difficulty, especially for *Cardisoma sensu stricto* and *Tuerkayana* n. gen., whose species reach very large dimensions, is the important mophological variation of the carapace and chelipeds according to growth: in large and very large specimens the carapace gets proportionately more swollen, increasingly rounded, becoming transversely subovate, with less defined anterolateral margins, also with a smoother dorsal surface, the lateral striae becoming less pronounced or even lost; heterochely can be more marked in larger males. The weak heterochely and heterodonty of males *Discoplax* and the moderate heterochely of males *Tuerkayana* n. gen. contrast with the strong heterochely and heterodonty of male *Cardisoma* that increase at largest sizes. The surprising disparities on the gecarcinid heterochely noted in the literature by Hartnoll *et al.* (2017: 947, table 4) can be at least partially explained when the identification of the cited taxa is updated. It should be noted that *Cardisoma guanhumi* has longevity of at least 20 years, whereas *Gecarcoidea natalis* may live for 13 years (Burggren & McMahon 1988; Linton & Greenaway 1997; Vogt 2012).

Genus *Discoplax* A. Milne-Edwards, 1867

TYPE SPECIES. — *Discoplax longipes* A. Milne-Edwards, 1867 (see N. K. Ng *et al.* in press: fig. 2C).

OTHER SPECIES. — *Discoplax gracilipes* Ng & Guinot, 2001 (see N. K. Ng *et al.* in press: fig. 2B); *D. michalis* Ng & Shih, 2015 (not examined).

DIAGNOSIS

Carapace not inflated (Fig. 4D, E), the maximum recorded size being 61.7 × 71.9 mm for *D. longipe*s; dorsal surface with regions distinctly marked, covered with granules; posterolateral regions with pronounced striae (Ng & Shih 2015: fig. 6); anterolateral margin well delimited, with a marked cleft (so "anterolateral margins unarmed", in the diagnosis of Gecarcinidae by Davie *et al.* 2015c: 1117, must be corrected); proepistome small, narrow, subquadrate; subhepatic and subbranchial areas heavily striated (Fig. 6A) (Ng & Shih 2015: fig. 7); orbit not closed laterally, with conspicuously granulated suborbital area; suborbital crest long, consisting of very small, close granules (Fig. 6A) (Ng & Guinot 2001: figs 5B, 6C, 9C; Ng & Shih 2015: fig. 7), here considered stridulatory pars stridens, rubbing on a thickened ridge (plectrum) located on inner magin of P1 merus (Fig. 11A), present in both sexes; male gonopore close to P5 coxo-sternal condyle and opening in middle of sternite 8 thus far from suture 7/8; penis proximally narrow, then more expanded (Fig. 5C); thoracic sternum not inclined posteriorly, wide, especially at level of sternite 4 (Fig. 5A, B) (Ng & Guinot 2001: fig. 4A; Ng & Shih 2015: figs 1G, 4D); sternites 1-3 forming a low plate; sternite 1 triangular, separated from sternite 2 by thick ridge anteriorly lined with granules (suture 1/2); sternite 2 short, flattened, separated from sternite 3 by thin, straight, complete sulcus (suture 2/3); no suture 3/4, without lateral trace; sternite 4 short and wide, with weakly concave lateral margins, thus only weakly restricted between the P1; very weak rim delineating margin of the sterno-pleonal cavity at level of telson; episternites 4-6 narrow, longitudinally directed; posterior sternites on same plane as preceding sternites; sternite 8 short but developed medially, the posterior emargination being far from reaching sternite 7; suture 7/8 rather short; thick and wide bridge at level of suture 6/7 (Fig. 5B, C) (Ng & Guinot 2001: fig. 4A); median line on sternite 8 and extending on sternite 7 only, not extending on sternite 6 (Fig. 5C); no visible portion of sternite 8 when pleon is folded; on sternite 5 acute press-buttons close to suture 4/5, observed in *D. longipes* (Fig. 5B) and *D. gracilipes* (character not mentioned in the description of *D. michalis*), however hardly visible due to dense setal cover (a trace in female *D. longipes* 32.6 × 37.0 mm) (Köhnk *et al.* 2017: fig. 19a), thus pleonal locking perhaps no longer functional over a certain size; socket on pleonal somite 6 not easily noticeable, except for small cuticular border (Köhnk *et al.* 2017: fig. 19b); sterno-pleonal cavity wide; pleon long, reaching sternite 3, subdistally wide; pleonal somite 4 especially broad; telson short, rounded (Fig. 5A) (Ng & Shih 2015: figs 8, 9); heterochely very weak, male chelipeds may be only slightly subequal; P2, P3 elongated and slender, covered with distinct granules and/or striae, appearing very rugose; dorsal margins of merus granulated; only lateral margins of propodus and dactylus with short stiff spines or setae (Ng & Shih 2015: fig. 10); G1 proportionally short (Ng & Shih 2015: figs 11, 13-15, *D. longipes* and *D. michalis*).

REMARKS

A particular character not previously noted in *Discoplax* is the presence of a large, laterally opened orbit, with the suborbital crest forming a stridulating pars stridens (Fig. 6A); a thickened ridge close to the inner margin of the cheliped merus represents the plectrum (Fig. 11A). This disposition has been observed in the both sexes of *D. longipes* and *D. gracilipes* of the MNHN collection. Given the similar morphology of the orbital area of *D. michalis* (Ng & Shih 2015: fig. 7G, H), a comparable stidulating apparatus may characterise this species. Note that stridulatory structures occur only in *Discoplax* and are lacking in *Cardisoma sensu stricto* and in *Tuerkayana* n. gen. (see below and Table 1).

The presence of a pleonal locking mechanism in *Discoplax* was a character overlooked by Ng & Guinot (2001), Ng & Davie (2012), Ng & Shih (2014, 2015) and subsequent authors. A structure is tangible in *D. longipes* (Fig. 5B) and *D. gracilipes*, i.e., a button close to suture 4/5 and surrounded by dense setae that obscure it (Köhnk *et al.* 2017: fig. 19a) (to be confirmed in *D. michalis*). This dense setal cover on the area probably makes the pleonal locking system non-functional in adults.

Genus *Cardisoma* Latreille, 1828 *sensu stricto*

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

OTHER SPECIES. — *Cardisoma armatum* Herklots, 1861; *C. carnifex* (Herbst, 1796); *C. crassum* Smith, 1870 (not examined).

REMARKS

Two species traditionally assigned to *Cardisoma*, *C. hirtipes* (see Appendix) and *C. rotundum*, are hereby assigned to a new genus *Tuerkayana* n. gen., to which are added *Discoplax celeste* of Ng & Davie (2012) and *D. magna* of Ng & Shih (2014).

The more significant features that characterise *Cardisoma sensu stricto* are the traditionally used ones that identify the type species *C. guanhumi* and, in addition, features based on the thoracic sternum.

DIAGNOSIS

Carapace inflated and thick (Fig. 4A-C: *C. guanhumi*, *C. carnifex*, *C. armatum*, respectively) (Bouchard *et al.* 2013: fig. 12C, *C. carnifex*); dorsal surface with regions weakly or hardly demarcated, smooth and without posterolateral striae; 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 1973: 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*). Proepistome prominently dome-shaped (Fig. 6B); suborbital margin entirely joining exorbital tooth; orbit closed laterally by right-angled margin; no suborbital crest (Fig. 6B) (Tavares 1989: fig. 3). Subhepatic and subbranchial areas not striated (Fig. 6B). Setose pterygostomial area usually narrow. Male chelipeds with strong heterochely and heterodonty: major chela very stout; fingers markedly gaping, with one main tooth on both prehensile margins; minor chela narrow, long; fingers elongated, weakly gaping. Thoracic sternum (Fig. 5D-F) inclined posteriorly, proportionally narrow, especially at level of sternite 4 that is restricted between the P1; anterior sternites forming a proportionally developed plate; sternite 2 semi-ovate, bluntly triangular; no suture 3/4, without lateral trace; sternite 4 anteriorly narrow and long, with more or less concave margins (Türkay 1970: fig. 8b, *C. guanhumi*; Türkay 1973: fig. 8, *C. armatum*; Türkay 1974a: fig. 11, *C. carnifex*); on sternite 4 a thick ridge forming the rim of the sterno-pleonal cavity at level of telson; a thick bridge at level of suture 6/7; sternite 8 rather large, developed medially; no visible portion when pleon is folded; suture 7/8 rather short. Median line on sternites 8, 7 and extending on the whole sternite 6, in front of transverse bridge (Fig. 5E, F) (Ng & Guinot 2001: fig. 3A, *C. guanhumi*; fig. 3B, *C. carnifex*; fig. 3C, *C. armatum*); correspondingly, a median septum at level of sternite 6, higher at level of sternite 7, visible after dissection of *C. carnifex*. Sterno-pleonal cavity very wide. Pleon elongated, may reach sternite 3; somite 6 narrow and conspicuously elongated; telson (Fig. 5D) (Türkay 1970: fig. 8b, *C. guanhumi*; 1973: fig. 8, *C. armatum*; Rathbun 1918: fig. 157, pl. 109, *C. crassum*); G1 (Türkay 1970: fig. 8b, *C. guanhumi*; Türkay 1973: fig. 4b, *C. carnifex*; 1974a: fig.11, *C. carnifex*). Locking structure absent: no press-button on smooth sternite 5, covered with setae (Fig. 5E) (Guinot 1979; Guinot & Bouchard 1998); no socket on pleonal somite 6, only some remants of a pleonal socket may be discernible in *C. carnifex* (Köhnk *et al.* 2017: fig. 20a, b). Male gonopore close to P5 coxo-sternal condyle; penis proximally narrow, then more expanded (Fig. 5F) (Guinot 1979: fig. 54A-C; Guinot *et al.* 2013: fig. 23A).

Genus *Tuerkayana* n. gen.

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TYPE SPECIES BY PRESENT DESIGNATION. — *Thelphusa rotunda* Quoy & Gaimard, 1824. The type material is preserved in the MNHN, and a lectotype will be selected by N. K. Ng *et al.* (in press: fig. 3B). Gender neuter.

OTHER SPECIES. — *Tuerkayana celeste* (Ng & Davie, 2012) n. comb.; *T. magnum* (Ng & Shih, 2014) n. comb.; *T. hirtipes* (Dana, 1851) n. comb. Seen as the type of *Cardisoma hirtipes* Dana, 1851 recently found in the USNM that was designated as lectotype by Ng (2017: figs 1-3) it matches well with the figures of Dana (1855: pl. 24, fig. 4). In order to avoid confusion regarding the identity and the morphology of the species, we will base our comparisons on the illustrations of these two authors. The complicated question about the identity of *C. hirtipes* is developed in the Appendix.

ETYMOLOGY. — Named in honour of our colleague and friend Michael Türkay, who died too soon in 2015, for his outstanding contribution to carcinology. He is the acknowledged specialist of land crab systematics, author of important papers in the 1970s devoted to the study of these crabs.

DIAGNOSIS

Carapace moderately inflated, convex tranversely and longitudinally; dorsal surface with poorly or well demarcated regions, smooth or granulated along anterolateral borders (Fig. 4F-I, *T.* aff. *hirtipes* n. comb., *T. rotundum* n. comb., *T. celeste* n. comb., *T. magnum* n. comb., respectively); weak but distinct posterolateral striae, may disappear in largest adults (Fig. 4F, *T.* aff. *hirtipes* n. comb.) (Ng 2017: fig. 2A, lectotype of *Cardisoma hirtipes*); anterolateral margin delimited by a row of fine granules (Fig. 4H, I, *T. celeste* n. comb., *T. magnum* n. comb., respectively) or by a continuous, long row of distinct granules (Fig. 4G, *T. rotundum* n. comb.) or anterolateral margin strongly convex, rounded (Fig. 4F, *T.* aff. *hirtipes* n. comb.); just behind the exorbital angle, a small notch or an indentation with small tooth (Fig. 4G-I, *T. rotundum* n. comb., *T. celeste* n. comb., *T. magnum* n. comb., respectively) (Ng 2017: fig. 2A, B, lectotype of *Cardisoma hirtipes*). Proepistome dome-shaped, wide but rather low (Fig. 6C-E) (Ng 2017: fig. 2B, lectotype of *Cardisoma hirtipes*); orbit with lateral gap closed by obliquous margin; no suborbital crest (Fig. 6C-E). Subhepatic and subbranchial areas not striated (Ng & Shih 2014: figs 9A-D, *Discoplax hirtipes*, *D.* celeste, *D. magna*, respectively). Setose pterygostomial area broad. Male chelipeds without maked heterochely: major chela moderately

Fig. 4. — Carapaces of Gecarcinidae: *Cardisoma* Latreille, 1828 (**A**-**C**), *Discoplax* A. Milne-Edwards, 1867 (**D**, **E**) and *Tuerkayana* n. gen. (**F**-**I**): **A**, *Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♂ 56.5 × 68.0 mm, Antilles, MNHN-IU-2013-14983 (= MNHN-B12270); **B**, *C. carnifex* (Herbst, 1796), ♂ 71.2 × 88.0 mm, French Polynesia, Society Islands, MNHN-IU-2013-14798; **C**, *C. armatum* Herklots, 1861, ♂ 51.6 × 65.2 mm, Benin, MNHN-IU-2017-11710 (= MNHN-B21986); **D**, *Discoplax longipes* A. Milne-Edwards, 1867, ♂ 32.4 × 37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **E**, *D. gracilipes* Ng & Guinot, 2001, paratype, ♂ 29.6 × 26.3 mm, Panglao Island, Bohol, Tawala Cave, MNHN-IU-2014-11217 (= MNHN-B27770); **F**, *Tuerkayana* aff. *hirtipes* (Dana, 1851), ♂ 61.0 × 79.0 mm, Loyalty Islands, Lifou Island, We cave, MNHN-IU-2017-8397 (= MNHN-B24811); **G**, *Tuerkayana rotundum* (Quoy & Gaimard, 1824) n. comb., ♀ 32.7 × 40.1 mm, Loyalty Islands, MNHN-IU-2013-3740 (= MNHN-B13141); **H**, *T. celeste* (Ng & Davie, 2012) n. comb., ♂ 44.4 × 52.2 mm, Australia, Christmas Island (ZRC 2012.0171); **I**, *T. magnum* (Ng & Shih, 2014) n. comb., ♂ 49.0 × 58.7 mm, Indonesia, Java, Cilacap (ZRC 2017.0252). Scale bars: 10 mm.

developed but becoming very stout in large adult males, fingers elongated (Ng & Shih 2014: fig. 6A-C, *Discoplax celeste*; Ng 2017: fig. 3A, B, lectotype of *C. hirtipes*) or swollen and with relatively short fingers (*T. rotundum* n. comb.); chela of large adult males of *T. magnum* n. comb. not especially enlarged in proportion to long fingers; fingers elongated, partially flattened laterally, sometimes appearing almost blade-like. Pereiopods variously shaped: short, relatively slender, especially merus and propodus (Ng 2017: fig. 3C-H, lectotype of *Cardisoma hirtipes*) or relatively stout, short, especially merus and propodus (*T. celeste* n. comb.), or relatively stout, short to slender (*T. magnum* n. comb.). Thoracic sternum (Fig. 5G-O) tilted posteriorly, proportionally wide, especially at level of sternite 4 that is not much restricted between the P1; sternite 1 small, triangular; sternite 2 broad, dome-shaped; suture 1/2 as a more or less arcuate, granulated thick ridge; suture 2/3 complete, straight; granulated thick ridge; suture 2/3 complete, straight; no suture 3/4, without lateral trace; sternite 4 proportionally wide and short; on sternite 4 a ridge forming the rim of sternopleonal cavity at level of telson; thick, wide bridge at level of suture 6/7; sternite 8 large, developed medially; no visible portion when pleon is folded; suture 7/8 rather short. Median line present on sternite 8 and extending on sternite 7 below median bridge (Fig. 5H, I, *T.* aff. *hirtipes* n. comb.; Fig. 5K, L, *T. celeste* n. comb.; Fig. 5N, O, *T. magnum* n. comb.) (Ng 2017: fig. 2D, E, lectotype of *Cardisoma hirtipes*); correspondingly, median septum lacking in dissected *T.* aff. *hirtipes*. Pleon (Fig. 5G, J, M) (Ng 2017: fig. 2E, F, lectotype of *Cardisoma hirtipes*) elongated, reaching sternite 3; somite 6 broad and short; telson short, bluntly tipped. G1: see Ng & Shih 2014: fig. 13A-E, F-J, K-O, as *Discoplax hirtipes*, *celeste*, *magnum*, respectively. Male gonopore close to P5 coxo-sternal condyle. Penis (Fig. 5I, L, O) with narrow proximal portion passing between sternite 7 and sternite 8, continuing by calcified cylindrical tube and then developing into large papilla (sometimes not exposed due to a short fusion of sternite 7 and sternite 8); sternite 8 usually exposed when pleon is folded.

Remarks

The features related to carapace and chelae considerably vary depending on the size, so the use to other more constant traits is required.

Tuerkayana n. gen. differs from *Discoplax* chiefly by: the body shape, more inflated; anterolateral margins slightly, hardly or not demarcated; posterolateral striae on carapace weaker and faint or lost at largest size (Fig. 4F, *T*. aff. *hirtipes*) (Ng 2017: fig. 2A, lectotype of *Cardisoma hirtipes*) (present in *Discoplax* even at large size, see Ng & Shih 2015: fig. 3); proepistome wide and dome-shaped (Fig. 6C-E) instead of narrow, subquadrate projection in *Discoplax* (Fig. 6A) (Ng & Shih 2015: fig. 7); orbit laterally closed, without stridulating suborbital crest (Fig. 6C-E) (Ng 2017: fig. 2B, C, lectotype of *Cardisoma hirtipes*); absence of smooth ridge (plectrum) on cheliped merus, thus no stridulatory apparatus; thoracic sternum proportionally longer and narrow, with posterior sternites steeply sloping; sternite 4 longer, narrower, much restricted between the P1, with concave lateral margins (Fig. 5G, H, J, K, M, N) (Ng 2017: fig. 2E, lectotype of *Cardisoma hirtipes*); sternite 2 rather broad, rectangular; thick pleonal rim on sternite 4; episternites 4-6 wide, horizontally directed; median line on sternite 7, not extending on sternite 6 (Fig. 5I, L, O); a moderate bridge at level of suture 6/7; long pleon, with elongate pleonal somite 6 (Fig. 5G, J, M) and long telson; absence of sternal press-button (Köhnk *et al.* 2017: 2111 as *Discoplax*; see also Guinot & Bouchard 1998).

Tuerkayana n. gen. differs from *Cardisoma sensu stricto* by: carapace moderately inflated, convex tranversely and longitudinally (Fig. 4F-I) (vs inflated and thick in *Cardisoma*, Fig. 4A-C); dorsal surface with poorly or well demarcated regions (vs regions weakly or hardly demarcated, smooth in *Cardisoma*); posterolateral striae weak but distinct (Fig. G-I), may disappear in largest adults (Fig. 4F) (without posterolateral striae in *Cardisoma*, Fig. 4A-C); proepistome dome-shaped but rather low (vs prominently dome-shaped in *Cardisoma*); male chelipeds without marked heterochely: major chela moderately developed but becoming very stout in large adult males (vs with strong heterochely and heterodonty: major chela very stout, minor chela narrow, long); sternite 4 wide and short (vs narrow and long); median line present only on sternites 8 and 7 below transverse bridge (vs on sternites 8, 7 and extending on the whole sternite 6, in front of transverse bridge); pleonal somite 6 (Fig. 5G, J, M) broad and short; telson short, bluntly tipped (vs pleonal somite 6 narrow and conspicuously elongated; telson elongated).

Tuerkayana rotundum n. comb., a species largely distributed in the Indo-West Pacific, living in the supralittoral or inland habitats and only occasionally found in caves (Türkay 1974a, as *Cardisoma*; Ng & Guinot 2001, as *Discoplax*; Innocenti & Vannini 2007, as *Discoplax*), only superficially looks like a *Discoplax* by the flattened carapace, with well delimited anterolateral margins (Fig. 4G) (Ng & Guinot 2001: figs 2B, 4B) and the dorsal surface granulose on lateroanterior regions and striated on lateroposterior regions (thus its name of "rugose land crab"). In contrast, *T. rotundum* n. comb. can be easily distinguished from *Discoplax* by numerous characters, in particular by: orbit laterally closed and lacking suborbital crest; wide, dome-shaped proepistome; and sternal and pleonal features; P2, P3 elongated but not so distinctly, only 2-3 times carapace length (in *D. longipes* and *D. gracilipes* far more elongated, at least 4-5 times carapace length); sternal button lacking and no clear socket, see Köhnk *et al.* (2017: fig. 20c-d, as *Discoplax*); also Guinot & Bouchard (1998) (in *D. longipes* [Fig. 5B] and *D. gracilipes*, button close to suture 4/5 and surrounded by dense setae that obscure it, so probably not an efficient locking mechanism, see Köhnk *et al.* 2017: fig. 19a).

Characters shared by *Leptograpsodes*, *Discoplax*, *Cardisoma* and *Tuerkayana* n. gen.

1) The orbit with a large lateral gap closed by an obliquous margin and long, finely ornamented suborbital ridge, extending laterally below and beyond orbit, are characters shared by *Leptograpsodes* (Figs 1G; 2C; 3D) and *Discoplax* (Fig. 6A), but absent in *Cardisoma* (Fig. 6B) and *Tuerkayana* n. gen. (Fig. 6C-E).

FIG. 5. — Pleon, thoracic sternum and genital region of Gecarcinidae. **A**, **D**, **G**, **J**, **M**, thoracic sternum (brushed) with pleon; **B**, **E**, **H**, **K**, **N**, thoracic sternum (brushed) without pleon; **C**, **F**, **I**, **L**, **O**, genital region with gonopore and penis: **A**-**C**, *Discoplax longipes* A. Milne-Edwards, 1867, ♂ 32.4×37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **D**-**F**, *Cardisoma guanhumi* Latreille *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♂ 56.5×68.0 mm, Antilles, MNHN-IU-2013-14983 (=MNHN-B12270); **G**-**I**, *Tuerkayana* aff. *hirtipes* (Dana, 1851) n. comb., ♂ 61.0×79.0 mm, Loyalty Islands, Lifou Island, We cave, MNHN-IU-2017-8397 (=MNHN-B24811); **J**-**L**, *Tuerkayana celeste* (Ng & Davie, 2012) n. comb., ♂ 44.4×52.2 mm, Australia, Christmas Island, ZRC 2012.0171; **M**-**O**, *T. magnum* (Ng & Shih, 2014) n. comb., ♂ 49.0×58.7 mm, Indonesia, Java, ZRC 2017.0252. Scale bars: 10 mm.

TABLE 1. — New nomenclatural terminology proposed for the Gecarcinidae.

Cardisoma Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828	
Cardisoma guanhumi	*Cardisoma guanhumi* Latreille, *in* Latreille, Le Peletier, Serville & Guérin, 1828 (type species)
Cardisoma armatum	*Cardisoma armatum* Herklots, 1861
Cardisoma carnifex	*Cardisoma carnifex* (Herbst, 1796)
Cardisoma crassum	*Cardisoma crassum* Smith, 1870
Discoplax A. Milne-Edwards, 1867	
Discoplax longipes	*Discoplax longipes* A. Milne-Edwards, 1867 (type species)
Discoplax gracilipes	*Discoplax gracilipes* Ng & Guinot, 2001
Discoplax michalis	*Discoplax michalis* Ng & Shih, 2015
Tuerkayana n. gen.	
Cardisoma rotundum	*Tuerkayana rotundum* (Quoy & Gaimard, 1824) n. comb. (type species)
Discoplax celeste	*Tuerkayana celeste* (Ng & Davie, 2012) n. comb.
Cardisoma hirtipes	*Tuerkayana hirtipes* (Dana, 1851) n. comb.
Discoplax magna	*Tuerkayana magnum* (Ng & Shih, 2014) n. comb.

2) The organisation of thoracic sternites 3 and 4, completely fused without any demarcation, is shared by *Leptograpsodes* (Figs 1C, D; 3A), *Discoplax* (Fig. 5A, B), *Cardisoma* (Fig. 5D, E) and *Tuerkayana* n. gen. (Fig. 5G, H, J, K, M, N).

3) The presence of a bridge at level of sternal suture 6/7 in *Leptograpsodes* (Figs 1D, E; 3A), very thick in *Discoplax* (Fig. 5B, C), less developed in *Cardisoma* (Fig. 5E, F, *C. guanhumi*) (see Ng & Guinot 2001: fig. 3A-C, *C. guanhumi*, *C. carnifex* and *C. armatum*, respectively), in *Tuerkayana hirtipes* n. comb., and in *T.* aff. *hirtipes* (Fig. 5H, I), *T. celeste* n. comb. (Fig. 5K, L), *T. magnum* n. comb. (Fig. 5N, O), and *T. rotundum* n. comb.

4) The genital disposition is similar in *Leptograpsodes* (Figs 1E; 3B), *Discoplax* (Fig. 5C), *Cardisoma* (Fig. 5F) and *Tuerkayana* n. gen. (Fig. 5I, L, O): the male gonopore, far from suture 7/8, occupies a posteriormost location in relation to sternite 8; it is close to P5 coxo-sternal condyle; the penis emerges just above this condyle, its proximal portion passing between sternite 7 and sternite 8. In *T. magnum* n. comb. (Fig. 5O) the gonopore is shortly separated from P5 condyle, the sternite 7 joining sternite 8 (a similar short joining is an individual variation observed in *T. rotundum* n. comb.). In contrast, the male gonopore is quite distant from the P5 coxa in other gecarcinids, see below, *Second gecarcinid subclade*.

5) A similar stridulatory apparatus is shared by *Leptograpsodes* and *Discoplax*: in both sexes, pars stridens formed by the suborbital ridge and plectrum on the inner margin of cheliped merus, showing as distinct, demarcated, whitish ridge in *Leptograpsodes* (Fig. 2C, D) (at least up to some certain size) and as thickened ridge closer to the merus margin in *Discoplax* (Fig. 11A); these structures are absent in *Cardisoma* and *Tuerkayana* n. gen.

The closest gecarcinid genus to *Leptograpsodes* is *Discoplax* with which it shares a wide, practically flat thoracic sternum, in the same plane (without inclination in the posterior portion, so the P1-P5 coxae are at a similar level), and a wide, not deeply hollowed sterno-pleonal cavity. Despite these similarities, there is no doubt that *Leptograpsodes* is not a gecarcinid. A main distinctive feature is the shape of sternite 8: weakly developed and unexposed medially in Leptograpsodidae n. fam., and developed medially in all Gecarcinidae, except for *Gecarcoidea*, see below. The thoracic sternum of *Leptograpsodes* and *Discoplax* is very wide, whereas it is narrower in *Cardisoma* and *Tuerkayana* n. gen. The sterno-pleonal cavity is broad, not deeply hollowed in large-sized *Leptograpsodes*, narrower and deeper in *Cardisoma* and *Tuerkayana* n. gen.

The current classification of Gecarcinidae does not reflect the existence of the two main subclades, supported by the congruence of morphological, larval and genetic data. Establishment of two subfamilies is strongly required but would not be appropriate in the present paper in respect of the project announced in Ng *et al.* (2008: 214).

Second gecarcinid subclade

INCLUDED GENERA. — *Gecarcinus* Leach, 1814; *Gecarcoidea* H. Milne Edwards, 1837; *Johngarthia* Türkay, 1970.

REMARKS

The second gecarcinid subclade forms a distinct gecarcinid group, with a higher degree of terrestriality, in contrast to the first subclade grouping *Discoplax*, *Cardisoma* and *Tuerkayana* n. gen. Gecarcinids of the second subclade may be distinguished from *Leptograpsodes* by a set of morphological characters, including the male gonopore that emerges far from the P5 coxo-sternal condyle (Fig. 7B, C and F, G, *Gecarcinus ruricola* and *Gecarcoidea lalandii*, respectively) and many other features including the shape of orbit, the proepistome, and sternal characters.

Genus *Gecarcinus* Leach, 1814

TYPE SPECIES. — *Cancer ruricola* Linnaeus, 1758, by subsequent designation by H. Milne Edwards (1837).

OTHER SPECIES. — *Gecarcinus lateralis* Fréminville *in* Guérin, 1832; *G. quadratus* Saussure, 1853; *G. nobilii* Perger & Wall, 2014.

Genus *Johngarthia* Türkay, 1970

TYPE SPECIES. — *Gecarcinus planatus* Stimpson, 1860, by original designation.

OTHER SPECIES. — *Johngarthia lagostoma* (H. Milne Edwards, 1837); *J. malpilenis* (Faxon, 1893); *J. weileri* (Sendler, 1912); *J. cocoensis* Perger, Vargas & Wall, 2011.

DIFFERENTIAL GENERIC DIAGNOSIS

Gecarcinus and *Johngarthia* are uniform with respect of selected characters: proepistome hardly discernible, inserted under the lower margin of narrow front (Fig. 7D, *Gecarcinus ruricola*; for *Johngarthia lagostoma* see Tavares 1989: fig. 9, as *Gecarcinus*; for *Johngarthia weileri* see N. K. Ng *et al.* 2007:

fig. 6H, as *Gecarcinus*); male gonopore emerging far from P5 coxo-sternal condyle (Fig. 7B, C, *G. ruricola*); for *J. planata* (see Guinot 1979: fig. 54D; Ehrardt 1968, as Gecarcinus; Guinot & Bouchard 1998: fig. 25A, as *Gecarcinus*); for *J. weileri* (see N. K. Ng *et al.* 2007: fig. 4H, as *Gecarcinus*); sternite 1 as a small triangular tooth, not separated by suture from sternite 2; sternite 2 semi-ovate; suture 2/3 horizontal or V-shaped; no suture 3/4, without lateral trace; completely fused sternites 3 + 4 with straight, obliquely directed margins, thus not restricted at level of P1 (Fig. 7B, C, *G. ruricola*); suture 7/8 rather short; sternite 8 not developed medially, the posterior emargination reaching sternite 7 at level of very a narrow median bridge at level of suture 7/8; another weak median bridge at level of suture 6/7 (Fig. 7B, C, *G. ruricola*), or only some traces of such bridges (*G. lateralis*, *G. quadratus*), or indistinct bridges (*Johngarthia*); deep median line only sternite 7 (Fig. 7B, C, *G. ruricola*). No exposed portion of sternite 8 when pleon is folded.

Johngarthia differs from *Gecarcinus* by the already known traits (Türkay 1970; Cuesta *et al.* 2007; Perger *et al.* 2011) and by the locking structures. Instead of a button covered by setae in *Gecarcinus ruricola* (Fig. 7B) and *G. quadratus* (see Köhnk *et al.* 2017: fig. 19c, d), there is a large, oblique prominence covered by setae in *Johngarthia* (Guinot & Bouchard 1998: fig. 25A, as *G. planatus*); but in both genera the pleonal sockets are not delineated, so the locking is no longer functional.

A stridulatory apparatus characterises species of *Johngarthia* and *Gecarcinus*, but it is quite distinct from those of *Leptograpsodes* (Figs 1G; 2C, D), *Discoplax* (Figs 6A; 11A) and *Epigrapsus*, all three with a suborbital pars stridens and a plectrum on cheliped merus. Oblique rows of tubercles on the subhepatic region are rubbed by the tuberculated cheliped merus in *G. quadratus* and by the cheliped palm in *G. lateralis* (see Klaassen 1973: figs 5, 6; Abele *et al.* 1973: fig. 1; Davie *et al.* 2015a). It was shown that in *G. lateralis* stridulation was part of communication system transmitted by substrate vibration (Klaassen 1973).

In *Gecarcinus* and *Johngarthia* the pterygostomial region is glabrous. Setal tufts of dense setae are located along the first pleonal somites instead of between the pereiopods (Rathbun 1918: figs 163, 165).

Genus *Gecarcoidea* H. Milne Edwards, 1837

TYPE SPECIES. — *Gecarcoidea lalandii* H. Milne Edwards, 1837 (see N. K. Ng *et al.* in press) by monotypy.

OTHER SPECIES. — *Gecarcoidea humei* (Wood-Mason, 1874); *G. natalis* (Pocock, 1889) (see Lai *et al.* 2017). All from the Indo-West Pacific.

DIAGNOSIS

Proepistome as small plate inserted under the lower frontal margin (Fig. 7H) (Tavares 1989: fig. 7); male gonopore emerging far from P5 coxo-sternal condyle (Fig. 7G); thoracic sternum (Fig. 7E-G) with 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,

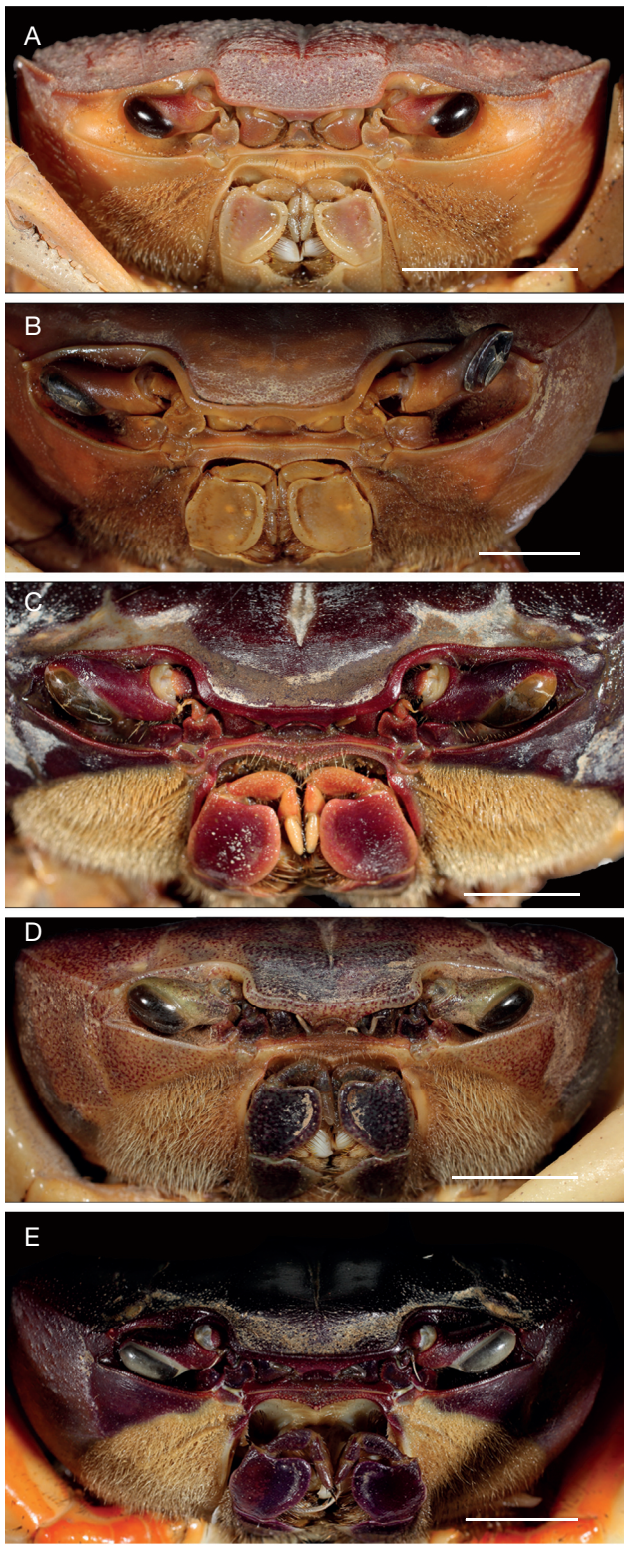

FIG. 6. — Ventral view of Gecarcinidae to show front, proepistome, cephalic appendages, orbit and mxp3: **A**, *Discoplax longipes* A. Milne-Edwards, 1867, ♂ 32.4 × 37.2 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815); **B**, *Cardisoma guanhumi* Latreille *in* Latreille, Le Peletier, Serville & Guérin, 1828, ♂ 56.5 × 68.0 mm, Antilles, MNHN-IU-2013-14983 (= MNHN-B12270); **C**, *Tuerkayana* aff. *hirtipes* (Dana, 1851) n. comb., ♂ 61.0 × 79.0 mm, Loyalty Islands, Lifou Island, We cave, MNHN-IU-2017-8397 (= MNHN-B24811); **D**, *T. celeste* (Ng & Davie, 2012) n. comb., ♂ 44.4 × 52.2 mm, Australia, Christmas Island, ZRC 2012.0171; **E**, *T. magnum* (Ng & Shih, 2014) n. comb., ♂ 49.0 × 58.7 mm, Indonesia, Java, ZRC 2017.0252. Scale bars: 10 mm.

no lateral trace; completely fused sternites 3 + 4 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 the sternal plate and becomes the bottom of the sterno-pleonal cavity (Fig. 7F, G); no portion of sternite 8 dorsally exposed when pleon is folded; locking button as large prominence occupying half proximal part of sternite 5, close to suture 4/5 (Fig. 7F), surrounded by setae (no delineated pleonal socket); on sternite 4 a thickened region forming hook-like edge close to suture 4/5 (Fig. 7F), resembling a clasping apparatus or safety catch, however apparently not functional (described by Guinot 1979: 153, as "cran d'arrêt" in some *Uca sensu lato*, and later recognised as a key innovation for the recognition of several distinctive genera within *Uca sensu lato*, see Beinlich & Hagen 2006: fig. 3b, c; Köhnk *et al.* 2017: fig. 19e). Numerous oblique rows of tubercles covering subhepatic region, but no known report in the emission of stridulation Pterygostomial region glabrous, as in *Gecarcinus* and *Johngarthia.* Dense tufts of hydrophilic setae located along margins of pleon and at its junction with carapace in *Gecarcoidea* (Fig. 7E-G), *G. natalis* and *G. lateralis* having setal tufts extending along first three pleonal segments and on e P5 coxae, such as in *Gecarcinus* (Fig. 7A-C) and *Johngarthia.*

Genus *Epigrapsus* Heller, 1862

Type species. — *Epigrapsus politus* Heller, 1862 by monotypy.

Other species. — *Epigrapsus notatus* (Heller, 1865).

Diagnosis

Carapace with lateral border defined in third part, and with weak subproximal indentation; no posterolateral striae. Proepistome as small plate inserted under lower frontal margin (Tavares 1989: figs 5, 6). Orbit not closed laterally (Tavares 1989: fig. 6), suborbital area granulated; suborbital crest very long, descending obliquely (instead of joining external angle of orbit), consisting of minute, close striae (stridulatory pars stridens), rubbing on ridge lined by short setae (plectrum) located on inner margin of P1 merus, present in both sexes. Male chelae with only minor heterochely or with clear heterochely (palm strongly inflated and with large gap between fingers). Thoracic sternum widened; sternite 1 small, triangular, seemingly fused with semi-ovate sternite 2 that bears medially setose transversal depression; suture 2/3 straight; sternites 3 + 4 not restricted at level of P1, thus with rather straight, obliquely directed margins; suture 7/8 short; sternite 7 wide; sternite 8 very wide, due to posterior emargination that does not reach sternite 7; only a minute portion of sternite 8 is dorsally exposed (below setae in *E. notatus)* when pleon is folded; no median bridge. Median line on sternite 8 and extending on whole sternite 7; its distal portion bumping at level of suture 6/7 into a median, weakly raised area that superficially units both sides of sternal plate and becomes the bottom of sterno-pleonal cavity. Pleon triangular, with short somite 6; long telson. Male gonopore emerging rather far from P5 coxo-sternal condyle and suture 7/8, sternite 7 joining sternite 8 for a rather long distance. Locking button remarkably large and inflated, occupying more than the middle of sternite 5, with strongly granulated prominence; pleonal socket with markedly calcified margin. Presence of conspicuous setal coxal pouches between P3/P4.

Remarks

Epigrapsus, unusual among gecarcinids with regards to the relatively small size at < 40 mm cw and the flatter carapaces of the two known species, *E. politus* and *E. notatus* (see Türkay 1974a; Ng *et al.* 1998; Ng 2003; Liu & Jeng 2005; Fujita 2017), was always considered apart from other land crabs. *E. villosus* Ng, 2003 is actually a junior subjective synonym of *E. notatus* (see Naruse *et al.* 2018b).

The disposition of the genital male region of *Epigrapsus*, with the gonopore remote from the P5 coxa, differs from those of *Cardisoma*, *Discoplax* and *Tuerkayana* n. gen. and is closer to those of other gecarcinids *Gecarcinus*, *Johngarthia* and *Gecarcoidea* studied below. The larval morphology (Cuesta *et al.* 2002, 2007) shows close relationships of *Epigrapsus* with this second subclade of gecarcinids. In contrast, the opened orbit with a long suborbital crest (see Ng *et al.* 1998b: fig. 2c), forming a pars stridens, looks more like the disposition of *Discoplax*, but the direction of suborbital crest is opposite: joining the orbit via a short granulous line in *Discoplax*, vs longer, obliquely descending, not connected to orbit in *Epigrapsus*. The presence in *Epigrapsus* of a thick setal coxa pouch between P3/P4 is unique to Gecarcinidae. Species of the first gecarcinid subclade, i.e., *Cardisoma*, *Discoplax* and *Tuerkayana* n. gen., lack setal coxal pouches and do not show distinct external terrestrial adaptations, except the inflated lateral regions of carapace to accommodate the the highly modified respiratory structures. The second gecarcinid subclade including *Gecarcinus* (Fig. 7A-C), *Johngarthia* and *Gecarcoidea* (Fig. 7E-G) have dense tufts of hydrophilic setae that are located along the margins of the pleon and at its junction with the carapace (see Terrestrial adaptations of grapsoids).

Two types of male chelae have been found in the two species of *Epigrapsus* by Hartnoll *et al.* (2017: figs 3-5, tables 2-4). In both *E. notatus* and *E. politus*, males either have morphologically similar chelae with minimal heterochely, or show a clear heterochely with different morphologies in the major and minor chelae; the proportion of heterochelous males increases in the larger mature size classes. Progressive polymorphism (i.e., when different chelar morphologies succeed each other within the mature phase, as recorded in *Johngarthia lagostoma*) needs to be confirmed.

Some aspects of the reproduction of both *Epigrapsus* species are also unusual: the fast and vigorous larval release behaviour (ovigerous females shake their whole body laterally to release the larvae instead of using fanning motions of the pleon) and the choice of surge channels as release sites (Liu & Jeng 2005). The affinities of *Epigrapsus* are so ambiguous to the point of questioning its status.

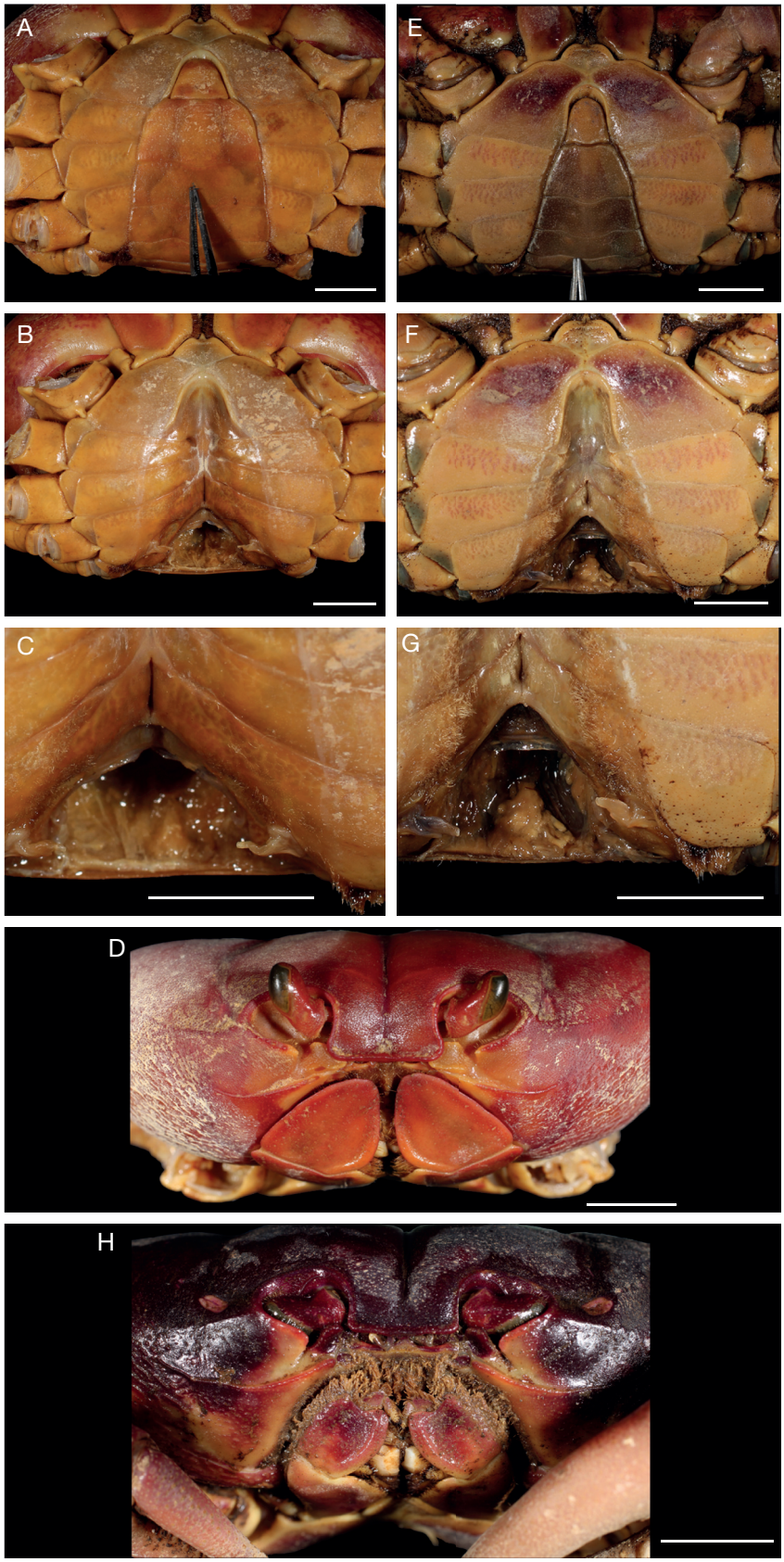

FIG. 7. —Thoracic sternum and frontal view: **A**-**D**, *Gecarcinus ruricola* (Linnaeus, 1758), ♂ 55.0 × 76.0 mm, Cuba, MNHN-IU-2017-8392 (= MNHN-B13155); **E**-**H**, *Gecarcoidea lalandii* H. Milne Edwards, 1837, ♂ 52.0 × 73.3 mm, Papua New Guinea, MNHN-IU-2013-13254: **A**, **E:** thoracic sternum (brushed) with pleon; **B**, **F**, thoracic sternum (brushed) without pleon; **C**, **G:** genital region with gonopore and penis, **D**, **H**, front, proepistome, cephalic appendages, orbit and mxp3. Scale bars: 10 mm.

Larval characters and molecular phylogeny of the two gecarcinid subclades

Morphological features of *Gecarcinus*, *Gecarcoidea* and *Epigrapsus* allow differentiation of two distinct gecarcinid subclades. In the cladistic analyses of Tavares (1989), which showed a sister-group relationship of Gecarcinidae-Grapsidae, Gecarcinidae was separated in at least two subclades: *Cardisoma* + *Discoplax* and *Gecarcinus* (including *Johngarthia*) + *Gecarcoidea*, with *Epigrapsus* seemingly closer to the second group.

The recent data from larval morphology or genetic analyses must take into account that *Cardisoma hirtipes* is hereby considered to be not a *Cardisoma* or a *Discoplax* and is assigned, instead, to another genus that we introduce, *Tuerkayana* n. gen. The results of our proposals for the new generic names of gecarcinids are provided in Table 1.

Larval characters emphasize the need to split the family Gecarcinidae (Willems 1982; Shokita & Shikatani 1990). According to Cuesta *et al.* (2002) zoeal features supported the recognition of two major groups: *Epigrapsus*, *Gecarcinus* and *Gecarcoidea* on one hand, and *Cardisoma* (*C. guanhumi*, *C. carnifex*) and *Tuerkayana hirtipes* n. comb. (as *Discoplax*) on the other hand, the setation of the maxillar endopodite separating the latter group from the rest of the Gecarcinidae. Based on overall similarities of zoeal morphology, Cuesta *et al.* (2002) and Cuesta & Anger (2005) suggested affinities of the group *Gecarcinus* + *Gecarcoidea* + *Epigrapsus* with Varunidae, whereas *Cardisoma* (our *Cardisoma sensu stricto*) and *Tuerkayana hirtipes* n. comb. (as *Discoplax*) shared with Sesarmidae antennal and pleonal morphologies, as well as the setation pattern of the maxillar endopodite. A new review of zoeal features of gecarcinids, with more complete data (Cuesta *et al.* 2007: tables 5, 6) distinguished the same two groups: one with *Cardisoma sensu stricto* (*C. guanhumi*, *C. carnifex*, *C. armatum*) and *Tuerkayana hirtipes* n. comb. (as *Discoplax*), and a second group with *Epigrapsus*, *Gecarcinus*, *Gecarcoidea*, and *Johngarthia*; interestingly, this paper shows that the megalopa of *Tuerkayana hirtipes* n. comb. (as *Discoplax*) differs from that of *Cardisoma sensu stricto*, which supports the distinction of *Tuerkayana* n. gen.

Genetic studies by Schubart *et al.* (2006) recovered *Cardisoma* as basal, followed by *Gecarcoidea-Gecarcinus.* N. K. Ng *et al.* (2007), noting that the orbital structure and the gonopore position were extremely variable within gecarcinids, recovered two groups: *Cardisoma sensu stricto* (*C. carnifex*, *C. crassum*) + "*Discoplax*" (i.e., *Tuerkayana hirtipes* n. comb. and *T. rotundum* n. comb.), and *Gecarcinus* + *Gecarcoidea*.

The molecular and larval analysis of Schubart & Cuesta (2010) demonstrated that the status of the apparently paraphyletic Gecarcinidae was still unresolved, with *Cardisoma* and *Discoplax* forming a sister-group to *Gecarcinus* and *Gecarcoidea*. Van der Meij & Schubart (2014: fig. 2) concluded that Gecarcinidae did not cluster together and also recovered two groups: *Cardisoma carnifex* + *Tuerkayana hirtipes* n. comb. (as *Discoplax*) and *Gecarcinus lateralis* + *Gecarcoidea lalandii*. Using molecular data from three markers (mitochondrial 12S and 16S rRNAs, and nuclear histone H3) and covering a total of 15 thoracotreme families, Tsang *et al.* (2018), as Chu *et al.* (2015), confirmed the polyphyly of Grapsoidea and Ocypodoidea, as well as that of Pinnotheroidea De Haan, 1833. Tsang *et al.* (2014: fig. 1) recognised a *Gecarcoidea* clade (*G. natalis* + *G. lalandii*) and a sister clade *Cardisoma-Tuerkayana* n. gen. (as *Discoplax*). Tsang *et al.* (2018: fig. 2) recognised two gecarcinid clades: a *Gecarcoidea* clade (*G. lalandii* and *G. natalis*) and a *Cardisoma* clade, actually including two genera: *Cardisoma* for *C. crassum* and *Tuerkayana* n. gen. for their "*Discoplax hirtipes*".

Biology of Gecarcinidae

According to Liu & Jeng (2007) biological aspects showed the same divergent tendency, the length of the breeding season being longer in species of *Cardisoma* (including *Cardisoma sensu stricto* and *Tuerkayana* n. gen.) compared to other gecarcinids. In terms of overall pattern of gecarcinid breeding migrations, opposing ends of the spectrum are presented by cavernicolous *Discoplax longipes* (eggs are laid and incubated in the caves where the adults live, and the females with ripe eggs migrate directly to the sea; no males migrate; see Ng & Guinot 2001) and by *Gecarcoidea natalis*, the iconic "Christmas Island red crab" (males and females migrate to the sea in similar numbers; only after both dip in the sea, does courtship and mating occur; see Hicks 1985; Hartnoll *et al.* 2010). *Johngarthia lagostoma* (mating and laying occur at all phases of the migration, and males migrate towards the sea in decreasing proportion with distance) and *Gecarcinus ruricola* (migrating crabs are mostly female with predominance of ovigerous females, so some females mate and lay eggs on the landward side, others on the seaward side; migrating females on average larger than migrating males) have a median position (Hartnoll *et al.* 2006a, b, 2007).

The relationships within Gecarcinidae can also be examined in relation to their landward migration stages, their degree of terrestrialisation. *Gecarcinus*, *Gecarcoidea* and *Johngarthia* form a group with markedly terrestrial habit: the megalopa is the landward migration stage in *Gecarcinus* and *Johngarthia* (the megalopa of *Gecarcinus ruricola* being the most terrestrially adapted megalopa described to date for locomotion on land: it is the returning stage from the sea into fully terrestrial habitats before moulting to the first crab instar (see Hartnoll & Clark 2006: 162; Rodríguez-Rey *et al.* 2016). On the contrary, the first crab in *Cardisoma sensu stricto* and *Tuerkayana* n. gen. (as "*Discoplax hirtipes*") form a second group, with less terrestrial habit. *Tuerkayana celeste* n. comb. migrates up streams as the megalopa and only emerges onto land as the first crab (Hartnoll *et al.* 2014, as *Discoplax*).

Family Grapsidae MacLeay, 1838

Included genera. — *Geograpsus* Stimpson, 1858; *Goniopsis* De Haan, 1833; *Grapsus* Lamarck, 1801; *Leptograpsus* H. Milne Edwards, 1853; *Metopograpsus* H. Milne Edwards, 1853; *Pachygrapsus* Randall, 1840; *Planes* Bowdich, 1825.

Remarks

Morphological comparison of Leptograpsodidae n. fam. with the family Grapsidae suffers from the lack of a consistent familial diagnosis for Grapsidae. In using the traditional and

recently published grapsid morphological characters (Banerjee 1960; Guinot & Bouchard 1998; Poore 2004; N. K. Ng *et al.* 2007; Davie *et al.* 2015a; Köhnk *et al.* 2017), we propose the diagnostic features of the family, essentially based on the type species of all genera. The question whether some distinctive features warrant the separation of Grapsidae into subfamilies is not the topic of our study.

Diagnosis

Carapace typically quadrilateral to quadrate; surface moderately flat, usually with marked striae, especially on branchial regions (Banerjee 1960: figs 1a-e, 5; Naderloo 2017: fig. 30.1), exceptionally faint in *Planes* (Chace 1951: table 1); anterolateral margins entire or with one, may be two, teeth behind exorbital angle; front wide, much broader than orbits, entire, strongly deflexed, widely overhanging epistome between short eyestalks; suborbital margin running vertically from orbital angle to meet end of suborbital crest directly, no overlap (N. K. Ng *et al.* 2007: fig. 5B); basal article of antenna immobile, bent; orbit small, open laterally; mxp3 leaving rhomboidal gape; both mxp3 merus and ischium with single longitudinal sulcus and lacking oblique setose crest (N. K. Ng *et al.* 2007: fig. 7D; Davie *et al.* 2015a: fig. 71-2.27N); flagellum of exopodite usually present, may be strongly reduced or absent (*Geograpsus*); absence of stridulatory suborbital crest; pterygostomial region sparingly setose, with setae simple, plumose, never arranged in reticulated pattern; male chelipeds homochelous (except in *Metopograpsus*, merus usually with developed spines on anterodistal margin, fingers apically spoon-shaped; walking legs robust, distinctly flattened, usually armed with spines and bristles; mobile setae on dactylus of P2-P5; sterno-pleonal cavity without rim at level of telson, may be a faint rim; male gonopore next to articular membrane adjacent to P5 coxa (sternal emergence being proved by dissection), and opening in middle of sternite 8 thus far from suture 7/8 (except in *Planes*); penis elongate, narrow (e.g. *Grapsus*) or wide, short (e.g. *Metopograpsus*), partially calcified; G1 short, sinuous or slightly curved, even twisted, usually with dense setae on apical part; pleon with six free somites plus telson; pleonal-locking mechanism of press-button type always present (but absent in *Geograpsus*), functional throughout life, usually very marked, close to suture 5/6 or slightly remote (*Goniopsis*), with round or acute buttons, exceptionally developed and half-moon-shaped (*Metopograpsus*); small but distinct socket usually next to intestine (Hartnoll 1965; Guinot & Bouchard 1998: fig. 22; Köhnk *et al.* 2017: figs 16, 17); vulva with operculum (McLay & Sal Moyan 2016). Tufts of hydrophilic setae generally lacking, but may be present between P3/P4 in some species of *Grapsus*, in *Goniopsis*, *Metopograpsus*, *Pachygrapsus* (Oliveira 2014: table 2) and chiefly in *Geograpsus*, the single terrestrial grapsid species (Greenaway 1988: fig. 7.2.B-D; Paulay & Starmer 2011).

Additional characters

For the sternal and male genital characters of Grapsidae that must be added, our diagnosis is based on the type genus *Grapsus* and its type species *G. grapsus*, but we have extended our study to numerous other genera.

Proepistome as a broad, more or less narrow, anteriorly convex (*Grapsus*) or straight (*Goniopsis*) septum, meeting frontal margin (Banerjee 1960: figs 2h, o, 4d; Komai *et al.* 2004: fig. 2B; N. K. Ng *et al.* 2007: fig. 6B; Bouchard *et al.* 2013: fig. 20D, F). Thoracic sternum wide (Fig. 8A, B) (Guinot & Bouchard 1998: fig. 22A-C); sternites 1-2 fused forming a small, more or less triangular plate, a trace of their separation may be however recognisable by a ridge or faint sulcus, lined by setae; suture 2/3 complete (Banerjee 1960: figs 1f, 4a, i); sternite 3 completely fused to sternite 4 without indication of a dorsally visible demarcation, thus absence of any suture 3/4; sutures 4/5-7/8 incomplete; sternite 7 with incomplete sulcus; suture 6/7 more obliquely directed forwards in *Metopograpsus* and *Leptograpsus*; episternite 7 variously shaped, for example extending posteriorly on the P5 coxa in *Goniopsis* (see Guinot 1979: fig. 52B); posterior emargination weak; sternite 8 very developed, largely exposed medially; no portion visible dorsally when the pleon is closed; suture 7/8 rather long, however shorter than preceding ones; median line long, present on sternite 8 and extending on sternite 7 (Fig. 8B, C: *Grapsus grapsus*) (Guinot & Bouchard 1998: fig. 22A: *G. tenuicrustatus* Herbst, 1783; fig. 22B, D: *Metopograpsus latifrons*). No medial bridge.

A male gonopore opening in the middle of sternite 8, thus far from suture 7/8, with a clear posteriormost location in relation to suture 7/8, occurs in all Grapsidae (Guinot 1979: fig. 52A) except in *Planes*. The penis emerges as a very thick, cylindrical tube (Fig. 8C) (Guinot 1979: fig. 52A-C; Sternberg *et al.* 1999; Karasawa & Kato 2001: fig. 2.19; N. K. Ng *et al.* 2007: fig. 4D; Guinot *et al.* 2013: fig. 23D), sometimes with a calcified proximal portion (e.g. in *Metopograpsus*). This pattern of genital disposition is shared by all examined genera, except by *Planes* (e.g. *P. minutus*), in which the gonopore is close to suture 7/8, the penis is short, lodged in a depression below suture 7/8, with only a tiny, hardly visible, sclerotised basal portion (Guinot 1979: fig. 52C).

Grapsids may swim; few of these do so extensively and exhibit significant swimming morphological adaptations, except species of *Planes*, which are wholly pelagic, clinging to floating marine animals such as sea turtles (Frick *et al.* 2011), and show fringes of setae on pereiopods for swimming ability (Hartnoll 1971: fig. 6d).

Leptograpsodidae n. fam. shares with Grapsidae: four postfrontal lobes, oblique striae on branchial regions, oblique ridges on the lateral surfaces of meri of P2-P5, an effective pleonal-locking mechanism, especially in *Grapsus*, in which the buttons on sternite 5 are generally acute (Köhnk *et al.* 2017: fig. 16a).

Comparison with Leptograpsodidae n. fam.

Leptograpsodidae n. fam. (Figs 1-3) differs from Grapsidae by: the shape of carapace with strongly convex margins, the proepistome obviously inserted into the frontal margin, the pleonal sockets close to the border of pleonal segment 6 (vs close to the intestine and not bordered by lateral edge of the pleon in Grapsidae, Köhnk *et al.* 2017: figs 16, 17). Another distinctive feature is the persistence of the locking

mechanism in adult females of *Leptograpsodes* (at least until cw carapace 20.6 mm), whereas it is lost in adult female grapsids. Pouches with tufts of hydrophilic setae are present between all pereiopods (generally absent in Grapsidae or, when present, only between P3/P4 such as in the terrestrial *Geograpsus*).

The main sternal features that differentiate Leptograpsodidae n. fam. from Grapsidae are: thoracic sternum less widened; sternite 1-2 individualised with suture 1/2 present (no suture 1/2 or only a sulcus or ridge in Grapsidae); a bridge at level of suture 6/7 (absent in Grapsidae); sternite 8 not developed, unexposed medially, no median line at this level (much expanded and largely exposed medially, with median line on sternite 8, in Grapsidae); a small portion of sternite 8 and also a tiny proximal part of penis dorsally visible when pleon is folded (not visible in Grapsidae); sterno-pleonal rim at level of telson rather thick (no rim or only faint rim in Grapsidae).

Leptograpsodidae n. fam., the first gecarcinid subclade (*Cardisoma*, *Discoplax* and *Tuerkayana* n. gen.) and Grapsidae share the same pattern of the genital region, except that the penis of Grapsidae, instead to be basally wedged above the P5 coxo-sternal condyle, is fully developed at its exit.

Previously suggested (Cuesta *et al.* 1997; Schubart *et al.* 2006; Schubart & Cuesta 2010) but also questioned (Kitaura *et al.* 2002; Wetzer *et al.* 2009), the monophyly of Grapsidae (*Leptograpodes* being excluded) was confirmed by Ip *et al.* (2015: figs 1-3) based on five molecular markers, including mitochondrial DNA and nuclear protein-coding markers. These results, which corroborated the 2011 Schubart's anlysis, showed with strong support: a paraphyletic *Pachygrapsus* (see also Wetzer *et al.* 2009; Schubart 2011; van der Meij & Schubart 2014); a paraphyletic *Planes*; *Metopograpsus* with clear differences in the number of zoeal stages (only 5) and also with distinctive morphological characters, so its basal position in the family (Cuesta *et al.* 2011: table 3; Landeira & Cuesta 2012; see also van der Meij & Schubart 2014). According to genetic studies, *Metopograpsus* was subdivided into two main clusters: the sister species *M. thukuhar* and *M. messor* on the one hand, and the remaining four species on the other (Fratini *et al.* 2018: fig. 2). From their phylogenetic tree, Wang *et al.* (2018a: fig. 1) found that *M. quadridentatus* Stimpson, 1858 and (*Grapsus tenuicrustatus* [*Grapsus tenuicrustatus* (Herbst, 1783) + *Pachygrapsus crassipes*] clustered in one branch with high nodal support value.

Larval characters

From a larval point of view, the grapsids were divided into two groups: 1) a first group, weakly supported, consisting of the monophyletic *Goniopsis* and a big cluster of all the *Grapsus* species together with three species of *Pachygrapsus*; 2) a second group that was a large assemblage of the remaining genera, e.g. the monophyletic *Geograpsus*, the monotypic *Leptograpsus* that branched off as a distinct clade, and all other species of *Pachygrapsus* (including the type species *P. crassipes*).

Family Glyptograpsidae Schubart, Cuesta & Felder, 2002

Included genera. — Based on available larval and DNA evidence, Schubart *et al.* (2002) established a new family for the American and east Atlantic genera *Glyptograpsus* Smith, 1870 and *Platychirograpsus* De Man, 1896, crabs occuring in shallow freshwater streams, from brackish waters at stream mouths to up to several hundred kilometers inland (see also Cuesta & Schubart 1998; Schubart *et al.* 2006: figs 1-4). Genetic results of van der Meij & Schubart (2014) showed that Glyptograpsidae appeared as sister-group of Heloeciidae H. Milne Edwards, 1852, a family currently included in Ocypodoidea (Ng *et al.* 2008).

Diagnosis

The most conspicuous adult morphological traits are: the striking heterochely shown by the males (unique in Grapsoidea), the dorsal carapace surface areolated and without striae, the broad mxp3 closing the buccal cavity without gaping and with three longitudinal sulci on the merus (N. K. Ng *et al.* 2007: fig. 7G), the pleon with somites 3 to 5 inflexible but with sutures, the G1 with a subproximal tuft of setae and elongate, uncinate distal portion, all characters well described by the cited authors.

To these synapomorphies corroborated by molecular studies, some characters must be added: absence of pleonal-locking mechanism, no button, no socket, the pleonal area where the socket is usually located being occupied by the G1's tip; sterno-pleonal cavity very broad, with conspicuous rim at level of telson; thoracic sternum (Fig. 8D, E): suture 2/3 well marked, sternite 1 extending into a narrow process between mxp3; sternite 2 with a membranaceous depression; sternite 8 rather wide but not greatly exposed medially; median line extending on sternite 7; male gonopore with a posteriormost location in relation to sternite 8; penis short, with a sclerotised proximal portion (Fig. 8F).

Comparison with Leptograpsodidae n. fam.

Glyptograpsidae shares with Leptograpsodidae n. fam. the median line extending on sternite 7, but the sternal emergence of the gonopore far from P5 coxa (N. K. Ng *et al.* 2007: fig. 4G), the dispositon of sternite 8, the shape of penis are distinctive characters. The glyptograpsid suborbital ridge (N. K. Ng *et al.* 2007: fig. 5G) does not consist in a stridulatory crest.

Family Percnidae Števčić, 2005

Included genera. — The family is monogeneric, with six species that show an active swimming capacity (Zenone *et al.* 2016) by means of a developed setation (rows of postero-dorsal setae) on the long pereiopods that allow them to cling to hard surfaces. Species of Percnidae are, with the Plagusiidae and Varunidae, the only grapsoids able to extensively swim thanks to specialised modifications.

Remarks

Based on Cuesta & Schubart (1998) and Schubart *et al.* (2000b, 2006) that questioned the placement of *Percnon* Gistel, 1848, Števčić (2005) established the new tribe Percnini, which was adopted as the subfamily Percninae within the Plagusiidae

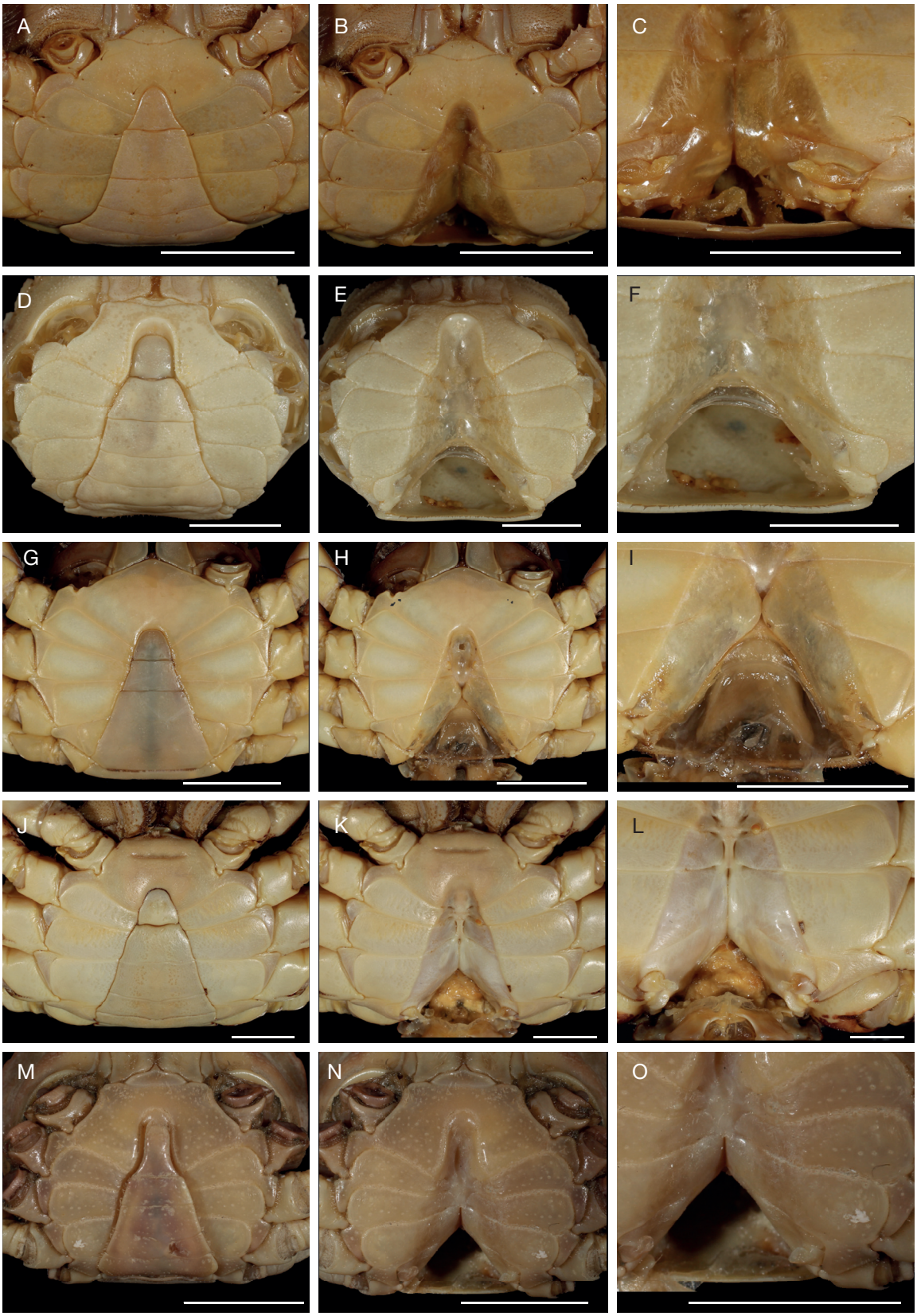

FIG. 8. — Pleon, thoracic sternum and genital region of Grapsoidea: **A**, **D**, **G**, **J**, **M**, thoracic sternum (brushed) with pleon; **B**, **E**, **H**, **K**, **N**, thoracic sternum (brushed) without pleon; **C**, **F**, **I**, **L**, **O**, genital region with gonopore and penis: **A**-**C**, Grapsidae: *Grapsus grapsus* Lamarck, 1801, ♂ 23.8×26.9 mm, Antilles, MNHN-IU-2013-10764 (=MNHN-B24641); **D**-**F**, Glyptograpsidae: *Glyptograpsus jamaicensis* (Benedict, 1892), ♂ 32.8×37.4 mm, Jamaica, MNHN-IU-2017-8401 (=MNHN-B127715); **G**-**I**, Percnidae: *Percnon planissimum* (Herbst, 1804), ♂ 29.7×27.7 mm, Réunion Island, MNHN-IU-2010-19798 (=MNHN-B24534); **J**-**L**, Plagusiidae: *Plagusia squamosa* (Herbst, 1790), ♂ 43.6×46.3 mm, Marquesas Islands, MNHN-IU-2011-8947; **M**-**O**, Xenograpsidae: *Xenograpsus testudinatus* N. K. Ng, Huang & Ho, 2000, ♂ 21.8×23.8 mm, NE Coast of Taiwan, MNHN-IU-2013-14995 (=MNHN-B30314). Scale bars: 10 mm.

(Ng *et al.* 2008) and then separated as a full family on the basis of larval morphology and combined evidence of mtDNA and nDNA by Schubart & Cuesta (2010), a currently adopted taxonomy (Davie *et al.* 2015c). Genetic results of van der Meij & Schubart (2014) showed that Percnidae was related to Mictyridae Dana, 1851, but with very long branches, "an unexpected hypothesis considering the large phylogenetic distance between these two families in the trees of Schubart *et al.* (2006) and Wetzer *et al.* (2009)."

Diagnosis

Sternal and male genital characters are here added. Proepistome very narrow. Thoracic sternum flat, remarkable by the absence of anterior sutures, seemingly except for faint suture 1/2, most noticeable medially posterior to small, triangular sternite 1; sternites 2-4 forming a smooth single piece, with straight margins (Fig. 8G, H). Episternite 7 long, narrowly extended. Despite a rather deep posterior emargination, sternite 8 very broad, widely exposed medially, although narrower in *P. gibbesi*. Sternite 8 forming raised protrusion that bears the gynglyme receiving P5 coxo-sternal condyle. When the pleon is closed, a rather large portion of sternite 8 dorsally exposed anteriorly; in addition, a very minute portion visible posteriorly (Guinot 1979: 209, pl. 23, fig. 2). Episternites 4-6 very narrow. Median line present on sternite 8 and extending on sternite 7. Located in posteriormost location in relation to sternite 8, male gonopore and penis very close to P5 coxa. Gonopore coming into contact with P5 coxo-sternal condyle in *P. planissimum* (see Guinot 1979: pl. 23, fig. 2; Rodríguez 1992: fig. 11E; Karasawa & Kato 2001: fig. 2.18), *P. affine*, *P. abbreviatum*, and *P. guinotae*; in contrast, in other species, e.g. *P. gibbesi*, episternite 7 long, very shortly joining the raised protrusion of sternite 8, therefore gonopore slightly separated. Penis narrow, showing a calcified proximal portion and then a tube (Fig. 8I) (Kienbaum *et al.* 2018: fig. 1). Presence of a strong press-button with wide base and corneous surface (Guinot 1979: pl. 23, figs 2, 3; Guinot & Bouchard 1998: 664; Davie *et al.* 2015c; Emmerson 2016).

The fusion of some pleonal somites is rare in Grapsoidea. In both sexes of Percnidae the pleonal somites 3 to 6 are inflexible although with distinct sutures, in contrast to somites 3-5 fused also with still evident sutures in Plagusiidae and Glyptograpsidae.

The female reproductive system of *Percnon gibbesi* studied by Kienbaum *et al.* (2018) exhibits a combination of morphological characters (connection of the oviduct through a separate cuticular duct and presence of a bursa) that has so far been only known in heterotreme crabs. This result supports the conclusion of Schubart & Cuesta (2010) that Percnidae represents a basal split within the Thoracotremata, with an independent phylogenetic origin. Molecular analyses by Tsang *et al.* (2014: figs 1, 2) and Chu *et al.* (2015: fig. 71-13.2) have also shown that Percnidae emerged basally with cryptochirids and xenograpsids.

A more complete comparison between Percnidae and Leptograpsodidae n. fam. is not necessary in view of their important morphological differences.

Family Plagusiidae Dana, 1851

Included genera. — *Plagusia* Latreille, 1804; *Davusia* Guinot, 2007; *Guinusia* Schubart & Cuesta, 2010; *Euchirograpsus* H. Milne Edwards, 1853; *Miersograpsus* Türkay, 1978.

Remarks

The Plagusiidae, traditionally treated as a subfamily of Grapsidae and comprising five genera (*Euchirograpsus* and *Miersograpsus* are not studied here), was raised to full family status by Sternberg & Cumberlidge (1998), Schubart & Ng (2000) (see also Cuesta & Schubart 1998; Davie 2002; Schubart *et al.* 2000b, 2002; Guinot 2007; N. K. Ng *et al.* 2007; Schubart & Cuesta 2010; Davie *et al.* 2015c). The genus *Percnon* was removed from the Plagusiidae and finally recognised as a separate family, Percnidae, by Schubart & Cuesta (2010).

Species of Plagusiidae, from rocky shores or on exposed reefs (Alcock 1900; Rathbun 1918; Dawson 1987; Emmerson 2016), are able to extensively swim (sideways swimming) thanks to specialised modifications: on the postero-dorsal regions of carpi, propodi and dactyli of P2-P5, dense fringes of long pinnate setae can stand erect for the propulsive stroke or lie flat for the forward recovery stroke; their swimming method gave them the name of "rafting crabs" (Hartnoll 1971: 44, figs 6b, 9A-C).

Additional sternal and male genital characters

Whereas the traditional differentiating characters of Plagusiidae are well established, sternal and male genital features must be documented. Proepistome either roughly triangular and prolonged inside median frontal incision (N. K. Ng *et al.* 2007: fig. 6D), or shorter, blunt and not deeply inserted into front. Thoracic sternum subcircular (Fig. 8J, K) (Schubart & Ng 2000: fig. 1D; Naderloo 2011: fig. 18f). Sternite 1 (narrow, triangular) and sternite 2 (of variable size and shape) forming a variously shaped, single piece located at a more or less lower level, but presence of suture 1/3, lined by setae. Suture 2/3 well marked, straight or curved. Sternites 3 and 4 completely fused without external mark, being only crossed medially by thick row of setae. Posterior emargination on sternite 8 low (*Plagusia*, *Davusia* and *Guinusia*). Sternite 8 wide, developed, exposed medially (Fig. 8L). Median line extending on sternite 8 and 7. (It should be noted that a long median line is already present [from somite 8 to 5] in the megalopa of *Guinusia dentipes*, as shown by Gonzáles-Gordillo *et al.* [2000: fig. 1C]). Male gonopore (Fig. 8L), in posteriormost location in relation to sternite 8, and penis very close to P5 coxa; however, junction of episternite 7 with sternite 8, thus gonopore separated: *Plagusia depressa* (Fabricius, 1775) (see H. Milne Edwards 1834, 1837, 1844, Atlas, pl. 23, fig. 3d; Guinot 1979: 209, fig. 52E), *P. squamosa* (see N. K. Ng *et al.* 2007: fig. 4C), *Guinusia dentipes* (see Karasawa & Kato 2001: fig. 2.17, as *P. dentipes*), and *Davusia glabra* (see Guinot 1979: pl. 18, fig. 9, as *Plagusia glabra*; 2007: 29); Guinot *et al.* 2013: figs 23B, 33B, C). Penis short, consisting of wide sclerotised portion and small papilla. Presence of strong, efficient press button, with remarkable microstructure, likely

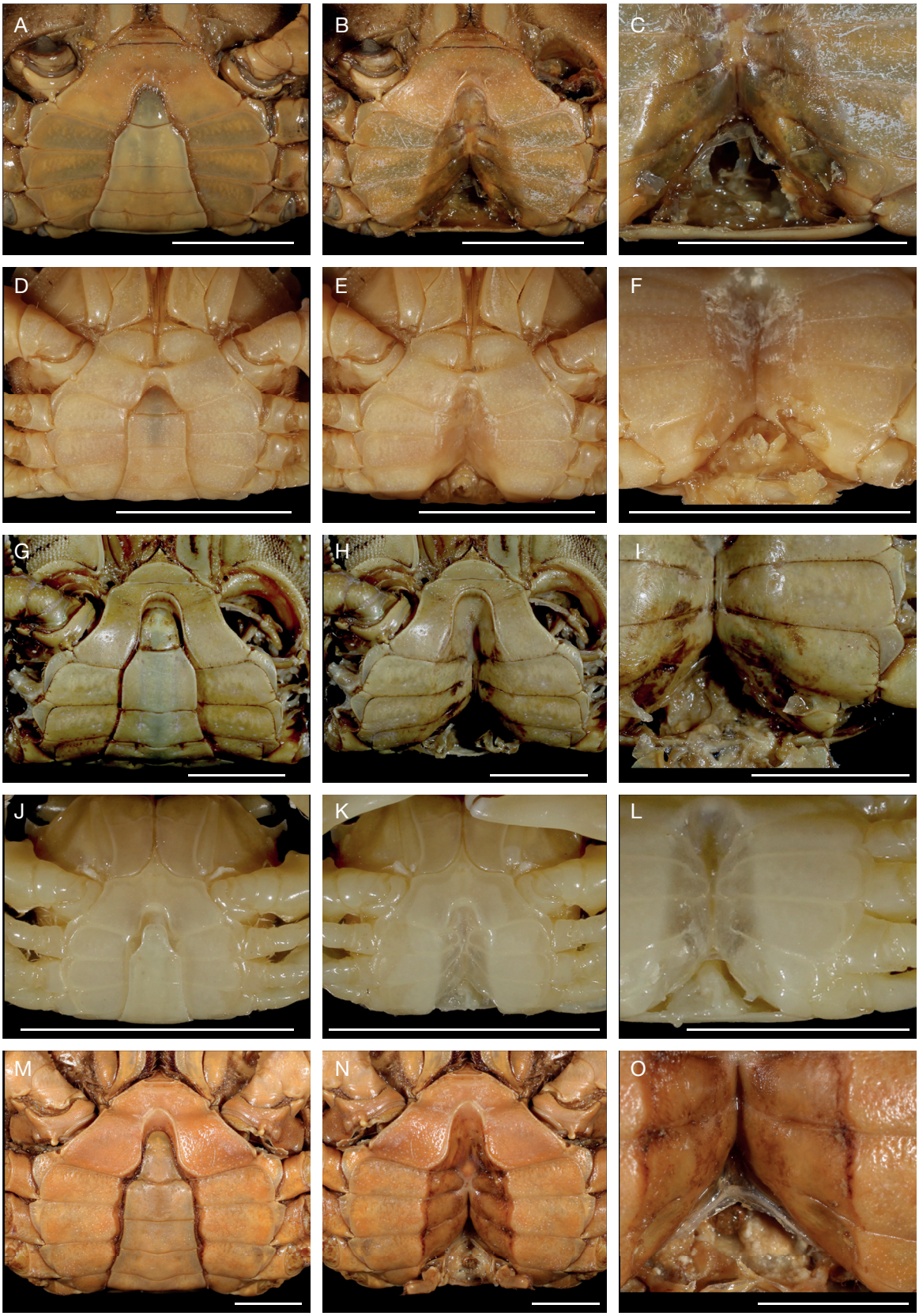

Fig. 9. — Pleon, thoracic sternum and genital region of Varunidae: **A**-**C**, Cyclograpsinae: *Cyclograpsus punctatus* H. Milne Edwards, 1837, ♂ 24.9 × 30.8.0 mm, South Australia, Kangaroo Island, MNHN-IU-2013-14994 (= MNHN-B12561); **D**-**F**, Gaeticinae: *Gaetice depressus* (De Haan, 1835), ♂ 15.7 × 18.0 mm, China, Amoy, MNHN-IU-2013-14990 (= MNHN-B12089); **G**-**I**, Heliceinae Sakai, Türkay & Yang, 2006: *Helice tridens* (De Haan, 1835), ♂ 28.7 × 34.2 mm, Japan, MNHN-IU-2016-10762 (= MNHN-B12098); **J**-**L**,Thalassograpsinae: *Thalassograpsus harpax* (Hilgendorf, 1892), ♂ 8.1 × 9.3 mm, Scattered Islands, MNHN-IU-2013-16120; **M**-**O**, Varuninae: *Varuna litterata* (Fabricius, 1798), ♂ 49.5 × 57.0 mm, Madagascar, MNHN-IU-2013-14987. Scale bars: A-K, M-O, 10 mm; L, 5 mm.

functional throughout life in females (Guinot & Bouchard 1998: 678, 680, figs 23D, 26F). Vulva with operculum, of varying complexity (see Guinot *et al.* 2013: 48; McLay & Sal Moyano 2016). Pleonal somites 3-5 fused, but sutures still evident.

Molecular analysis and larval morphology

Based on a molecular analysis and larval morphology, three main phylogenetic clusters have been recognised by Schubart & Cuesta (2010): *Davusia*, phylogenetically basal to other plagusiids; another cluster including *P. depressa* (type species), *P. squamosa*, *P. immaculata* Lamarck, 1818, and *P. speciosa* Dana, 1852; a third cluster consisting of the two species of *Guinusia*, *G. chabrus* and *G. dentipes.*

We do not find any close similarities between Plagusiidae and Leptograpsodidae n. fam.

Family Sesarmidae Dana, 1851

Remarks

The Sesarmidae, which contains nearly 300 species (Davie *et al.* 2015c), is known as a solid monophyletic clade, supported by genetic sequences (van der Meij & Schubart 2014) and larval morphology (Cuesta *et al.* 2006; Shahdadi & Schubart 2017). The massive ecological and morphological speciation should be the result of convergent evolution (Schubart *et al.* 1998; see also Fratini *et al.* 2005). According to Schubart *et al.* (2006), *Sesarmoides* Serène & Soh, 1970, now *Karstama* Davie & Ng, 2007, occupies a basal position within the family. Despite the species richness and ecological diversity (typically inhabitants of soft-sediment littoral habitats like marshes and mangroves, also in freshwater and terrestrial habitats, may be found in bromeliad leaf axils, rock rubble, empty snail shells, caves and mountain streams, thereby showing complete independence from the sea, see Schubart & Koller 2005), the family has not been splitted into subfamilies. The external morphology (e.g. carapace quadrate to quadrangular; suborbital, pterygostomial, subbranchial, subhepatic regions and lateral walls of carapace covered in uniform reticulated network of short, hooked, closely-set setae (Felgenhauer & Abele 1983: figs 1-4); orbits with lower border as channel running obliquely downwards towards buccal cavern; oblique setose ridge running across merus and ischium of mxp3) is unambiguously different from that of Leptograpsodidae n. fam.

Additional characters

Sternal and male genital features are added, based on a limited number of selected genera. Proepistome usually very developed, transwerse, broad, variously widened (Abele 1992: fig. 2d; N. K. Ng *et al.* 2007: fig. 6C; Komai *et al.* 2004: figs 4C, 5C, 6B, 8B, 9B; Ragioneri *et al.* 2012: figs 1, 7d); epistome as complex structure, with Vervey's groove in which the water from the exhalent openings flows towards antenna and orbit, emptying a thin stream over the reticulate network of setae (Hagen 1978: fig. 2; Abele 1992; Felgenhauer & Abele 1983: fig. 1; Reimer *et al.* 1998: fig. 2f). Thoracic sternum variously widened, strongly restricted at P1 level. Sternites 1 and 2 separated by suture 1/2. Suture 2/3 well marked, straight or curved, often lined by setae. Sternite 3 completely fused to sternite 4, no suture 3/4, even no lateral trace (Fig. 10A, B) (Davie & Ng 2013: fig. 9). Sternite 8 developed, either exposed medially and with median line or narrowing medially and without median line. Median line extending on sternite 7 (e.g. *Sesarma reticulatum*, *Chiromantes dehaani*), even on sternite 5. (e.g. *Neosarmatium meinerti*). Male sternal gonopore (Fig. 10C) located posterior to suture 7/8, adjacent to variously expanded episternite 7, shortly separated from P5 coxa (Guinot 1979a: fig. 52D; N. K. Ng *et al.* 2007: fig. 4B; Schubart *et al.* 2009: 4; see also Karasawa & Kato 2001: fig. 2.20). Penis rather long, well developed, generally basally calcified, may be foliaceous, showing as longitudinal, oblique or horizontal tube variously oriented; may show as seemingly lying in small depression excavated at base of G1 endopodite (Guinot *et al.* 2013: fig. 35: *Metasesarma aubryi* (A. Milne-Edwards, 1869)).

Karstama ultrapes (previously in *Sesarmoides*) is a remarkable exception. It shows a triangular proepistome, which is wedged between two frontal projections, and a widened thoracic sternum. The male gonopore, in contact with the P5 coxosternal condyle, and the penis, resting in a depression of the developed sternite 8 (Ng *et al.* 1994: fig. 8B, as *Sesarmoides*), also represent an unusual dispositon.

The pleonal locking mechanism, of press-button type, is various in Sesarmidae: occasionally functional at any (moulting stage) size of the individuals, or present but disappearing at a particular moult (button becoming smaller or obsolete, with increasing body size), or absent (Guinot & Bouchard 1998). A recent study of species of *Parasesarma* De Man, 1895 and *Perisesarma* De Man, 1895 has shown that a button is either absent or indistinct, or developed (Shahdadi & Schubart 2017: fig. 7).

Molecular analysis

Chiromantes neglectum (De Man, 1895) was found "within an intermingled 'Grapsoidea & Ocypodoidea' clade" (Xing *et al.* 2016: 461, fig. 1). Study of complete mitochondrial genome by Xin *et al.* (2107b) indicated that Sesarmidae, Xenograpsidae and Varunidae have close relationships.

Given all the differences in many respects, it is easy to distinguish Leptograpsidae n. fam. from the Sesarmidae.

Family Varunidae H. Milne Edwards, 1853

Remarks

Guinot (1978, 1979) implied that the systematic status of the Varuninae must be raised to a full family. The delimitation of the family has been subsequently supported by congruent larval and adult morphology and by molecular studies (Sternberg & Cumberlidge 1998; Cuesta 1999; Schubart *et al.* 2000b; N. K. Ng *et al.* 2007). Five subfamilies were recognised by Ng *et al.* (2008): the nominotypical Varuninae H. Milne Edwards, 1853, Asthenognathinae Stimpson, 1858, Cyclograpsinae

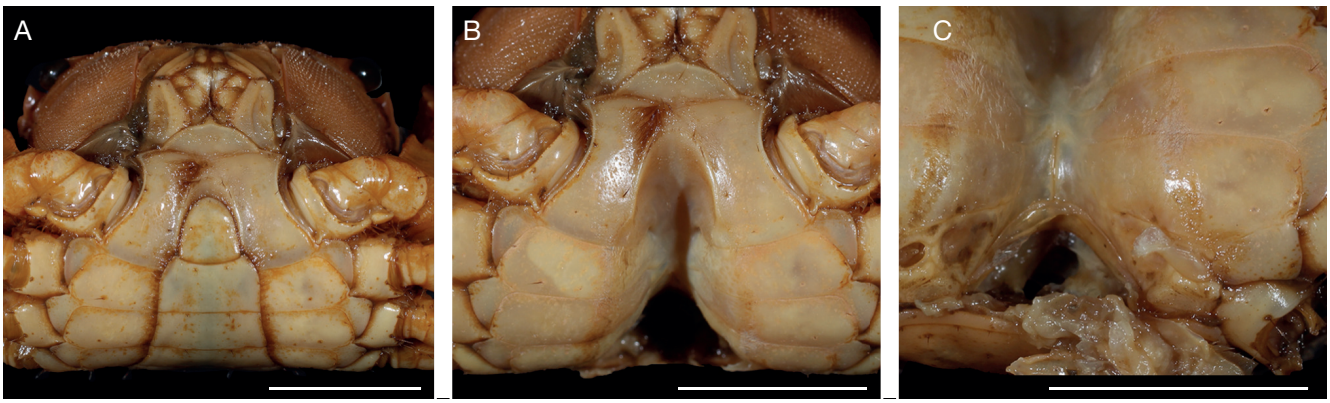

FIG. 10. — Sesarmidae: *Sesarma reticulatum* Say, 1817, ♂ 22.1 × 27.0 mm, New Jersey, MNHN-IU-2017-8399 (= MNHN-B25784): **A**, thoracic sternum (brushed) with pleon; **B**, thoracic sternum (brushed) without pleon; **C**, genital region with gonopore and penis. Scale bars: 10 mm.

H. Milne Edwards, 1853 (as Cyclograpsacea), Gaeticinae Davie & N. K. Ng, 2007, and Thalassograpsinae Davie & N. K. Ng, 2007. In contrast, according to Števčić (2005) the Varuninae and Cyclograpsinae were grapsid subfamilies, besides the Grapsinae, Gecarcininae and Sesarminae. Later, Števčić (2013), recognising a family level to Gecarcinidae, added two varunine tribes, one grapsid subfamily Gaeticinae Davie & N. K. Ng, 2007, and elevated Asthenognathinae to family level, with two subfamilies Asthenognathinae and Aphanodactylinae Ahyong & Ng, 2009. Based on a morphology-based cladistic analysis, Karasawa & Kato (2001) suggested the monophyly of Varuninae and Cyclograpsinae under Grapsidae. Varunids are known since the Miocene (Karasawa 2018).

According to genetic sequences (Kitaura *et al.* 2002, 2010; Schubart *et al.* 2002, 2006; N. K. Ng *et al.* 2007; van der Meij & Schubart 2014; Tang *et al.* 2017), the Varunidae is paraphyletic and its current subfamilies are not monophyletic. In view of the traditional morphology, the subfamilial divisions remain confuse, and it is probable that not only the subfamilies (at least some of them) are paraphyletic but, in addition, certain genera or species are at risk of standing clearly outside the major varunid grouping and must be excluded to recover the monophyletic status of the Varunidae. For example, Kitaura *et al.* (2002) have shown a sister-group relationship between varunine species and *Macrophthalmus* Desmarest, 1823, which revealed distinct from studied ocypodid genera (see also Barnes 2010); similarly, van der Meij & Schubart (2014) and Tsang *et al.* (2014) recovered strong support for a Varunidae + Macrophthalmidae Dana, 1851 relationship. According to Tsang *et al.* (2018) the Aphanodactylidae Ahyong & Ng, 2009, considered a monophyletic family, is more closely related to Macrophthalmidae and Varunidae than to Pinnotheridae De Haan, 1833. The high diversity of mating strategies described by Brockerhoff & McLay (2005) concerns various varunids, instead of grapsids.

The diversity of morphological characters exhibited by the Varunidae demonstrates how a coherent diagnosis of the family is difficult and does not support its monophyly.

The varunid subfamilies Cyclograpsinae H. Milne Edwards, 1837, Gaeticinae Davie & N. K. Ng, 2007, Thalassograpsinae Davie & N. K. Ng, 2007, Varuninae H. Milne Edwards, 1853 cannot accommodate *Leptograpsodes* (see N. K. Ng 2006: table 1 and key p. 41; N. K. Ng *et al.* 2007; Davie *et al.* 2015c: 71). In only one subfamily, the Cyclograpsinae H. Milne Edwards, 1837, a few representatives of *Cyclograpsus* H. Milne Edwards, 1837 share some similarities with Leptograpsodiae n. fam. (see below, Cyclograpsinae).

Asthenognathinae, previously within the polyphyletic family Pinnotheridae, was transferred to Varunidae by Cuesta *et al.* (2005) based on molecular results. It was raised to separate familial status by Števčić (2005) within the Grapsoidea. Thus, members of Asthenognathinae (type genus: *Asthenognathus* Stimpson, 1858) were moved from Pinnotheroidea to Varunidae in their own subfamily Asthenognathinae (see Števčić 2005; Ng *et al.* 2008: 226; Davie *et al.* 2015b, c) or its own family Asthenognathidae Stimpson, 1858 (Cuesta *et al.* 2005; see also Palacios-Theil *et al.* 2009; Guinot *et al.* 2013: table 7). Asthenognathinae was recently found to be nested within Varunidae instead of aligning with pinnotherids (Tsang *et al.* 2018). Given the numerous differences, a comparison with Leptograpsodidae n. fam. is superfluous.

Subfamily CYCLOGRAPSINAE H. Milne Edwards, 1837

POSITION OF *CYCLOGRAPSUS*

Guinot (1979: 209) was the first to recognise that the sesarmines including *Cyclograpsus* and allied genera showed the same sternal male gonopore structure as varunines (see also Guinot & Bouchard 1998). Ng *et al.* (2001: 41, 44) included *Cyclograpsus* into Varuninae but did not recognise the Cyclograpsinae as a separate taxon, similarly to Schubart *et al.* (2000b). Karasawa & Kato (2001) and Davie (2002: 207) are credited for resurrecting the subfamily Cyclograpsinae H. Milne Edwards, 1853 (= Cyclograpsacea H. Milne Edwards, 1853, long treated as synonymous with Sesarminae Dana, 1851), although they took however the conservative approach of treating the Grapsinae, Sesarminae, Cyclograpsinae and Varuninae as grapsid subfamilies (see also Davie & Xuan 2003; Sakai *et al.* 2006). In the revision of Varuninae by

N. K. Ng (2006: 26, 39, 54, 469), which included 16 species of *Cyclograpsus*, *L. octodentatus* was not studied. Larval studies and, chiefly, molecular phylogenetic researches, as those of Schubart & Cuesta (1998), Schubart *et al.* (2000b, 2002: 39, figs 7, 8, table 1), Kitaura *et al.* (2002), supported close relationship of *Cyclograpsus* to the Varunidae or Varuninae. Today, Cyclograpsinae is accepted as a distinct clade within the Varunidae (N. K. Ng 2006: 11, 36, 469, 476, 478; N. K. Ng *et al.* 2007: 234; Ng *et al.* 2008: 226; Davie *et al.* 2015a: 41, 2015c: 1120).

So varied is the subfamily Cyclograpsinae that it is difficult to make general statements. *Cyclograpsus* seems to be the closest member to *Leptograpsodes*, thus our study will first focus on this genus. As *Cyclograpsus*, a genus that probably exceeds 20 worldwide distributed species (Davie & N. K. Ng 2007; Ng *et al.* 2008; Naruse & N. K. Ng 2012; Naruse 2015), is probably not monophyletic, we will restrict our study to the type species *C. punctatus* (by subsequent designation of Rathbun 1918: 328) and only its allies. They show a small orbit, a real infraorbital margin lacks, and a variously ornamented (granules, tubercles, elongated structures) suborbital crest is present. In cyclograpsines, the strongly developed and suborbital crest can be stridulatory in conjunction with cheliped merus, which is either only thickened and without a differentiated structure, or bears a horny ridge, usually sexually dimorphic (Tesch 1918; Guinot-Dumortier & Dumortier 1960; Sakai *et al.* 2006; Davie *et al.* 2015a). See *Stridulatory structures in grapsoids*.

The biology of *Cyclograpsus punctatus*, a species restricted to southern Africa (see Rathbun 1918; Barnard 1950; Garth 1957; Griffin 1968; Fagetti & Campodonico 1971; Emmerson 2016), provides some similarities with that *Leptograpsodes octodentatus*: it develops aerial respiratory adaptations, so is highly resistant to desiccation, lives semi-terrestrially, enters estuaries and diggs more or less elaborate burrows in the muddy banks of the rivers (Broekhuysen 1941; Alexander & Ewer 1969: fig. 3b; Emmerson 2016). *Leptograpsodes octodentatus* lacks the fine reticulated pattern of short curved setae that entirely covers the pterygostome and results in a fine film of water over the setae, characteristic of *Cyclograpsus punctatus* and sesarmids (Alexander & Ewer 1969: fig. 4).

Comparison of *C. punctatus* and *Leptograpsodes*

The comparaison between *Leptograpsodes octodentatus* (especially when small specimens are examined, see Fig. 2A-C) and *Cyclograpsus punctatus*, which is a relatively small species, reveals a lot of distinguishing characters. *Leptograpsodes* differs from *C. punctatus* by, e.g. carapace margin strongly convex and with three weak teeth (only slightly convex, almost straight, with margin subcristate, entire or indistinctly notched in *C. punctatus*); anterolateral margin normal (carinate and ventrally hollowed in *C. punctatus*); presence of several postero-lateral striae (at most 2-3 faint ridges obliquely connecting to posterolateral margin in *Cyclograpsus*); two pairs of frontal lobes (absent in *C. punctatus*); carapace dorsal surface grooved (flat and smooth in *C. punctatus*); developed suborbital tooth (absent in *Cyclograpsus*); sunken, faint, finely granulose suborbital margin, continuous to near inner limit of orbit and paralleled by developed stridulatory suborbital crest (a thickening encircling and surrounding base of eyestalk in middle of orbit, eclipsed by prominent suborbital crest having a stridulatory role in *C. punctatus*); shape of epistome; mxp3 merus without oblique setose crest (with oblique setose crest in *C. punctatus*); pterygostome with shallow, simple vertical groove, parallel to buccal cavity (without vertical groove in *C. punctatus*); subhepatic, pterygostomial and subbranchial regions covered by pubescence lacking reticulate pattern (reticulated network of short hooked setae in *C. punctatus*).

The shape of the orbit, with a stridulating suborbital crest in both genera, merits careful comparison: a close scrutiny reveals their discrepancy. In *Cyclograpsus punctatus* the orbit is small and closed laterally, a real infraorbital margin lacks and there is only a strongly developed, coarsely granulated suborbital crest that acts in conjunction with variously thickened inner margin of cheliped merus. In *Leptograpsodes* the large orbit is opened laterally, there is a faint but very distinct suborbital margin, with, in addition, subparallel to and below, a suborbital crest consisting of numerous, very fine and regular granules; this crest (pars stridens) is stridulatory in conjunction with a smooth, delimited crest (plectrum) at inner face of cheliped merus.

The status of all other *Cyclograpsus* is uncertain. That *Cyclograpsus* is not monophyletic was shown by the specific disparity of larval features (Gore & Scotto 1982; Cuesta & Rodríguez 1994) and of locking-pleonal mechanism (Guinot & Bouchard 1998; Köhnk *et al.* 2017). As a result, all species assigned to Cyclograpsinae need a reevalution, as Naruse & N. K. Ng (2012) has done for *Cyclograpsus lophopus* Nobili, 1905 that revealed to be a sesarmid and became *Cyclorma lophopus* (Nobili, 1905). *C. granulosus* H. Milne Edwards, 1853, a conspicuous species occurring on rocky shorelines in southeastern Australia including Tasmania (Campbell & Griffin 1966; Griffin 1971), and known by its completely sequenced mitochondrial genome (Tan *et al.* 2016), is morphologically quite distinct from *Leptograpsodes octodentatus*.

The junction of the proepistome to the front is rather similar in the two genera. In *Leptograpsodes* sternal suture 1/2 strongly marked, sternites 1 + 2 semi-ovate; suture 2/3 straight (in *C. punctatus* sternite 1 individualised, with thick ridge at the location of suture 1/2, see Fig. 9A, B); in *Leptograpsodes* sternite 8 only developed laterally, a minute portion visible posteriorly when pleon is folded (Fig. 3C) (in *C. punctatus* sternite 8 developed, medially exposed, and with large portion visible dorsally when pleon is folded); in *Leptograpsodes* male gonopore close to P5 coxa and far from suture 7/8; penis long, emerging on sternite 8, not very far from suture 7/8, see Fig. 3B) (in *C. punctatus* male gonopore far from P5 coxa; penis short, see Fig. 9C).

Other genera of Cyclograpsinae

The status of all other genera included in Cyclograpsinae, e.g. *Helograpsus* Campbell & Griffin, 1966, *Metaplax* H. Milne Edwards, 1852 (see Karasawa & Kato 2001: fig. 2.24; Davie &

Xuan 2003), *Paragrapsus* H. Milne Edwards, 1853 (e.g. with *P. laevis* (Dana, 1851), the "mottled shore crab" from Southeastern Australia), deserves a thorough examination.

Subfamily Gaeticinae Davie & N. K. Ng, 2007

Included genera. — The subfamily consits of only a few genera, notably *Gaetice* Gistel, 1848, type genus (type species *Gaetice depressus* (De Haan, 1833)), *Acmaeopleura* Stimpson, 1858, *Gopkittisak* Naruse & Clark, 2009, *Pseudopinnixa* Ortmann, 1894, *Proexotelson* Naruse, 2015; *Sestrostoma* Davie & N. K. Ng, 2007 (see Davie & N. K. Ng 2007; Komai & Konishi 2012; Naruse 2015).

Remarks

This subfamily is remarkable for having mouthparts and thoracic sternum highly modified for suspension feeding, and male pleonal somites 3-6 functionally fused. In gaeticines (see Davie & N. K. Ng 2007: figs 5H, 7B, *Gaetice depressus*; Komai & Konishi 2012: fig. 2D, E, *Pseudopinnixa carinata* Ortmann, 1894; Naruse 2015: fig. 1a-d: *Gaetice depressus*, *Sestrostoma balssi* (Shen, 1932), *S. depressum* (Sakai, 1965), *Acmaeopleura parvula* Stimpson, 1858, respectively), the first sternites are peculiar, being medially hollowed to receive the setal brush of mxp3 palp. Sternite 1 is triangular; sternite 2 is distinctly produced anterolaterally and easily recognisable; the well marked suture 2/3 encompasses diverse patterns (Davie & N. K. Ng 2007: 216), in particular in *Proexotelson*, in which the long sterno-pleonal cavity (together with long pleon, long G1) completely covers the sternal plate and joins the buccal cavity (Naruse 2015: figs 6B, 8).

In the type genus and species *Gaetice depressus* (Fig. 9D-F) the first sternites are highly modified as precedingly indicated, which makes difficult interpretation of sutures. A suture 2/3 is clearly visible; sternites 1 and 2 are fused, the line of setae that crosses not seemingly being a true suture; sternite 8 is broad, developed medially, and with a median line (not clearly visible in the figure of Davie & N. K. Ng 2007: fig. 5H); the exposed lateral portion is transversally crossed by a deep, complete sulcus that joins the gonopore to the P5 coxo-sternal condyle. A large portion of sternite 8 is exposed laterally when pleon is folded. The median line extends on sternite 8 and 7. The male sternal gonopore (Guinot 1979: fig. 52G; Davie & N. K. Ng 2007: fig. 5H) is far from P5 coxa and from suture 7/8. The penis of *Gaetice* resembles that of *Varuna* and seems to be able to be applied against the gonopore (as in *Varuna*, see Guinot *et al.* 2013: fig. 36).

Naruse & Clark (2009: 66, fig. 2b) described the male gonopore of *Gopkittisak* as "appearing from distal end of thoracic sternite 8" (Guinot *et al.* 2013: 144 erroneously accepted this interpretation): the suture that is figured between the gonopore and the P5 coxa does not denote the suture 7/8 but, instead, probably represents the complete sulcus above-mentioned; the visible sternite only corresponds to sternite 8 crossed by this sulcus (instead of sternites 7 and 8 as in the caption). Acording to Ng (2012: fig. 5B), in *Brankocleistostoma* Števčić, 2011 the very short sternites 1 and 2 are completely fused, being separated from the longitudinally narrow sternite 3 by a rim: we do not agree with this interpretation, the distinct suture supposedly separating sternites 3 and 4 actually should correspond to suture 2/3. In *Gopkittisak*, in which anterior sternites are only slightly concave to accommodate setae of mxp3 palp, Komai (2011: fig. 2F) described that thoracic sternites 1-3 were fused, a transverse rim being the bordering of sternite 4.

The differences between Gaeticinae and Leptograpsodidae n. fam. are so numerous that a comparison is not warranted.

Sufamily Heliceinae Sakai, Türkay & Yang, 2006

Included genera. — *Helice* De Haan, 1833 (type genus); *Helicana* K. Sakai & Yatsuzuka, 1980; *Neohelice* Sakai, Türkay & Yang, 2006; *Chasmagnathus* De Haan, 1833.

Remarks

Heliceinae, replacement name for Helicinae Kossmann, 1877 (considered a *nomen oblitum*), is here recognised. A diagnosis of the subfamily lacks since Kossmann (1877: 57) established the taxon only in a key, whereas Sakai *et al.* (2006: 2, 7) did not formally provide one in their study of the "*Helice/Chasmagnathus complex*", only listing the characters shared by the two genera. *Austrohelice* Sakai, Türkay & Yang, 2006 and *Pseudohelice* Sakai, Türkay & Yang, 2006 are not included for now, waiting for further investigations.

Diagnosis

Carapace subquadrate, lateral margins varying from subparallel to strongly convergent, usually armed with two epibranchial teeth behind exorbital tooth. Front much narrower than half exorbital width; exorbital width not markedly exceeding carapace length. Orbit long, not closed laterally. Eyestalks not nearly as broad as front. Proepistome as wide triangular or pentagonal plate, its very narrow tip inserted under front (Tavares 1989: fig. 21, as *Chasmagnathus granulatus* Dana 1851, now *Neohelice granulata*). Stridulatory apparatus usually present (e.g. *Helice*, *Helicana*, *Chasmagnathus*): pars stridens formed by suborbital ridge composed of granules or tubercules, sexually dimorphic (ridge often heteromorphic in males), rubbed by prominent horny ridge on inner margin of cheliped merus; may be absent. Reticulation on pterygostomial regions poorly developed. Thoracic sternum wide; sternite 1 separated from sternite 2 by convex ridge; suture 2/3 straight; sternite 8 developed, exposed medially, not deeply notched by posterior emargination. Deep median line usually extending from sternite 8 to sternites 6 and even 5, but intermittently. Male gonopore in posteriormost location in relation to suture 7/8. G1 with suture of sperm channel usually torsioned towards dorsal face, except in *Chasmagnathus*.

Remarks

The wide thoracic sternum (Fig. 9G, H) is typical in having a deep median line intermittently extending from sternite 8 to sternites 5 or at least 6, this corresponding to a variously developed and high median plate (see Sakai *et al.* 2006: figs 1,

2, 14, 15, 23; note that on their fig. 1 "Mp" corresponds to the median line). The thoracic sternite 1 is triangular; suture 1/2 is strong, convex; sternite 3 is completely fused to sternite 4 as in all Grapsoidea (on fig. 1 of Sakai *et al.* 2006, "III" actually corresponds to sternite 2): both fused sternites 3 and 4 are separated from sternite 2 by a conspicuous suture (suture 2/3) as shown by N. K. Ng *et al.* (2018: 6, fig. 1B); when pleon is folded, sternite 8 is exposed, widely (*Helice*) or narrowly (*Chasmagnathus*). The male gonopore (Fig. 9I) emerges in middle of sternite 8, far from P5 coxa and from suture 7/8; in *Helice* (see Guinot 1979: fig. 52I; Sakai *et al.* 2006: figs 1, 14), *Helicana* (Sakai *et al.* 2006: figs 14, 35) and *Neohelice* (Sakai *et al.* 2006: fig. 92), a conspicuous complete sulcus joins the gonopore to the P5 coxo-sternal condyle; it is incomplete in *Chasmagnathus* (see Sakai *et al.* 2006: fig. 7). The opercular cover of the vulva in *Helice* and *Chasmagnathus* shows a correspondence between the direction and torsion of the G1 and the shape of the vaginal aperture (Sakai *et al.* 2006: 6; see also Shih & Suzuki 2008; Guinot *et al.* 2013: 36).

The stridulatory apparatus (Guinot-Dumortier & Dumortier 1960: fig. 5b, f), well documented by Sakai *et al.* (2006: figs 3, 10c, 17, 38-40, 57, 58, 60-66, table 3), is present in most members of the subfamily; the species in which the plectrum lacks in both sexes do not stridulate. Shih & Suzuki (2008) criticised the key morphological characters used by Sakai *et al.* (2006) and, in particular, their variations within species and between sexes.

The poorly known and probably paraphyletic *Pseudohelice* is for the moment not included in the subfamily because of its sternal features: median line and median septum only developed on sternite 7 and very small or absent on sternites 5 and 6 (Sakai *et al.* 2006: figs 2, 51); male gonopore indicated as close to sternal suture 7/8 (Sakai *et al.* 2006: fig. 50); G1 with or without torsion; absence of stridulatory plectrum, at least in some members. *Austrohelice* is not included for the same reasons: median line and septum not developed; faint sulcus on sternite 8 (Sakai *et al.* 2006: figs 2, 86, 87); no plectrum.

Genetic studies including *Helice* and allied genera are related to their intrarelationships (e.g. Shih & Suzuki 2008; Yin *et al.* 2009; Zang *et al.* 2009; Ituarte *et al.* 2012; Xu *et al.* 2012) or interrelationships (Kitaura *et al.* 2002; Schubart *et al.* 2006; Xu 2010; Xin *et al.* 2017a; Tang *et al.* 2018).

Subfamily Thalassograpsinae Davie & N. K. Ng, 2007

Included genera. — The subfamily is monotypic, with its type genus *Thalassograpsus* Tweedie, 1950 with a single species, *Thalassograpsus harpax* (Hilgendorf, 1892), that lives under coral stones or rocks in sheltered rocky shores (Davie 2002; Bouchard *et al.* 2013; Naderloo 2017).

Remarks

Davie & N. K. Ng (2007) have listed the unique apomorphies of the subfamily, e.g. frontal margin with short distinct lateral sulcus just posterior to lateral frontal margin, and separated from inner orbital margin (in other Varunidae frontal margin continuous with orbital margin); mxp3 not gaping when closed (more or less gaping in Varuninae, Cyclograpsinae and Gaeticinae); mxp3 merus and ischium lacking visible longitudinal sulcus (distinctly visible in other varunine subfamilies); male pleon with segments 5 et 6 functionally fused, but sutures visible. The assertion of Davie & N. K. Ng (2007: 262) that the medial groove is proportionately wide on sternites 8 and 7 (other subfamilies with narrower medial groove in sternite 8) in our opinion corresponds in *Thalassograpsus* to the much more developed sternite 8 (thus more dorsally visible than in *Cyclograpsus*) and to a suture 7/8 as long as preceding sutures and reaching the bottom of the sterno-pleonal cavity, thus much more longer than in *Cyclograpsus*. We agree with the first part of the sentence of Davie & N. K. Ng (2007: 258) "suture of thoracic sternite 3/4 not visible" but not with the second term of the alternative, "slightly visible in all other subfamilies": the suture 3/4 lacks, as in all Grapsoidea.

Other characters of the subfamily are: sternites 1 and 2 fused (no suture 1/2), sternite 1 narrow and distinctly tapering at tip; suture 2/3 present but thin (Fig. 9J-K); suture 3/4 absent; sutures 4/5-7/8 interrupted; sternite 8 developed; median line visible on long portion of sternite 8 and extending on sternite 7 (Fig. 9K, L); episternites 5 and 6 very narrow and long; male gonopore in middle of sternite 8, far from suture 7/8 and from P5 coxa, a large part of sternite 8 being intercalated between gonopore and P5 coxo-sternal condyle; proepistome not forming developed structure (Bouchard *et al.* 2013: fig. 26B, D); stridulatory apparatus: suborbital crest separated in at least three portions (pars stridens) rubbing against marked thickening (plectrum) on inner edge of cheliped merus (Fig. 11B, C) (Tweedie 1954; Davie & N. K. Ng 2007); press-button mechanism typical.

Comparison with Leptograpsodidae n. fam

Leptograpsodidae n. fam. shares with Thalassograpsinae the presence of a stridulatory apparatus, however different. In *Leptograpsodes* suborbital crest is composed of homomorphic granules and the plectrum is a delimited ridge on P1 merus (Figs 1G; 2C, D; 3D); in *Thalassograpsus harpax* the suborbital crest consists of heteromorphic tubercles and the plectrum is only a thickening on P1 merus, see Fig. 11B, C).

Subfamily Varuninae H. Milne Edwards, 1853

Included genera. —The Varuninae includes a large number of genera. Main features of Varuninae are provided by N. K. Ng (2006: 37 and table 1, 2007) and Davie *et al.* (2015c: 1119).

Comparison with Leptograpsodidae n. fam

The traditional characters that may be used to differentiate Leptograpsodidae n. fam. from Varuninae could be, e.g. carapace rounded, with very convex margins in Leptograpsodidae n. fam. (in Varuninae varying from quadrate to quadrangular, lateral margins varying from subparallel to moderately convex); front about half width of carapace (vs less than half maximum carapace width); two pairs of postfrontal lobes (vs

without four postfrontal lobes); pterygostome, subbranchial, subhepatic regions setose (vs glabrous); suborbital crest stridulatory (vs not stridulatory); mxp3 largely gaping when closed, with antero-external angle of merus not produced, (vs small, rhomboidal gape; antero-external angle of merus strongly produced and auriculate).

For the sternal and male genital features, we will focus our comparison to the type genus *Varuna* H. Milne Edwards, 1830 and its type species *V. litterata*. In all examined varunines: male gonopore far from P5 coxa and from suture 7/8, but distance between the genital orifice and suture 7/8 varying among genera. In *V. litterata* thoracic sternum characterised by: sternite 1 triangular; sternites 1 + 2 separated from sternite 3 by suture; sternite 4 weakly restricted at level of chelipeds; episternites 4-6 elongated and narrow (Fig. 9M, N); episternite 7 practically joining P5 coxo-sternal condyle; sternite 8 developed medially, not deeply notched by narrow posterior emargination, and largely exposed when pleon is folded; conspicuous rim on sterno-pleonal cavity at level of telson; marked, deep, long median line on sternites 8, 7 and 6 (Fig. 9N, O); typical press-button and persistent throughout the life in males, with socket slightly remote from pleonal margin (Guinot & Bouchard 1998: fig. 23A). Male gonopore, located far from P5 coxa, opening on vertical slope of sterno-pleonal cavity; P5 coxo-sternal condyle prolonged by incomplete sulcus. Penis, directed obliquely, showing calcified basal portion and well-developed, foliaceous papilla that may clearly invaginate inside gonopore, with calcified portion acting as operculum (Fig. 9O) (Guinot 1979: fig. 52H, pI. 20, fig. 5; N. K. Ng *et al.* 2007: fig. 4E; Guinot *et al.* 2013: fig. 36).

For the genital disposition of species of *Eriocheir* De Haan, 1835 and allies, see Bouvier 1940: fig. 186B; Guinot 1979: fig. 53F; Guinot & Bouchard 1998: fig. 23B; N. K. Ng *et al.* 1999: figs 2Ci, 2Cii, 4A. In fresh material of *Platyeriocheir formosa* there is evidence of an invagination of the penis, at least of the papilla, the calcified basal portion of the penis acting as an operculum.

The median line extends along sternites 8-6 in *Neoeriocheir leptognathus* (Rathbun, 1913) as shown by N. K. Ng *et al.* (1999: figs 2Ci), likewise in *Varuna*, but only on sternites 8 and 7 in *Eriocheir sinensis* and *Platyeriocheir formosa*, see N. K. Ng *et al.* (1999: figs 2Cii, 4A, respectively). Such divergences are not necessarily valid indices to assess generic or even subfamilial status, but a new morphological examination is needed. For other genera, see data in Guinot *et al.* 2013: 143.

Molecular analysis

The complete mitochondrial genome is known for some species of *Varuna* (Lin *et al.* 2018) and *Eriocheir* (Tang *et al.* 2003; Liu *et al.* 2015; Li *et al.* 2016; Wang *et al.* 2016; Xin *et al.* 2017b). Assignation of *Eriocheir* to the Varuninae by Balss (1957) and Guinot (1979), to Varunidae Schubart *et al.* (2000b) in a molecular study, and by Clark (2006). Analysis of the nucleotide sequences of the 13 mitochondrial protein-coding genes showed that *Eriocheir sinensis*, *E. hepuensis* Dai, 1991, *E. japonica*, and *Helice latimera* Parisi, 1918 clustered together with high statistical support, these species having a

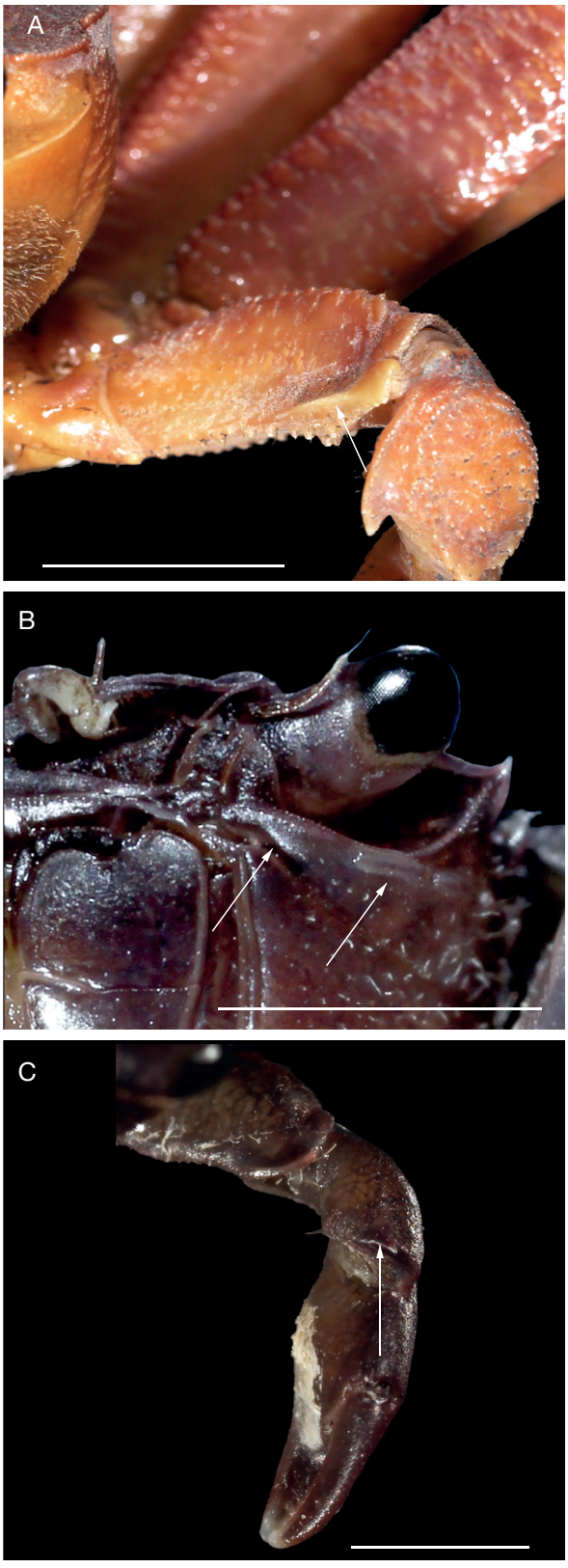

Fig. 11. — Stridulatory apparatus: **A**, *Discoplax longipes* A. Milne-Edwards, 1867, ♀ 32.6 × 37 mm, Loyalty Islands, Lifou, Inegoj Cave, MNHN-IU-2008-11402 (= MNHN-B24815): plectrum as a ridge on cheliped merus (see arrow); **B**, **C**, *Thalassograpsus harpax* (Hilgendorf, 1892), ♂ 5.3 × 5.7 mm, Scattered Islands, MNHN-IU-2013-16120; **B**, pars stridens consisting of elongated tubercles on suborbital ridge (see arrows); **C**, plectrum as a thickening (see arrow) on inner edge of cheliped merus. Scale bars: A, 5 mm; B, C, 2 mm.

sister-group relationship (Xin *et al.* 2017b, as *Eriocheir japonica sinensis*, *E. japonica hepuensis* and *E. japonica japonica*, respectively). The molecular data of Chu *et al.* (2003: table 2) had previouly shown substantial divergences between species of *Eriocheir sensu lato* and *Varuna litterata*, and led to the conclusion that the five "mitten crab" species, always clustering together, constituted a monophyletic group genetically distinct from *V. litterata*. The unstable state of the Varuninae accepted as including *Eriocheir* and *Varuna* was confirmed. A new reappraisal based on reliable morphological characters will probably lead to some changes in the systematics of the subfamily.

Family Xenograpsidae
N. K Ng, Davie, Schubart & Ng, 2007

Included genera. — *Xenograpsus* Takeda & Kurata, 1977.

Remarks

The unusual genus *Xenograpsus* (Takeda & Kurata 1977), originally assigned to the Varuninae, shares some morphological characters with other grapsoid families, but evidence from adult and larval morphology (Jeng *et al.* 2004a) has shown that it should be regarded as belonging to a separate family. Family Xenograpsidae, established by N. K. Ng *et al.* (2007), only includes three *Xenograpsus* species all associated with shallow hydrothermal vents: *X. novaeinsularis* Takeda & Kurata, 1977 (type species) from the Ogasawara Islands and the Marianas Arc; *X. testudinatus* Ng, Huang & Ho, 2000 from the Taiwan Arc and Japan (N. K. Ng *et al.* 2014: in the title of that paper the family is erroneously referred to Grapsidae, owing to a *lapsus muris*); and *X. ngatama* McLay, 2007 from Brothers Mount in New Zealand. They are the only grapsoids that live in such a harsh environment (Jeng *et al.* 2004b; N. K. Ng *et al.* 2014; Hu *et al.* 2016).

The absence of gap between the quadrate mxp3 (vs a rhomboidal gap in Leptograpsodes), considered a diagnostic character of the family Xenograpsidae by N. K. Ng *et al.* (2007: 250) and considered unique amongst the Grapsoidea, is in fact a character also shared by Glyptograpsidae (see Schubart *et al.* 2002: fig. 1; N. K. Ng *et al.* 2007: fig. 7G), Plagusiidae, and various varunid genera of the subfamily Gaeticinae that show a characteristic structure of mxp3 related to suspension feeding (Davie & N. K. Ng 2007; Naruse 2015: table 2).

Molecular analysis

Genetic sequences by Schubart (2011), with *Varuna litterata* as outgroup, and by Ip *et al.* (2015) indicate a close relationship of *Leptograpsodes* to Xenograpsidae, even a possible sister-taxon relationship with *Xenograpsu*s. The question is therefore to test whether the xenograpsid morphology provides the accurate traits to corroborate the DNA data or whether there is another case of incongruence between the currently adopted classification and molecular phylogenetics. *Xenograpsus testudinatus* was shown to have distinct gene order (Ki *et al.* 2009). According to the gene order analysis of brachyuran mitochondrial genomes by Basso *et al.* (2017), in which Brachyura appears to be a hot-spot of gene order diversity within the phylum Arthropoda, XenGO is an apomorphy currently known only for *X. testudinatus*. According to Wang *et al.* (2018b: 39, fig. 6), based on the complete mitochondrial DNA (mtDNA) sequences, *Xenograpsus testudinatus* and Sesarmidae was found forming a group with close relationships.

The morphological characters of *Xenograpsus testudinatus* have been studied and illustrated by N. K. Ng (2006) and N. K. Ng *et al.* (2007). The comparative characters are: proepistome inserted as thin tongue into lower margin of front (N. K. Ng *et al.* 2007: figs 3B, 6A) (also thin tip in *Leptograpsodes*); orbit almost complete, in the form of deep sunken cavity (N. K. Ng *et al.* 2007: fig. 5A) (partially opened laterally in *Leptograpsodes*); suborbital margin not stridulatory (N. K. Ng *et al.* 2007: fig. 5G) (suborbital margin with stridulatory function in *Leptograpsodes*); mxp3 broad, operculiform, lacking rhomboidal gap (N. K. Ng *et al.* 2007: fig. 7A) (gaping in *Leptograpsodes*); typical pleonal-holding mechanism present: rather big sternal button and deep pleonal socket (as in *Leptograpsodes*); G1 strongly calcified, short and stout (long, quite slender, with blunt, horny tip and flap on sternal surface in *Leptograpsodes*).

Additional sternal and male genital characters

In Xenograpsidae (our data are only based on *X. testudinatus*, the only species that we have examined), the thoracic sternum (Fig. 8M, N) (N. K. Ng *et al.* 2007: fig. 3H) shows: complete suture 2/3 and no anterior suture or depression that could be suture 1/2; sutures 4/5-7/8 incomplete, suture 7/8 being shorter; rather wide sternite 8 but, as notched by deep triangular posterior emargination, not exposed medially and only lateral; median line on sternite 7 only (not clearly shown by N. K. Ng *et al.* 2007: fig. 3H); no traces of bridge. Male gonopore (Fig. 8O) (N. K. Ng *et al.* 2007: fig. 4A) opening on sternite 8 by wide aperture along lateral margin of posteriorly expanded episternite 7; aperture rather far from suture 7/8 but close to P5 coxo-sternal condyle; expanded episternite 7 joining P5 coxo-sternal condyle, extending in direction of sternite 8, thus getting very close to it but without reaching it; penis short, not exposed when pleon is folded.

Concerning the sternal and male genital features, Xenograpsidae and Leptograpsodidae n. fam share: sterno-pleonal cavity very wide; press-button typical; male gonopore not far from P5 coxo-sternal condyle; sternite 8 reduced to its lateral portion due to pronounced posterior emargination reaching sternite 7; median line on sternite 7 only. But they differ by the obvious traditional traits already known and also by: suture 1/2 convex as complete, thickened ridge, and suture 2/3 complete in Leptograpsodidae n. fam. (only suture 2/3 in Xenograpsidae, although two anterior sutures are figured for *X. testudinatus* by N. K. Ng *et al.* 2000: fig. 3B and by N. K. Ng *et al.* 2007: fig. 3H); presence of thick sternal bridge in Leptograpsodidae n. fam. (no bridge in Xenograpsidae); very small portions of penis and sternite 8 dorsally visible in Leptograpsodidae n. fam. (nothing visible in Xenograpsidae).

The genital condition of *Xenograpsus* presents some similarities with that of Plagusiidae (Fig. 8L) (Guinot 1979: fig. 52E; N. K. Ng *et al.* 2007: fig. 4C) where the elongated episternite 7 joins the sternite 8 and separates the gonopore from the P5 coxa.

DISCUSSION

The resolution of problems encountered in the current classifications and phylogenetic trees requires modern diagnoses, with an unambiguous terminology, primarily making use of intrinsic, fundamental characters, allowing more rigorous comparisons. Traits that are largely independent of the behaviour and ecology represent the best support for the systematics and phylogeny of Brachyura, but non-morphological characters such as behaviour tend to be currently analysed in a phylogenetic context. Whereas carapace, the mxp3, the gonopods, the pleon and the pereiopods are the currently studied and used characters, others that are retained from the groundplan, being not subject to variation and having a strong phylogenetic component, are often neglected, even overlooked. These are: the proepistome, the thoracic sternum, including all sternites and all sutures, the median line, the location of the male gonopore with the penis, and the press-button.

Proepistome

The proepistome in Brachyura, i.e., the sternite of antennular somite, often called "interantennular septum", is a structure often ignored by carcinologists and even not distinguished from the epistome (sternite of antennal somite). It is, however, an important structure of the body that connects the sternal surface and the carapace thanks to its junction with the rostrum or the front. It is the same in both sexes, and apparently does not to change during growth. Exceptionally absent in a few Brachyura, it shows a consistent shape within a genus. For example in Grapsidae, the proepistome shows as a broad septum meeting the frontal margin but not obviously inserted into. This area was well represented by Tavares (1989: figs 3-9, 10) in Gecarcinidae, in which its shape enables to differentiate the three genera of the first subclade. Proepistome is dome-shaped in both *Cardisoma* (Fig. 6B) (Ng & Guinot 2001: figs 1, 2A) and *Tuerkayana* n. gen. but less prominently in the later (Fig. 6C-E) (Ng & Shih 2014: fig. 9, as *Discoplax*); in contrast, it shows as a narrow projection in *Discoplax* (Fig. 6A) (Ng & Shih 2015: figs 4C, 7). In the Gecarcinidae of the second subclade, the proepistome is hardly discernible in *Gecarcinus* (Fig. 7D) and *Johngarthia* or shows as small plate inserted under the lower frontal margin in *Gecarcoidea* (Fig. 7H).

Thoracic sternum

The morphology of the thoracic sternum mirrors (at least partly) the internal organisation of the body, and its transversal compartmentalisation can be interpreted as the original one, hence its crucial importance, particularly for the recognition of homologous structure. And yet, although increasingly figured, it is not or only partially described, even when establishing new taxa. According to Guinot (1977, 1978, 1979) the widening of the thoracic sternum in Eubrachyura was considered a determining factor in the evolution of the genital region in both sexes: the female gonopore or vulva, instead of being located on the P3 coxa (as in other decapods and podotremes), is sternal (Heterotremata Guinot, 1977 and Thoracotremata); the broadening of the posterior half in males determines the location of the male gonopore from the P5 coxa to the sternite 8 (Thoracotremata). Depending on the groups, the ejaculatory duct on sternite 8 emerges with a more or less accentuated distance with respect to the P5 coxa, and the male gonopore occurs in various locations, either along suture 7/8 or in the middle of sternite 8 (Guinot *et al.* 2013: fig. 1B vs fig. 1D, E). These changes, supposedly related to the evolutionary process of carcinisation, should be re-examined from a new perspective.

The thoracotreme condition occurs in crabs having a variously widened thoracic sternum, with all sutures 4/5-7/8 that are interrupted, which corresponds to a median fusion of the somites and increases the median distance between the endosternites. The morphology of various sternal parts required our attention.

Sternites 1-3

In most heterotremes, the anterior portion of the thoracic sternum (sternites 1-3), usually much narrower that the posterior sternites, shows as a variously developed "anterior shield", with approximately a triangular shape in many families, but sometimes more or less quadrangular in others (e.g. in fossil and extant Hexapodidae, see De Angeli *et al.* 2010; Rahayu & Widyastuti 2018). Sternites 1-3, more or less recognisable, show various patterns: sternites 1-2 (sternites of mxp1 and mxp2, respectively) are fused or not, a suture 1/2 being either complete or only lateral or indiscernible; typically, sternite 3 (sternite of mxp3) is distinctly recognisable from sternite 4 (sternite of cheliped). Actually, the suture 3/4 is either complete or incomplete, sometimes only laterally located (often well marked, as e.g. in Dorippidae Miers, 1886), consistently in such a way that the sternite 3 is clearly identifiable. The separation of somites 3 and 4 by a variously developed suture 3/4 seems to be a heterotreme characteristic (vs an entire fusion in grapsoids, and probably in all thoracotremes, see below). Even in Trapeziidae Miers, 1886, in which the fusion of anterior sternites is made evident by shortening of first sternites in the form of a reduced triangle, the boundary between the sternites 3 and 4 remains distinguishable (Castro 1997: fig. 2B, D, F). The case of primarily freshwater crabs is apart: for example, Potamidae Ortmann, 1896 shows a complete suture 2/3 and a suture 3/4 either discernible by an incomplete suture or a marginal cleft, or not all discernible (Yeo & Ng 2007; Huang *et al.* 2014; Huang 2018; Naruse *et al.* 2018a); Gecarcinucidae Rathbun, 1904 and Parathelphusidae Alcock, 1910 provide the both cases, either with or without discernible suture 3/4 (Bahir & Yeo 2005, 2007; Pati *et al.* 2017), the pattern of the suture 3/4, discernible or undiscernible, being constantly used by these authors in their diagnoses. The modalities of fusion of sternites 3 and 4 and trace of suture 3/4 must be checked in all primarily freshwater families.

Conversely to most heterotremes, the thoracotreme thoracic sternum shows a weak development of the anterior shield, with a general flattening of the anterior portion and its incorporation into the sternal plate, to varying degrees (Guinot 1979). Sternite 1 is a very small triangular plate inserted between the mxp3, usually demarcated from sternite 2 by a suture (suture 1/2). (We should point out that sternites 1-3 are fused, with a hardly recognisable sternite 3 in extant podotremes, and that sternites 4 to 8 are fused in the basal families [Guinot 1995, 2008; Guinot & Tavares 2003]: this refers to the question of the relationship between the polarisation of character state transformations and the rooting of phylogenetic trees).

We have to consider the question of whether the entire fusion of sternite 3 to sternite 4, with a complete incorporation into the sternal plate, can be a new thoracotreme synapomorphy: no demarcation between sternites 3 and 4, no visible suture 3/4 (and generally also no depression), even on lateral borders. The only discernible mark between the two somites should be, for example as in some Varunidae (Fig. 9M, N), the location of the gynglyme (i.e., the socket hollowed on the side of the sternal plate) that receives the sterno-coxal condyle of mxp3, i.e., the location of the articulation of mxp3 on the thoracic sternum. In Sesarmidae the articulation of mxp3 on the sternum is at a marked angle representing the lateral margin of sternite 3, below suture 2/3: this is well obvious in *Sesarma reticulatum* (Fig. 10A, B). Although only a relatively small number of sesarmids has been examined, we may postulate that sternite 3 is entirely fused to sternite 4 in this large family.

Karasawa & Kato (2001: fig. 1, tables 2, 3), in a cladistic analysis, seem to be the only ones who have taken into consideration the complete fusion of sternites 3 and 4 in grapsoids, as formulated in their matrix of characters (suture between sternites 3 and 4 recovered as 'indistinct') and have illustrated it in their diagrammatic representation of the thoracic sternum.

A clarification is indispensable, as there are some misinterpretations in the literature. For example, in the figure of *Sesarmoides ultrapes* by Ng *et al.* (1994: fig. 8A) (now *Karstama ultrapes*, see Davie & N. K. Ng 2007) the region "st 2+3" in fact represents only the sternite 2, posteriorly demarcated by suture 2/3: the sternite 3 is completely fused to sternite 4. The "almost straight, setae-lined ridge" indicated as separating the sternites 3 and 4 in *Labuanium scandens* Ng & Liu, 2003 by Ng & Liu (2003: 606, fig. 2A) is not the suture 3/4, but, instead, the suture 2/3. On the opposite, in the figure of the sesarmid *Haberma tinghok* Cannicci & Ng, 2017 (Cannicci & Ng 2017: fig. 4G) the sternite 3 is correctly shown fused to sternite 4. Another source of misunderstanding in the illustration of the thoracic sternum is to draw a depression like it was a suture: for example in the figure of the varunid gaeticine *Sestrostoma balssi* (Shen, 1932) by Davie & N. K. Ng (2007: fig. 7B) the transversal line drawn below the medial groove is probably not a suture that should correspond to a suture 3/4 but just a deep depression (effectively at the normal location of suture 3/4). An identical pattern occurs in *Gaetice depressus* that is correctly drawn with a depression in the same paper (Davie & N. K. Ng 2007: fig. 5H), as in our figure (Fig. 9D, E). In the varunine *Scutamara enodis* Ng & Nakasone, 1993, the short suture drawn by N. K. Ng & Komai (2000: fig. 2A, B) in the prolongation of the conspicuous gynglyme receiving the coxo-sternal condyle of P4 coxa, and supposedly corresponding to a lateral suture 3/4, is probably incorrect; the close species *Pseudograpsus albus* does not show such a suture, and sternite 3 is completely fused to sternite 4 in both species; similarly, the thoracic sternum of *P. setosus* (Fabricius, 1798) figured by N. K. Ng *et al.* (2002: fig. 4A, B) does not display a suture 3/4. Sternite 3 of *Davusia* described by Guinot (2007: 28) as "markedly delimited from sternite 4 by suture 3/4" must be corrected.

Shape and segmental condensation of anterior thoracic sternites exhibit various patterns in thoracotremes. In Grapsoidea, below the suture 1/2, a suture 2/3 either separates sternite 2 from sternite 3 or may be lacking (e.g. Percnidae, remarkable by a faint suture 1/2 and sternites 2-4 forming a smooth and flat single pièce, Fig. 8G, H). Leptograpsodidae n. fam. is characterised by the presence of both conspicuous sutures 1/2 and 2/3 (Figs 1C, D; 2B; 3A), so retains the original metamery in the anterior sternal part (plesiomorphy), but lacks suture 3/4 as all other grapsoids.

Sternites 4 to 8

Sternite 4, always the more developed, is recognisable by the variously pronounced concavities receiving the arthrodial cavities of the chelipeds; they are sometimes hardly or not delineated, as in some gecarcinids, i.e., *Gecarcinus ruricola* and *Gecarcoidea lalandii* (Fig. 7A, B and 7E, F, respectively). Sternite 7 is much expanded posteriorly in all grapsoid families.

Development of the last thoracic sternite, the sternite 8, is a key character. It may be either dorsally visible, with a various portion exposed on each part of the pleon, or not at all exposed when pleon is folded. In fact, structure of sternite 8 is highly dependent on the shape and size of the emargination that posteriorly excavates the plastron for the insertion of the pleon into the sterno-pleonal cavity. If the posterior emargination is wide and semicircular (such as in Leptograpsodidae n. fam.) or narrower but long enough to reach the sternite 7 (such as in Xenograpsidae), the sternite 8 is reduced, unexposed medially, only visible laterally, without median line, and it is limited by a short suture 7/8. If the posterior emargination is weak, sternite 8 is normally developed (practically as developed as the preceding sternites or sometimes only a little less wide), well exposed medially, limited by a long suture 7/8: in this case only, sternite 8 may be longitudinally crossed by the median line. Sternite 8, which has not yet been examined from the standpoint of its posterior emargination and never studied so far in Grapsoidea, might be a valuable diagnostic feature and could provide important new insights into the brachyuran evolution. The implementation of the pleon, its bending and flexion within the sterno-pleonal cavity, the reduction of the last thoracic sternite and its impact on the posterior portion of the axial skeleton are all characters that necessitate to be studied with related internal structures, i.e., the interosternites 7/8 and the endosternal intertagmal phragma (formed of an anterior plate derived from the thorax and a posterior plate derived

from the pleon) and the brachyuran sella turcica (Secretan 1998; Guinot *et al.* 2013; Keiler *et al.* 2017).

Shape of sternite 8 considerably varies in Grapsoidea, and this morphological disparity desserves to be taken into account. In Leptograpsodidae n. fam. (Figs 1D; 3A) sternite 8 is poorly developed, widely notched by the posterior emargination, thus restricted to its lateral portion and unexposed medially, therefore without median line at this level. In the gecarcinids of the second subclade, the posterior emargination (more or less triangular in *Gecarcinus* Fig. 7B, C, *Johngarthia* and *Gecarcoidea* Fig.7F, G) is long and reaches sternite 7 just at level of the median bridge (very prominent in *Gecarcoidea*), so that sternite 8 is unexposed medially and cannot have a median line; suture 7/8 is short. In contrast, in gecarcinids of the first subclade (*Discoplax*, *Cardisoma*, *Tuerkayana* n. gen.) the posterior emargination is far from reaching sternite 7, so the sternite 8 is not reduced, is exposed medially and vertically crossed by the median line. Xenograpsidae (Fig. 8O) is the only other grapsoid family to show, likewise Leptograpsodidae n. fam., a reduced sternite 8. In Grapsidae (Fig. 8C) and all other grapsoid families the sternite 8 is well developed, as wide as preceding sternites, not deeply notched by posterior emargination, thus exposed medially and longitudinally crossed by clear median line.

The complete fusion of thoracic sternites 4-8, which takes place medially in all thoracotremes and corresponds to the pattern 5 defined by Guinot *et al.* (2013: fig. 56), encompasses a variety of phylogenetic groups, as well heterotremes as thoracotremes. Several subpatterns may be defined by taking into account the arrangement of the median line and median plate. The correlation (it is not always absolute) between the median line and the development median plate has been well documented in the *Helice*/*Chasmagnathus* complex by Sakai *et al.* (2006: fig. 2).

Median line and median plate

The median line axially crosses a various number of thoracic sternites and generally represents the external mark of the internal median septum (median plate), of variable height, on which the endosternites of the axial skeleton are connected; it corresponds to a sternal invagination at the connection points of the endosternites. The observations thus far made by Guinot *et al.* (2013: 72, fig. 56) have highlighted that a monophyletic taxon seems to display a similar sternal pattern of both median line and median plate, with only a few variants. These characters had not been generally used in taxonomy, with a few exceptions, as in the varunid *Helice*/*Chasmagnathus* complex (Sakai *et al.* 2006): a wide and high posterior emargination leads to a reduced sternite 8, only developed laterally, and to the absence of median line on sternite 8. The median line that is present along posterior sternites in the megalopa of *Cardisoma armatum* (see Cuesta & Anger 2005: 652, fig. 4C) properly corresponds to the median line on sternites 8, 7 and 6 of adults.

There are different modalities of the median line in thoracotremes, which correspond to subpatterns of pattern 5: absent (as in *Macrophthalmus* Desmarest, 1823, see Guinot & Bouchard 1998: fig. 24A) or present, but with various modalities. For example, in *Ocypode* Weber, 1795 (Ocypodidae Rafinesque, 1815) and *Ucide*s Rathbun, 1897 (Ucididae Števčić, 2005) the median line extends along sternites 5-8, the median plate being either continuous or discontinuous (Guinot *et al.* 2013: fig. 57A, B, respectively).

Median bridge(s)

In Leptograpsodidae n. fam., a transverse ridge at the level of suture 6/7 forms a thick triangular bridge that superficially units the both sides of the sternal plate and extends forward to become the bottom of the sterno-pleonal cavity (Figs 1D, E; 3A).

A bridge similar to that of *Leptograpsodes* is present in Gecarcinidae *pro parte* (see Table 1). In *Cardisoma* (Fig. 5E, F), *Discoplax* (Fig. 5B, C) and *Tuerkayana* n. gen. (Fig. 5H, I, K, L, N, O) a transverse ridge about at the level of sternal suture 6/7 (or a little lower) forms a kind of bridge that superficially units the two sides of the sternal plate; then, this bridge extends anteriorly to become the bottom of the sterno-pleonal cavity. The median line either stops at this level, thus is confined to sternite 7 (*Tuerkayana* n. gen.), or reappears on sternite 6 (*Cardisoma*, see Fig. 4E, F). A similar bridge is present on the widened thoracic sternum of females.

The second subclade of Gecarcinidae exhibits a distinctive pattern. In *Gecarcinus* the disposition varies along species: a weak triangular median bridge at level of suture 6/7 and a very narrow bridge at level of suture 7/8 (Fig. 7B, C, *G. ruricola*), or only some traces of such bridges (*G. lateralis*, *G. quadratus*), or even indistinct bridges in *Johngarthia*. *Gecarcoidea* (Fig. 7F, G) shows similar but still narrower transverse bridges: a small triangular bridge at level of sternal suture 6/7 plus a narrow transverse bridge at level of suture 7/8.

Note that such a tranverse ridge, but in this case at the level of suture 7/8, has allowed the division of Potamidae into two different subfamilies: Potaminae Ortmann, 1896 with a ridge (thus a median line interrupted); Potamiscinae Bott, 1970 with no trace of tranverse bridge (thus a median line continuous on sternites 8 and 7) (Yeo 2000: 33; Yeo & Ng 2004: 1224, figs 1, 2; Shih *et al.* 2009).

Male gonopore and penis

The thoracotreme male gonopore is sternal. Even in *Cardisoma* (*C. guanhumi* [Fig. 5F] or *C. carnifex* (Guinot *et al.* 2013: fig. 23A)), *Discoplax* (Fig. 5C) and *Tuerkayana* n. gen. (Fig. 5I, L, O), cases in which the male duct is close to the membrane between the P5 coxa and the thoracic sternum, the ejaculatory duct does not perforate or enter the P5 coxa. A dissection of *D. longipes* has proved the specific location of its exit, i.e., the sternal emergence of penis, without a detour by the P5 coxa. The same disposition was found by a dissection of *Plagusia squamosa* (see Guinot *et al.* 2013: fig. 33A).

In thoracotremes, the male gonopore occurs in several locations, either along suture 7/8 or in the middle of sternite 8. The main feature is its position in relation to the P5 coxo-sternal condyle. Penis emerges from a perforation through the thoracic sternite 8, either very close to the P5 coxa, as

in Leptograpsodidae n. fam. (Figs 1D; 3B), all Grapsidae (Fig. 8C), (Guinot 1979: fig. 52A-C), Gecarcinidae *pro parte*, i.e., in the "first subclade" (Fig. 5C, F, I, L, O) (Guinot 1979: fig. 54A-C; Guinot *et al.* 2013: fig. 23A) or far from the coxa, but to a varying extent, in remaining Gecarcinidae, i.e., in the "second subclade" (Fig. 7C, G) (Guinot 1979: fig. 54D) and in *Epigrapsus*, in Percnidae (Fig. 8I), Plagusiidae (Fig. 8L) (Guinot 1979: fig. 52E; Guinot *et al.* 2013: figs 23B, 33A), Glyptograpsidae (Fig. 8F) (N. K. Ng *et al.* 2007: fig. 4G), Xenograpsidae (Fig. 8O) (N. K. Ng *et al.* 2007: fig. 4B), and Varunidae (Fig. 9C, F, I, L, O) (Guinot 1979: fig. 52H). In contrast, in the Ocypodoidea (Ucididae and Ocypodidae) the male gonopore always exits very far from the P5 coxa and is located on suture 7/8 (Guinot *et al.* 2013: figs 23C and 23E, F, respectively). In Heloeciidae, a family considered close to Ocypodidae (Türkay 1983; Sternberg & Cumberlidge 2001b; Števčić 2005; Ng *et al.* 2008; Davie *et al.* 2015c), the gonopore is very close to the P5 coxo-sternal condyle (Guinot *et al.* 2013: fig. 26A), thus with a disposition of the penial region similar to that of *Cardisoma*, *Discoplax* and *Tuerkayana* n. gen., which is unusal for an ocypodoid. The unique morphological traits of Heloeciidae (others than those that show a resemblance to *Uca* or allies) discussed at length by Guinot *et al.* (2013: 119), with evidence of a separate status for this monotypic family, were not cited by Shih *et al.* (2016: fig. 2) whose genetic results reveal that *Heloecius* is not closely related to the Ocypodidae, such as in Schubart *et al.* (2006: fig. 1).

In all varunids that we have examined, the male gonopore opens far from the P5 coxa (and also from suture 7/8), with a distance varying among the genera. A special disposition has been observed in fresh material of *Varuna litterata* where the penial papilla is supposed to invaginate inside the gonopore, the calcified portion acting as an operculum (Guinot *et al.* 2013: fig. 36).

A clear posteriormost location of the sternal male gonopore in relation to suture 7/8 occurs in all Grapsoidea: Leptograpsodidae n. fam. (Fig. 3A), Grapsidae (Fig. 8C) (Guinot 1979: fig. 52A) (except *Planes*, see Guinot 1979: fig. 52C), Gecarcinidae (Figs 5C, F, I, L, O; 7C, G), Plagusiidae (Fig. 8L) (Guinot 1979: fig. 52E; Guinot *et al.* 2013: 23B, 33A), Percnidae (Fig. 8I) (Guinot 1979: pl. 23, fig. 2), Glyptograpsidae (Fig. 8F) (N. K. Ng *et al.* 2007: fig. 4G), Varunidae (Fig. 9C, F, I, L, O) (Guinot 1979: fig. 52G-J; N. K. Ng *et al.* 2007: fig. 4F; N. K. Ng 2010: fig. 3C), and Xenograpsidae (Fig. 8O) (N. K. Ng *et al.* 2007: fig. 4B). In the cases where the gonopore opens far from the P5 coxa (e.g. Plagusiidae, Varunidae), a sulcus crosses the sternite 8, either being only proximal ("incomplete sulcus") or reaching the P5 coxo-sternal condyle ("complete sulcus") ("*sillon complet*" or "*sillon incomplet*", see Guinot 1979).

The penis shows various shapes in thoracotremes. When it is close to P5 coxa, either it is cylindrical, entirely (or almost) of the same width, with a short basal portion and large papilla (e.g. Grapsidae); or it is wedged between the P5 coxo-sternal condyle and sternite 7, with a narrow exposed proximal portion, and then continues through a developed, sometimes foliaceous papilla: Gecarcinidae (*Discoplax longipes*: fig. 5C; *Cardisoma guanhumi*: Fig. 5F; species of *Tuerkayana* n. gen.: fig. 5I, L, O), and *Leptograpsodes* (Figs 1D, E; 3A, B). When the penis emerges far from the P5 coxa, it shows as a variously developed papilla. In some thoracotremes the quite distal end of the papilla can be invaginated into the papilla: e.g. in some grapsoids, like *Leptograpsus variegatus* (see Brocchi 1875: fig. 103) and *Varuna litterata* (Guinot *et al.* 2013: 143, fig. 36).

Pleon-locking mechanism

Existence of a system that holds or locks the pleon closely to the body is a synapomorphy of Brachyura. Thoracotremata display multiple pleon-holding mechanisms (press-button, clasping apparatus, overhanging edge) or do not show any specific structures (Guinot & Bouchard 1998; Köhnk *et al.* 2017: fig. 28). The thoracotreme locking mechanisms have emerged in crabs displaying a variety of behaviours and habitats: swimming (Grapsidae), rafting by clinging to floating objects (Plagusiidae), may be invasive (Percnidae), climbing mangrove trees (Sesarmidae), terrestrial, walking during migrations over considerable distances (Gecarcinidae), and often burrowing (Leptograpsodidae n. fam., Gecarcinidae *pro parte*). If correctly documented, the presence of pleonal holding and its modalities could be an important source of information for the families and subfamilies: a typical and supposedly functional press-button mechanism (e.g. Grapsidae, Glyptograpsidae, Plagusiidae, Percnidae, Leptograpsodidae n. fam.); either present or absent (Varunidae, obviously paraphyletic, see below); present but seemingly not functional (Gecarcinidae *pro parte*).

Varunidae is heterogeneous in respect of the locking system: some species, e.g. *Varuna litterata*, have typical sternal button and pleonal socket, but many representatives, e.g. *Cyclograpsus*, have apparently completely lost a holding mechanism in adults; the system is not functional, and only small vestiges of the holding structures are present in some species (Guinot 1979: pl. 20, fig. 5, pl. 23, fig. 1; Guinot & Bouchard 1998: fig. 23A, B, as Varuninae; Köhnk *et al.* 2017: figs 21, 22). A study dealing with the character state in the varunid subfamilies still lacks.

Stridulatory structures in grapsoids

The function of the suborbital crest acting as a pars stridens and the more or less specialised structure on the inner magin of P1 merus acting as a plectrum is for the first time identified as a stridulatory apparatus in species of *Leptograpsodes*, *Discoplax*, and *Epigrapsus*.

In *Leptograpsodes octodentatus* the finely granulated suborbital margin represents a stridulatory structure, the pars stridens (Figs 1G; 2C; 3D); the plectrum or "scraper" (Fig. 2D) is a short but distinct smooth, whitish ridge on the inner surface of the cheliped merus, just adjacent to the inner distal margin. The suborbital crest, smooth at small size, appears made of flattened granules in largest males. The stridulatory apparatus is seemingly no more functional at a great size (as in the male 51.8 × 68.3 mm), the merus of the massive major

cheliped not being facing the suborbital crest. In the female 27.0 × 34.0 mm the apparatus is present, with a practically smooth suborbital crest and a rather faint meral ridge, but it could be probably effective.

The stridulatory apparatus of *Leptograpsodes* is similar to that of *Discoplax*: both of them have a comparable suborbital margin forming the pars stridens (Figs 1G; 2C; 3D and Fig. 6A, respectively) and the plectrum on inner margin of P1 merus, represented by a delimited crest in *Leptograpsodes* (Fig. 2D) (disappearing at a larger size) and a thickened ridge in *Discoplax* (Fig. 11A). Both sexes of the two examined species of *Discoplax*, *D. longipes* and *D. gracilipes*, display a stridulatory apparatus. It is the first time that such a pattern of stridulation is described in the family Gecarcinidae. It is true that there is no record demonstrating that *Leptograpsodes* and *Discoplax* produce an acoustic signal, but the morphology leaves no doubt about this function. The genus *Discoplax* is probably the first cavernicolous brachyuran genus in which stridulatory structures are identified.

The two species of the gecarcinid *Epigrapsus*, *E. politus* and *E. notatus*, were not known as stridulating. And yet, there can be no doubt that the long, striated suborbital crest, which is not externally connected to orbit, is a pars stridens and the ridge located on inner magin of P1 merus represents the plectrum. The stridulatory apparatus is present in both sexes.

According to Bennett (1964: 84, figs 94-97), *Leptograpsodes octodentatus* (as *Brachynotus*), *Cyclograpsus audouinii* H. Milne Edwards, 1837, *Hemigrapsus sexdentatus* (H. Milne Edwards, 1837) and *Metaplax crenulata* (Gerstaecker, 1856) (as *Hemigrapsus crenulatus*) exhibit stridulatory structures in both sexes, with the pars stridens formed by the suborbital margin and the plectrum located on the P1. Previously, Chilton & Bennet (1929) heard the stridulation produced by a pair of cyclograpsine crabs *in copula* outside the water in an intertidal rocky station near Christchurch, New Zealand: their presence could be detected, before being seen, thanks to clicking sounds "almost like distant artillery". Another varunid, *Thalassograpsus harpax* (Thalassograpsinae) also displays a stridulatory apparatus but in this species the suborbital margin composed of about three portions (pars stridens) rubbs against a thickening (plectrum) of inner edge of cheliped merus (Fig. 11B, C) (Tweedie 1954; Davie & N. K. Ng 2007). Although that a sound production has not been demonstrated, the conspicous stridulatory structures that are present in most members of the Heliceinae (Guinot-Dumortier & Dumortier 1960: fig. 5b, f; Sakai *et al.* 2006: figs 3, 10c, 17, 38-40, 57, 58, 60-66, table 3; Shih & Suzuki 2008) are so specialised that an acoustic function could not be doubted, all the more so individual communication is well known in these burrowing crabs. Surprisingly, *Neohelice granulata* (Dana, 1851), which is described by Sakai *et al.* (2006: 64, fig. 95c) without stridulatory mechanism (suborbital crest bearing two unequal rows of isomorphic granules in both sexes, but P1 merus lacking the typical plectrum of *Helice tridens*), would be able to produce two distinct acoustic emissions, one of these, the multi-pulses rasp, conveying messages involved in the sexual interactions (Filiciotto *et al.* 2018).

A stridulatory apparatus, apparently unique within Sesarmidae, occurs in the three species of the genus *Sesarmoides sensu stricto*. Described by Davie & Ng (2007: fig. 1) in *S. borneensis* (Tweedie, 1950), it is formed by the practically smooth (only distinctly milled) suborbital margin rubbing against a short, smooth ridge adjacent to the inner surface of cheliped merus. Although transferred in the close genus *Karstama* Davie & Ng, 2007, initially supposed devoid of stridulatory structures (Davie & Ng 2007), *K. ultrapes* should be able, from our point of view, to exhibit a stridulatory apparatus comparable to that figured by Davie & Ng (2007: fig. 1) in S. *borneensis*. The case of *K. philippinarum* Husana, Naruse & Kase, 2010, from two anchialine caves in the Philippines, with a thinly raised suborbital margin forming a keel lined with microscopical granules, and described as close to *K. ultrapes* (Husana *et al.* 2010: fig. 3C), should be revisited; also the cases of new *Karstama* species described by Wowor & Ng (2009; 2018) in which there is no mention of stridulating structures. Recently, two species of *Karstama* were presumed to display a stridulatory mechanism (Poupin *et al.* 2018: 394): in male *K. jacksoni* (Balss, 1934), from Christmas Island, a salient, coarsely granulated 'stridulating' ridge on the inner face of the major chela would rub against the developed flange of the P1 merus (Poupin *et al.* 2018: fig. 8B, E); by contrast, in male *K. vulcan* Poupin, Crestey & Le Guelte, 2018 from lava tubes of the volcano 'Piton de la Fournaise', Réunion Island, the stridulating organs are the suborbital margin and the granulated ridge on the inner surface of P1 palm (Poupin *et al.* 2018: figs 1D, E, 2B).

These patterns of stridulation differ from that of other Sesarmidae that are known to show sound production structures and emit acoustic signalling, but with a different mechanism by rubbing their chelae together: pars stridens composed of tubercles on the dactylus on one cheliped; plectrum consisting in a double row of pectinated setae on the propodus of the other cheliped (Tweedie 1954: fig. 2; Guinot-Dumortier & Dumortier 1960: fig. 22; Boon *et al.* 2009: figs 1-5; Chen *et al.* 2014, 2017).

Another type of acoustic signals, however truly distinct, is found in Gecarcinidae. A stridulation, without a differentiated plectrum, is performed by two species of *Gecarcinus*: the subhepatic region, with oblique rows of tubercles, is rubbed by the tuberculated cheliped merus in *G. quadratus* (see Abele *et al.* 1973: fig. 1), or is scraped by the cheliped palm in *G. lateralis* (see Klaassen 1973: figs 5, 6). In addition, a communication system, a substrate vibration signal, is performed by percussion, drumming, rapping, striking of a body part (chela or legs) on the substrate, with typical sequences of pulses that inform congeners: threatening, sexual display, appeasement (Klaaseen 1973: figs 1-4) (see also von Hagen 1975; Davie *et al.* 2015a).

Terrestrial adaptation of grapsoids

Level of terrestriality varies substantially among grapsoid crabs. *Leptograpsodes octodentatus* shows a high degree of terrestrial adaptation: the coxae of P2-P4 and, to a lesser extent, the P1 coxa form setal pouches bearing dense, long tufts of hydro-

philic setae, thicker and longer on P3, P4 (Figs 1C, D; 2B). Such setae, which are usually attached to the opening of the Müller's channel (situated between P3 and P4) and function to transport water into the branchial chamber, are related to terrestrial life (Hartnoll 1973: 151; 1988: 27; Wolcott 1984: fig. 2; Greenaway 1988: fig. 7.2B-D; Oliveira 2014). Tufts of setae are found in some grapsids (Balss 1944: 557): they occur between the P3/P4 coxae, e.g. in the terrestrial *Geograpsus* (see Greenaway 1988: fig. 7.2.B-D; Paulay & Starmer 2011), in *Goniopsis*, in some *Grapsus* as *G. fourmanoiri*, and seemingly at a lesser extent in *Pachygrapsus*, e.g. *P. crassipes*, *P. transvs* (Gibbes, 1850) (see Oliveira 2014: table 2).

Gecarcinidae of the first subclade (*Cardisoma*, *Discoplax* and *Tuerkayana* n. gen.) lack coxal setal pouches. Instead, in Gecarcinidae of the second subclade (*Gecarcinus*, *Johngarthia*, *Gecarcoidea*) dense tufts of of hydrophilic setae are located along the margins of the pleon and at its junction with the carapace, facing row of setae on adjacent portions of last sternites (Bliss 1963; Wolcott 1984): these species are devoid of Müller's channel (Oliveira 2014). Ability to absorb water from the substrate is well developed in *Gecarcoidea natalis* and *G. lateralis*, in which setal tufts extend along the first three pleonal segments 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 *Gecarcinus ruricola* and *Gecarcoidea lalandii* (Fig. 7A, B and 7E, F, respectively) the posterior margin of sternite 7 is lined with dense hydrophilic setae in contact with tufts of setae on P5 coxa and pleonal somites 1-3.

A conspicuous setal pouch between P3/P4 occurs in both species of *Epigrapsus*, *E. notatus* and *E. politus*. This feature is unique within the Gecarcinidae, since the first subclade (including *Cardisoma*, *Discoplax* and *Tuerkayana* n. gen.) lack setal pouches, and the second gecarcinid subclade (including *Gecarcinus*, *Johngarthia* and *Gecarcoidea*) have tufts of hydrophilic setae along the margins of the pleon and at its junction with the carapace (Rathbun 1918: figs 163, 165). This demonstrates that Müller's channel unexpectedly exists in *Epigrapsus*.

In Varunidae, the setal insertion occurs between P2/P3 and P3/P4 coxae in *Cyclograpsus* (see Hartnoll 1988: 27) and *Neohelice* (see Oliveira 2014: fig. 22). By comparison, in Ocypodidae large setal tufts are found only between P3/P4 (Bliss 1968: fig. 15; Wolcott 1984: fig. 2; Greenaway 1988; Matsuoka & Suzuki 2011: 14, 15, figs 1B, 10, 11; Oliveira 2014: table 2), as well as in Heloeciidae (see Türkay 1983). Tufts of setae are situated on coxal processes of P2 and P3 in some Sesarmidae (Komai *et al.* 2004: figs 4I, 9F), and on P3 to P5 in the mangrove tree crab *Aratus pisonii* (see Greenaway 1988; Hartnoll 1988: fig. 2.8.F; Niem 1993: fig. 4b-d; Oliveira 2014: table 2). Setal tufts also occur in species of Dotillidae Stimpson, 1858: for example, in *Dotilla* Stimpson, 1858, *D. fenestrata* Hilgendorf, 1879 seems unique in having water uptake setae on the pleon (smooth setae arising from the posterior margin of the pleonal somite 4 and the water passing to the space between lateral openings on the pleonal somite 5 and the thoracic sternum) (Hartnoll 1973: 144-145, 150, fig. 3a-c); in *Scopimera* De Haan, 1833 uptake setae are situated between the coxae of P2/P3 (Wolcott 1984); in *Dotilloplax* Kemp, 1919 and *Tmethypocoelis* Koelbel, 1897 setae are located between P2/P3 and P3/P4 (Hartnoll 1973; Davie & Kosuge 1995); hydrophilic setae are absent in other genera currently grouped in the Dotillidae. The remarks by Hartnoll (1973: 150) about the water uptake in Mictyridae through long, curved setae arising from the rear of the carapace and the first pleonal segment were confirmed by video camera records showing the behaviour patterns of water uptake and circulation in *Mictyris guinotae* Davie, 2010: the tufts of long setae are inserted into the substratum and collect water by capillary action (Matsuoka *et al.* 2012: figs 2, 4-6).

CONCLUSION

The recognition of Leptograpsodidae n. fam., monotypic and monogeneric, is fully justified. The new family is unique among extant Grapsoidea by the shape of the body, the presence of two oblique grooves on the carapace dorsal surface, and numerous other traits. It shares with Gecarcinidae, especially with *Discoplax*, several characters, notably: the shape of the orbit, the long suborbital crest (with stridulatory function), the location of the male gonopore, the presence of sternal bridges at level of sternal suture 6/7. But the distinguishing features that separate Leptograpsodidae n. fam. from *Discoplax* are unambiguous: rather wide dome-shaped proepistome (very narrow, subquadrate in *Discoplax*), anterior sternites well separated, with sutures 1/2 and 2/3 marked (only 2/3 present in *Discoplax*), shape of sternite 8 only laterally developped (well developped and exposed medially in *Discoplax*), median line only on sternite 7 (on sternites 8 and 7 in *Discoplax*). Erection of the new genus *Tuerkayana* n. gen. quite changes the currently accepted taxonomy: it is the result of a carefully considered decision, with full consciousness of the consequences, from a taxonomic and ecological points of view, as well from legal and strategies of conservation aspects, in the ecosystems where gecarcinids are key species.

Analysis of characters (mostly of the thoracic sternum) here proposed for the reconstruction of the phylogenetic relationships among the major groups of the superfamily Grapsoidea in conjunction with the pre-existing suite of features from other body parts, could provide a basis for a strongly supported new classification. The groups outlined in this more modern way are most often corroborated by molecular phylogenetics based on the complete genome, so the past incongruences between traditional taxonomy and genetics tend to vanish and, instead, both approaches become complementary tools.

Recent molecular data confirmed that Grapsoidea does not form a monophyletic group (Tsang *et al.* 2014; Chu *et al.* 2015; Basso *et al.* 2017; Xin *et al.* 2018; Wolfe *et al.* in press). Despite the superfamily Grapsoidea, such as many superfamilies in Eubrachyura, suffering from the lack of consistent diagnosis, without clear apomorphies, we have used by convenience this superfamilial name in the present study to limit the investigations.

According to Schubart *et al.* (2006), at higher taxonomic level it became evident that Grapsoidea and Ocypodoidea

were not monophyletic in their current composition, suggesting that longstanding morphological evidence be put aside and members of these two families should be merged under a single taxon within Thoracotremata, corresponding to the Grapsoidea *sensu lato* Rathbun, 1918 that has a similar composition. Grapsidae and Varunidae were recognised polyphyletic not only by reference to genomic analysis but also to morphology (Kitaura *et al.* 2002, 2010). According to Tsang *et al.* (2009, 2014) based on nuclear and mitochondrial sequences, to Xing *et al.* (2016) based on complete mitogenome, and to Basso *et al.* (2017) based on gene order analysis of brachyuran mitochondrial genome, Grapsoidea and Ocypodoidea were recovered as polyphyletic. According to Ji *et al.* (2014: fig. 3), Grapsoidea and Ocypodoidea formed a monophyletic group.

Based on molecular results, Schubart *et al.* (2000a: fig. 1; 2000b: fig. 1), without retaining a suprafamilial Gecarcinoidea as proposed by Guinot (1978), gave additional evidence for close relationship between grapsids and gecarcinids and for their treatment at the same taxonomic rank, even suggesting that Gecarcinidae evolved within the Grapsidae. Morphological data show that the Grapsoidea are paraphyletic (Davie *et al.* 2015b: 957), and that some included taxa, e.g. the Varunidae, require further investigations.

The main synapomorphy of Thoracotremata, and arguably a major change in brachyuran evolution, is the displacement of the male gonopore and penis from the plesiomorphic P5 coxal position to being fully sternal (Guinot 1977; 1978: table p. 214; 1979). However it is not that simplistic, and phylogenetic relationships within the Thoracotremata remain still contentious. For example the sternal location of the male gonopore in Hymenosomatidae MacLeay, 1838, in contradiction to all morphological characters that indicate a heterotreme affiliation supported by the molecular data, is a controversial question (Guinot 2011). It should be possible, after a least verification, to propose, a second synapomorphy of Thoracotremata: the complete fusion of thoracic sternites 3 and 4 without any visible external suture, even laterally; the only discernible mark should be the lateral hollow (the gynglyme) corresponding to the articulation of mxp3 on the thoracic sternum (the coxo-sternal condyle), for example in some Varunidae, e.g. *Varuna litterata* (Fig. 9M, N).

It is worth reminding that the reciprocal monophyly of the eubrachyuran subsections Heterotremata and Thoracotremata have received strong support from genetic studies (Tsang *et al.* 2008; Wetzer *et al.* 2009; Palacios-Theil *et al.* 2009; Tsang *et al.* 2014; Chu *et al.* 2009, 2015), whereas their monophyly was not supported by sperm morphology that suggested inclusion of Thoracotremata within Heterotremata (Jamieson *et al.* 1995; Jamieson & Tudge 2000). The broad acceptance of these two subsections was also called into question by morphological cladistic analyses (Scholtz & Richter 1995; Sternberg & Cumberlidge 2001a, b; Dixon *et al.* 2003). Modern molecular methods (Tang *et al.* 2017; 2018) led to a new classification, with Eubrachyura consisting of four groups: Raninoida De Haan, 1839 (i.e., Gymnopleura Bourne, 1922, see Guinot *et al.* [2013]), Heterotremata, Thoracotremata, and Potamoidea Ortmann, 1896, with a high nodal support value separating these groups.

The Thoracotremata can be defined by three putative spermatozoal synapomorphies: 1) loss of the acrosome ray zone; 2) unique development of an apical button, filling a central perforation of the operculum; and 3) the presence of concentric lamellae in the acrosome (Jamieson *et al.* 1995, 1996; Jamieson & Tudge 2000; Tiseo *et al.* 2017). According to Benetti *et al.* (2012) ultrastructural sperm morphology lends support for the monophyletic origin of the Thoracotremata and further attests the low level of variability within the thoracotreme clade. More generally, the brachyuran sperm ultrastructure is increasingly proving to be an effective tool to adjust phylogenetic relationships when used in association with molecular data (Camargo *et al.* 2018) and proper morphology.

We cannot refrain from making one last remark: the striking similarities of the carapaces between certain thoracotremes, e.g. gecarcinids and *Leptograpsodes*, and primary freshwater crabs (heterotremes) such as *Thelphusula* Bott, 1969, *Terrathelphusa* Ng, 1989 (Gecarcinucidae) and *Isolapotamon* Bott, 1968 (Potamidae): see figures in P. K. L. Ng & P. Y. C. Ng (2018: figs 1A, 2A, B, 6E, F). With its unique representative *Leptograpsodes octodentatus*, a supratidal brachyuran never found immersed or rarely entering in the sea, inhabiting brackish waters but also remaining out of water (Hale 1927a; George 1962; Griffin 1971), the family Leptograpsodidae n. fam. may be compared to other thoracotreme families that are found outside the sea for part of their life cycle, the secondary freshwater crabs (Yeo *et al.* 2008; Cumberlidge 2016).

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APPENDIX

NOMENCLATURAL ISSUES

Nomenclatural status of authorship of H. Milne Edwards (1837) brachyuran names

H. Milne Edwards (1834, 1837), the author of *Histoire naturelle des Crustacés*, has proposed many new nominal taxa at rank of the family group (and also class-series nomina, see Guinot *et al.* 2013: 17, *Nomenclatural ranks*) by providing substantial diagnoses, keys and list of included taxa. His "tribes", which often correspond roughly to our superfamilies, and his families were introduced in French, not in latinised form, so that they were practically all rejected for the account of authors who first latinised them, as MacLeay (1838), De Haan & Dana (see Dubois 2012).

The question of whether H. Milne Edwards's names are scientific names or vernacular names needs to refer to the *Code*. On this point of discussion, although ambiguous depending on the *Code* articles in which the definitions of "vernacular name" are not absolutely similar in the English and French glossaries, we would note that the H. Milne Edwards's names were proposed "only for zoological nomenclature" as opposed to names "of an animal or animals in a language used for general purposes" (*Code*, Article 1 and Glossary p. 109), see discussion in Kottelat (2001: 609). Another point is that the criterion of latinisation is nowhere required by the *Code*: the Article 11.3 and the appended examples very explicitly permit the use of non-Latin words.

In any event, the family-group names, when first published not in latinised form by H. Milne Edwards (1834, 1837), meet all the criteria in accordance with the provisions of the ICZN (*Code*, Art. 11.7). They are available with their original authorship and date since, when they have been latinised by the first author, they have been explicitely recognised to first belong to H. Milne Edwards and they were later generally accepted as valid by the majority of authors interested in the group and, most often, as dating from that first publication in original form (*Code*, Art. 11.7.2).

Thus, in view of the general acceptance, most of names in the *Histoire naturelle des Crustacés* shoul be credited to H. Milne Edwards. We will examine here the case of the Gécarciniens H. Milne Edwards, 1837, whereas the case of Grapsoïdiens H. Milne Edwards, 1837 will be treated in another paper.

Gécarciniens H. Milne Edwards, 1837

The family-group name Gécarciniens was coined by H. Milne Edwards (1837: 7, 16) for a tribe of crabs, but was first published not in latinised form. Only one year later, MacLeay (1838: 63) latinised the name in writing "Gecarcinidae, M. E.". Later, H. Milne Edwards (1853: 200 [166]) latinised it as Gecarcinacea. Another cited authorship is Dana, 1851, for example by Rathbun (1918: 339) and Davie (2002: 184). The great specialist of gecarcinids M. Türkay (1970: 335) ascribed authorship to H. Milne Edwards (1837) in his famous "Gecarcinidae of Amerikas", such as some authors as Prahl & Manjares (1984: 151) and Tavares (1989 in the title of his revision of the family). Great scientists, and not the least, as Miers (1886: xiv, 216, as Geocarcinidae [sic, recte Gecarcinidae]), Rathbun (1918: 339), and Manning & Holthuis (1981: 248) all cite *Gecarciniens H. Milne Edwards, 1837* (with or without an accent on the "e") just after or under Gecarcinidae MacLeay, 1838 or Gecarcinidae Dana, 1851, and provide the original reference of 1837. Ng *et al.* (2008: 30, 214) indicate below Gecarcinidae MacLeay, 1838 " = *Gecarciniens H. Milne Edwards, 1837 (not in Latin, unvailable name)*", a conclusion to which we do not agree.

The family-group name Gécarciniens H. Milne Edwards, 1837 meets all the criteria of availability in accordance with the provisions of the ICZN (*Code*, Art. 11.7, 11.7.2). Authority of H. Milne Edwards is widely recognised, and in view of this general acceptance authorship of the family-group name Gecarcinidae is hereby ascribed to H. Milne Edwards, 1837.

The case of the family-group name Grapsoïdiens H. Milne Edwards, 1837, also first published not in latinised form by H. Milne Edwards (1837: 7, 68, and, after p. 70, in the table of included genera) for a tribe of crabs, then latinised by MacLeay (1838: 64) as stirp "Grapsisna", and family "Grapsidae M.E", must be treated in another paper.

Nomenclatural and taxonomical status of *Gecarcinus hirtipes* Lamarck, 1818 and *Cardisoma hirtipes* Dana, 1851

Gecarcinus hirtipes Lamarck, 1818 (p. 521; see also 1838: 462), created with a two-line description and whose the type material from Mauritius has not been found in the collection of the MNHN, has a complicated story, briefly exposed here. When establishing a new *Cardisoma* species from the Fiji Archipelago, Dana (1851: 253; 1852: 376; 1855: pl. 24, fig. 4) used the same binomen as Lamarck (1818). Türkay (1975: 168) proposed to suppress the name "*Gecarcinus hirtipes*" by arguing that the description provided by Lamarck (1818) was too brief to define the species. For the proposed suppression of *Gecarcinus hirtipes* Lamarck, 1818, vs *Cardisoma hirtipes* Dana, 1851, see Holthuis (1980) and the reply by Türkay (1980). Ultimately, the specific name *hirtipes* as published in the binomen *Gecarcinus hirtipes* Lamarck, 1818; see also Lamarck 1838 has been suppressed and placed on the Official List of Rejected and Invalid Specific names in Zoology (Opinion 1205 in *Bulletin of Zoological Nomenclature* 1982, 39, pt 2: 102-103).

Cardisoma hirtipes Dana, 1851 has therefore been considered a valid species by most authors. Türkay (1974a: 229) listed its distinctive characters from the close species *Cardisoma rotundum* (Quoy & Gaimard, 1824: pl. 77, fig. 1), senior synonym of *Cardisoma frontalis* H. Milne Edwards, 1853 (see N. K. Ng *et al.* in press). Later, however Türkay (1987: 145) included *C. hirtipes* Dana, 1851 (and also *C. rotundum*) in *Discoplax* without further justification. Ng *et al.* (2000, 2001),

Ng & Guinot (2001), Ng *et al.* (2008), Ng & Shih (2014, 2015) and many others agreed for such an allocation, which today we consider to be erroneous. In the present paper the species *hirtipes*, *magnum* and *rotundum* are referred to *Tuerkayana* n. gen. (see above, under *Discoplax*, *Cardisoma*, and *Tuerkayana* n. gen.). In the following discussion, for an easier understanding we will however use the names as applied in the previous literature.

On the occasion of the erection of the new species *Discoplax celeste* from Christmas Island in the eastern Indian Ocean, Ng & Davie (2012), relying on the fact that the type material of *C. hirtipes* Dana, 1851 was no longer extant, selected as neotype a recently collected male specimen from Fiji (ZRC 2010.0415). This neotype designation might appear to be unwarranted, since Evans (1967: 410) had previously listed a syntype specimen of *C. hirtipes* Dana, 1851 in the NHM, with the catalogue number 1861.44. Ng & Clark (2014) made clear the available evidence that this NHM specimen was not a type of *C. hirtipes* (it was in fact *C. carnifex*), so that the specimen selected by Ng & Davie (2012) was eligible for neotype designation. But the recent discovery (Ng 2017) in the USNM of old boxes containing the dried type material of the land crabs *Cardisoma hirtipes* Dana, 1851 (and also of *C. obesum* Dana, 1851, see below) called everything into question. The original specimen, a male (47.4 × 58.2 mm) from Fiji collected during the U.S. Exploring Expedition (USNM 2356), displaces the neotype selected by Ng & Davie (2012) and becomes the name-bearing type, the lectotype, of C. *hirtipes* Dana, 1851. This lectotype (Ng 2017: figs 1-3) has roughly subequal homochelous male chelipeds (Ng 2017: fig. 3A, B), which does not conform with the strongly heterochelous chelipeds of some *hirtipes* that become very stout, with elongate fingers in largest adult males (Ng & Shih 2014: fig. 5, as *Discoplax*).

The problem we now face is knowing the identity of the crab that hides under the name *C. hirtipes* in the collections and literature. Ng & Shih (2014), who examined a considerable material, assumed that the *Cardisoma hirtipes* of Türkay (1974a: 229) actually recovered at least two species: the true *D. hirtipes* and a new species, *D. magna*, to which corresponded the fig. 12 of Türkay (1974a). The same difficulty arises when are examined the numerous *D. hirtipes* from various localities figured by Ng & Shih (2014: figs 5, 10: carapace and ventral surface): some are not conclusive enough, especially when *D. hirtipes* must be distinguished from *D. magna*; for example, the figures 5B and 10C of a male 87.4 × 68.3 mm from Angaur Island, Palau (fig. 5B: carapace seemingly without defined anterolateral margin; fig. 10C: pleonal somite 6 elongated; episternites triangular) apparently do not show the same species that those from other localities figured next. A key allowing a clear differentiation of these two close species (here *Tuerkayana hirtipes* n. comb. and *T. magnum* n. comb.) was unfortunately lacking.

In the list of the examined material of their *Discoplax hirtipes*, Ng & Shih (2014: 116) included a specimen from Loyalty Islands deposited in the MNHN, a male 61.0 × 79.0 mm, Lifou Island, We Cave, coll. Richer de Forges B, 14 July 1993, MNHN-IU-2017-8397 (= MNHN-B24811). The examination of this specimen (Fig. 4F) showed that the inflated carapace and the undefined carapace margins do not exactly conform to those of the lectotype of *Cardisoma hirtipes* (see Ng 2017: fig. 1A-C), which is smaller 47.4 × 58.2 mm. These differences may be attributed to the sizes of specimens, since most gecarcinids display significant morphological variations of carapace and chelipeds according to the growth: in large adults the carapace becomes proportionately more swollen and rounded, with less defined anterolateral margins, and the chelipeds are modified. The male specimen of Lifou is obviously different from *D. magna* (here *Tuerkayana magnum* n. comb.) from Java and Christmas Island with defined carapace margins that we have examined (Fig. 4E). For the moment we identify the specimen from Lifou as *Tuerkayana* aff. *hirtipes* n. comb. A further revision is required.

These specific identification problems do not affect the new generic taxonomy that is proposed concerning *Cardisoma*, *Discoplax* and *Tuerkayana* n. gen.

Cardisoma obesum Dana, 1851

A comment is in order about the type material of *Cardisoma obesum* Dana, 1851 (1851: 252; 1852: 376; 1855: pl. 24, fig. 1) recently found in the dried collection of the USNM (Ng 2017: figs 4, 5), a specimen 90.6 × 70.0 mm from Peacock Island (= Ahe Atoll), Tuamotu. This species is currently regarded as a junior subjective synonym of *Cardisoma carnifex* (Herbst, 1796) (see Türkay 1974a: 224). Ng (2017: 6) finally expressed some doubts about the identity *C. obesum* found in the USNM.

As for us, we do not suspect it is not the type material of Dana since the excavated and extremely extended area laterally to the orbit (Ng 2017: fig. 5) conforms to the figure of Dana (1855: fig. 1). This peculiar feature is not observed in the first subclade of gecarcinids including *Cardisoma*, *Discoplax* and *Tuerkayana* n. gen. and may at most look like the disposition found in *Gecarcoidea lalandii* H. Milne Edwards, 1837 (see Fig. 7H) of the second gecarcinid subclade; but the dome-shaped proepistome of the typical *obesum* is distinctive. The gecarcinid fauna of French Polynesia includes several species, all from the first gecarcinid subclade: *C. carnifex*, *Discoplax longipes*, *Tuerkayana rotundum* n. comb., perhaps *T. hirtipes* n. comb. (see discussion in Ng & Shih 2014: 125, as *Discoplax hirtipes*), and *Epigrapsus politus* (see Poupin 1994, 1996; Poupin & Juncker 2010; Bouchard *et al.* 2013). *Gecarcoidea lalandii* and other species from the second gecarcinid subclade have never been recorded from French Polynesia. In conclusion, the taxonomical status of *C. obesum* Dana, 1851 requires further researches.

Type material of *Cyclograpsus punctatus* H. Milne Edwards, 1837 (Cyclograpsinae)

The type series of *Cyclograpsus punctatus* H. Milne Edwards, 1837 consists of three syntypes in dry condition: 2 ♂ 27.9 × 34.1 mm, 29.0 × 37.5 mm, MNHN-B3368, and 1 ♀ 20.9 × 25.8 mm, MNHN-B3372, Indian Ocean, M. Reynaud coll. This material collected by Reynaud, a naturalist cited by H. Milne Edwards in the introduction of his "*Histoire*

naturelle" (1834: xxvii), is presumed to be the type series. As the number of specimens on which was based the description was not clearly specified in the original publication, it is possible that the nominal species-group taxon was based on more than one specimen. The male 27.9 × 34.1 mm in good condition designated as holotype by Campbell & Griffin (1966: 142) is here chosen as lectotype by inference of this holotype designation (*Code*, Art. 74.6). The lectotype keeps the original number MNHN-IU-2000-3368 (= MNHN-B3368), whereas the other male 29.0 × 37.5 mm of the type series becomes a paralectotype, with the new registration number MNHN-IU-2000-1116 (= MNHN-B3368). The syntype ♀ 20.9 × 25.8 mm, MNHN-IU-2000-3372 (= MNHN-B3372), also becomes a paralectotype.