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A new subfamily classification of the highly diversified Dorippidae H. Milne Edwards, 1837 (Crustacea, Decapoda, Brachyura, Dorippoidea), using morphological, molecular and palaeotonlogical data, with special emphasis on its unique female reproductive system

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Detail of colour print *The ghost of Taira Tomomori along with the anchor he drowned with, and heikegani with faces of fallen soldiers* by Utagawa Kuniyoshi in 1851 showing *Heikeopsis japonica* (von Siebold, 1824), the 'heike-gani' or 'samurai crab', during the naval battle at Dan-no-ura (1185) in Japan's Inland Sea.

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Dedicated to the memory of my colleague and dearest friend Ngan Kee NG (1966-2022)

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ABSTRACT

A new and revised classification of the small family Dorippidae H. Milne Edwards, 1837, which previously comprised two distinct subfamilies (Dorippinae H. Milne Edwards, 1837 and Ethusinae Guinot, 1977), each of which was subsequently elevated to a familial rank supported by traditional data and genetic phylogenies, is presented on the basis of a morphological analysis involving a large number of characters. The family is in fact highly diverse, at all levels. Several features are described and depicted in detail here for the first time, e.g. the presence of a diversely developed strip along the protrudingly rimmed posterior margin of the carapace; on the dorsally exposed thoracic sternite 8, a process acting as an additional pleonal-retention mechanism in the females of three genera (*Dorippe* Weber, 1795; *Philippidorippe* Chen, 1986; *Phyllodorippe* Manning & Holthuis, 1981); a callosity at the base of the coxa of the third pereiopod, variously shaped, in two genera (*Dorippe* and *Dorippoides* Serène & Romimohtarto, 1969). The generic and specific taxonomy masterfully stabilised by Holthuis & Manning (1991) is undisputed and still valid, except for the composition of the genus *Heikeopsis* Ng, Guinot & Davie, 2008 that may well contain in northern China a form not entirely consistent with the typical *Heikeopsis japonica* (von Siebold, 1824) of Japan. A second exception concerns the genus *Paradorippe* Serène & Romimohtarto, 1969 *sensu* Holthuis & Manning (1991) that may not be monophyletic. The validity of *Medorippe crosnieri* Chen, 1988, questioned by Holthuis & Manning (1990), could not be confirmed here: its distinctive morphological characters from *M. lanata* (Linnaeus, 1767) suggest that it could be recognised one day. The synthesis of conventional and new characters allows the traditional taxonomic approach to be updated and modernised, more complete and robust diagnoses to be constructed, and groups of genera to be circumscribed. We propose a new subfamily classification whereby the family Dorippidae is recognised as monophyletic but with seven genera assigned to subfamily-level rank, leading to the recognition of seven distinct subfamilies: the Dorippinae H. Milne Edwards, 1837 n. stat. (*Dorippe*), Dorippoidinae n. subfam. (*Dorippoides*), Medorippinae n. subfam.

(*Medorippe* Manning & Holthuis, 1981), Heikeopsinae n. subfam. (*Heikeopsis*, *Neodorippe* Serène & Romimohtarto, 1969, *Nobilum* Serène & Romimohtarto, 1969), Paradorippinae n. subfam. (*Paradorippe*), Philippidorippinae n. subfam. (*Philippidorippe*) and Phyllodorippinae n. subfam. (*Phyllodorippe*). There is a high degree of concordance between several elements of our proposal: 1) the main morphological patterns of the male gonopods lead to the recognition of seven subfamilies; 2) the main morphological patterns of the vulvae correspond to the seven observed gonopod types and lead to the recognition of the same seven subfamilies; 3) the recognition of several subfamilies is supported by the well-defined clades obtained by the molecular analyses; and 4) the female reproductive system, recently documented by histologists in most genera of Dorippidae, which differs from that of all other eubrachyurans studied so far, with an arrangement that undoubtedly represents a new type of organisation, unparalleled in the Brachyura Brünnich, 1772: it further shows unexpected diversity, with a degree of divergence similar to that of the gonopods and vulvae, in accordance with the subfamilies here recognised. A new interpretation of the two main grooves on the dorsal surface of the carapace is widely discussed. The authorship of the family-group name Dorippidae is here ascribed to H. Milne Edwards (1837). The study of Dorippidae is a particular example of how the integration of data from various fields, such as morphological and molecular phylogenetics, larval and post-larval features, behaviour and palaeontology, offers opportunities for reciprocal illumination. The early diversification of the family and its basal position among the Eubrachyura Saint Laurent, 1980 are supported not only by morphological traits but also by other characters, such as spermatozoal ultrastructure, carrying behaviour, forward locomotion and forward burying behaviour, all of which set the family apart from all other Eubrachyura. The substantial morphological variety of female reproductive systems within the Dorippidae, with the discovery in some species of external fertilisation sites, in contrast to the internal fertilisation that is assumed to define all eubrachyurans, challenges several previous ideas on the evolution of sperm storage in Eubrachyura and raises more questions than it answers. According to histologists, the arrangement of the Dorippidae suggests that the family could be sister to a clade including the Heterotremata Guinot, 1977 and the Thoracotremata Guinot, 1977. Two keys to the subfamilies, one based on gonopods and vulvae, the second based on other morphological characters, are provided. The taxonomy, including extant and fossil forms, is accompanied by justifications for the arrangement we propose. The Dorippidae proves to be a special lineage within the Eubrachyura: its diverse and unique features are discussed. The dorippids in legend and myth are the subject of Appendix 1. Fossil Dorippidae and Ethusidae Guinot, 1977 are reviewed, as well as the two extinct dorippoid families (Telamonocarcinidae Larghi, 2004; Tepexicarcinidae Luque, 2015), and also fossil families that were at one time considered to belong to the Dorippoidea, such as Goniochelidae Schweitzer & Feldmann, 2011 (see Appendix 2).

KEY WORDS
New characters,
new diagnoses,
identification keys,
carapace grooves,
female reproductive system,
molecular analysis,
fossil taxa,
Ethusidae,
samurai crab,
new status,
new subfamilies.

RÉSUMÉ

Une nouvelle classification subfamiliale de la famille hautement diversifiée des Dorippidae H. Milne Edwards, 1837 (Crustacea, Decapoda, Brachyura, Dorippoidea), fondée sur des données morphologiques, moléculaires et paléontologiques, et plus particulièrement sur le système unique de reproduction chez les femelles.
Une classification nouvelle et révisée de la petite famille des Dorippidae H. Milne Edwards, 1837, qui comprenait auparavant deux sous-familles distinctes (Dorippinae H. Milne Edwards, 1837 et Ethusinae Guinot, 1977), chacune ayant été élevée ensuite au rang de famille soutenu par les données traditionnelles et la phylogénie moléculaire, est présentée sur la base d'une analyse morphologique impliquant un grand nombre de caractères. De fait, la famille s'est révélée hautement diversifiée, et ce à tous les niveaux. Plusieurs caractères sont ici décrits et représentés en détail pour la première fois, comme par exemple la présence d'un rebord diversement développé le long du bord postérieur proéminent de la carapace ; sur le sternite 8 dorsalement exposé, un prolongement agissant comme un mécanisme additionnel de rétention du pléon chez la femelle de trois genres (*Dorippe* Weber, 1795; *Philippidorippe* Chen, 1986; *Phyllodorippe* Manning & Holthuis, 1981) ; une callosité à la base de la coxa du troisième péréiopode, de formes différentes, chez deux genres (*Dorippe* et *Dorippoides* Serène & Romimohtarto, 1969). La taxonomie générique et spécifique magistralement stabilisée par Holthuis & Manning (1991) est incontestée et toujours valide, sauf dans le cas de la composition du genre *Heikeopsis* Ng, Guinot & Davie, 2008, qui pourrait bien contenir dans le nord de la Chine une forme ne correspondant pas entièrement au *H. japonica* (von Siebold, 1824) typique du Japon. Une deuxième exception concerne le genre *Paradorippe* Serène & Romimohtarto, 1969 *sensu* Holthuis & Manning (1991) qui pourrait ne pas être monophylétique. Quant à *Medorippe crosnieri* Chen, 1988, dont la validité mise en doute par Holthuis & Manning (1991) n'a pu être vérifiée, ses caractères morphologiques distinctifs de *M. lanata* (Linnaeus, 1767) laissent à penser qu'elle sera reconnue un jour. La synthèse des caractères conventionnels et nouveaux permet d'actualiser et de moderniser l'approche taxonomique traditionnelle, de construire des diagnoses plus complètes et plus robustes, et de circonscrire des groupes de genres. Nous proposons une nouvelle classification sous-familiale, selon laquelle la famille des Dorippidae est reconnue monophylétique mais avec

sept genres assignés à un rang sous-familial, conduisant à la reconnaissance de sept sous-familles distinctes : les Dorippinae H. Milne Edwards, 1837 n. stat. (*Dorippe*), Dorippoidinae n. sous-fam. (*Dorippoides*), Medorippinae n. sous-fam. (*Medorippe* Manning & Holthuis, 1981), Heikeopsinae n. sous-fam. (*Heikeopsis* Ng, Guinot & Davie, 2008, *Neodorippe* Serène & Romimohtarto, 1969, *Nobilum* Serène & Romimohtarto, 1969), Paradorippinae n. sous-fam. (*Paradorippe*), Philippidorippinae n. sous-fam. (*Philippidorippe*) et Phyllodorippinae n. sous-fam. (*Phyllodorippe*). Il y a un haut degré de concordance entre plusieurs éléments de notre proposition : 1) les principaux patrons morphologiques des gonopodes mâles conduisent à la reconnaissance de sept sous-familles ; 2) les principaux patrons morphologiques des vulves correspondent aux sept types de gonopodes observés et conduisent à la reconnaissance des mêmes sept sous-familles ; 3) la reconnaissance de plusieurs sous-familles est soutenue par les clades bien définis obtenus par les analyses moléculaires ; 4) l'appareil reproducteur femelle, récemment documenté par les histologistes chez la plupart des genres de Dorippidae diffère de celui de tous les autres eubrachyoures étudiés jusqu'à présent, avec une disposition qui représente sans aucun doute un nouveau type d'organisation, sans équivalent chez les Brachyura Brünnich, 1772 : de plus, il montre une diversité inattendue, avec un degré de divergence similaire à celui des gonopodes et des vulves, en accord avec les sous-familles ici reconnues. Une nouvelle interprétation des deux principaux sillons de la face dorsale de la carapace est largement discutée. La paternité du nom de groupe famille Dorippidae est attribuée à H. Milne Edwards (1837). L'étude des Dorippidae est un exemple particulier de la façon dont l'intégration des données provenant de divers domaines, tels que la phylogénie morphologique et moléculaire, les caractéristiques larvaires et post-larvaires, le comportement et les données paléontologiques, offre des perspectives d'illumination réciproque. La diversification précoce de la famille et sa position basale parmi les Eubrachyura Saint Laurent, 1980 sont soutenues non seulement par des traits morphologiques mais aussi par d'autres caractères, comme l'ultrastructure du sperme, le comportement de portage, ainsi que la locomotion et l'enfouissement vers l'avant, qui placent la famille à part de tous les autres Eubrachyura. L'importante variété morphologique des systèmes reproducteurs femelles au sein des Dorippidae, avec la découverte chez certaines espèces de sites de fertilisation externe, en contradiction avec la fertilisation interne qui est supposée définir tous les eubrachyoures, remet en question plusieurs idées antérieures sur l'évolution du stockage des spermatozoïdes chez les Eubrachyura et soulève plus de questions qu'elle n'apporte de réponses. Selon les histologistes, la disposition des Dorippidae suggère que la famille pourrait être le groupe frère d'un clade comprenant les Heterotremata Guinot, 1977 et les Thoracotremata Guinot, 1977. Deux clés pour les sous-familles, l'une basée sur les gonopodes et les vulves, la seconde basée sur les autres caractères morphologiques, sont fournies. La taxonomie, incluant les formes actuelles et fossiles, est accompagnée de justifications pour l'arrangement en sous-familles que nous proposons. La famille des Dorippidae s'avère comme une lignée particulière au sein des Eubrachyura, et ses caractéristiques diverses et uniques sont discutées. Les dorippides dans la légende et le mythe font l'objet de l'Annexe 1. Sont passés en revue les Dorippidae et les Ethusidae Guinot, 1977 fossiles, les deux familles éteintes de Dorippoidea (Telamonocarcinidae Larghi, 2004 ; Tepexicarcinidae Luque, 2015), ainsi que les familles fossiles ayant été à un moment donné considérées comme appartenant aux Dorippoidea, comme par exemple les Goniochelidae Schweitzer & Feldmann, 2011 (voir l'Annexe 2).

MOTS CLÉS
Caractères nouveaux,
diagnoses nouvelles,
clefs d'identification,
sillons de la carapace,
système reproducteur femelle,
analyse moléculaire,
taxons fossiles,
Ethusidae,
crabe des samouraï,
statut nouveau,
sous-familles nouvelles.

INTRODUCTION

With the renewed interest in the phylogeny of the Brachyura Latreille, 1802, a consensus on the phylogenetic position of Dorippidae H. Milne Edwards, 1837 began to emerge among morphologists and molecular systematists. The confusion between the podotreme Cyclodorippidae Ortmann, 1892 and the Dorippoidea H. Milne Edwards, 1837 (Eubrachyura Saint Laurent, 1980), still pursued by neontologists in the recent past, has been facilitated by their many similarities: carapace structure with a human 'face' delineated on the dorsal surface by unique grooves; reduction of the branchiostegite; respiratory modifications of the mouthparts (the oxystomatous condition) and unique afferent branchial orifices; first pleonal somites on the same level as the dorsal carapace; albeit distinctive, pleonal-locking system generally present; reduction and dorsal position of the last two pereiopods; and carrying behaviour.

It should be noted that the Dorippidae was in fact the starting point for the distinction between coxal and sternal female gonopores in the Brachyura, an issue that deserves comment. It is actually in relation to the Dorippidae that Bouvier (Bouvier 1897a: 786; 1897b: 56, 57; 1898: 104; see also A. Milne-Edwards & Bouvier 1902: 71) introduced the terms *péditrème* and *sternitrème*, emphasising the major difference within this family that at that time included species with both female and male coxal gonopores (being in fact the Cyclodorippidae, which are now treated as podotreme crabs) and those with female sternal gonopores (vulvae) corresponding in fact to the family Dorippidae (and that of Palicidae

Bouvier, 1898). It was not until Gordon (1963: 55; 1966: 353) that all 'peditremen' were excluded from Brachyura and only 'sternitremen' were considered true brachyurans. Guinot (1977: 1049) showed the distinction between the podotreme crabs and all other crabs, and formally established a new section, the Podotremata Guinot, 1977 (Guinot *et al.* 2013: 96; 1978: 216, fig. 1, table p. 214). A heterotreme position for the Dorippidae was unequivocally supported by the sperm ultrastructure investigated in an Australian dorippid from Queensland (Jamieson & Tudge 1990, 2000).

Previously, the Dorippidae comprised two distinct subfamilies, Dorippinae (traditionally with MacLeay, 1838 as the authorship, here corrected to H. Milne Edwards, 1837, see below) and Ethusinae Guinot, 1977, still clearly distinguished by Castro (2005) under this rank but in fact distinctive enough to warrant a family level (Guinot *et al.* 2013). The recognition of the family Dorippidae has been successfully implemented, after the rejection of the section Oxystomata H. Milne Edwards, 1837, thanks to its elevation to the suprafamilial rank Dorippoidea (Guinot 1978: 245) and the proposal of a new classification scheme for Brachyura that excluded from Dorippoidea all crabs with coxal female gonopores (Guinot 1977, 1978, 1979a, b). Following a pioneering study by Serène & Romimohtarto (1969) dividing the Indo-Pacific *Dorippe* Weber, 1795 into several new genera and subgenera, the major revision of Holthuis & Manning (1990, as Dorippinae), albeit still at the subfamily level, stabilised the taxonomy of the group (Davie *et al.* 2015b: 945; 2015c: 1076). The evidence for family status within the crown group Dorippoidea, exclusively composed of two families in the living fauna, was well reflected in the classification of Ng *et al.* (2008).

The Dorippidae is a quite small family, with a total of only nine genera, as recognised by Holthuis & Manning (1990, as Dorippinae), and is represented by only 21 living species, including some doubtful ones, and thus belongs in the tree of life to the groups without substantial species richness. Three genera (*Nobilum* Serène & Romimohtarto, 1969, *Philippidorippe* Chen, 1986, *Phyllodorippe* Manning & Holthuis, 1981) are monospecific, whereas *Medorippe* could include a second species, *M. crosnieri* Chen, 1988, which is close to the type species *M. lanata* (Linnaeus, 1767) (see *Remarks about the validity of* Medorippe crosnieri *Chen, 1988*). Three genera (*Dorippoides* Serène & Romimohtarto, 1969, *Heikeopsis* Ng, Guinot & Davie, 2008, and *Neodorippe* Serène & Romimohtarto, 1969) are represented by only two species (but see below the Remarks paragraph under the genus *Heikeopsis*). *Dorippe* and *Paradorippe* Serène & Romimohtarto, 1969 comprise seven and four species, respectively. Only three new species have been described since 1990: two in the genus *Dorippe*, *D. glabra* Manning, 1993 and *D. trilobata* Manning, 1993, both never found since their description (see the remarks on their respective status), and one in the genus *Neodorippe* (*N. simplex* Ng & Rahayu, 2002).

As we agree with Holthuis & Manning's (1990) reassessment of the taxonomy and new nomenclature, supported further by many excellent drawings, we will not repeat here the synonyms of each genus and species and will only build new emended descriptions by adding new characters. There are, however, several problems. The first problem is the composition of the complex genus *Heikeopsis* (as *Heikea* Holthuis & Manning, 1990): the type species *H. japonica* would indeed be widespread outside Japan, but northern China is supposed to harbour a different form whose status is difficult to interpret, see *Status of non-Japanese* Heikeopsis japonica, H. taiwanensis *(Serène & Romimohtarto, 1969), and* H. arachnoides *(Manning & Holthuis, 1986): a major problem*. A second problem concerns the genus *Paradorippe*, which seems to recover two distinct entities, thus perhaps a new genus needs to be established after due comparisons of the four species allocated to it: we were only able to examine the type species, *P. granulata* (De Haan, 1841) and to check with some difficulty the identity of the species in the literature (see see *Preliminary note*, p. 279). A third problem concerns the validity of *M. crosnieri* Chen, 1988, questioned by Holthuis & Manning (1990), which future research should well confirm, see *Remarks about the validity of* Medorippe crosnieri *Chen, 1988*. Lastly, the validity of some poorly known species of *Dorippe*, including those described by Manning & Holthuis (1986) and some added by Manning (1993), needs to be examined (see below under the genus *Dorippe*).

Dorippids are characterised by striking similarities: long second and third pereiopods, last two pereiopods reduced and carried dorsally, a generalised carrying behaviour (Guinot & Wicksten 2015), a forward locomotion and a partial burying, also forward, well shown by *in situ* live videos. They show a similar general facies, with a comparable pattern of main grooves on the dorsal surface of the carapace that draws a strange 'human face' (Fig. 1). This resemblance has inspired legends and myths in Japan, in particular the best known tale of the 'samurai crabs' known as 'heike-gani', the crabs of the Japanese feudal family Heike. The deceased spirits of the Heike samurai heroes annihilated at Dan-no-ura, in the Inland Sea of Japan, Yamaguchi Prefecture, during a desperate naval battle in 1185, appeared in the guise of crabs, inspiring magnificent paintings by the famous painter Utagawa Kuniyoshi, the last great master of Japanese woodblock print and painting. In one painting, some crabs recognisable by their paddle-like last legs are portunid swimming crabs. Another one (Figs 2; 39) shows crabs with human face and reduced last two legs carried on the back: they are undoubtedly Dorippidae and the true Heike-gani, namely a barely stylised *Heikeopsis japonica* (von Siebold, 1824), the emblematic 'samurai crab' common in this area (Fig. 1). In many countries, particularly in Asia, dorippids have vernacular names that allude to the crabs' resemblance to a human face (see Appendix 1).

Dorippids are mostly tropical or subtropical in distribution, and are totally absent from the New World (at least in the living fauna), occurring throughout the Indo-West Pacific, from the East African coast (Red Sea, South Africa and Madagascar) to Japan, and Australia, but do not reach Polynesia or New Zealand. Two species inhabit the eastern Atlantic, along the West African coast to South Africa, with *Medorippe lanata* (Linnaeus, 1767) also occurring in the Mediterranean Sea,

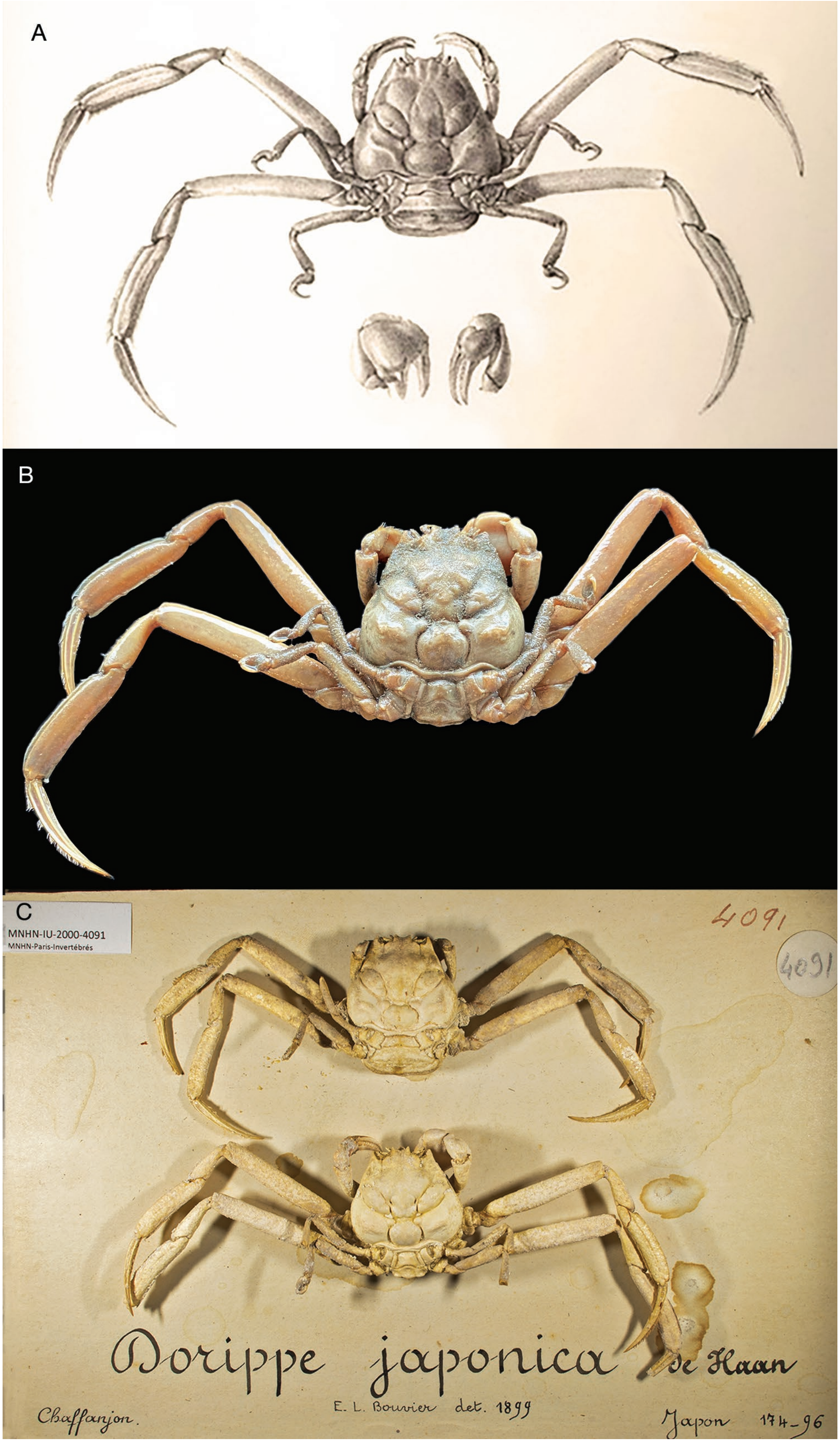

FIG. 1. — A typical dorippid crab, *Heikeopsis japonica* (von Siebold, 1824), the iconic 'samurai crab' known in Japan as 'heike-gani', whose carapace looks like a human face: **A**, the species represented by De Haan (1839: pl. 31, fig. 1, as *Dorippe japonica*) in *Fauna Japonica*: *top,* a female; *below*, chelae of a male; **B**, lectotype selected by Yamaguchi & Baba (1993: 300, fig. 90-A.a-2, as *Heikea japonica*) from type series material labelled "Types, Japan, 1823, Leg. P. H. von Siebold", RMNH CRUS D 822 (see Fransen *et al.* 1997: 83); **C**, ♂ 25.0 × 27.3 mm, ♀ 23.5 × 26.7 mm, Japan, Chaffanjon, 174-96, E.-L. Bouvier det. 1899 *Dorippe japonica*, dry condition, MNHN-IU-2000-4091 (= MNHN-B4091).

Fig. 2. — Colour print by Utagawa Kuniyoshi in 1851: *The ghost of Taira Tomomori along with the anchor he drowned with, and heikegani with faces of fallen soldiers*; **A**, *Heikeopsis japonica* (von Siebold, 1824), the 'heike-gani' or 'samurai crab', during the naval battle at Dan-no-ura (1185) in Japan's Inland Sea; **B**, close-up view of the crabs, easily recognisable by their carapaces bearing like a human face, their last two legs, reduced and carried dorsally, and the dorsally visible pleon (See also Fig. 39).

where the Lessespian species *Dorippe quadridens* (Fabricius, 1793) has been introduced from the Red Sea; and *Phyllodorippe armata* (Miers, 1881), exclusively West African. Most dorippid species occur on soft sediments, sand or mud, in shallow coastal waters and on the continental shelf depths, with the exception of *Philippidorippe philippinensis* Chen, 1986, endemic to the seas around the Philippines, which lives in slightly deeper waters.

The incomplete folding of the pleon in all dorippid species is probably one of the most important characters found in basal Brachyura: it corresponds to a strong posterior curvature of the thoracic sternum, that is, a modification of

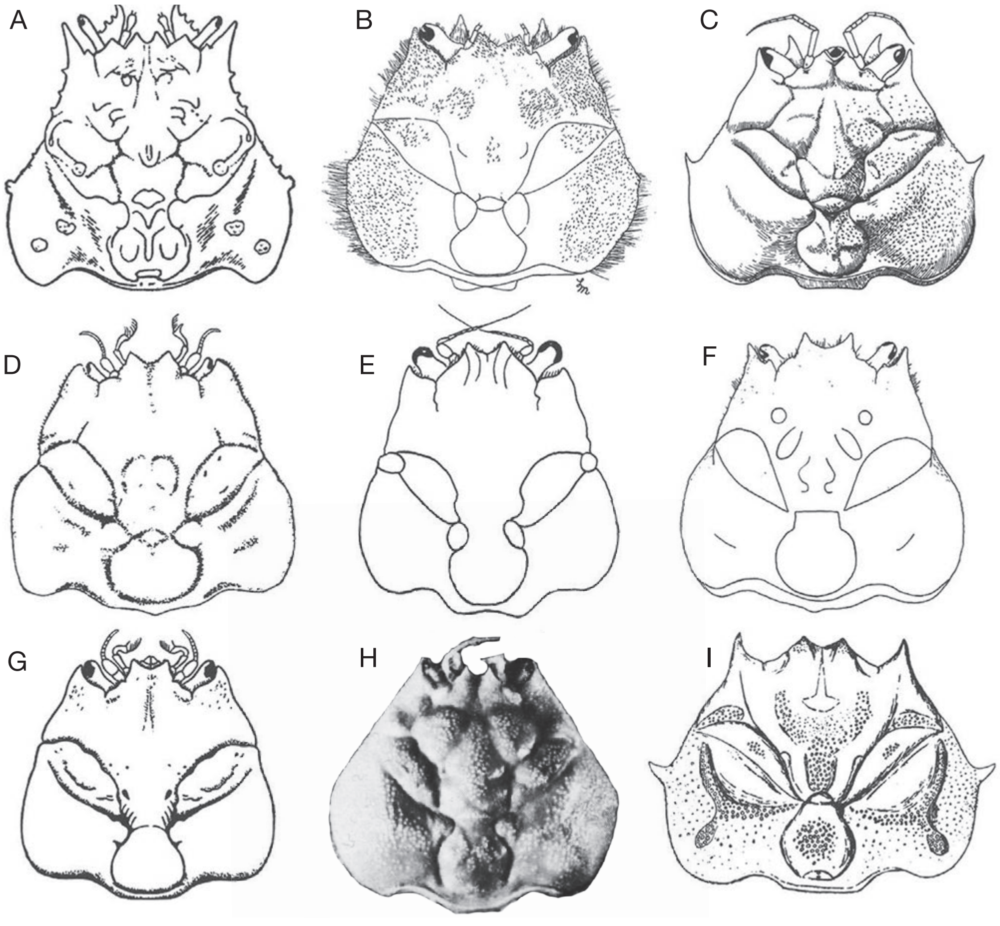

Fig. 3. — Carapace diversity in the nine dorippid genera: **A**, *Dorippe* Weber, 1795 (*D. quadridens*); **B**, *Dorippoides* Serène & Romimohtarto, 1969 (*D. facchino*); **C**, *Medorippe* Manning & Holthuis, 1981 (?*M. crosnieri*); **D**, *Heikeopsis* Ng, Guinot & Davie, 2008 (*H.* aff. *japonica*); **E**, *Neodorippe* Serène & Romimohtarto, 1969 (*N. callida*); **F**, *Nobilum* Serène & Romimohtarto, 1969 (*N. histrio*); **G**, *Paradorippe* Serène & Romimohtarto, 1969 (*P. cathayana*); **H**, *Philippidorippe* Chen, 1986 (*P. philippinensis*); **I**, *Phyllodorippe* Manning & Holthuis, 1981 (*P. armata*). **A**-**G**, **I**: modified from Sin *et al.* (2009: fig. 3); **H**, from Chen (1986: pl. 1, fig. 3). The strip, which is shown here only in *Dorippoides facchino* (Herbst, 1785) and *Medorippe* ?*crosnieri* Chen, 1988, is in fact present in all species of dorippids.

the alignment of the arthrodial cavities of the pereiopods. Such a change induces here a dorsal location of P4 and P5 as well as an elongated G1 protopodite generating a long penial structure. Dorippids are (together with ethusids) the only extant eubrachyurans to perform a carrying behaviour using the last two pereiopods, palicids only using the last one. A sternum/pterygostome junction involving sternite 3 (Figs 4; 7C) is a unique arrangement that affects the inhalant entrances for water passing into the branchial chamber. The afferent branchial orifices (Milne Edwards openings) appear as ovate, elongated slits in the pterygostome and separated from the chelipeds, which is also a unique organisation (Fig. 7C) (H. Milne Edwards 1834, Atlas, pl. 20, fig. 12; Ihle 1916: fig. 45; Guinot *et al.* 2013: fig. 42C; Davie *et al.* 2015a: 41, fig. 71-2.14A).

It should be noted that the thoracic sternum has never been studied or depicted (only partially seen in figures showing the vulvae) in any dorippid, except for a sketch of *Medorippe lanata* (Guinot 1979a: fig. 28, as *Dorippe lanata*; reproduced by Davie *et al.* 2015a: fig. 71-2.18A) and a photograph of the ventral surface of *Dorippe quadridens* by Takeda *et al.* (2019: pl. 3, fig. F). The thoracic sternum of Ethusidae Guinot, 1977, to our knowledge, has only rarely been represented (e.g. by photographs in Rathbun 1937: pls 23, 25, 29; Hendrickx 1989: pl. 1b, d; Spiridonov & Türkay 2007: figs 3b, d, f, 9b, f; Guinot *et al.* 2013: fig. 42A; Ocampo *et al.* 2014: fig. 1d); some partial sketches are in Guinot *et al.* (2013) and Vehof (2020: fig. 4A, C).

Apparently, the carapace of dorippids varies little in outline (Fig. 3) and presents a rather uniform pattern of main grooves that are the same whether the dorsal carapace is weakly areolated – in which case they are almost the only ones present – or whether it is quite heavily sculptured. The dorsal surface allows the Dorippidae to be roughly divided into two groups: an uneven surface bearing small or strong tubercles, several grooves, and a cardiac region with a distinct V- or Y-shaped ridge (*Dorippe*, *Medorippe*) (Figs 3A, C; 5A, B); only two deep main grooves, rounded branchial lobes and a cardiac region without ridge (*Dorippoides*, *Heikeopsis*, *Neodorippe*, *Nobilum*, *Paradorippe*, *Philippidorippe*, *Phyllodorippe*) (Fig. 3B, D-I).

Although more or less marked depending on the genera, the groove pattern, which is somewhat reminiscent of that of basal crabs, poses a problem of homology in relation to that of podotremes and other Eubrachyura, and its interpretation is

TABLE 1. — Comparison of main characters between Dorippidae H. Milne Edwards, 1837 and Ethusidae Guinot, 1977. Abbreviations: see Material and methods.

	Dorippidae	**Ethusidae**
Carapace	usually subovate, broader than long, with posterior part widest; sometimes longer than broad	often longitudinally subrectangular, subtriangular or pear-shaped, longer than broad
Posterior rim	thick, protruding may extend to varying degrees along the posterolateral margins	sometimes quite wide but very low, barely demarcated and not extending laterally
Strip	always present	no strip (to be checked)
Dorsal surface of carapace	smooth to granular	smooth, rarely densely or coarsely granular
Precervical and cervical grooves	deep, well marked 'human face' often well-delineated	usually faint and shallow
Thoracic sternum/pterygostome	junction	no junction
Milne Edwards openings	narrow, separated from chelipeds, as pterygostomial slits	circular or oval, contiguous to chelipeds
Mxp3	with epipodite not occluding Milne Edwards opening; exopodite without flagellum	with epipodite completely occluding Milne Edwards opening; exopodite with multiarticulated flagellum
Thoracic suture 5/6	strongly concave, with press-button in a curve	weakly concave or straight
Male pleon	more or less triangular, sometimes with distinct teeth on somites 2-4; six somites free, plus telson	usually narrow and with nearly parallel sides, rarely wide; four somites, plus telson (somites 3-5 fused)
P4, P5 (reduced, carried dorsally)	with chelate mechanism	with only strongly recurved ending
G1	extremely diverse, variously shaped, ending in two or numerous lobes or processes (see *Key to dorippid subfamilies based on G1 and vulva*)	simple, slender to slightly stout, straight or curved, rarely conspicuously bent, without multiple distal lobes or processes
G2	short	as long as or longer than G1
Coxo-sternal condition	multistate characters	probably a single modality

a challenge (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae*).

Guinot & Bouchard (1998: figs 15C, D, 16) have highlighted the most striking and often unique characteristics of the dorippids, as follows: thoracic sternum (Fig. 4) in the form of a very wide plate, especially at level of somite 5; all sutures 4/5-7/8 interrupted; episternites very small and delimited; sterno-pleonal cavity fairly deep; male pleon in a posterior position, of variable in length, the tip of telson slightly or clearly extending beyond suture 5/6; press-button typical, as an acute, hooked protuberance constantly lodged in a curve (variously pronounced) of sternal suture 5/6 (dorippid synapomorphy); pleonal sockets deep, providing together with press-button an efficient pleonal-locking mechanism; persistence of acute buttons and defined sockets in postpubertal females, with the locking remaining functional even in ovigerous females of some species; locking protuberances located very close to vulvae (Fig. 4B). In addition, the female pleon can be maintained in species of certain genera by two other devices, the most remarkable being a process of sternite 8 that overhangs the second pleonal somite (Figs 8C; 9C).

Dorippoidea is recovered as monophyletic, morphologically and genetically (Tsang *et al.* 2014), but it is important to recall the main differences between the Dorippidae and Ethusidae, based on extant species (Table 1). In contrast to the Dorippidae, the Ethusidae is a large family of about 80 species, mainly from tropical and subtropical waters of all major ocean basins, and which rarely inhabit waters shallower than 100 m and prefer deep waters, up to more than 5000 m. Ethusidae comprises four Recent genera: *Ethusa* Roux, 1830, *Ethusina* Smith, 1884, *Parethusa* Chen, 1997 and *Serpenthusa* Naruse, Castro & Ng, 2009 (Naruse *et al.* 2009). Both families are oxystomatous and have sternal extensions between the pereiopods (for more details, see Castro 2005; Guinot *et al.* 2013; Naruse *et al.* 2009; Castro 2020; present paper, see *Table 1*, *Palaeontological data* and *Appendix 2*).

The monophyly of the dorippids is supported by morphological features (Guinot *et al.* 2013; Davie *et al.* 2015b, c), larval and post-larval data (Rice 1980, 1981, 1983; Quintana 1987), behavioural traits, particularly carrying behaviour (Guinot & Wicksten 2015) combined with forward burying, and molecular analyses (Ahyong *et al.* 2007; Sin *et al.* 2009; Chu *et al.* 2015).

Despite the similarities mentioned above, the Dorippidae is highly diversified and constitutes fascinating model of complexity. The discrepancies revealed by the first gonopod morphology between the genera, already widely reported by Serène & Romimohtarto (1969), were highlighted by the key based on this single trait by Holthuis & Manning (1990: 6, as Dorippinae), and their diversity well illustrated by the summary figure of Sin *et al.* (2009: fig. 4) (Fig. 31). The extreme diversity of the Dorippidae is also evidenced by the disposition of the male genital, penial region. The Dorippidae, previously diagnosed by carcinologists as having male gonopores either coxal (Ortmann 1901: 1157, Dorippinae *pro parte*; Alcock 1896: 273, Dorippinae *pro parte*; Bouvier 1940: 195; Barnard 1950: 387) or sternal (De Haan 1841: 120; 1849: xvii; Miers 1886: 326; Alcock 1896: 273, Dorippinae *pro*

Fig. 4. — Dorippid thoracic sternum exemplified here by *Medorippe lanata* (Linnaeus, 1767), Mediterranean Sea, dehydrated specimens for skeletal preparation by Sylvie Secretan (MNHN): **A**, ♂; **B**, ♀. Abbreviations: **b.p.**, press-button located in curved sternal suture 5/6; **cx4**, P4 coxa: **e**, episternite; **G1**, **G2**, first and second gonopods; **j**, sternum/pterygostome junction; **m**, membrane; **m.o.**, Milne Edwards opening as pterygostomial slit; **p**, perforation at the end of sternal suture 3/4; **r**, sternal ridge; **s.p.**, sternal prominence; **v**, vulva; 1-8, thoracic sternites 1-8; 2/3-7/8, sternal sutures 2/3-7/8. Photographs by Barry van Bakel.

parte; Balss 1957: 1608, 1610, Dorippinae; Glaessner 1969: R492, Dorippinae *pro parte*), actually shows a perforation of the P5 coxa by the male ejaculatory duct, and therefore has coxal gonopores. Nevertheless, the family does display a transformation series of the penial condition, from a nearly coxal condition in *Medorippe lanata* to a variously developed coxo-sternal condition in other species (Guinot 1978: 244; 1979b: 45, fig. 2A; Guinot & Bouchard 1998: fig. 16; Guinot *et al.* 2013: figs 15-19; Davie *et al.* 2015a: fig. 71-2.19H). In contrast, the Ethusidae exclusively shows a complete and fully advanced coxo-sternal condition (Guinot 1979b: figs 2B3, 3; Guinot *et al.* 2013: figs 20-22).

Very often, in Eubrachyura the lack of data on female genitalia severely limits our understanding of genital evolution. The morphology of dorippid vulvae (Fig. 32) also reveals a high degree of variability (Holthuis & Manning 1990, as Dorippinae; this paper) and allows the hypothesis that this diversification reflects a coevolution between male and female external genitalia, which probably contributed to the rapid divergent evolution of the family.

Closer examination shows that other fundamental structures, independent of size or sex, differ greatly from one genus to another: the antennule, antenna, endostome disposition, thoracic sternum, male pleon, male genital area, vulva, and female reproductive system. The antennule and antenna are closely situated in the same single fossa, only separated from the eyestalk by the basal antennal article, which is more or less mobile. The morphology of the cephalic appendages, which was studied in *Dorippe quadridens* by Ihle (1916: figs 41, 45, as *Dorippe dorsipes* (Linnaeus, 1764)), displays several valuable patterns in dorippids, but its taxonomic usefulness has not been considered by most authors, including Holthuis & Manning (1990). On closer examination, even the shape of the carapaces is diverse (Fig. 3). All these features prove to be subfamilial diagnostic characters.

The variability of morphological features in the Dorippidae is also reflected in the female reproductive system, which has recently been studied in many species by several histologists (Hayer *et al.* 2016a; Vehof *et al.* 2017, 2018a, b; Vehof 2020). This new area of investigation highlights that the organisation is far from uniform in the family and, moreover, challenges prevailing and conventional ideas about the evolution of reproduction in Eubrachyura, which is a major finding. Histological and micro-computed-tomographic analyses revealed at least a 'novel type' of sperm storage organ with different modalities, implying in some cases external rather than internal fertilisation and supporting the family as a putatively early-diverging lineage of eubrachyurans. Although a vulva opens on the 6th thoracic somite as in other eubrachyurans, the question arises to as to how far the dorippid condition actually corresponds to a plesiomorphic state. An obvious similarity to what exists in podotreme crabs naturally raises the question of how the dorippid arrangement might be evolutionarily related to the podotreme intersegmental spermathecae. In any case, it will be of interest to test whether the character transformation series observed in dorippid female reproductive systems is congruent with the transformation series of other morphological characters. The different arrangements exhibited by the Dorippidae are reviewed here since only a reliable assessment of the high degree of variability encountered within the family in this area will allow us to consolidate the separation of the Dorippidae into subfamilies in accordance with those established on the basis of more usual morphological characters. For comparison, we present a brief survey of the reproductive systems in other Brachyura. We refute the assertion of Kienbaum *et al.* (2018b) that Guinot *et al.* (2013) used parallel trends in evolutionary transformation as 'proper characters'. Like von Sternberg (1996), we quote this sentence of Mayr (1988: 435): "In many, if not most, phyletic lines there is an indication of trends […]. It is now quite obvious that such trends are the necessary consequence of the unity of genotype which greatly constrains evolutionary potential".

A molecular analysis by Ahyong *et al.* (2007: 583, figs 2, 4) recovered *Dorippoides facchino* (Herbst, 1785) as a sister taxon to the freshwater hymenosomatoid *Amarinus lacustris* (Chilton, 1882), and indicated a dorippid + hymenosomatid clade within the Heterotremata Guinot, 1977, with the large clade majoids-hymenosomatids-dorippoids lying as sister to the remainder of Eubrachyura. Teske *et al.* (2009: 29, 31, figs 3, 4) combined sequence data of the hymenosomatids with previously published brachyuran sequences (including representatives from several major brachyuran families) of Porter *et al.* (2005: fig. 2, table 1) using 16S mtDNA, 18S and 28S rRNA, and the histone H3 gene. The conclusion of Teske *et al.* (2009) that the Hymenosomatidae MacLeay, 1838 ('secondary freshwater' crabs, with exclusively freshwater species reproducing by direct development, see Ng & Chuang 1996, and, on the contrary, those from the marine stock with three zoeal stages that are not followed by a typical megalopa) is not part of the Majoidea Samouelle, 1819, must be considered preliminary. Significantly, their results strongly support a sister-taxon relationship of the Hymensomatidae with a primary freshwater crab, *Geothelphusa* sp. (Potamidae Ortmann, 1895, Potamiscinae Bott, 1970) (from the data inferred by Porter *et al.* 2005: fig. 2, table 1; see also Bracken *et al.* 2009: table 1).

A phylogeny inferred from nuclear protein-coding genes by Chu *et al.* (2009b: figs 1, 3) suggested a basal position of the Dorippidae, clustering with the Majoidea. Such a position contrasted with a larger multigene study by Tsang *et al.* (2014) that returned Dorippidae as sister to Leucosiidae Samouelle, 1819, at some distance from Majidae Samouelle, 1819. The basal position of Dorippidae, long based on morphology (Guinot 1978; Guinot *et al.* 2008, 2013, 2019), is recognised by the latest molecular phylogenetic analyses (Chu *et al.* 2015; see also Chu *et al.* 2009a), which place the family among the most basal heterotremes (see also Bracken *et al.* 2009). However, this basal position is not supported by the genetic results obtained by Wolfe *et al.* (2022, pers. comm.), which tend to show relationships between Dorippidae and Leucosiidae, which has not yet been documented by morphology.

Links could be inferred from: the female reproductive system (with the seminal receptacles of Dorippoidea being the most basal state known, that of Leucosiidae could be the 'missing link' between Dorippoidea and other eubrachyuran families, see Hayer *et al.* 2017: 280); from the 'advanced larva' in both families, and also in Hymenosomatidae and Pinnotheridae De Haan, 1833, these specialised larval stages being considered representing "end-points of Brachyuran evolution stages" (Rice 1980: 358). All these results may call into question the validity of our research findings, but, in our view, this is due to the fact that both Hymenosomatoidea MacLeay, 1838 and Dorippoidea are the oldest of the divergent lineages within the Heterotremata (see *Discussion*, p. 327), making interpretation difficult and even distorting it.

Analysis of phylogenetic relationships using DNA sequence data from 10 of the 13 known dorippid genera (Sin *et al.* 2009: fig. 1) revealed a robust framework where each genus forms a distinct and strongly supported clade, complementing preliminary results based on four Chinese genera (Fan *et al.* 2004). The partial COI sequence from a Japanese specimen of *Paradorippe granulata* is also noteworthy (Yamada & Watanabe 2012). The very high sequence divergences between the two dorippoid families Dorippidae and Ethusidae testify to their deep separation in evolutionary history (Sin *et al.* 2009; Chu *et al.* 2015). To test the correlation between morphological characters and molecular divergences, a new analysis of publicly available sequences was attempted (see *DNA Evidence,* page 328 and Fig. 38).

As highlighted above, within the Brachyura that appears to be a hot-spot of gene order diversity within the phylum Arthropoda (Basso *et al.* 2017), the Dorippidae exhibits extreme underlying morphological diversity. The diversification patterns are not reflected in the current classification (Ng *et al.* 2008: 59). The reappraisal of traditional morphological characters in the present study suggests several groupings that justify the recognition of clearly distinct subfamilies, in fact seven, as follows: Dorippinae n. stat. (*Dorippe*); Dorippoidinae n. subfam. (*Dorippoides*); Heikeopsinae n. subfam. (*Neodorippe*, *Heikeopsis*, *Nobilum*); Medorippinae n. subfam. (*Medorippe*); Paradorippinae n. subfam. (*Paradorippe*); Philippidorippinae n. subfam. (*Philippidorippe*); and Phyllodorippinae n. subfam. (*Phyllodorippe*).

Evidence for the monophyly of the Dorippidae inferred from several putative synapomorphies is not questioned. Some scientists disparage the establishment of subfamilies, especially if they are monotypic and particularly in the classification of a small, apparently well-known family, arguing that, despite considerable divergence, it is unnecessary and more informative to leave genera grouped with their relatives. We obviously agree with Vences *et al.* (2013) that it is impractical to name all the clades in a phylogenetic tree as taxa and that redundant naming in a subfamilial classification (sometimes including a single genus in each subfamily) may seem superfluous. But we argue that this 'economy of change' is not relevant in the present situation: a monotypic subfamily emphasises the disparity in question, thus avoiding the danger of losing a considerable amount of phylogenetic distinctiveness. The search for ancestral divergence pattern of early crabs such as Dorippidae has been hampered not only by the great developmental divergence between and within taxa but also by uncertainties about their phylogenetic relationships. Phylogeny-based classifications of taxonomically complex and morphologically heterogeneous clades such as the Dorippidae are essential to pave the way for further taxonomic studies of genera and groups of genera, as well to track the course of morphological evolution, speciation and extinction patterns. The objective of the present study is to produce a subfamilial classification based on robust morphological evidence, supported by comprehensive generic-level sampling and representative species-level sampling. To make this work taxonomically sound, we have primarily used the type genera and their type species.

Some morphological structures peculiar to the Dorippidae remain poorly described. One intriguing structure on the coxa of P3, decribed for the first time by Serène (1982: 1130, pl. 1, fig. 1, pl. 2, figs 1, 4, as *Dorippe miersi* Serène, 1982) as a large whitish cup-shaped growth at the P3 base, then referred to as a 'sausage-like callosity' by Holthuis & Manning (1990: 2, 8), is a unique novelty of species of *Dorippe* (Figs 9C, D; 10A-C; 15A, C, E-J; 33C-H) and *Dorippoides* (Fig. 33A), featuring several patterns. It is shown here in detail for the first time and described as well as figured in all examined species of these two genera. The 'spur-like process' found by Holthuis & Manning (1990: 2, 48, fig. 26F) on the ischium of P3 in females of *Dorippoides* will also be examined (Figs 8D; 9A). The erect spine on sternite 8 in females of *Heikeopsis*, *Neodorippe*, *Nobilum* (Heikeopsinae n. subfam), and *Phyllodorippe* (Phyllodorippinae n. subfam) (Figs 9B; 29D, respectively) is unusual.

In addition, particular structures not previously documented in dorippids are investigated here: 1) the posterior margin of the carapace has a particularly thick margin, the 'rim', extending variously on posterolateral margins; it is bordered posteriorly by a 'strip', present in all species (Figs 5C; 8A-C; 9C), which is apparently an exclusivity of the family (such a strip is absent in the Ethusidae we have examined); and 2) females of many dorippids (e.g. *Dorippe*, *Dorippoides*, *Philippidorippe*, *Phyllodorippe*) exhibit a process on the dorsally exposed portion of sternite 8 that overhangs the pleonal somite 2 and acts as a pleonal holding device (Figs 8C; 9C). Females of these same species possess an additional modality of retention: the telson is engaged in the constricted sterno-pleonal cavity between the edges of sternite 5 so that the pleon is secured at this level (Figs 8D; 9A). All these new data are incorporated in the present study (see *Some particular morphological characters of Dorippidae,* page 246).

Holthuis & Manning (1990: 2) have already pointed out how surprisingly little is known about dorippids, even though most species are large-sized and at least some are fairly common. Likewise, their biology is poorly recorded. Their carrying behaviour has not been documented in all species. Their forward-burying (as opposed to back-burying) and forward locomotion (as opposed to sideways locomotion) are known mainly from field videos (see Guinot *et al.* 2013) and a few rare studies (Mori 1986; Ng & Tan 1986; Tan & Ng 1988; Shen 2006; Rossetti *et al.* 2006).

The evolutionary history of the Dorippoidea has been documented by fossils since the Early Cretaceous, and this early occurrence had confirmed that they were, with the Majoidea, the earliest splitting brachyuran branches (Luque 2015; Guinot *et al.* 2013, 2019; Charbonnier *et al.* 2017; Guinot 2019; Vega *et al.* 2019; Van Bakel *et al.* 2020). Our view that Hymenosomatoidea is even more basal in Eubrachyura, with its relationship to Dorippoidea (Guinot 2011) apparently supported by consistent data sets, will be discussed in light of the recent discovery of even older hymenosomatoid fossil representatives, namely in the Barremian (Mendes *et al.* 2022). We will review the fossil dorippid species in the light of the data from extant representatives and the extinct families attributed to the Dorippoidea.

Based on the brachyuran fossil material studied at hand, the current view is that the earliest Eubrachyura (heterotremes) did not appear until the Early Cretaceous, but there are arguments for dating the first 'true crabs' to the Jurassic. This is what is suggested in our recent article (Guinot 2019), admittedly provocative and containing assumptions that will certainly prove false, but hopefully not in vain. For example, for the Late Jurassic Lecythocaridae Schweitzer & Feldmann, 2009, which do not appear to be podotreme crabs as currently believed, there is conclusive evidence to advocate for their eubrachyuran, probably majoid, affiliation, implying that the evolutionary history of Brachyura started much earlier than assumed (Guinot *et al.* 2019: fig. 13A-C; Guinot 2019: 768, 782, fig. 10A-D; see *Appendix 2*, *Fossils assigned to Lecythocaridae Schweitzer & Feldmann, 2009*). Based on phylogenomic divergence time estimates and using 36 newly vetted fossil calibrations, Wolfe *et al.* (2022, pers. comm.; see also Wolfe *et al.* 2019) inferred that brachyurans most likely diverged in the Triassic (but see Iniesto *et al.* 2019), with family-level splits in the Late Cretaceous and Early Paleogene, and stated that Eubrachyura could be as old as the mid-Jurassic (183-161 Ma), with the oldest event, encompassing the freshwater heterotreme groups Potamoidea Ortmann, 1896, Gecarcinucoidea Rathbun, 1904, and Pseudothelphusoidea Ortmann, 1893, occurring in the upper Cretaceous, with others in the Cenozoic (Davis *et al.* 2022).

MATERIAL AND METHODS

Terminology essentially follows Guinot *et al.* (2013) and Davie *et al.* (2015a). Measurements are provided in millimetres, being taken at the maximum of the carapace (including rostrum and lateral teeth if present) and are reported as carapace length (cl) × width (w), respectively. The thoracic somites are numbered from 1 to 8. Pleonal somites are numbered from 1 to 6. Thoracic sternal sutures are designated by the number of the two thoracic sternites that they involve, and thus are numbered from 1/2 to 7/8. The exposed pleurites at the level of the pereiopods are numbered from 5-7, corresponding to their respective sternites. Various specimens that had to be cleaned before being photographed were brushed so that the setae are not normally represented.

In order to facilitate future identifications in a group where there has been much confusion in the past, each diagnostic character is accompanied by a list of the main illustrations in the literature.

ABBREVIATIONS

Institutions

AM	Australian Museum, Sydney;
ICZN	*International Code of Zoological Nomenclature*, referred to as 'the *Code*' throughout the text;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	Natural History Museum, formerly British Museum (Natural History) BM (NH), London;
NHMUK	Palaeontology Collections, The Natural History Museum, London;
RMNH	The Naturalis (ex Rijksmuseum van Natuurlijke Historie), Leiden;
SMF	Senckenberg Research Institute and Natural History Museum, Franfurt am Main;
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.;
ZRC	Zoological Reference Collection, Lee Kong Chian, Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore.

Morphology

G1	male first pleopod;
G2	male second pleopod;
mxp1, mxp3	first, third maxillipeds, respectively;
P1-P5	pereiopods 1-5, respectively.

MOLECULAR STUDY

Sequences of the molecular markers 16S rRNA, 12S rRNA and COI produced for the Dorippoidea (including the Ethusidae) by Sin *et al.* (2009) and 16S rRNA by Fan *et al.* (2004, as Dorippinae) were retrieved from GenBank to be re-analysed, with the kind help of Valentin de Mazancourt (MNHN). Each dataset was aligned independently using Muscle algorithm (Edgar 2004) implemented in MEGA 7 (Kumar *et al.* 2016). Quick Neighbor-Joining analyses performed with the same program showed no incongruencies among single-gene datasets. The concatenated dataset partitioned by gene and codon position for the COI was analysed with PartitionFinder (Lanfear *et al.* 2012) to determine the best-fit molecular evolution model of the three datasets using corrected Akaike Information Criterion. The following models were retained: GTR + I for 16S, 12S and COI 3rd codon position, SYM + I for COI 1st position and GTR + I for COI 2nd position. Using the partition and models, a Bayesian Inference (BI) phylogenetic analysis was performed with MrBayes 3.2 (Ronquist & Huelsenbeck 2003) implemented in the CIPRES online platform (Miller *et al.* 2010). BI analyses consisted of four Markov chains and 10 000 000 generations with default number of chain swaps and sampling frequency of one tree in each 2 000 generations. A chain temperature of 0.05 was used in all analyses. The convergence of each analysis was checked using Tracer ver. 1.4.1 (Rambaut *et al.* 2014); the two runs were considered converged if all effective sample size (ESS) values exceeded 200. Consensus trees were calculated after discarding the first 25% trees as burn-in. Independently, a Maximum Likelihood (ML) phylogenetic analysis was run with RaxML (Stamatakis 2014) also implemented in CIPRES. The robustness of nodes was assessed using rapid bootstrapping with 1000 bootstrap replicates.

Material examined and/or photographed

Dorippe frascone (Herbst, 1785). **Philippines** • 1 ♂ 29.7 × 31.0 mm, 1 prepubertal ♀ 23.3 × 24.4 mm; Philippines, Panglao Island; stn D12; Exp. PANGLAO 2004; 28.VI.2004; T. Naruse det. *D. quadridens*; 11.IX.2008; ZRC 2008.0076. **Papua New Guinea** • 1 juvenile; Kavieng Lagoon; N coast of Manne I., silty coral slope to mud near mangrove; KAVIENG Exp. 2014; stn KR36; 02°40.8'S, 150°42.7'E; 1-11 m; 8.VIII.2014; MNHN coll.; L. Corbari det. 2014; MNHN-IU-2014-2247 • 1 ♀ juvenile 15.8 × 16.4 mm; Kavieng Lagoon, Nusa Channel, patch reed; KAVIENG Exp 2014; stn KD26; 02°39.4'S, 150°40.3'E; 8-12 m; 14.VI.2014; MNHN coll.; L. Corbari det. 2014; MNHN-IU-2014-2486 • 2 juveniles; Kavieng Lagoon, N coast of Manne I., sand with Caulerpa; KAVIENG Exp. 2014; stn KD11; 02°40.6'S, 150°42.5'E; 15 m; 8.VI.2014; MNHN coll.; G. Poore & L. Corbari det. 2014; MNHN-IU-2016-1010 and MNHN-IU-2016-1011.

Dorippe glabra Manning, 1993. **Holotype**. **Australia** • 1 ovigerous ♀ 24.3 × 26.7 mm; Chambers Bay, NT; 12°13'S, 131°35'E; Otter trawl; 38 m; A. A. Racek; 7.XI.1959; AM P13363.

Dorippe irrorata Manning & Holthuis, 1986. **Holotype**. **Andaman Sea** • ♂ 21.5 × 22.0 mm; south of Mergui Archipelago; 9°54'N, 97°42'E; International Indian Ocean Expedition, *Anton Bruun Cruise 1*; stn AB-21; 73 m; 24.III.1963; USNM 172495.

Dorippe quadridens (Fabricius, 1793). **Egypt** • 2 ♂, dry condition; Timsah Lake; Chen det. *Dorippe frascone*; Guinot det. *D. quadridens* 19.IV.2023; MNHN-IU-2000-19818 (=MNHN-B19818). **Madagascar** • 5 specimens (including 1 ♀ 29.5 × 30 mm); NW Madagascar, Ambaro Bay, N.O. *Vauban*; A. Crosnier coll.; II.1959; trawling; 5 m; mud; Chen det. *D. frascone*; Manning redet. *D. quadridens*; MNHN-IU-2018-5193 (= MNHN-B18279) • 5 ♂, 1 ♀, 4 ovigerous ♀ (including ovigerous ♀ 30.0 × 31.0 mm); NW Madagascar, Ambaro Bay; trawling; 24.III.1965; R. Plante coll.; Manning det. 1984; revid. Chen H. 1987; MNHN-IU-2018-5198 (MNHN-B11172). **Vietnam (= Indochine)** • 3 ♂ (including 1 ♂ 33.0 × 33.5 mm), 1 ♀, 1 ovigerous ♀; Campagne du *de Lanessan* 1925-1929, N°116: Don A. Krempf 1930; Entry MNHN 7-1930; initially *Dorippe dorsipes*, Manning 1984 det. *D. quadridens*; MNHN-IU-2021-8757 (= MNHN-B11177). **South China Sea** • 1 ♂, 4 ♀ (including ♀ 38.1 × 33.7 mm); about 30 miles from Horsburgh Lighthouse; Hee Huat det. *D. frascone*, redet. *D. quadridens*; ZRC 1984.6307 • 1 ♂ 36.3 × 38.1 mm; near Singapore, Hee Huat; 16.IX.1983; det. *D. frascone*, redet. *D. quadridens*, ZRC 1984.6308. **Thailand** • 2 ♂ 39.0 × 41.4 mm, 34.5 × 38.9 mm; Pattani Province, Movig Chik District, Bang Tawa crab fishing village (DY 03-04); DCJ Yeo *et al.*; 20.II.2003; ZRC 2003.0126.

Dorippe sinica Chen, 1980. **China** • 1 ♂ 36.2 × 39.5 mm, 1 ♀ 34.8 × 38.9 mm; Guangdong, Nanao Island, Y Cai & NK Ng; 12.XI.1998; ZRC 1999.0470. **Japan** • 1 ♂ 36.6 × 38.6 mm; Kochi, Shikoku, Tosa Bay, Netzabfahl von Fischern; 150-200 m; K. Sakai coll. and ded.; SMF 57855 • 1 ♂; Kochi, Shikoku, Tosa Bucht; 33°29.049'N, 133°35.707'E; leg. K. Sakai; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 1 ♂; Kochi, Usa, Kenoura; 33°26.316'N, 133°28.003'E; 18.X.1984; leg. K. Sakai; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 2 ♂; Kochi, Shikoku, Tosa Bucht; 33°29.049'N, 133°35.707'E; R.V. *Toyohata-maru*; leg. K. Sakai; XII.2005; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 9 specimens; Wakayama, Tanabe-Bay; 33°43.001'N, 135°19.103'E; 40 m; 26-27.X.1988; leg. K. Sakai; ded. K. Sakai; XI.2005; Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856a (tissues extracted from 1 ♂ and 1 ♀ for genetic analysis) • 1 ♂; Wakayama, Tanabe-Bay; 33°43.001'N, 135°19.103'E; 26.X.1988; leg. K. Sakai; ded. K. Sakai; XI.2005; Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 1 ♂; Kagoshima, Nagashima; XI.1963; leg. K. Sakai; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856.

Dorippe tenuipes Chen, 1980. **Vietnam** • ♂ 19.0 × 20.0 mm, holotype of *Dorippe miersi* Serène, 1982; Nhatrang Bay; collect 2541, trawlers catches, 15-20 m, muddy shell sand, Nguyen, Van Luom coll.; 24.VII.1969; MNHN-IU-2008-12890 (= MNHN-B7279) • 2 paratypes of *Dorippe miersi* Serène, 1982, 1 ♀ 23.0 × 25.0 mm; same data as for holotype; 24.VII.1969; MNHN-IU-2008-10599 (= MNHN-B7280) • 1 ♀ 24.0 × 26.0 mm; same data as for holotype; MNHN-IU-2008-10600 (= MNHN-B11180). **South China Sea** • 1 ♀ 24.0 × 26.0 mm, paratype of *Dorippe miersi* Serène, 1982 (as. 48.927); same data; MNHN-IU-2008-10600 • 1 ♂ 21.0 × 25.0 mm; 20°30'N, 113°00'E; 68 m; Chen H. coll.; 18.IV.1960; MNHN-IU-2018-5192 (= MNHN-B8937) • 1 ♂ 13.2 × 14.2 mm, 1 ovigerous ♀ 17.3 × 19.6 mm; 21°00'N, 113°00'E; mud-sand; coll. Qi; 10.II.1960; ZRC 1999.0009.

Dorippe trilobata Manning, 1993. **Holotype**. **Australia** • ♂ 20.5 × 21.1 mm; off Mitchell River, Admiralty Gulf, Western Australia; 13°52'S, 126°45'E; Otter trawl over silty bottom; 18 m; C. O'Connor; 18.IV.1978; AM P27124.

Dorippoides facchino (Herbst, 1785). **India** • 8 ♂, 6 ♀ (including 1 postpubertal ♀ 19.0 × 22.0 mm); Pondicherry Bay; Maindron coll. 1882; Chen det. 1987; MNHN-IU-2018-5199 (= MNHN-B19817). **South China Sea** • 1 ovigerous ♀ 21 × 25 mm; trawl; 37 m; Chen leg. 1987; MNHN-IU-2018-5195 (= MNHN-B18802) • 1 ovigerous ♀ 20.3 × 26.2 mm; *c.* 150 miles, off Singapore, Hee Huat; 28.VIII.1983; ZRC 1984.5347 • 1 ♂ 25.3 × 32 mm; Malaysia, Johore, Pontian; CM Yang; 31.III.1991; ZRC 1991.6672.

Dorippoides nudipes Manning & Holthuis, 1986. **Madagascar** • 1 ♂ 18.0 × 20.0 mm; Ambaro Bay; trawling; 3 m; zone d'herbier; A. Crosnier coll.; XI.1959; Chen H. det. 1986; MNHN-IU-2018-5200 (MNHN-B18276). **Iran** • 1 ♂ 16.2 × 19.4 mm; M. Safael; V.2020; ZRC 2017.1227. **South Africa** • 1 ♀ 21.6 × 29.5 mm; vicinity of Tugela river mouth; trawled 15-35 m; coll. S. Fennesy; 27-31.V.2006; ZRC 2009.0885. **India** • 1 ♂ 12.2 × 13.5 × mm, 1 ♀ 15.8 × 18.1 mm; Muttom fish port; shallow water trawlers; Tamil Nadu, southwestern India; coll. and det. PKL Ng, III.2017; ZRC 2017.0874.

Heikeopsis japonica (von Siebold, 1824). **Japan** • 1 ♂ 25.0 × 27.3 mm, ♀ 23.5 × 26.7 mm; Chaffanjon coll. & leg.; entry MNHN 174-1896; E.-L. Bouvier det. 1899 *Dorippe japonica*; dry condition; MNHN-IU-2000-4091 (= MNHN-B4091) • 1 ♀ 16.8 mm; dry condition; Japan Sea; MNHN-IU-2000-34 (= MNHN-B34) • 5 ♂, 2 ♀; Tokushima, Yoshinogawa; 34°3.489'N, 134°38.697'E; vend. Iuchi, K. Sakai coll.; det. *Heikea japonica* (Von Siebold, 1824), D. Guinot verif., XII.2021; SMF 57849 • 8 ♂, 5 ♀; Tokushima, Komatsujima; 6.XI.2001; leg. K. Sakai; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 15 ♂ (22.5 × 24.3 mm, 24.2 × 25.4 mm), 8 ♀; Tokushima, off Okrnose, Tsuda-Tokushima; 14.II.2002; leg. Iuchi; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 8 ♂, 10 ♀ (some damaged); Hiroshima, Honshu, Inland See, Onomichi bei, Fukuyama; 34°25'N, 135°26'E-34°25'N, 135°26'E; 10 m; VI.1979-VIII.1979; N. Wasaki det. *Heikea japonica* von Siebold (1824); D. Guinot verif. XII.2021; SMF 57856 and ex 15130 • 1 small specimen; Wakayama, Tanabe-Bay; 33°43.001'N, 135°19.103'E; 40 m; 26-27.X.1988; leg. K. Sakai; ded. K. Sakai XI.2005, Dorippidae indet.; K. Sakai coll., D. Guinot det. XII.2021; SMF 57856 (tissue extracted for genetic analysis) • 4 specimens; Tokushima, Komatsu-Jima; 9.VI.1991; leg. K. Sakai; ded. K. Sakai Dorippidae indet., K. Sakai coll.; D. Guinot det. XII.2021; SMF 57864b • 3 ♂; no further information; leg. K. Sakai; ded. K. Sakai Dorippidae indet.; K. Sakai coll. D. Guinot det. XII.2021; SMF 57856 • 1 ovigerous ♀; Wakayama, Honshu, Halbinsel Kii, Minabe, Sakai (Village), Shrimp-Net; V.1951; ded. Kohno Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856.

?Heikeopsis aff. *japonica* (von Siebold, 1824). **North China Sea** • 1 ♂ 29.0 × 30.3 mm, 1 ovigerous ♀ 24.4 × 26.5 mm; coll. 10.XII.1959; H. Chen det. *Dorippe japonica* and leg.; MNHN-IU-2018-5197 (= MNHN-B18801). **China** • 1 ♂ 21.9 × 24 mm, 1 ♀ 23.4 × 26.4 mm; seas off Qingdao, Tuanda, Fishermen, via P. K. L. Ng; 23-25.VIII.2002, det. *H. japonica*; ZRC 2002.0491.

Medorippe lanata (Linnaeus, 1767). **Benin** • 7 ♂, 3 ♀, 3 ovigerous ♀ (including 1 ♀ 22.4 × 28.6 mm); Dahomey Coasts; Stn CH40; 6°11'N, 2°12'E; 40-45 m; 21.VII.1964; A. Crosnier coll. et det. *Dorippe armata*; MNHN-IU-2018-5196 (= MNHN-B16380, *pro parte*) • 1 ♂ 18.5 × 23.2 mm; Dahomey Coasts; 6°11'N, 2°12'E; 40-45 m; A. Crosnier coll.; IV.2009; Guinot det. *M. lanata*; ZRC 2009.0411 (ex MNHN). **Senegal** • 5 specimens (including 1 ♂ 26.0 × 32.0 mm); off Joal, *Gérard Tréca*; V.1949, Cremoux coll., Monod Th. 1952 det.; MNHN-IU-2009-2000 (= MNHN-B21493). **Republic of Congo** • 3 specimens (including 2 ♂ 26.0 × 30.0 mm and cw 27.5mm, damaged); north of mouth of Congo River; R.O.C.); 20-30 m; VIII.1963; MNHN-IU-2009-2001 (= MNHN-B13583). **Morocco** • 8 specimens (including 1 ♀ 18.0 × 24.0 mm); *Vanneau*; Stn 70; 30°25'N, 09°51'W; 85 m; 24.VIII.1925; MNHN-IU-2009-2002 (= MNHN-B26115). **No data** • 1 ♂ 23.2 × 28.9 mm, 1 ♀ 23.2 × 28.9 mm; no data; ZRC 2009.0412 (ex MNHN). **Israel** • 1 ovigerous ♀ 21.2 × 27.7 mm; Haifa Bay; 43 m; Galil; V.1997; ZRC 1999.0632. **?Mediterranean Sea** • dissected 3 ♂, 2 ♀ (including 1 ♀ 17.8 × 23.0 mm); dehydrated specimens for skeletal preparation by Sylvie Secretan (MNHN-IU-2021-8745) • 5 ♂ and 10 ♀ (incomplete), in alcohol; specimens for skeletal preparation by Sylvie Secretan (MNHN-IU-2021-8746).

?Medorippe crosnieri Chen, 1988. **Holotype. Madagascar** • ♂ 15.7 × 19.9 mm; N. W. Madagascar; Campagne CREVETTIERE 1972; N.O. *Vauban*; Stn CH47; 15°20'S, 46°12'E; 245-250 m; low-calcareous sandy silt; A. Crosnier coll.; 7.XI.1972; MNHN-IU-2009-1995 (= MNHN-B18269, erroneously B18219 in Chen 1988). **Paratypes. Madagascar** • 2 ♂ 10.0 × 12.0 mm, 13.0 × 15.8 mm; Campagne CREVETTIERE 1972, N.O. *Vauban*; Stn CH44; 15°26'S, 46°01'E; 200-210 m moderately calcareous sands; A. Crosnier coll.; 7.XI.1972; MNHN-IU-2009-1996 (= MNHN-B18358) • 1 ♀ 9.9 × 12.0 mm; Campagne CREVETTIERE 1972, N.O. *Vauban*; Stn CH52; 15°21'S, 46°12'E; 150 m; sandy silt moderately calcareous; A. Crosnier coll.; 8.XI.1972; MNHN-IU-2009-1997 (= MNHN-B18365) • 1 ♂ 21.1 × 25.9 mm; Mozambique Channel, Maputo transect; MAINBAZA Expedition; R.V. *Vizconde de Eza*; CP 3132; 25°11'S, 35°02'E, 101-102 m; Bouchet, Rosado & Strong coll.; 10.IV.2009; MNHN-IU-2009-1998 • 1 ♂ young 12.0 × 15.0 mm; Maputo transect; MAINBAZA Expedition; R.V. *Vizconde de Eza*; CP 3130; 25°53'S, 33°07'E; 112-127m; Bouchet, Rosado & Strong coll.; 09.IV.2009; Guinot det., MNHN-IU-2009-1999.

Neodorippe callida (Fabricius, 1795). **China** • 2 ♀, dry condition; Amoy, N°70; VII.1932; Entry MNHH 1-1937, MNHN-IU-2000-28984 (= MNHN-B28984) • 5 ♂, 3 ♀ (including 1 ♂ 12.0 × 12.0 mm, 1 ♀ 13.5 × 14.3 mm); Amoy, C. F. Wang coll.; VII.1925; Manning det.; MNHN-IU-2021-8738 (= MNHN-B11170). **Singapore** • 1 ♂ cl 11 mm, 1 ♀; Ng P. K. L. coll.; 30.V.1991; det. et leg.; MNHN-IU-2021-8739 (= MNHN-B29083). **Thailand** • 1 ♂ 13.5 × 14 mm, 1 ♀ 14.0 × 15.0 mm; Andaman Sea, Phuket, S. Chaitiamuong *et al.* coll.; XII.1998, P. Ng det. and leg.; MNHN-IU-2016-10754 (ex ZRC 1998.1116). **Malaysia** • 1 ♂ 15.6 × 14.1 mm, 1 ♀ 16.1 × 15.8 mm; off Kuala Lumpur; ZRC1993.386-391. **Singapore** • 1 young ♂ 10.1 × 10.3 mm, 1 ♀ 11.2 × 11.5 mm; Changi Point Beach; HH Tan *et al.*; 8.III.2001; ZRC 2018.0445.

Neodorippe simplex Ng & Rahayu, 2002. **Paratypes** • **Indonesia** • 1 ♂, 1 ♀; Irian Jaya, Freeport, Timika; Stn EM870; Trawled; 16.XII.1997; ENU workers coll.; MNHN-IU-2014-11222 (ex ZRC 2001.2272).

Nobilum histrio (Nobili, 1903). **China** • 1 ovigerous ♀ 24.0 × 27.0 mm; Amoy; Wang C. F. coll.; VII.1925; MNHN-IU-2021-8740 (= MNHN-B11171). **Malaysia** • 1 ♂ 21.0 × 22.4 mm, 1 ovigerous ♀ 22.1 × 24.7 mm; Johore, Pontian; CM Yang; 31.III.1991; ZRC 2002.0491 • 1 ♂ 23.4 × 23.7 mm; Johore; Pontian; ZRC 1984.57445747.

Paradorippe granulata (De Haan, 1841). **China** • 1 ♂, 1 ♀ 22.7 × 24, 7 mm; Tuandao, off Qingdao; fishermen coll.; 23-25.VIII.2002; P. Ng det.; 25.VIII.2002; MNHN-IU-2016-10753, ex ZRC 2002.0492. **Japan** • 1 ♂ 11.0 × 11.0 mm; vicinity of Tokyo; Harmand J. coll.; 1906; MNHN-IU-2021-8743 (= MNHN-B11181) • 2 damaged specimens (♀ cw 17.0 mm); Boucard coll. et leg.; entry MNHN 83-1898, MNHN-IU-2021-8744 (= MNHN-B19825). **Taiwan** • 1 ♂ 23.6 × 27.3 mm; NE Taiwan, I-Lan county, Tahsi; K. X. Lee; 2000; ZRC 2001.0014 • 1 ♂; NE coast of Taiwan, off Suao; Fishing boat *Rih-Jheng 101* Taiwan 2004; CP263; 101-106 m; 24°31.45'N, 121°53.34'E; Chan & Cosel leg.; 1.IX.2004; MNHN-IU-2016-5224. **Japan** • 1 ovigerous ♀; 23.2 × 25.7 mm, off Hota, Uchibo coast off Boso Peninsula; T. Komai; 22.VIII.1997; ZRC 1999.0082 • 2 ♂, 15 ♀; Kochi, Shikoku, Tosa Bucht vor Mimase, Trawl, 60-70 m; 23.X.1979; M. Türkay leg. and det. *Heikea japonica*, D. Guinot det. X.2021; SMF 57856 • 7 specimens; Tokushima, Komatsu-Jima; 9.VII.1991; leg. K. Sakai, K. Sakai coll.; ded. Dorippidae indet.; D. Guinot det. XII.2021; SMF 57856 • 1 ♀ (large, without pleon); Wakayama, Honshu, Halbinsel Kii, Minabe, Sakai (Village), Shrimp-Net; V.1951; ded. Kohno Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 3 ♂, 2 ♀, 2 ovigerous ♀; Kochi, Shikoku, Tosa Bucht; 33°29.049'N, 133°35.707'E; leg. K. Sakai; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856 • 2 ♂, 1 ♀, 1 ovigerous ♀; Mie, Toba, leg. Yamashita; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57860 • 1 ♂; no further information; 30 m; 5.II.1986; R.V. *Toyohata-maru*; ded. K. Sakai Dorippidae indet.; K. Sakai coll.; D. Guinot det. XII.2021; SMF 57856.

Philippidorippe philippinensis Chen, 1986. **Philippines** • **Holotype.** ♂ 25.2 × 30.0 mm; between Luçon & Lubang; Campagne MUSORSTOM 2; N.O. *Coriolis*; Stn CP06; 13°56'N, 120°22'E; 136-152 m; Bouchet coll.; 20.XI.1980; MNHN-IU-2008-10971 (= MNHN-B18190) • 1 ♂, 1 ♀ 26.0 × 33.0 mm; W Luçon; Campagne MUSORSTOM 3, N.O. *Coriolis*; stn CP101; 14°00'N, 120°18'E; 194-196 m; Bouchet & Triclot coll.; 1.VI.1985; MNHN-IU-2018-5201 (= MNHN-B18913) • 1 ♂ 23.0 × 29.3 mm; 1 ovigerous ♀ 25.2 × 33.2 mm; Bohol Province, NW of Panglao Island; J. Arbasto; 2006; ZRC 2016.0240.

Phyllodorippe armata (Miers, 1881). **Côte d'Ivoire** • 42 specimens (including 1 ♀ 13.0 × 19.0 mm); Guinean Trawling Survey II; *La Rafale*, Dr 8; 5°09'N, 4°39'W; 15 m; 31.III.1964; MNHN-IU-2021-8731 (= MNHN-B24199). **Benin** • 2 ♂ (including 1 ♂ 20.0 × 25.5 mm), 1 ♀; Dahomey (= Benin); Stn CH40; 6°11'N, 2°12'E; 40-45 m; A. Crosnier coll. et det.; 21.VII.1964; MNHN-IU-2009-2004 (= MNHN-B16380 *pro parte*). **Sierra Leone** • 1 ♂ 15 × 21 mm; Gulf of Guinea, Sherbro Island; Calypso 1956 Expedition; N.O. *Calypso*, St. CH11; 7°20'N, 12°39'W; 30-34 m; Marche-Marchad coll.; 19.V.1956; MNHN-IU-2009-2006 (= MNHN-B13555). **Republic of Congo** • 1 ovigerous ♀ 15.0 × 22.8 mm; Congo, off Pointe Noire; Crosnier coll.; Guinot det.; MNHN-IU-2009-2005 (= MNHN-B16385). **Guinea** • 1 ♂ 12.3 × 16.2 mm, 1 ovigerous ♀ 11.9 × 16.6 mm; Guinean Trawling Survey, Guinea II; 15 m; *La Rafale*; 3.IV.1964; ZRC 2009.0413 (ex MNHN-B24202).

Correct authorship of brachyuran names by H. Milne Edwards (1837): the case of the Dorippidae

The concept of authorship in zoological taxonomy and nomenclature has evolved over time, and nowadays the *Code* credits authorship of a nomen to the publication (with its original author and date) where it was first published and made nomenclaturally available (ICZN 1999, 2012; Dubois 2012).

Henri Milne Edwards (1834, 1837), in *Histoire naturelle des Crustacés*, proposed many new nominal taxa at the rank of the family group and also class-series nomina (see Guinot *et al.* 2013: 17, *Nomenclatural ranks*) by providing substantial diagnoses, keys and lists of included taxa, often in 'tribes' that roughly correspond to higher-ranked taxa (= class-series taxa). He establised the foundations of brachyuran carcinology. His new groups, including families, were introduced in French, not in Latinised form, so that virtually all of them were rejected on account of the authors who first Latinised them, such as MacLeay (1838), De Haan or Dana at various dates.

The question of whether H. Milne Edwards's names are scientific names or vernacular names must be referred to the *Code*. This point of discussion remains ambiguous since, according to the articles of the *Code*, the definitions of 'vernacular name' are not absolutely similar in the English and French glossaries. It should be noted that the H. Milne Edwards's nomina were proposed "only for zoological nomenclature" as opposed to "nomina of an animal or animals in a language used for general purposes" (*Code*, Article 1 and Glossary p. 109), see the discussion in Kottelat (2001: 609). Another point is that the criterion of Latinisation is nowhere required by the *Code* (Article 11.3) and the annexed examples very explicitly allow the use of non-Latin words. In any event, the family-group names, when first published in non-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 were Latinised by the first revisor, they were explicitely recognised as belonging first to H. Milne Edwards and were then generally accepted as valid by the majority of authors interested in the group and most often as dating from that first publication in its original form (*Code*, Art. 11.7.2). Thus, given the general acceptance, in strict application of the ICZN rules and if the international spirit of fairness can prevail, most of the names in the *Histoire naturelle des Crustacés* should be credited to H. Milne Edwards (see Davie *et al.* 2015c: 1052; also Poore 2016: 249).

Here we will consider the particular case of the tribe Dorippiens, which is similar to the cases of the family-group names Homolidae H. Milne Edwards, 1837 (Homoliens H. Milne Edwards, 1837) treated by Guinot *et al.* (2013: 301) and Gecarcinidae H. Milne Edwards, 1837 (Gécarciniens H. Milne Edwards, 1837) treated by Guinot *et al.* (2018: 601). The family-group name Dorippiens was coined by H. Milne Edwards (1837: 151, 153) (spelt Dorypiens p. 99) for a tribe of crabs (within the 'family' Oxystomes, p. 96) with a diagnosis mentioning the main characters (unusual inhalant respiratory openings, broad and posteriorly tilted thoracic sternum, dorsal insertion of the last two pereiopods) but in a non-Latinised form. Only a year later, MacLeay (1838: 55, 69, 71), according to whom (p. 5) H. Milne Edwards based his groupings on "analogies […] mistaken for affinities", Latinised the name for the 'stirpe' [sic] he called Dorippina without any mention of the Dorippiens and with only a brief indication of characters. The nomen was emended to Dorippidae by White (1847: 53). According to Holthuis & Manning (1985:

305) the attribution to De Haan (1841) of the family name Dorippidae on the Official List of Family Names in Zoology (as Name no. 355, in Opinion 688 of the International Commission on Zoological Nomenclature) was inaccurate, hence their proposal to "correct this error" by acknowledging MacLeay's "first use".

However, leading scientists, not least, have recognised the priority of H. Milne Edwards: De Haan (1841: 119, 120) who writes "Dorippidea, Edwards"; Alcock (1896: 273) who writes "Dorippiens, Milne Edwards"; Miers (1886: 326) who first cites "Dorippiens H. Milne Edwards, 1837"; Chen & Sun (2002: 208) who first cite "Dorypiens" and "Dorippiens" of H. Milne Edwards; and Holthuis & Manning (1990: 5) first mentioning the name of H. Milne Edwards for the family Dorippidae but explicitly regarding "Doryppiens" and "Dorippiens" as French vernacular names. For most carcinologists including Guinot *et al.* (2013, 2019) and Ng *et al.* (2008: 59), although the priority of H. Milne Edwards is implicitly or explicitly acknowledged, the authorship is commonly attributed to MacLeay, 1838 (Davie 2002: 155; Poore 2004: 324), or sometimes to De Haan, 1833 (Guinot 1977, 1978), or to Dana, 1852 (Ortmann 1892: 553; Rathbun 1937: 75).

With reference to the above considerations, the family-group name Dorippiens H. Milne Edwards, 1837 meets all the criteria of availability in accordance with the provisions of the *Code* (ICZN, Art. 11.7, 11.7.2). This Art. 11.7.2 indeed stipulates – and this is the case here as shown as the many examples of quotes listed above show – that "If a family-group name was published before 1900, in accordance with the above provisions of this Article but not in latinized form, it is available with its original author and date only if it has been latinized by later authors and has been generally accepted as valid by authors interested in the group concerned and as dating from that first publication in vernacular form". Therefore, the authorship of the family-group name Dorippidae is hereby ascribed to H. Milne Edwards (1837).

HISTORICAL ACCOUNT

The first mention of a dorippid, *Notogastropus* Vosmaer, 1763 or *Noto-gastropus* Vosmaer, 1765, from Indonesia, appeared in a non-binominal work, so this generic name is not available and has been placed on the Official Index of Rejected and Invalid Generic Names in Zoology (International Commission 1987b: 132) in Opinion 688 (International Commission 1964: 17). It corresponds to the *Cancer frascone* of Herbst (1785), a valid species now known as *Dorippe frascone* (Herbst, 1785).

In establishing *Dorippe*, Weber (1795: 93) listed several species, including *Cancer quadridens* Fabricius, 1793 (Fabricius 1793) and *Cancer lanatus* (Linnaeus, 1767), and only with questionable allocation and without type designation. *Dorippe* Fabricius, 1798, junior homonym and junior objective synonym of *Dorippe* Weber, 1795 is an invalid generic name. At that time, *Dorippe astuta* Fabricius, 1798 and *Dorippe callida* Fabricius, 1798 (Fabricius 1798) were both *nomina nuda*. Therefore, as *Cancer quadridens* Fabricius, 1793, the only valid species included in the original description of *Dorippe*, was selected as type species of *Dorippe* by Holthuis (1962: 54, 55), the name was placed on the Official List of Generic Names in Zoology (International Commission 1987b: 83) in Opinion 688 (International Commission 1964: 16). A synonym of *Dorippe quadridens* (Fabricius, 1793) is the *Cancer dorsipes* of Linnaeus (1764), later the *Dorippe dorsipes* of many authors, a species often misidentified, so that many *D. dorsipes* in the literature actually belong to another species, *Dorippe sinica* Chen, 1980. The *Cancer dorsipes* of Linnaeus (1758), based on a figure from Rumphius (1705: pl. 10, fig. 3) showing a crab from 'India', is not a dorippid but is a raninoid now known as *Notopus dorsipes* (Linnaeus, 1758) (Holthuis 1962).

Before 1969, the family Dorippidae contained only those species that were all assigned to the genus *Dorippe*. In their revision, Serène & Romimohtarto (1969) divided *Dorippe* into three genera and two subgenera: *Dorippe*, comprising the nominotypic subgenus and the new subgenus *Dorippoides*; the new genus *Neodorippe*, including the nominotypical subgenus and their new subgenus *Nobilum*; and the new genus *Paradorippe.* They recognised 10 species within their Dorippinae. Subsequently, Manning & Holthuis (1981) added two new genera, *Medorippe* and *Phyllodorippe*, and raised all of the subgenera recognised by Serène & Romimohtarto (1969) to genus level. Meanwhile, Chen (1980) described from China two new species of *Dorippe*, *D. sinica* and *D. tenuipes*, the latter being the senior synonym of the contemporary *D. miersi* of Serène (1982). Chen (1986a) described the new genus and species *Philippidorippe philippinensis.* In 1986, Manning & Holthuis gave preliminary accounts of four new species: *Dorippe irrorata*, *Dorippoides nudipes*, *Nobilum arachnoides*, and *Paradorippe cathayana* (see *Subsequent misdesignation of paratypes by Holthuis & Manning (1990)*). Chen (1988) described *Medorippe crosnieri* from Madagascar. Dai & Yang (1991: 51), not yet having seen the revision by Holthuis & Manning (1990) and taking into consideration the 'common' characters and 'similarities' shared by the subgenera recognised by Serène & Romimohtarto (1969), had preferred to recognise only one genus *Dorippe*, the species being distinguished mainly by their first gonopods as indicated in their identification key.

Holthuis & Manning (1985: 304, 305), stating that the new genus *Neodorippe* Serène & Romimohtarto (1969: 3, 4, 11) was clearly based on a misidentified type species, *Dorippe astuta* Fabricius, 1798 (a junior synonym of *Cancer facchino* Herbst, 1785), submitted a proposal to the International Commission on Zoological Nomenclature. Under its Plenary Powers, the Commission designated *Dorippe callida* Fabricius, 1798 as the type species of *Neodorippe* and placed both *Neodorippe* and *Dorippoides* (with *Dorippe facchino* as the type species) on the Official List of Generic Names in Zoology (1987a: 139, Opinion 1437; 1987b). The *Dorippe astuta* of Weber (1795, *nomen nudum*) and of Fabricius (1798) is synonymous with *Dorippoides facchino* (Herbst, 1785).

The revision of Holthuis & Manning (1990), based on examination of type specimens of the oldest species in the museums of Washington, Copenhagen, Leiden, London and Paris, and reordering all the names in the literature, revealed the need for considerable changes in nomenclature. These authors have contributed greatly to a better understanding of the group by studying each species at length, by providing several keys, long diagnoses and descriptions, numerous figures, as well as a complete re-evaluation of synonymies, biological and geographical considerations. The result was the recognition of 17 species and nine genera, including a new genus, *Heika. Dorippe quadridens* was removed from the synonymy of *Dorippe frascone* (Herbst, 1785), and *Medorippe crosnieri* was considered a synonym of *M. lanata* (Linnaeus, 1767) (see Figs 22; 23 and *Remarks about the validity of* Medorippe crosnieri). Two new species of *Dorippe*, *D. glabra* and *D. trilobata*, found among the collection in the Australian Museum, Sydney (see Springthorpe & Lowry 1994; Davie 2002), were established by Manning (1993). *Neodorippe* Serène & Romimohtarto, 1969, previously monotypic, was augmented by a new species, *N. simplex* from Irian Jaya, by Ng & Rahayu (2002). Ng *et al.* (2008) proposed the replacement name *Heikeopsis* for *Heikea* Holthuis & Manning, 1990 (type species: *Dorippe japonica* von Siebold, 1824) that is a junior homonym of *Heikea* Isberg, 1934, a bivalve mollusc. No other new species or genera have been created since then.

In the first application case of the Autopoiesis Theory (derived from the cognitive neuroscience) to crustacean taxonomy, Watabe (2007: 56) recognised: the Dorippidae (represented only by the genus *Dorippe*), the Heikeidae (represented by the Recent genera *Heikea*, *Medorippe*, *Neodorippe*, and *Nobilum*), the Paradorippidae represented only by the genus *Paradorippe*), and the Philippidorippidae (represented only by the genus *Philippidorippe*). But these taxa are not available since they do not fulfil the requirements of the International Code of Zoological Nomenclature (ICZN 1999).

SUBSEQUENT MISDESIGNATION OF PARATYPES BY HOLTHUIS & MANNING (1990)

In anticipation of their major revision in 1990, Manning & Holthuis were led in 1986 to pre-describe several new species by extracting only certain data. They explain in the introduction (Manning & Holthuis 1986: 363) that, due to the unforeseen delay in the publication of their revision and to satisfy requests from colleagues for species pre-labelled in some museums with new but unpublished names, they will make the names of these new taxa available in a preliminary note, i.e., in 1986: there they describe the new species on the basis of a single specimen, the holotype, and with a minimum of figures. But later in their revision (Holthuis & Manning 1990) they designated paratypes for the same species, even in some cases from a provenance other than that of the type or type series. This subsequent action is not admissible under the ICZN rules, and these paratypes are invalid.

The four cases of invalid paratypes are listed below:

Dorippe irrorata Manning & Holthuis, 1986. In Manning & Holthuis (1986: 363): holotype, male 21.5 × 22.0 mm, Andaman Sea, south of Mergui Archipelago; 09°54'N, 97°42'E; 73 m, International Indian Ocean Expedition, *Anton Bruun* (USNM 172495) (Fig. 14H, I). But a female from the same expedition and from a close provenance, and indicated as deposited in the same institution, was designated as a paratype by Holthuis & Manning (1990: 15).

Dorippoides nudipes Manning & Holthuis, 1986. In Manning & Holthuis (1986: 364): holotype, male 17.00 × 19.00 mm, Massawa, Ethiopia, Red Sea, RMNH no. D.35530. But numerous specimens from the Red Sea (including the holotype), as well as lots from the Gulf of Aden, Gulf of Oman, Persian Gulf and Madagascar, are designated as paratypes by Holthuis & Manning (1990: 66-68) ("All specimens examined, other than the holotype and the two specimens from Karachi, are paratypes") and listed as deposited in several different institutions.

Nobilum arachnoides Manning & Holthuis, 1986. In Manning & Holthuis (1986: 364): holotype, male 15.8 × 16.7 mm, Japan, Inland Sea, near Kobe, *Challenger*; 19 May1875, BM (NH) 84.44. But two males from the Inland Sea are designated as paratypes by Holthuis & Manning (1990: 72, as *Heikea arachnoides*) and indicated as deposited in the British Museum (currently NHM) with the numbers 1903.6.7.5 and 1903.6.7.10.

Paradorippe cathayana Manning & Holthuis, 1986. In Manning & Holthuis (1986: 365): holotype, male 16.8 × 18.2 mm, China, Jimei, Fujian Province, USNM 57762. But several specimens from China are designated as paratypes by Holthuis & Manning (1990: 113) and indicated as deposited in the British Museum (currently NHM) and the USNM.

All such paratype designations should be mentioned as invalid on all listed specimens of the species cited above and deposited at the relevant institutions.

MORPHOLOGICAL FEATURES OF DORIPPIDAE

Interpretation of grooves on the carapace dorsal surface in Dorippidae

It is difficult to interpret adequately the grooves in brachyuran families and to recognise homologies, especially between podotremes and eubrachyurans. In their revision of the Dorippidae, Holthuis & Manning (1990: fig. 1, as Dorippinae) provided a schematic figure (Fig. 5A) showing the terminology they use to refer to grooves and elevations of the carapace. The branchiocardiac groove, sometimes flanked by a pair of branchial lobes, is placed as usual and is not questioned. But the two main grooves that cross the carapace, both meeting medially in their figure, are problematic. The anterior one, drawn somewhat straight, which separates the mesogastric and metagastric regions, is called the 'cervical groove'; the second, much more posterior and concave, is called the 'branchial groove'. Unfortunately, such a pattern of grooves is not found in any dorippid. Examination of dorippid specimens of all species shows that, quite consistently, the anterior groove is convex and the posterior groove concave (according to Holthuis & Manning, usually 'cervical' and 'branchial', respectively). In fact, Holthuis & Manning's (1990) interpretation corresponds to that of various authors: Bouvier (1897b: 60) for whom the grooves in dorippids are the same as those of Dromiidae De Haan, 1833 (including the Homolodromiidae Alcock, 1900), with two major transverse grooves: cervical, bearing the pair of gastric pits, and branchial; Bouvier (1898: 103) who stated that the Dorippidae "must be considered as modified Dromiidae"; Ihle (1916: 98, figs 30, 46, in *Ethusa*) who depicted the cervical and branchial grooves as in Dromioidea De Haan, 1833. Our interpretation for the Eubrachyura is quite different (see below).

Significantly, however, Holthuis & Manning (1990) have introduced in their descriptions of several species an additional groove, a 'precervical groove', which is not shown in their fig. 1 and is only occasionally mentioned in the text: p. 17 for *Dorippe irrorata*; p. 39 for *D. sinica*; p. 43 for *D. tenuipes*; p. 98 for *Neodorippe callida*; p. 114 for *Paradorippe cathayana*. Sometimes (e.g. on their p. 8 for the diagnosis of *Dorippe*) a 'precervical ridge' is quoted instead; in other cases it is not mentioned at all, when in fact it is present. Comparing the grooves as named in their descriptions and depicted in the corresponding drawings, we must admit that we have not been able to recognise homologous grooves, making their interpretation unclear.

The explicit description by Holthuis & Manning (1990: 114, fig. 46) of *Paradorippe cathayana* Manning & Holthuis, 1986 does not match their figure 1 (Fig. 5A), and is difficult to comprehend in this context: "Precervical groove deeper and better marked than cervical, deepest at lateral margins, forming distinct indentation there"; no mention is made of a branchial groove. However, in other species of *Paradorippe*, a genus that is very homogeneous in its groove pattern, the description changes radically, e.g. in *P. australiensis* (Miers, 1884), where no mention is made of a precervical groove: "Cervical and branchial grooves well marked but shallow, only faintly indicated across midline" (Holthuis & Manning 1990: 110, figs 44, 45a). The mention of a precervical groove in only one *Paradorippe* species (*P. cathayana*) and not in the other four species is inconsistent. As in the case of *P. cathayana*, the diagnosis of *Neodorippe callida* (Fabricius, 1798) mentions a precervical groove: "deep cervical, precervical, and branchiocardiac grooves" (Holthuis & Manning 1990: 98, figs 40, 41a, 42a) (Fig. 20A, B). Again, a contradiction can be found between the generic and specific descriptions of *Nobilum* and *N. histrio* (Fig. 21A) "Cervical and branchial grooves distinct" versus "Branchial and branchiocardiac grooves very distinct, precervical grooves also distinct but less deep" (Holthuis & Manning 1990: 104 and 105, respectively, see fig. 43a). The genus *Dorippe* (Figs 10; 12A; 14A, E, H; 15A, C, E, F), with a strongly sculptured carapace, is diagnosed by "a short, precervical ridge [instead of a 'precervical groove'] placed before distal part of cervical groove, forming its anterior margin; indistinct groove branching forward from cervical groove, just mediad of precervical ridge, turning inward and encircling protogastric region" and by a very deep branchial groove (Holthuis & Manning 1990: 7, figs 2a, 3, 4a, 5a, 6a, 7a, 8-11, 12a, 13a, 15, 16a). Later, Manning (1993) did not mention a precervical groove or ridge for his two new species of *Dorippe*.

In any case, the question that concerns us is to clearly determine the dorippid grooves: first to identify the true cervical groove, in relation to that of the other Brachyura, and then to clearly define the groove located anterior to it. It does not seem possible to us that the dorippid convex anterior groove is homologous to the cervical groove of the other Brachuyra. In our opinion, the true cervical groove of dorippids is the concave groove, as typically found in eubrachyuran crabs, and the convex groove could correspond to the 'precervical' groove of Holthuis & Manning (1990) (Fig. 5B-D). Why introduce a 'precervical' groove in the Dorippidae (when a groove of this name has never, to our knowledge, been given to other brachyuran crabs) except that this groove pattern is unique? It is not mentioned in the *Crustacea Glossary* and, moreover, it is very exceptionally mentioned in other crustaceans. Furthermore, in the papers on Dorippidae published after Holthuis & Manning (1990), which are rather rare for the extant fauna but more numerous for the fossils dorippoids (see below, *Palaeontological data* and *Appendix 2*), there is no mention of a precervical groove. Is this dorippid precervical groove not homologous to the other brachyuran grooves? Is it exclusive to the family? This is our conviction.

A historical reminder is in order. According to H. Milne Edwards (1851: 9-32, pl. 8, figs 6-10), the cervical groove demarcates the boundary between the cephalic arch and the scapular arch ("arceau céphalique" and "arceau scapulaire", respectively), and is located just behind the urogastric area in the eubrachyuran species studied. These data and figures, together with the topographic nomenclature of the carapace regions by Dana (1851), have been compiled and illustrated by schematic reconstructions (Fig. 6A-D) (Guinot 1976: 6-9, fig. 1; 1979a: 37-46, fig. 7). According to Davie *et al.* (2015a: 35, fig. 71-2.11A), who reproduced without modification the schematic figure 1 of a dorippid published by Holthuis & Manning (1990: fig. 1), "the cervical groove lies transversely across the middle of the carapace between the gastric and cardiac region, and is sometimes considered to separate head and thorax". This corresponds to the (1851) H. Milne Edwards' interpretation (Fig. 6A, B) and means that the cervical groove must be more posterior than shown in their schematic figure 1. In other words, the brachyuran cervical groove of H. Milne Edwards (1851) does not partition the gastric region but separates it from the cardiac region.

The interpretations of many authors correspond to that of H. Milne Edwards (1851): Pearson (1908: 10-12, fig. 2) for *Cancer* Linnaeus, 1758; Schmitt (1921: fig. 6) for a cancrid, adapted from Pearson (1908); Rathbun (1918) showing a grapsoid crab; and Balss (1940: 45, fig. 31) reproducing a Rathbun's figure. Chace & Hobbs (1969: 49, 224, Glossary, fig. 4, for a generalised crab, freshwater or terrestrial) consider that the cervical groove separates "the gastric and hepatic regions from the cardiac and branchial regions". Poore (2004: 553, Glossary) situates the "cervical groove across the middle of the carapace between gastric and cardiac regions". In contrast, Abrahamczik-Scanzoni (1942) places the cervical groove between the metagastric and urogastric areas, above the location of the gastric pits. In the schematic views of her numerous important revisions, Rathbun (1918: 4, 6, fig. 1, for a grapsoid; and 1930: fig. 1 for a portunid) correctly represents the cervical groove (as 'cervical sulcus') and interprets it as separating the gastric regions from the branchial and cardiac regions, thus behind the urogastric region. However, in the diagrammatic view of a majoid (Rathbun 1925: fig. 1), the location of the cervical groove is unclear: between the metagastric and urogastric areas or posterior to the urogastric area? The diagrammatic figure of Rathbun (1937: fig. 1), in her revision of *Oxystomatous and allied crabs of America* that includes the podotreme crabs, does not indicate any groove in *Ethusa* Roux, 1830, and two grooves (often called 'sutures'), cervical and branchial, are considered.

According to H. Milne Edwards (1851: 12), "the approximate direction of the cervical groove is first recognised by two small pits which correspond to the insertion of the posterior stomach muscles and which are usually seen in the middle of the carapace near the midline, a little in front of the posterior margin of the cephalic arch" (*on en reconnaît approximativement la direction, d'abord à l'aide de deux petites fossettes qui correspondent à l'insertion des muscles postérieurs de l'estomac, et qui se voient d'ordinaire au milieu de la carapace près de la ligne médiane, un peu en avant du bord postérieur de l'arceau céphalique*). The gastric pits are lying on the groove that separates the metagastric region from the urogastric region and mark the boundary between these two regions. They cannot therefore mark the cervical groove, which is posterior; they were depicted by H. Milne Edwards (1851: pl. 12, figs 6, 9, respectively) on the carapaces of *Mithrax spinosissimus* (Lamarck, 1818) and *Zosimus aeneus* (Linnaeus, 1758) (Fig. 6A, B). However, according to some authors (including Holthuis & Manning 1990), the gastric pits are associated with the cervical groove, being located on its course, and, in fact, their location is represented in a highly variable way in the literature (see Discussion in Guinot 1976: 6; 1979a: 37, fig. 7).

Depending on the authors and groups considered (and even more so if podotreme crabs are included), it appears that the interpretation of the cervical groove in relation to the gastric pits is highly variable, with the gastric pits (also called 'cervical pits') being positioned either behind the cervical groove or on the cervical groove itself, leading to confusions (Klompmaker *et al.* 2019, 2020). Numerous surveys have been conducted on the carapace and its grooves in Decapoda by neontologists (Boas 1880; Huxley 1877; Bouvier 1896; Pearson 1908; Renaud 1977) and many palaeontologists (e.g. Van Straelen 1925; Glaessner 1933, 1969; Secretan 1964, 1966, 1972; Bishop 1978: fig. 4; Förster 1979: fig. 4; 1985; Müller *et al.* 2000; Starzyk 2013, 2020; Krzemińska *et al.* 2021; Artal *et al.* 2022: fig. 2; Ferratges *et al.* 2022: fig. 3), and others. Recently, Van Bakel *et al.* (2020: 1, 3, 7, 14, 19) discussed "branchial condensation", i.e., "the ratio between the median carapace portion and the relative distance of the branchial groove to the cervical groove", and its various gradations: developed in basal forms and reduced or even absent in more derived forms, with the branchial groove gradually shifting towards the cervical groove, the two grooves finally morphing into a single groove, the cervical groove.

The conspicuous markings that outline a 'human face' on the dorsal surface of basal crabs correspond to the points of the internal muscle attachments (sigilla) (Abrahamczik-Scanzoni 1942: 354, figs 50, 63; Glaessner 1969: R408, fig. 224; Renaud 1977: 577, fig. 4; Klompmaker *et al.* 2019). In the process of carapace evolution in Decapoda, the transformation of the cylindrical cephalothorax of long-bodied decapods, which possess a much elongated attractor epimeralis muscle, into a shortened carapace results in the forward displacement of the posterior end of this muscle insertion (Glaessner 1933: 184, fig. 3; 1960: 36, fig. 16; 1969: R408, figs 224, 225, 227). One of the consequences of this transformation is the displacement of several muscles, which makes it difficult to establish a homology between their attachment areas on the carapace and the corresponding grooves. This major change probably also explains the problem of finding homologies between the grooves of podotremes and eubrachyurans. Only a thorough and modern study (including fossils) of the carapace, its regions and grooves should be able to identify homologies and provide new diagnostic characters for a better understanding of the ground plan of brachyurans. It is beyond the scope of this paper to address these points, and we will focus on the Dorippidae.

Ortmann (1892), Alcock (1896), Serène & Romimohtarto (1969) in their revisions of Dorippidae, as well as Chen in several papers (Chen 1980, 1986a, b, 1988, 1993) and probably Chen & Sun (2002, Chinese text) do not address the issue of grooves on the carapace at all. In their papers on fossil dorippoids, Larghi (2004), Luque (2015) and Van Bakel *et al.* (2020) refer only to the terminology of schematic figure 1 of Holthuis & Manning (1990), without any discussion of the newly introduced precervical groove in the nomenclature of the brachyuran integumentary system. Ng & Rahayu (2002) in describing a new *Neodrippe* follow Holthuis & Manning (1990) in identifying a cervical groove and a branchial groove.

It should be noted that the name 'hepatic furrow' is given to the precervical groove by some palaeontologists, such as the eminent Morris & Collins (1991: 5, as *Dorippe* (*Dorippe*) *frascone tuberculata*) and Collins *et al.* (2003: 200, as *Heikea tuberculata*), in their record of a true dorippid from the Miocene: they do not mention a branchial groove and describe a wide, fairly deep, and broadly V-shaped 'cervical groove' and a 'hepatic furrow'. A hepatic groove, corresponding to the precervical groove, is also recognised by Crônier & Boursicot (2009: fig. 2) and by Collins *et al.* (2020: 42, fig. 8A). A convex precervical groove is also visible in some telamonocarcinids, the extinct representatives of the Dorippoidea (see Appendix 2).

By comparison, in the Ethusidae the carapace has only faint grooves on the dorsal surface, which sometimes is not even grooved at all; it usually seems to be slightly more subdivided in *Ethusina* Smith, 1884 than in *Ethusa.* In fact, the two cervical and branchial grooves corresponding to the figure 1 of Holthuis & Manning (1990) for the Dorippidae (Fig. 5A) are usually so faint and shallow in ethusids that it is difficult to recognise a convex precervical groove, at least in extant species. These grooves are merely mentioned by Rathbun (1937, as 'sutures'), by Castro (2005) in his revision of the subfamily Ethusinae, by Castro (2013) in *Ethusa*, and by Ahyong & Ng (2008) in two new species of *Ethusina*.

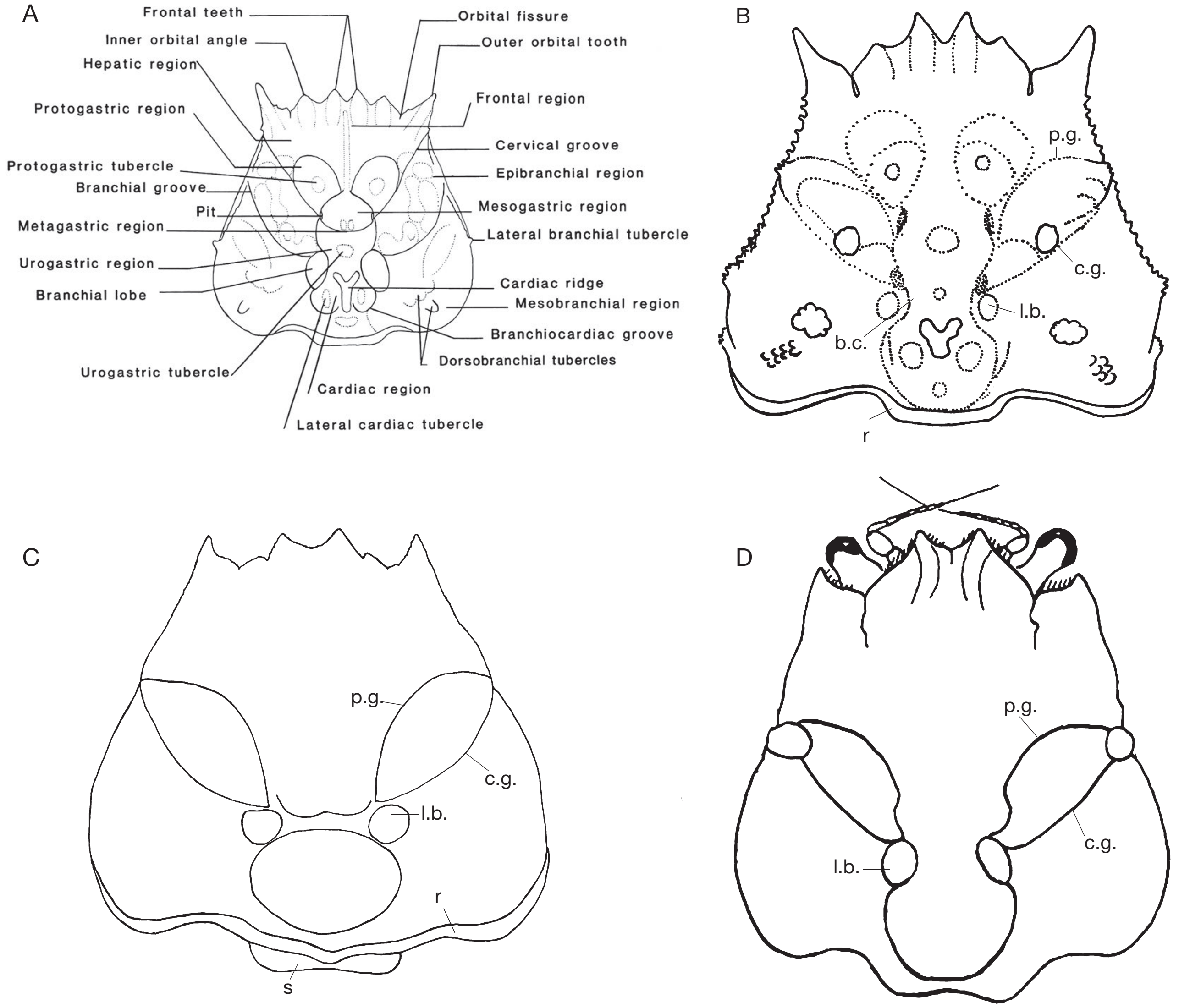

Fig. 5. — Terminology of main grooves on dorsal carapace of Dorippidae: **A**, diagrammatic figure of Holthuis & Manning (1990: fig. 1, based on a *Dorippe* species) without any mention of 'precervical groove'. **B**-**D**, terminology used in the present paper and only partially used by Holthuis & Manning (1990). **B**, *Dorippe tenuipes* Chen, 1980: after Holthuis & Manning (1990: fig. 18a); **C**, *Heikeopsis japonica* (von Siebold, 1824): after Holthuis & Manning (1990: fig. 30a, as *Heikea japonica*); **D**, *Neodorippe callida* (Fabricius, 1795): after Holthuis & Manning (1990: fig. 39). The strip, which runs posteriorly along the rim, was only figured in **C**. Abbreviations: **b.c.**, branchiocardiac groove; **c.g.**, cervical groove; **l.b.**, branchial lobe; **p.g.**, precervical groove; **r**, rim; **s**, strip.

Our purpose is not to criticise, but only to identify and name the two main grooves of the Dorippidae. As the family displays in many respects a wide range of original characters that are not shared with other Brachyura, we will choose to retain the denomination, although unusual, of 'precervical' for the anterior convex groove. There remains the question of the posterior V-shaped groove: is it cervical or branchial? In fact, the term 'branchial' is not used to designate a groove in extant Eubrachyura. It is found mainly in descriptions of podotreme crabs: Dromiidae (Rathbun 1937; McLay 1993: 166, fig. 17a, b; Guinot & Tavares 2003); Dynomenidae Ortmann, 1892 (McLay 1999: fig. 1a); Homolidae H. Milne Edwards, 1837 (Rathbun 1937; Guinot & Richer de Forges 1995: fig. 1A, B); Homolodromiidae (Guinot 1995: fig. 2B), and thus very frequently in the descriptions of fossil species. We have therefore decided, on the basis of our interpretation in accordance with that of H. Milne Edwards (1851) (Figs 5B-D; 6), to call the long concave, V-shaped posterior groove 'cervical', following Holthuis & Manning (1990) descriptions of *Paradorippe cathayana* and *Nobilum histrio*, but not their schematic figure 1 (Fig. 5A) and most of their text. In species of *Dorippe* (Figs 5B; 10, 12A; 14A, E, H; 15A, C, E, F) and in *Medorippe lanata* (Fig. 22A, B), whose gastric area is clearly subdivided into meso-, meta- and urogastric regions, the pair of gastric pits is visible just behind the metagastric region and not on the cervical groove, in accordance with H. Milne Edwards' (1851) definition. In other species whose dorsal surface is poorly sculptured and whose metagastric region is not well delimited from the mesogastric region, the gastric pits are located at the base of the meso-metagastric region, just in front of the groove that separates it from the urogastric region, thus as observed in other Eubrachyura. In

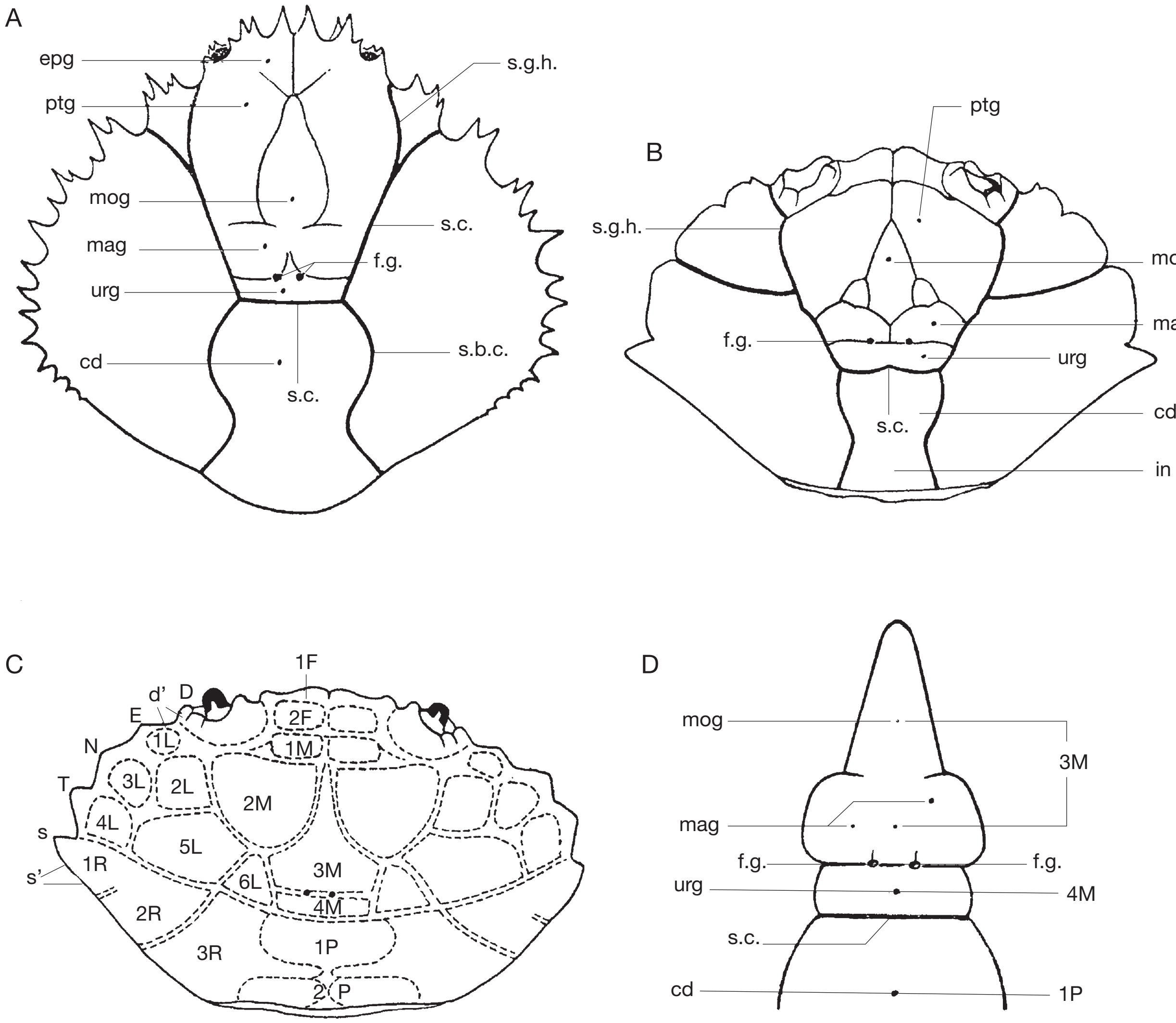

Fig. 6. — **A**-**C**, nomenclature of various carapace regions and location of cervical groove in Eubrachyura, exemplified by: **A**, *Mithrax spinosissimus* (Lamarck, 1818); **B**, by *Zosimus aeneus* (Linnaeus, 1758), according to H. Milne Edwards (1851: pl. 8, figs 6, 9, respectively); **C**, by a species of '*Cancer* group' with numbered regions, according to Dana (1851: 95-98, fig. 1); **D**: homology of gastric regions defined by H. Milne Edwards (1851) and those numbered by Dana (1851) (after Guinot 1979a: fig. 7D). Abbreviations: **cd**, cardiac region; **epg**, epigastric lobe; **f.g.**, gastric pit; **in**, intestinal region; **mag**, metagastric region; **mog**, mesogastric region; **ptg**, protogastric lobe; **s.c.**, cervical groove; **s.b.c.**, branchiocardiac groove; **s.g.h.**, hepatic groove; **urg**, urogastric region.

fact, in dorippids the gastric pits are very small and not clearly discernible at first sight, but examination of many specimens finally allows us to detect them always in the same location. Dissections confirm that in Dorippidae the two tiny gastric pits correspond to two robust endophragmata as stated by Guinot (1979a: 44). The dorippid gastric pits should not be confused with two other deeper, longer and more visible oblique pits, positioned more anteriorly on either side of the mesogastric region.

It should be noted that the two dorsal grooves are already distinct in the megalopa and first crab stage of *Heikeopsis japonica*, and arranged as in adults (Quintana 1987: fig. 8A, C, as *Nobilum japonicum japonicum*); in *Paradorippe granulata* only the trace of a curved groove is visible in the megalopa, but the two main ones are discernible in the first stage (Quintana 1987: fig. 15C, E, respectively); no groove is detectable in the megalopa and first stage of *Dorippe sinica* (Quintana 1987: fig. 3B, D, as *Dorippe frascone*), a species in which the adults have a more sculptured and tuberculate dorsal surface.

The fact that the original groove pattern requires the use of special nomenclature in the Dorippidae is not really unexpected and is consistent with the many other characters that are unique to this family and set it apart from other Eubrachyura. The region bounded by the precervical and cervical grooves, the narrow epibranchial region is obliquely oriented in living and fossil dorippids, an arrangement very rarely found in other Eubrachyura.

There are also even more enigmatic carapace grooves in the Hymenosomatidae that are likewise unique to Brachyura and are autapomorphic, but they are difficult to compare with the dorippid grooves. Nevertheless, the proposal (Guinot 2011) of possible relationships between dorippids (Heterotremata) and hymenosomatids (still considered until recently as "part of the Thoracotremata", see Kienbaum *et al.* 2018b: 518, also

Kienbaum 2019) could remain valid, unless the shared features (Guinot *et al.* 2013: 221) correspond only to evolutionary transformation and convergence, which would require a re-evaluation of this hypothesis.

Some particular morphological characters of Dorippidae

Dorsal exposure of first pleonal somites. The incomplete folding of the pleon and the strong posterior thoracic curvature lead to a dorsal exposure of the first pleonal somites, which are thus located in the prolongation of the dorsal carapace and visible dorsally in both sexes, generally more pronounced in females: the first and second pleonal somites are exposed dorsally in males (Figs 1B; 7A, B; 8B; 9D), whereas the first three somites and often part of the fourth are exposed dorsally in females (Figs 1A, C; 8A, C; 9C). This feature is shared with many podotremes and, to a lesser degree, with various eubrachyurans such as *Corystes* Bosc, 1801, *Carcinus* Leach, 1814, *Litocheira* Kinahan, 1856 or *Ocypode* Weber, 1795.

Articular membranes at the flexion site of pleonal tergites. The unfolded pleon of long-bodied Decapoda requires simultaneous extension and flexion of each pleonal somite through special integumentary joining structures and hinges by which they articulate with each other, thus allowing movements (Drach & Jacques 1982). The reduced pleon of Brachyura does not require such movements and differs essentially in the arrangement of the articulation hinge between the somites. However, some podotremes with a variously curved and arched pleon exhibit different character states of pleonal articulation; they maintain plesiomorphically externally conspicuous articular membranes between the pleonal somites at the site of tergite flexion, in fact between the first four or five somites such as in Homolodromiidae and Homolidae (Guinot *et al.* 2013: fig. 51C, E, respectively). In Eubrachyura, where the pleon generally becomes flattened and straighter, the articular membranes at the site of tergite flexion tend to be lost. However, in the Dorippidae small articular membranes (laterally narrowing) are located at the sites of flexion of pleonal tergites, i.e., between all pleonal somites and across the width of each somite in both sexes, such as in *Medorippe lanata* (Fig. 7D), and more or less developed depending on the species (difficult to quantify). A review of the pleonal articulation would deserve a study in all brachyuran families.

Dorsal exposure of last thoracic sternites. Posterior thoracic curvature, clearly correlated with incomplete pleonal unfolding, may affect the posterior part of the thoracic sternum to a greater or lesser extent in both sexes, usually more marked in females. An inclination of the last thoracic sternites relative to the preceding ones characterises podotremes (Dromiidae, see Guinot & Tavares 2003; Homolidae, see Guinot & Richer de Forges 1995; Guinot *et al.* 2013; Homolodromiidae, see Guinot 1995; Cyclodorippidae and in particular Cymonomidae Bouvier, 1897, see Poore 2004; Ahyong & Ng 2008, 2017; Ahyong 2019). But in basal podotremes, the P5 and P4 coxae are adjacent to pleonal somites and no sternal part is exposed dorsally.

In Dorippidae the dorsal exposure of the first two pleonal somites is complemented in both sexes by dorsal exposure of sternites 8 and 7, which are thus also visible dorsally (Figs 1; 7A, B; 8; 9C, D; 33). In females of some genera, sternite 8 bears a tubular process, called here 'retention process', which overhangs the pleon in the proximal part of somite 2 and holds the female pleon at its base (Figs 8C; 9C) (see below, *Pleonal-locking retention process of sternite 8 in females*, p. 250).

A large dorsal exposure of thoracic sternites 7 and 8 in both sexes is a truly unique dorippoid feature (Dorippidae and Ethusidae, see Table 1), in fact the condition that allows P4 and P5 to be carried dorsally. In Palicidae, another family of eubrachyurans in which there is also carrying behaviour but only through the dorsal location of P5, a very small portion of sternite 8, namely the anterior margin, is exposed dorsally (Guinot *et al.* 2013: fig. 32A, B, E). In Retroplumoidea Gill, 1894, with no known carrying behaviour, a tiny portion of sternite 8 and a large portion of sternite 7 are exposed dorsally (Saint Laurent 1989: fig. 23a; Guinot *et al.* 2013: 138, fig. 34). In Litocheiridae Kinahan, 1856, a small portion of sternite 8 is exposed (see Guinot *et al.* 2013: 117, fig. 25F). In Hexapodidae Miers, 1886, which shows a strong modification of somite 8, the dorsally visible sternal portion varies in size, shape, and orientation between species (see Guinot *et al.* 2013: 121, fig. 27).

Dorsal location of both P4 and P5 (Figs 1; 8, 9 *sqq*.). The incomplete folding of the pleon and the posterior thoracic curvature lead to a dramatic change in the alignment of the arthrodial cavities and induce a dorsal location of P4 and P5, which become instrumental for carrying behaviour. They are reduced, subdorsal/dorsal, mobile to the point of being held on the back, and provided with a specialised subchelate ending, in a manner that resembles the pattern of basal podotremes (Guinot *et al.* 1995: 387, figs 4A, 5D; Guinot & Wicksten 2015: fig. 71-11.8.A-C).

Dorsal exposure of lateral portions of pleurites 5-7 (Fig. 7A, B). In Dorippidae, pleurites 5-7 have part, albeit reduced, of their latero-external ends exposed and inserted into a gutter, termed the 'setting gutter' (Guinot *et al.* 2013: figs 46A, B, 47A, B, *Medorippe lanata*). These exposed pleurites, on which each corresponding pereiopod is articulated by its coxo-pleural condyle, are not parts of the carapace but belong to the axial skeleton that is uncovered at this level. Pleurite 4, at the cheliped level, is entirely covered by the carapace, as it normally is, but this is not the case for pleurites 5-7. Pleurite 5, at the P2 level, is partially exposed, its posterior portion forming a small but salient sclerite (sclerite 5); pleurite 6, at the P3 level, is largely exposed across the entire breadth of the P3 coxa and is crossed by the gutter in which the carapace margin lies; the exposed pleurite 7, at the P4 level, is obliquely oriented, narrow, and also receives the carapace margin; no pleural part is exposed at the P5, which is dorsally oriented and serves for carrying behaviour. This peculiar disposition, not noticed until recent years, is unique to Dorippoidea and thus represents a synapomorphy

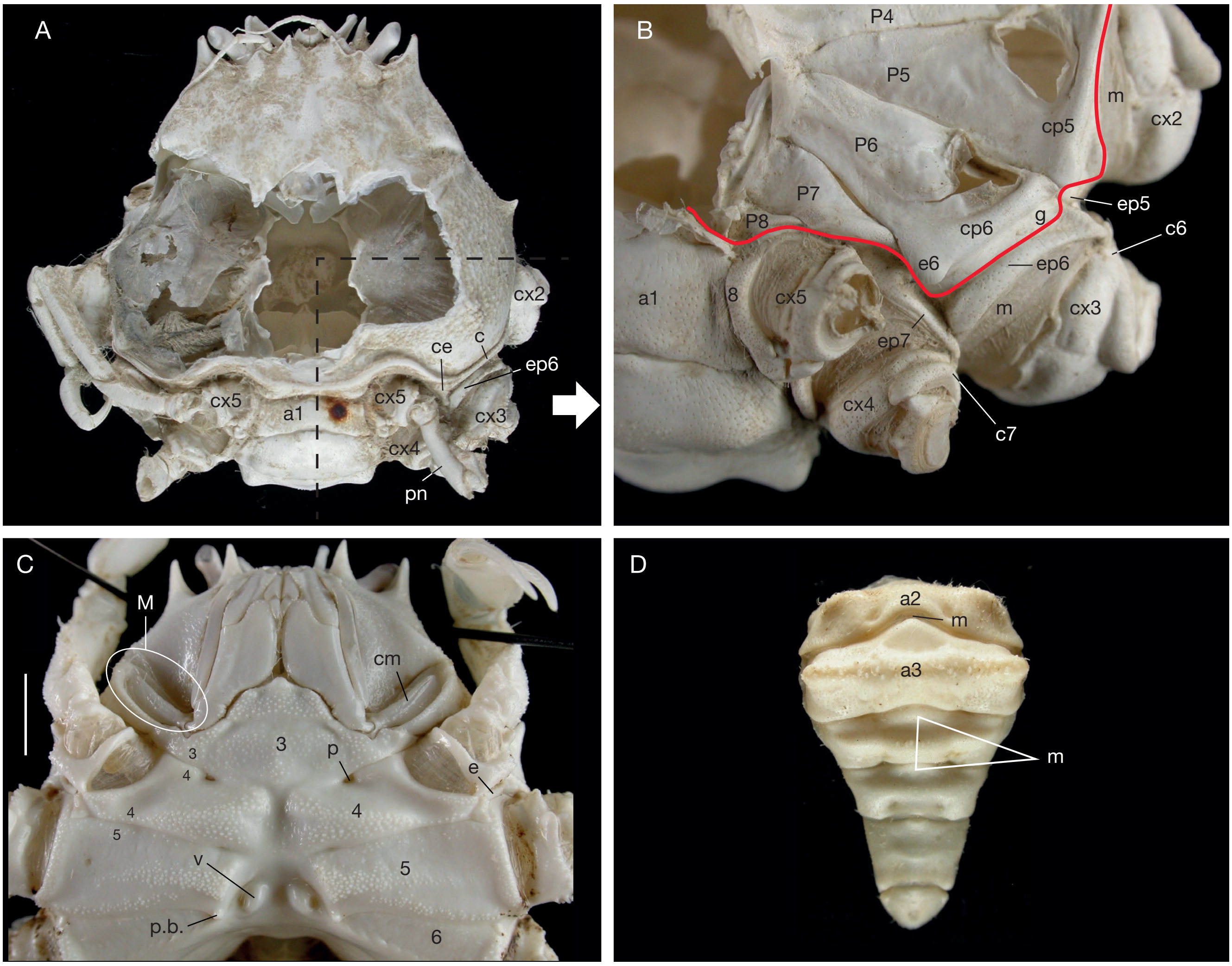

Fig. 7. — **A**, **B**, exposure of latero-external ends of pleurites 5-7 in *Medorippe lanata* (Linnaeus, 1767), skeleton prepared by S. Secretan, MNHN: **A**, carapace (partially removed) covering all pleurites except exposed latero-external portions of pleurites 5-7; **B**, close-up view of lateroposterior region of carapace to show calcified exposed external portion of pleurites 5-7, with setting gutter for carapace; **red line** indicates location of carapace margin. Modified from Guinot *et al.* (2013: fig. 46A, B). **C**, thoracic sternum/pterygostome junction, oxystomatous condition, Milne Edwards openings in *Medorippe lanata* (Linnaeus, 1767), ♀ 17.8 × 23.0 mm, Mediterranean Sea (MNHN, skeleton prepared by S. Secretan). Modified from Guinot *et al.* 2013: fig. 42C. **D**, articulation of pleonal somites, dorsal view of female *Medorippe lanata* (Linnaeus, 1767). Modified from Guinot *et al.* (2013: fig. 51G). Abbreviations: **a1-a3**, first to third pleonal somites; **c**, carapace margin; **ce**, ventral extension of carapace posterior margin; **cm**, mxp3 coxa; **cp5**, **cp6**, calcified portion of pleurites 5, 6 covered by carapace; **cx2**-**cx5**, coxae of P2-P5; **c6**, **c7**, coxo-pleural condyles of P3, P4; **e**, sternal extension; **e6**, extension of pleurite 6 covered by carapace; **ep5**-**ep7**, exposed pleurites 5-7; **g**, setting gutter of carapace; **M**, Milne Edwards openings as pterygostomial slits; **m**, articulating membrane; **p**, sternal boutonniere of suture 3/4; **pn**, penis; **pt**, pterygostome; **p.b.**, press-button; **r**, rim; **s**, strip; **t**, telson; **v**, vulva on a prominence and with operculum; **3-6**, thoracic sternites 3-6; **8**, exposed portion of thoracic sternite 8; **3/4**, **4/5**, thoracic sternal sutures 3/4, 4/5.

of the superfamily (Guinot *et al.* 2013). In this paper, the modalities of exposure of the lateral parts of pleurites 5-7 in the different species could not be documented because this examination requires extensive cleaning of the carapace in the region of the pereiopod joints and its removal at this point, which could damage the specimens.

To recapitulate, consistent features in dorippids are: pleurite 5 exposed posteriorly as small but variously prominent and ornamented sclerite; pleurite 6 widely exposed across the entire width of P3 coxa; and pleurite 7 forming narrow, obliquely oriented exposed sclerite. Interpretation is sometimes difficult in species with developed callosities (Figs 9D; 33) (see below, *Callosities, unique structures at the base of P3 in Dorippinae n. stat. and Dorippoidinae n. subfam.*, p. 309).

Branchiostegite. The branchiostegite (portion of the carapace that covers the branchial chamber at the thoracic level) is variously reduced in the Dorippidae: more or less strongly restricted, it may be missing at the level of the last pereiopods. In contrast, the branchiostegite is present in the Ethusidae (Guinot *et al.* 2013: fig. 42A).

Respiratory system and thoracic sternum/pterygostome junction. The Dorippidae is characterised by an oxystomatous disposition (Fig. 7C), i.e., the forward extension of the buccal frame: closure of the endostomal gutter by the mxp1, their calcified endopods forming the floor of the gutter; openings of exhalant channels being at the extremity of the elongated endostome produced forwards, these efferent openings being

Fig. 8. — Particular structures of some dorippids: **A**, **B**, rim and strip along posterior margin of carapace: **A**, *Dorippoides facchino* (Herbst, 1785), ovigerous ♀ 20.3 × 26.2 mm, South China Sea, ZRC 1984.5347; **B**, *Paradorippe granulata* (De Haan, 1841), ♂ 23.6 × 27.3 mm, NE Taiwan, ZRC 2001.0014; **C**, retention of female pleon by process of sternite 8 overhanging pleonal somite 2: *Dorippe quadridens* (Fabricius, 1793), ♀ 38.1 × 33.7 mm, South China Sea, Hee Huat, ZRC 1984.6307; **D**, retention of telson engaged between edges of sternite 5: *Dorippoides facchino* (Herbst, 1785), ovigerous ♀ 20.3 × 26.2 mm, same data as **A**. Abbreviations: **cx3**-**cx5**, coxae of P3-P5; **p**, process of sternite 8; **p2**, **p3**, pereiopod 2, 3; **r**, rim; **s**, strip; **sp**, spur-like process on P3 ischium; **1**, pleonal somite 1; **7**, **8**, dorsally exposed thoracic sternites 7, 8.

visible or not in dorsal view depending on the genera; afferent branchial openings pre-chelipedal, receiving the developed, calcified mxp3 coxa; Milne Edwards openings ovate, elongated, margins surrounded by dense setae, separated from the chelipeds due to the fusion of sternite 3 with pterygostome (thoracic sternum/pterygostome junction). The exopodite of mxp3 lacks a flagellum.

Sternal extensions. Lateral outgrowths of the sternites connect the thoracic sternum to the carapace at the suture levels. Formed by two consecutive sternites (i.e., double), they are inserted respectively between P1 and P2, between P2 and P3, and between P3 and P4 respectively (Guinot *et al.* 2013: fig. 42C). The arthrodial cavities of the pereiopods are surrounded by sclerites.

Coxo-sternal condition. The male gonopore is coxal and the penis very long in Dorippidae. The coxo-sternal condition (Guinot 1978: 244; 1979b: 45 footnote) is but one of several mechanisms for the protection of the penis, only a variant of the coxal condition, with the ejaculatory duct perforating the P5 coxa. The Dorippidae offers multistate characters of penis protection (Guinot *et al.* 2013: 99-105, figs 15-19), varying from a (nearly) coxal pattern in *Medorippe lanata* to various patterns in other genera. Such a configuration is not found in any family of Eubrachyura, and such a range of variation within a family is also unparalleled.

New morphological features of Dorippidae

Rim of carapace posterior margin and posterior strip (Figs 5C; 8A-C; 9C, D sqq.)

In Dorippidae, the straight posterior margin of the carapace (concave in fossil representatives, see Guinot *et al.* 2019: 300; and below, *Palaeontological data* and *Appendix 2*) forms a thick, often protruding rim that, depending on the species, may extend to varying degrees along the posterolateral margins, shaping a more or less deep concavity at the level of each P5 coxa and gradually narrowing laterally. In addition, this rim may be lined posteriorly in both sexes by a smooth, more or less conspicuous and individualised strip that separates the

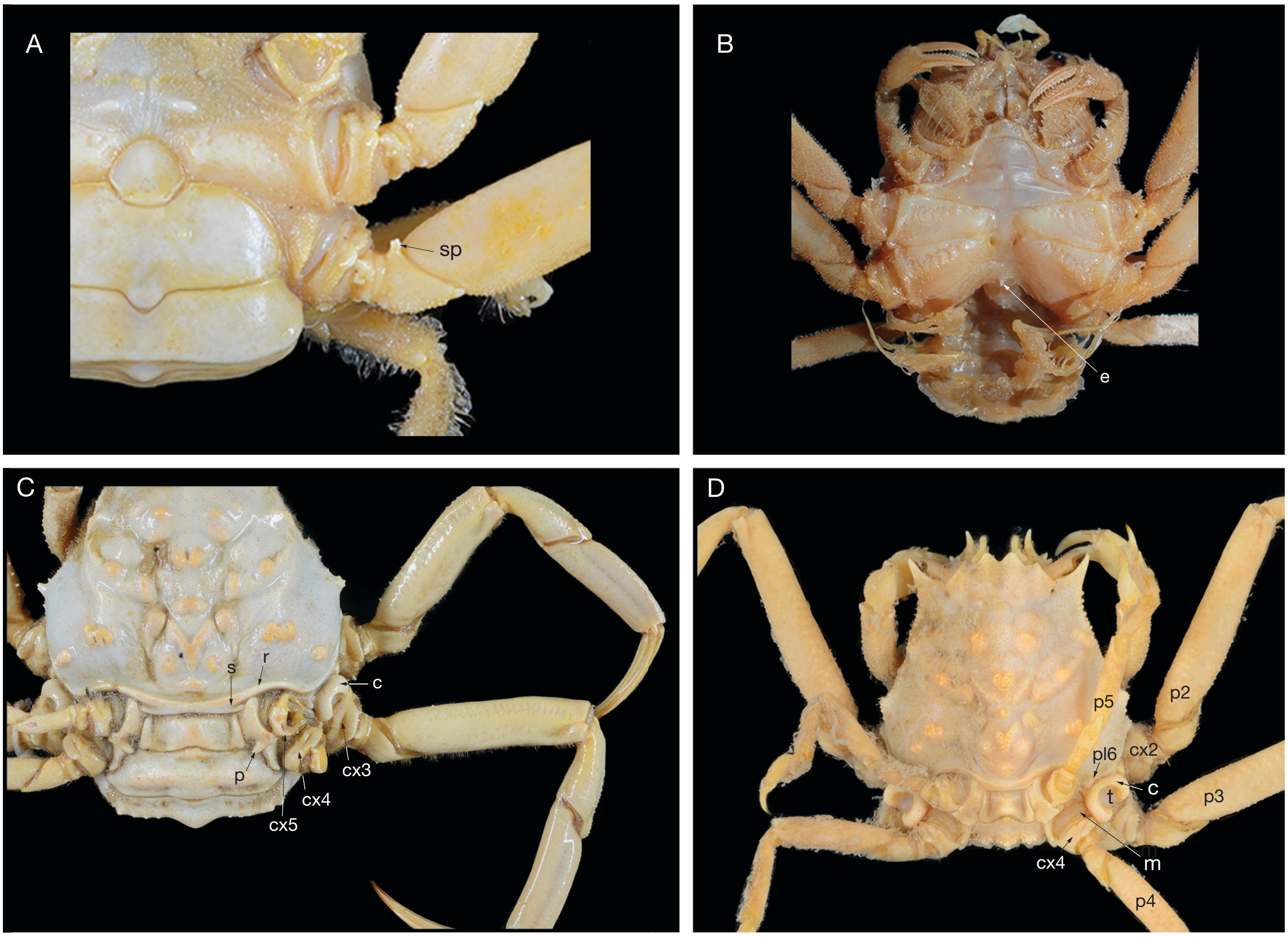

Fig. 9. — Particular structures of some dorippids: **A**, spur-like process on ischium of P3 and sometimes P2: *Dorippoides facchino* (Herbst, 1785), postpubertal ♀ 19.0 × 22.0 mm, Pondicherry Bay, Maindron coll. 1882, MNHN-IU-2018-5199 (= MNHN-B19817). **B**, erect spine on sternite 8: *Neodorippe callida* (Fabricius, 1795), ovigerous ♀ 13.5 × 14.3 mm, Amoy, MNHN-IU-2021-8738 (= MNHN-B11170). **C**, **D**, callosity at base of P3: **C**, *Dorippe sinica* Chen, 1980, ♀ 34.8 × 38.9 mm, China, Guangdong, Nanao Island, ZRC 1999.0470; **D**, *Dorippe tenuipes* Chen, 1980, ♂ 13.2 × 14.2 mm, South China Sea, ZRC 1999.0009 (the granules on P2 and P3 are not visible in the photograph). Abbreviations: **c**, callosity; **cx2-cx5**, coxae of P2-P5; **e**, erect spine; **m**, articulating membrane; **p**, process of sternite 8; **pl6**, exposed pleurite 6; **p2-p5**, pereiopods 2-5; **r**, rim; **s**, strip; **sp**, spur-like process; **t**, special texture area.

rim from the first pleonal somite and which should not be confused with the latter. This strip has nothing to do with an integument connecting the pleon to the carapace either. When the authors' drawings are too rough, or the photographs are too small or blurred (as in Serène & Romimohtarto 1969), it is not possible to clearly distinguish the arrangement at the posterior margin of the carapace. The existence of this strip, not mentioned by Holthuis & Manning (1990) although depicted in their drawings of most species, has not been reported in the literature, except for one figure of *Medorippe lanata* by Guinot (1979a: fig 28, as *Dorippe lanata*, '*ce*' meaning 'ventral extension of carapace posterior edge') and a brief commentary by Guinot *et al.* (2019: 299, fig. 46A) establishing it as a peculiarity of the Dorippidae.

As it should normally conform to the adjacent pleon, which is narrower in males than in females, the strip should be sexually dimorphic, but this is not always the case (e.g. in species of *Dorippe* where it has about the same shape and size in both sexes, see below). The strip varies in shape and size. It is indistinct in one taxon, *Phyllodorippe armata*, in both sexes (Fig. 29A, B). In *Philippidorippe philippinensis*, the thin rim is bordered posteriorly by a weakly developed strip in males, hardly thickened laterally in females (Fig. 27A, B). In *Medorippe lanata*, there is also a thin strip, slightly thicker on each lateral side in females (Fig. 22A, B). In *Heikeopsis*, *Neodorippe* and *Nobilum* (Figs 1; 19A, B, E, F; 20A, B; 21A), the strip is narrow, thinner medially than laterally, thus slightly concave in both males and females. In species of *Dorippe*, the narrow and straight strip is similar in both sexes (Figs 9C, D; 10; 12A; 14A, E, H; 15A, C, E, F). In males and females of *Dorippoides facchino* (Figs 8A; 16A, B) and *D. nudipes* (Fig. 16C, D), the strip is so enlarged at each posterior corner that it appears to be flanked by two lateral extensions. In male *Paradorippe granulata* (Figs 8B; 24A), a straight, narrow but truly distinct strip seems to be inserted between the carapace and the first pleonal somite, whereas in the females (Fig. 24B) the strip, slightly depressed medially and bordered by a dense fringe of setae, seems continuous with the rim. What is the nature, the function of this structure that, on close examination, appears to be embedded in the rim itself and to correspond simply to an extension, a thickening that varies according to species, being more or less long, straight, laterally widened, or depressed? In any case, the strip is a part of the rim. In fossil dorippids, a rim is clearly present, whereas a strip is most often difficult to recognise, depending on the state of preservation of the carapace.

In the Ehusidae there is also a rim, sometimes quite wide but very low, barely demarcated and not extending laterally, in both sexes. The absence of a strip in all the extant ethusids we have examined could be another major difference between the two families. In contrast, in fossil ethusids, provided they are correctly identified, the rim would appear to be more pronounced, whereas a strip is mostly not perceptible; and the grooves and areolation of the carapace would sometimes be more apparent.

Pleonal-locking retention process of sternite 8 in females (Figs 8C; 9C)

A particular pleonal-retention mechanism, which has not been reported so far in the Dorippidae and, to our knowledge, not in other Brachyura either, characterises the females of *Dorippe*, *Heikeopsis*, *Nobilum*, *Philippidorippe* and *Phyllodorippe*, i.e., all dorippid genera except *Dorippoides*, *Medorippe*, *Neodorippe* and *Paradorippe*. Sternite 8, exposed dorsally at the level of P5 coxa, bears a tubular process that overhangs the pleon in the proximal part of somite 2. This device serves to retain the female pleon at its base, hence the name 'retention process' given here. It is easily visible in dorsal view of the females (and thus in photographs showing them in dorsal view) since both the sternites 7 and 8 and the first pleonal somites are exposed dorsally. This feature appears to be exclusive to the family Dorippidae (seemingly not present in Ethusidae, but not all have been examined), possibly unique to Brachyura, and needs to be documented.

In the same genera, the females have an additional modality of retention: the telson is engaged in the sterno-pleonal cavity that is narrower and constricted between the more or less raised edges of sternite 5 so that the pleon is also secured there, forming a kind of clasping apparatus.

Spur-like process on P3 ischium of females (Figs 8D; 9A; 18A, B)

A spur-like process on the ischium of P3 and sometimes also a smaller one on P2 are present in females of Dorippoidinae n. subfam. In both species of *Dorippoides*, *D. facchino* and *D. nudipes*, but only in females, the ischium of P3 bears a narrow, granular, variously tuberculated 'spur-like process' on its anterior margin, as termed by Holthuis & Manning (1990: 2, 48, fig. 26F). Given its position, its function would be to prevent the leg, when it folds, from straightening beyond a certain extent and to allow it to rest on the raised edge of the arthrodial cavity of the coxa. This spur-like process is absent in all other dorippids.

Erect spine on sternite 8

An erect axial spine in the fused medial part of sternite 8 (erroneously indicated on 'sternite 4' or 'sternite of P4' by Holthuis & Manning 1990) is present in females of four genera: *Heikeopsis*, *Neodorippe* (Figs 9B; 20G, H), *Nobilum*, and *Phyllodorippe* (Fig. 29D), and is absent in other dorippids.

Callosity on P3 coxae (Figs 9C, D; 33)

A unique novelty within the Brachyura characterises the species of Dorippidae belonging to only two genera, *Dorippe* and *Dorippoides*. Serène (1982: 1130, pl. 1, fig. 1, pl. 2, figs 1, 4, as *Dorippe miersi* and pl. 1, fig. 3, as *D. frascone*) described in two species of *Dorippe*, *D. tenuipes* and *D. quadridens* respectively, a whitish, cup-shaped outgrowth at the base of P3. This structure was later reported 'on the coxae of P3' and referred to as a 'sausage-like callosity' by Holthuis & Manning (1990: 2, 8, 48). But in fact several modalities can be actually recognised (Fig. 33): a simple pattern in the Dorippoidinae n. subfam. and three complex patterns, variously developed in the Dorippinae n. status. Only the external morphology will be described here, pending histological analysis.

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977

Superfamily DORIPPOIDEA H. Milne Edwards, 1837

Dorypiens H. Milne Edwards, 1837: 99.

Dorippiens H. Milne Edwards, 1837: 151, 153 *pro parte.*

Dorippina – MacLeay 1838: 69.

Dorippidea – De Haan 1841: 120; 1849: xvii (incorrect spelling [Opinion 688]).

Dorippoidea – Glaessner 1969: R492. — Guinot 1978: 245. — Guinot & Bouchard 1998: 673. — Ng *et al.* 2008: 59. — Guinot *et al.* 2013: 10; 2019: 288. — Davie *et al.* 2015b: 941; 2015c: 1076. — Emmerson 2016: 329. — Sasaki 2019: 7769.

REMARKS

The superfamily encompasses two families, Dorippidae and Ethusidae (as Ethusinae in 2005 Castro's revison) in the extant fauna. The family Orithyiidae Dana, 1852 is sometimes regarded as a third potential member (see *Relationships between Dorippidae and Orithyiidae*, p. 292).

Family DORIPPIDAE H. Milne Edwards, 1837

Dorippiens H. Milne Edwards, 1837: 151, 153 *pro parte.*

Dorippidae – Dana 1852: 390, 398; 1853: 1427 *pro parte.* — Miers 1886: 326 *pro parte.* — Ortmann 1892: 553 *pro parte.* — Bouvier 1897a: 784 *pro parte*; 1897b: 54-70 *pro parte*; 1898: 103-105 *pro parte*; 1940: 195 *pro parte.* — A. Milne-Edwards & Bouvier 1902: 35-39 *pro parte.* — Gordon 1963: 55; 1966: 353. — Serène & Romimohtarto 1969: 1-35. — Kim 1973: 287, 290 *pro parte.* — Guinot 1978: 247; 1979a: 101, 130, 139, 171, 176, 195, 241, 260, tables 3, 5; 1979b: 45, table 1. — Chen 1993: 316. — Dai & Yang 1991: 50. — Guinot & Bouchard 1998: 649. — Ng *et al.* 2008:

59; 2017: 35. — Guinot *et al.* 2013: 10; 2019: 300. — Davie *et al.* 2015c: 1077. — Luque 2015: 253. — Emmerson 2016: 330. — Sasaki 2019: 7770.

Dorippinae – Alcock 1896: 136, 273, 275-286 *pro parte.* — Ihle 1916: 137 *pro parte.* — Rathbun 1937: 75 *pro parte.* — Balss 1957: 1609. — Manning & Holthuis 1981: 28. — Chen 1986a: 181; 1986b: 119. — Holthuis & Manning 1990: 1-151. — Chen & Xu 1991: 57. — Guinot & Bouchard 1998: 649. — Chen & Sun 2002: 208.

Dorippidae – Dorippinae – A. Milne-Edwards & Bouvier 1900: 21.

Recognition of seven subfamilies within the Dorippidae

The species of Dorippidae, before 1969 all assigned to the single genus *Dorippe* Weber, 1795, were subsequently distributed into three new genera and two new subgenera (Serène & Romimohtarto 1969) and two further new genera (Manning & Holthuis 1981, as Dorippinae). Finally, a total of nine genera, including a new genus, were recognised by Holthuis & Manning (1990) in a comprehensive revision resolving a great number of previous misidentifications and confusions, which contributed considerably to a better understanding of the group. These authors were probably conscious of the differentiation within the group (at the time Dorippinae) as they provided a separate key to the genera based on the G1s that highlighted their extreme diversity. Since then, two new *Dorippe* species from Australia have been added (Manning 1993) and one species of *Neodorippe* described (Ng & Rahayu 2002); no new dorippid taxa have been established recently. Currently, the family contains a total of only nine genera and 27 species (Ng *et al.* 2008).

Although a small group with apparently similar general facies, the Dorippidae, on closer examination, displays great diversity in body form. The extent of variation and the occurrence of significant divergence patterns within the family have never led to the formal recognition of subfamilies, however. A tentative grouping of genera into a new taxonomic arrangement is proposed here, based on a re-evaluation of morphological characters, including the cephalic appendages, the configuration of the thoracic sternum, the male genital area, the gonopod structure, the vulvae, and the female reproductive system. Seven subfamilies are recognised: Dorippinae H. Milne Edwards, 1837 n. stat., Dorippoidinae n. subfam., Medorippinae n. subfam., Heikeopsinae n. subfam., Paradorippinae n. subfam., Philippidorippinae n. subfam., and Phyllodorippinae n. subfam.

Our results are congruent with known recovered molecular data. A first molecular analysis based on 16S rRNA gene sequence data from five species and four genera supported the recognition of the Dorippidae as a monophyletic family, consisting of two main clades, with the genus *Dorippe* appearing basal (Fan *et al.* 2004: figs 1, 2). A more complete phylogenetic tree inferred from three mitochondrial genes (16S rRNA, 12S rRNA, and COI) (Sin *et al.* 2009) showed several distinct clades, consistent with previous groupings based on overall carapace morphology and other traits, including G1 structure. The results were as follows: two main groups were supported, one with *Dorippe*, *Dorippoides*, *Medorippe*, and the other with *Heikeopsis*, *Neodorippe* and *Nobilum*; *Philippidorippe*, somewhat ambiguous, could be associated with the preceding three genera, however with relatively low branch support; the species of *Paradorippe* also formed a distinct clade, with a high intra-generic divergence, and could be a sister to *Heikeopsis*/*Neodorippe*.

Dorippids are characterised by simultaneous carrying behaviour using reduced, mobile, dorsally carried and subchelate P4 and P5 to hold various materials), forward locomotion (mixed with movements in all directions, including sideways) and fast forward burying: they can be categorised as 'forward-buriers' by relying on their bodies to penetrate soft substrates rapidly (see below).

Subfamily Dorippinae H. Milne Edwards, 1837
n. status

Type genus. — *Dorippe* Weber, 1795 (type species by subsequent designation by Holthuis [1962]: *Cancer quadridens* Fabricius, 1793; the type species of *Dorippe* Fabricius, 1798 is *Cancer quadridens* Fabricius, 1793 by subsequent selection by Latreille [1810], see Holthuis [1962]: 54; Holthuis & Manning [1990]: 7). Other included species: *Cancer frascone* Herbst, 1785; *Dorippe glabra* Manning, 1993; *Dorippe irrorata* Manning & Holthuis, 1986; *Dorippe sinica* Chen, 1980; *Dorippe tenuipes* Chen, 1980; *Dorippe trilobata* Manning, 1993.

Description

Carapace (Figs 10; 12A; 14A, E, H; 15A, C, E, F)

Carapace wider than long, being much wider than long in larger individuals, but always narrowing distinctly forward. Dorsal surface strongly sculptured, subdivided into several regions, rough, uneven, with distinct tubercles, often with setae obscuring surface ornamentation; meso-, meta- and urogastric regions well recognisable. Precervical groove irregular, indistinct. Cervical groove distinct, wide. Branchiocardiac groove deep, clearly defined. A pair of small branchial lobes. At base of meso-metagastric region, two small, oblique, hardly distinct submedian gastric pits. Between base of outer orbital tooth and cervical groove, anterolateral margin of carapace long, with a few or many tubercles or denticles, otherwise smooth. Posterior margin of orbit with fissure. Outer orbital tooth triangular, slender and pointed, reaching beyond frontal teeth. Epibranchial angle marked, may be with spine. Front consisting of two closely spaced triangular submedian teeth, separated by more or less deep V-shaped emargination. Inner orbital teeth about as large as frontal teeth, reaching less far forward. Lower orbital margin with spines on outer margin of inner suborbital tooth. Carapace rim extending along posterolateral margin, lined posteriorly by narrow, straight strip, similar in both sexes.

Illustrations: *Dorippe glabra*: Manning 1993: fig. 1a, b. *D. frascone*: Herbst 1785: pl. 11, fig. 70 (reproduced by Holthuis & Manning 1990: fig. 3); Serène & Romimohtarto 1969: figs 1, 5, 10, 15A, B, pl. 1, figs A, B, pl. 3, figs A-C, as *Dorippe* (*Dorippe*) *frascone*); Chen 1980: fig. 3.2, pl. 2, figs 1, 6, *as D.* (*D.*) *frascone*; Holthuis & Manning 1990: fig. 2a. *D. irrorata*: Holthuis & Manning 1990: fig. 4a-c. *D. quadridens*: Latreille 1818: pl. 306, fig. 1; Guérin ?1831-1833: pl. 13, fig. 2, as *D. nodulosa* (reproduced by Holthuis & Manning 1990: fig. 10A); Griffith & Pidgeon 1833: pl. 13, fig. 2, as *D. nodulosa* (reproduced by Holthuis & Manning 1990: fig. 10B); De Haan 1839: pl. 31, fig. 3, as *D. quadridens* (reproduced by Holthuis & Manning 1990: fig. 15); Borradaile 1903: pl. 22, fig. 1, as *D. dorsipes* (reproduced by Holthuis & Manning 1990: fig. 11b); Shen 1931: fig. 5 (reproduced by Holthuis & Manning 1990: fig. 11a; by Sin *et al.* 2009: fig 3A); Chen 1980: fig. 2a, b (reproduced by Holthuis & Manning 1990: fig. 12a); Holthuis & Manning 1990: figs 5a, 7a, 8, 9; Chen & Sun 2002: fig. 89.3, pl. 2.3; Naruse *et al.* 2014: fig. 2c; Takeda *et al.* 2019: 13, pl. 3E, F; Wong *et al.* 2021: fig. 8a, pl. 2B. *D. sinica*: Chen 1980: fig. 1.2 (reproduced by Holthuis & Manning 1990: fig. 16a), pl. 1, figs 1, 3, 5, as *D.* (*D.*) *sinica*; Miyake 1983: pl. 6, fig. 2; Takeda 1983: 231, fig. p. 121, as *D. frascone*; Quintana 1987: fig. 20A, as *D. frascone*; Holthuis & Manning 1990: figs 13a, 15; Yamaguchi & Baba 1993: fig. 89A, B; Chen & Sun 2002: fig. 90.1; Wong *et al.* 2021: fig. 9a, pl. 2C. *D. tenuipes*: Serène 1982: pl. 1, fig. 1, pl. 2, fig. 1, as *Dorippe miersi*; Chen 1980: fig. 2.1, as *D.* (*D.*) *tenuipes* (reproduced by Holthuis & Manning 1990: fig. 18a); Chen 1986a: figs 1, 2a; Holthuis & Manning 1990: fig. 17a; Chen & Sun 2002: fig. 91.1; Takeda & Manuel-Santos 2006: fig. 6B. *D. trilobata*: Manning 1993: fig. 2a, b.

Cephalic structures (Figs 12B; 14B, F; 15G)
Eyestalk elongated, slender, pointed; cornea ventrolateral. Antennule folded or incompletely folded into fossa. Antenna: article 2 + 3 long and immobile, wedged in narrow fossa, partially visible; articles 4 and 5 widened, very setose, directed forward; flagellum slightly bent outwards. Lower orbital margin with cluster of several spines.

Illustrations: *Dorippe frascone*: Chen 1980: fig. 3.1, as *D.* (*D.*) *frascone*; Holthuis & Manning 1990: fig. 3. *Dorippe glabra*: Manning 1993: fig. 1b. *D. quadridens*: Ihle 1916: figs 41, 45, as *D. dorsipes*; Holthuis & Manning 1990: figs 6b, c, 12a; Chen & Sun 2002: fig. 89.1; Wong *et al.* 2021: fig. 8b. *D. sinica*: Chen 1980: fig. 1b (reproduced by Holthuis & Manning 1990: fig. 16b); Quintana 1987: fig. 20A-a, as *D. frascone*; Holthuis & Manning 1990: fig. 13b, c; Chen & Sun 2002: fig. 90.1; Wong *et al.* 2021: fig. 9b. *D. tenuipes*: Chen 1980: fig. 2.2, as *D.* (*D.*) *tenuipes* (reproduced by Holthuis & Manning 1990: fig. 18b); Holthuis & Manning 1990: fig. 17b, c. *D. trilobata*: Manning 1993: fig. 2b.

Oxystomatous disposition (Figs 12B; 14B; 15G)
Openings of exhalant channels not visible in dorsal view.

Illustrations: *Dorippe frascone*: Holthuis & Manning 1990: fig. 3. *D. quadridens*: Holthuis & Manning 1990: figs 8, 10, 11; Wong *et al.* 2021: fig. 8b. *D. sinica*: Quintana 1987: fig. 20a, as *D. frascone*; Holthuis & Manning 1990: fig. 15; Wong *et al.* 2021: fig. 9b.

Pereiopods (Figs 10; 12A; 14A, B, E, F; 15A, B, E, H, I)
Chelipeds equal in females and small males, but heterochely usually in large males. Carpus either smooth and naked or with distinct granules or tubercles and short hairs. Major cheliped with palm smooth or variously granulated, swollen, higher than long dorsally; lower margin convex, lacking teeth or tubercles. Minor cheliped with fingers 2-3 times longer than palm; both fingers with two grooves separated by ridge; cutting edges with 12-16 subequal triangular teeth, regularly distributed over edge.

Illustrations: *Dorippe glabra*: Manning 1993: fig. 1c. *D. irrorata* Holthuis & Manning 1990: fig. 4d. *D. frascone*: Chen 1980: fig. 3.3, pl. 2, figs 1, 2, 4, 6, as *D. (D.) frascone*; Chen 1986a: fig. 1c, as *D. tenuipes*; Holthuis & Manning 1990: fig. 2b. *D. quadridens*: Holthuis & Manning 1990: figs 5d, 6d; Wong *et al.* 2021: fig. 8c, d. *D. sinica*: Chen 1980: fig. 1.3, as *D. (D.) sinica* (reproduced by Holthuis & Manning 1990: fig. 16c), pl. 1; Holthuis & Manning 1990: fig. 13d; Chen & Sun 2002: fig. 90.2. *D. tenuipes*: Chen 1980: fig. 2.3 (reproduced by Holthuis & Manning 1990: fig. 18c), pl. 2, figs 3, 5, 7, 8, as *D.* (*D.*) *tenuipes*; Holthuis & Manning 1990: fig. 17d; Chen & Sun 2002: fig. 91.2. *D. trilobata*: Manning 1993: fig. 2c.

P2, P3 long or very long, P3 longest. Meri of P2 and P3 either nearly cylindrical or compressed, setose or glabrous, without dorsal spines or spinules, with numerous more or less acute granules in *D. tenuipes*. Sexual dimorphism of P2, P3 meri setation slight in *D. frascone*, with naked meri in males, hairy in females (Fig. 14A, B and E, F, respectively), much more pronounced in *D. sinica* with merus of adult males (Fig. 10C) covered by dense pubescence but almost completely naked in females (Fig. 10D). Propodi and dactyli entirely naked; dactyli of P2, P3 without hair fringes, naked or nearly so. P4, P5 reduced, with subcheliform apparatus.

Illustrations: *Dorippe glabra*: Manning 1993: fig. 1d. *D. irrorata* Holthuis & Manning 1990: fig. 4 e, f. *D. frascone*: Holthuis & Manning 1990: fig. 2c, d. *D. quadridens*: Holthuis & Manning 1990: figs 5e, f (reproduced by Sin *et al.* 2009: fig. 4A), 6e, f, 7b; Wong *et al.* 2021: fig. 8e, f. *D. sinica*: Holthuis & Manning 1990: fig. 13e, f; Wong *et al.* 2021: fig.9c. *D. tenuipes*: Holthuis & Manning 1990: fig. 17e, f. *D. trilobata*: Manning 1993: fig. 2d.

Thoracic sternum (Figs 11; 12B-E; 13; 14B, C, F; 15B, D, G)
Thoracic sternum strongly sculptured in both sexes; thickened laterally at distal part of sternites 4 and especially 5, 6. Sternites 1 and 2 as pentagonal, raised shield: sternite 1 with small visible pointed portion; sternite 2 narrow, demarcated from sternite 3 by thick ridge; sternite 3 lowered, developed, separated from sternite 4 by short lateral suture (suture 3/4) that may or may not end in small boutonniere; sternite 4 with two strong curved submedian elevations or complete ridge; sternite 5 crossed by strong ridge; sternite 6 crossed by two elevations. Sutures 4/5-7/8 interrupted; 5/6 to 7/8 obliquely oriented; suture 5/6 strongly curved backwards, with press-button in curve. Female thoracic sternum extremely tilted backwards at level of ridge crossing entire sternite 6.

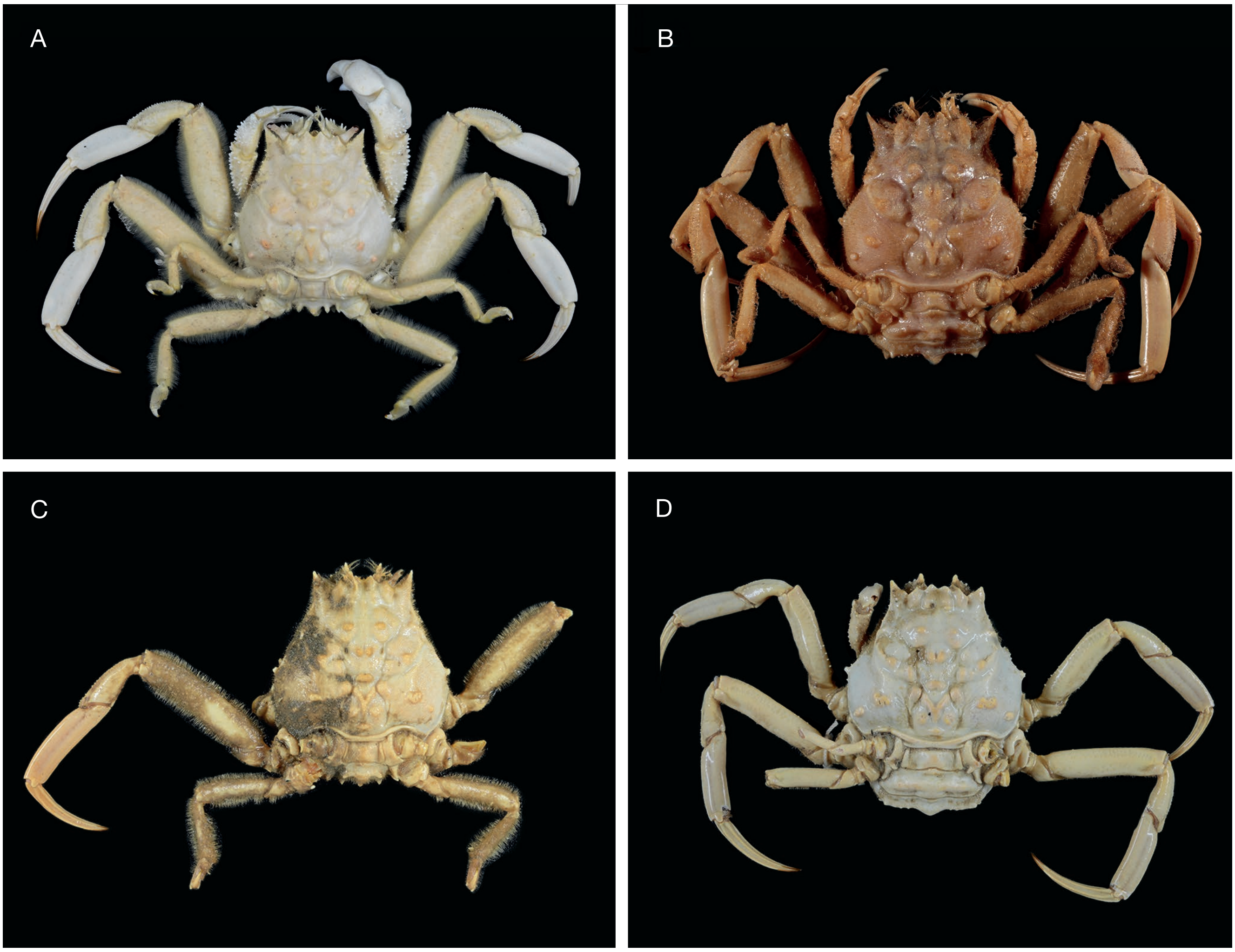

Fig. 10. — Dorippinae H. Milne Edwards, 1837 n. stat.: habitus: **A**, **B**, *Dorippe quadridens* (Fabricius, 1793): **A**, ♂ 36.3 × 38.1 mm, China Sea near Singapore, Hee Huat, ZRC 1984. 6308; **B**, ♀ 29.5 × 30 mm, NW Madagascar, Ambaro Bay, MNHN-IU-2018-5193 (= MNHN-B18279). **C**, **D**, *Dorippe sinica* Chen, 1980, China, Guangdong, Nanao Island, ZRC 1999.0470: **C**, ♂ 36.2 × 39.5 mm; **D**, ♀ 34.8 × 38.9 mm, specimen brushed.

Pleon and telson (Figs 8C; 9A, C, D; 10; 11B; 12A, C; 13A, C; 14B, C, F, I; 15A-H)

Male pleon with all somites free; somite 1 trapezoidal, widening slightly posteriorly; somites 2, 3 each with transverse row of three strong teeth (*Dorippe frascone*, *D. quadridens*, *D. sima*, *D. trilobata*) or blunt granular elevations (*D. irrorata*, *D. tenuipes*); somite 4 narrower, narrowing posteriorly, with single median tooth (*D. frascone*, *D. quadridens*, *D. sima*, *D. trilobata*) or with granular elevations (*D. irrorata, D. tenuipes*); somite 5 laterally constricted; somite 6 posteriorly narrowing, with more or less produced posterolateral angles enclosing base of telson; telson triangular, with rounded apex, tip exceeding level of suture 5/6.

Illustrations: *D. irrorata*: Holthuis & Manning 1990: fig. 4g, h. *D. frascone*: Chen 1980: fig. 3.4, pl. 2, figs 1, 2, as *D.* (*D.*) *frascone*; Holthuis & Manning 1990: fig. 2e, f. *D. quadridens*: Chen 1980: fig. 2b, as *D.* (*D.*) *frascone* (reproduced by Holthuis & Manning 1990: fig. 12b); Holthuis & Manning 1990: figs 5g-i, 7c, d (reproduced by Davie *et al.* 2015a: fig. 71-2.22J); Chen & Sun 2002: fig. 89.2. *D. sinica*: Chen 1980: fig. 1.4, as *D.* (*D.*) *sinica* (reproduced by Holthuis & Manning 1990: fig. 16d), pl. 1, figs 2, 6; Miyake 1983: pl. 6, fig. 2; Holthuis & Manning 1990: fig. 14c, d, e, f; Chen & Sun 2002: fig. 90.3. *D. tenuipes*: Chen 1980: fig. 2.4 (reproduced by Holthuis & Manning 1990: fig. 18d), pl. 2, figs 3, 5, as *D.* (*D.*) *tenuipes*; Holthuis & Manning 1990: fig. 17g, h; Chen & Sun 2002: fig. 90.3. *D trilobata*: Manning 1993: fig. 2e, f.

Female pleon narrow in immature individuals, widening greatly in adults. Somites 3-5 with conspicuous transverse ridges; ridges on somites 3, 4, each with a median and two lateral teeth or low elevations, occasionally with small denticles; telson a little longer than wide, apex rounded (see below, *Female pleonal-retention mechanism*) (the triangular female pleon of *D. frascone* figured Fig. 14F belongs to a prepubertal female).

Illustrations. *Dorippe glabra*: Manning 1993: fig. 1e. *D. frascone*: Chen 1980: pl. 2, figs 4, 6, as *D.* (*D.*) *frascone*. *D. quadridens*: Holthuis & Manning 1990: fig. 6h. *D. sinica*: Chen 1980: pl. 1, figs 3, 4, as *D.* (*D.*) *sinica*; Holthuis & Manning 1990: fig. 14a, b.

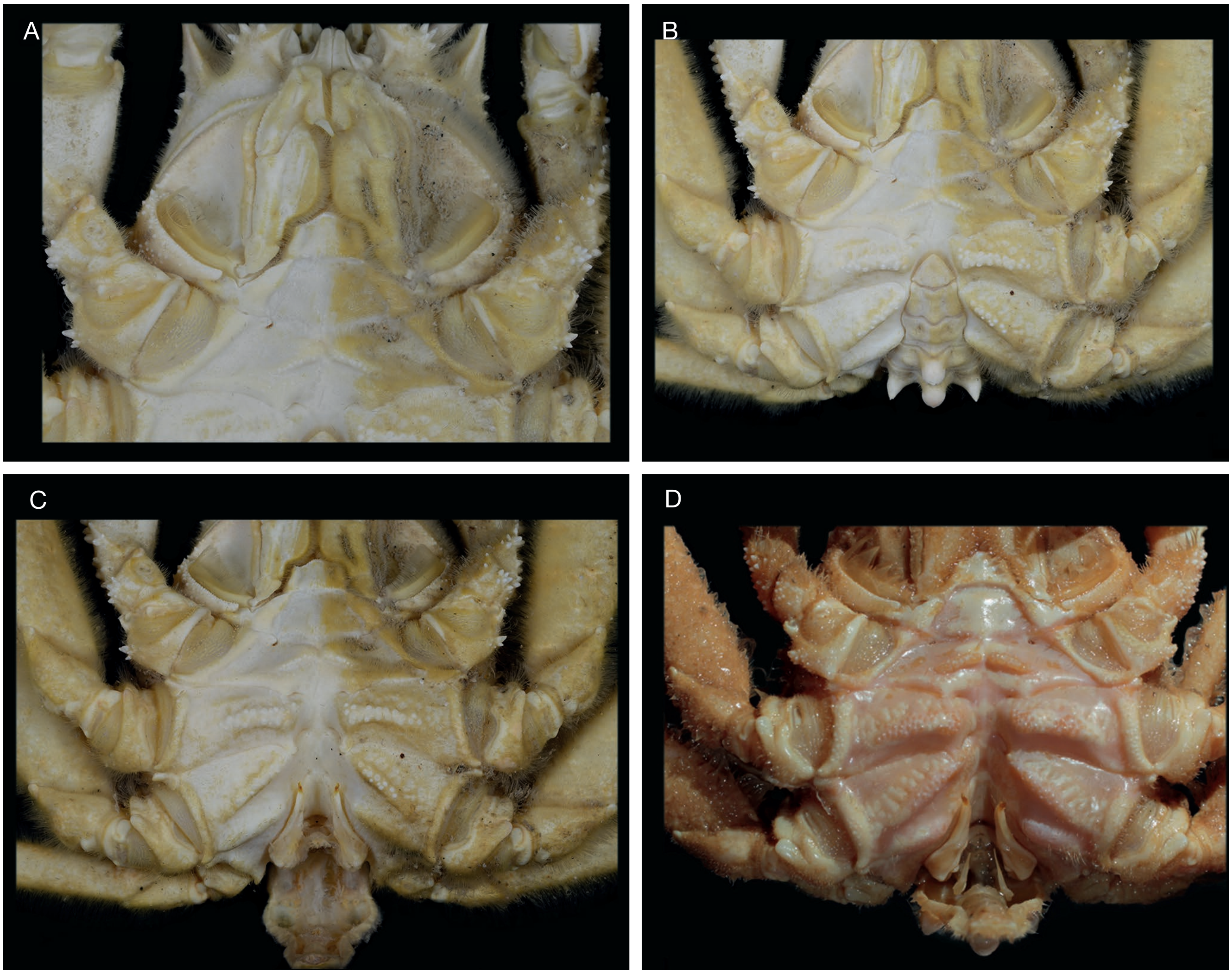

Fig. 11. — Dorippinae H. Milne Edwards, 1837 n. stat.. *Dorippe quadridens* (Fabricius, 1793): **A**-**C**, ♂ 38.1 × 36.3 mm, China Sea near Singapore, Hee Huat, ZRC 1984.6308. **A**, anterior region; **B**, thoracic sternum with pleon; **C**, thoracic sternum without pleon, G1. **D**, ♂ 16.6 × 17.0 mm, NW Madagascar, Ambaro Bay, MNHN-IU-2018-5193 (= MNHN-B18279): thoracic sternum without pleon, G1 and G2.

Pleonal-locking mechanism by press-button (Figs 11C, D; 12D, E; 13B, D; 14B, C, F, I; 15B, D, G, H)

Press-button as small spine in curve of sternal suture 5/6 in both sexes.

Additional female pleonal-retention mechanism (Figs 8C; 9C, 10B, D; 12A; 15E, F)

In females, strong retention by wide process of dorsally exposed portion of sternite 8 overhanging pleonal somite 2. Small telson engaged between raised edges of sterno-pleonal cavity at level of sternite 5 (Figs 12; 13C; 15G, H).

Male gonopore and penis

Male gonopore coxal. Coxo-sternal condition. Penis markedly angled, with membrane between inclined and vertical portions; penial bulb thick, sclerotised; exposed proximal penial portion sclerotised; next portion covered by pleon. Sternites 7 and 8 expanded over penis, very close to each other for short distance, then not completely joined in some cases; sternite 8 with bifid process over P5 coxo-sternal condyle, partially covering penial bulb, overhanging inclined portion of penis.

Illustrations: *Dorippe quadridens*: Guinot *et al.* 2013: 102, fig. 16A-C. *D. tenuipes*: Guinot *et al.* 2013: fig. 17A, B.

Gonopods (Figs 11C, D; 13B; 14D; 31A)

G1 relatively simple, rather straight, short, gradually tapering to single apex; subdistal setae; with narrow tongue-shaped corneous distal process; tip bluntly rounded; basal lobe present, covered with small denticles and with cluster of pappose setae at tip.

Illustrations: *Dorippe frascone*: Chen 1980, fig. 3.5, as *Dorippe* (*Dorippe*) *frascone*; Holthuis & Manning 1990: fig. 2g; Dai & Yang 1991: fig. 25.1, as *D.* (*D.*) *frascone*. *D. irrorata*: Holthuis & Manning 1990: fig. 4i, j. *D. quadridens*: Stephensen 1946: fig. 4A, as *D. dorsipes*; Holthuis & Manning 1990: fig. 7e, f (reproduced by Sin *et al.* 2009: fig. 4A); Guinot *et al.* 2013: 102, fig. 16C, D; Chen & Sun 2002: fig. 89.4; Davie *et al.*

Fig. 12. — Dorippinae H. Milne Edwards, 1837 n. stat.. *Dorippe quadridens* (Fabricius, 1793): **A**-**D**, ovigerous ♀ 38.1 × 33.7 mm, South China Sea, Hee Huat, ZRC 1984.6307: **A**, habitus; **B**, anterior region, ventral view; **C**, thoracic sternum and pleon; **D**, vulvae. **E**, ovigerous ♀ 28.0 × 29.0 mm, NW Madagascar, Ambaro Bay, MNHN-IU-2018-5193 (= MNHN-B18279): thoracic sternum and vulvae.

2015a: fig. 71-2.22J. *D. sinica*: Chen 1980: fig. 1.5, as *D.* (*D.*) *sinica* (reproduced by Holthuis & Manning 1990: fig. 16e, f); Holthuis & Manning 1990: fig. 13g; Dai & Yang 1991: fig. 25.2, as *D.* (*D.*) *sinica*; Chen & Sun 2002: fig. 90.4, 5; Hayer *et al.* 2016a: figs 2, 3A; Vehof 2020: fig. 10A-C. *D. tenuipes*: Chen 1980: fig. 2.5, as *D.* (*D.*) *tenuipes* (reproduced by Holthuis & Manning 1990: fig. 18e); Holthuis & Manning 1990: fig. 17i; Dai & Yang 1991: fig. 26, as *D.* (*Dorippe*) *tenuipes*; Chen & Sun 2002: fig. 91.4. *D. trilobata*: Manning 1993: fig. 2g.

Illustrations: *Dorippe quadridens*: Stephensen 1946: fig. 4B, as *D. dorsipes*; Guinot *et al.* 2013: 102, fig. 16E.

G2 straight.

Illustrations: *D. quadridens*: Guinot *et al.* 2013: fig. 16E; *D. sinica*: Vehof 2020: fig. 10D.

Vulvae (Figs 12D, E; 13D; 14G; 32A)
Vulva at the summit of elevated portion of sternite 6 and at extremity of setose raised sternal ridge; opening quite large, rounded, not recessed, well exposed, covered by operculum leaving inverted V-shaped opening.

Illustrations: *Dorippe glabra*: Manning 1993: fig. 1f. *Dorippe quadridens*: Holthuis & Manning 1990: fig. 6g. *Dorippe sinica*: Hayer *et al.* 2016a: figs 1, 2, 3A; Vehof *et al.* 2017: fig. 1D, E. *Dorippe quadridens* and *D. sinica*: Vehof *et al.* 2017: fig. 2A.

Female reproductive system
Studied in *Dorippe quadridens* by Vehof *et al.* (2017) and in *D. sinica* by Hayer *et al.* (2016a), Vehof *et al.* (2017) and Vehof (2020). See Figs 35A, B; 36B; 37 and below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae*.

Callosities
In both sexes, dorsal part of P3 coxa bearing a callosity, variously developed according to the species: a simple thickening and elongated calcified bulge in *Dorippe quadridens* (Fig. 33C); or in the form of a hemicircular structure in *D. sinica* (Figs 9C; 10C, D; 33D, E), *D. frascone* (Fig. 33F), *D. trilobata* (Fig. 15A, C, J), *D. glabra* (Fig. 15E, F, I); or more complex and taking the form of a double calcified bulge with a central part showing a special texture in *D. tenuipes* (Figs 9D; 33G, H). The callosity, partially concealed by the P5, is visible in the photograph by Takeda & Manuel-Santos (2006: fig. 6B). It was not possible to detect whether a callosity is present in *D. irrorata* (Fig. 14H).

DISTRIBUTION AND HABITAT
Dorippe quadridens is the most widely distributed dorippid in the Indo-West Pacific. It is a Lessespian species introduced into the Mediterranean Sea through the Suez Canal (Monod 1937, as *D. dorsipes*), in Egyptian waters (Timsah Lake and Port Said), along the coasts of Israel (Galil 2005, 2011; Galil & Shlagman 2010; Brockerhoff & McLay 2011), perhaps Syria (Hasan 2008). Its range extends from the Red Sea, Persian Gulf (Apel 2001), Gulf of Aden (Zarenkov 1971), Gulf of Oman, the Seychelles, southeast Africa to the west and east coasts of India (Dev Roy & Nandi 2007, 2008; Dev Roy 2008; Dev Roy & Bhadra 2011: 117; Varadharajan & Soundarapandian 2014; Dev Roy & Rath 2017; Vidhya *et al.* 2017; Beleem *et al.* 2019: 20, fig. 1a; Gosavi *et al.* 2021: table 3), the Andaman and Nicobar Islands (Venkataraman *et al.* 2004: 312, as *Dorippe dorsipes*), the Philippines, Singapore, Indonesia, Vietnam (André 1931: 638, as *Dorippe dorsipes*), Peninsular Malysia (Razak *et al.* 2022: fig. 6.11), Thailand, China and Hong Kong (Chen & Sun 2002; Wong *et al.* 2021), Taiwan (Wang *et al.* 2017; Ng *et al.* 2017), Australia, and also southern Japan (Takeda *et al.* 2019: 13, pl. 3, fig. E, F). Many records of *Dorippe quadridens* with its synonyms cannot reliably be referred to this species, and all Japanese records probably refer to *D. sinica*; the ranges of the two species (both often incorrectly identified as *Dorippe frascone* in early publications) overlap over most of southern China and probably Taiwan (Holthuis & Manning 1990; Ng *et al.* 2017). Recent data on the distribution and ecology of *D. quadridens* and *D. sinica* have been provided by Osman *et al.* (2015); Ng *et al.* (2001, 2017); Ng & Davie (2002); Thoma (2007); Beleem *et al.* (2019); also Zairion *et al.* (2018). The depth from which *D. quadridens* has been reported varies from 1 to 73 m, with most records between 1 and 30 m. It is found on rather flat bottoms of mud and/or sand, sometimes with weeds, corals, or sponges; it has also been reported on coral reefs and oyster beds (Holthuis & Manning 1990).

Recent records of *Dorippe quadridens* in the Middle East do not reliably refer to this species. It appears that the carapaces of *D. quadridens* and *Dorippoides nudipes* (both previously cited in the "Annotated checklist of the decapod crustaceans of the Gulf of Oman" by Naderloo *et al.* 2015: table 2) studied and represented in the *Atlas of crabs of the Persian Gulf* by Naderloo (2017: figs 7.1 and 7.3, respectively) were mistakenly interchanged, whereas the keys to both species, the figures of the G1s and the distribution maps (Naderloo 2017: 47, fig. 4.2.e and 4.2.f, respectively, and fig. 7.2) are correct. Subsequently, crabs from the northwestern Persian Gulf, Iraq, identified as *Dorippe quadridens* by Yasser & Naser (2019: fig. 2) and Al-Khafaji *et al.* (2019: fig. 2a, table 2) are *Dorippoides nudipes* instead of *Dorippe quadridens* (see under *Dorippoides nudipes*).

Most of the specimens reported in the literature as *Dorippe frascone* are either not recognisable from the available data or belong to *D. quadridens* or to *D. sinica*. *Dorippe frascone* is known with certainty only from the Philippines, Indonesia and Papua New Guinea (present paper), at depths between 1-10 m on a sandy bottom, and questionably from southern China (Dai & Yang 1991, as *Dorippe* (*Dorippe*) *frascone*). Records of *D. frascone* by Jeyabaskaran *et al.* (2000: 46, pl. 31c, as *D.* (*D.*) *frascone*) from India in the Gulf of Mannar, by Venkataraman *et al.* (2004: 312) in Tamil Nadu, and by Krishnamoorthy (2007: 90) on the Chennai Coast probably correspond to *D. quadridens*. So far, *Dorippe sinica* reported from East Asia (Chen & Sun 2002; Ng *et al.* 2017; Wong *et al.* 2021) is the only species of the genus known with certainty from Japan (Minemizu 2000: 189; Takeda *et al.* 2006, 2011, 2019); the ranges of *D. sinica* and *D. quadridens* overlap in southern China. *Dorippe sinica* is probably present in Taiwan (Ng *et al.* 2017; Wong *et al.* 2021). The species is reported from the shoreline, on the tidal flat (Yamaguchi *et al.* 1987) and at depths between 15-50 and 118 m; specimens are collected from mud, sand bottoms, and from "volcanic sand, shells, and rock" (Holthuis & Manning 1990).

Dorippe tenuipes is known from Vietnam, the Philippines (including Balicasag Island, Bohol, see Takeda & Manuel-Santos 2006: fig. 6B), eastern Indonesia and southern China, at depths ranging from 15-20 m (Serène 1982), 52-92 m (Chen 1980), 76-70 m (Serène & Vadon 1981), 49-53 m (Holthuis & Manning 1990) and 33-128 m (Chen 1986b), and is found on muddy sand, sand and shell bottoms. According to Trivedi

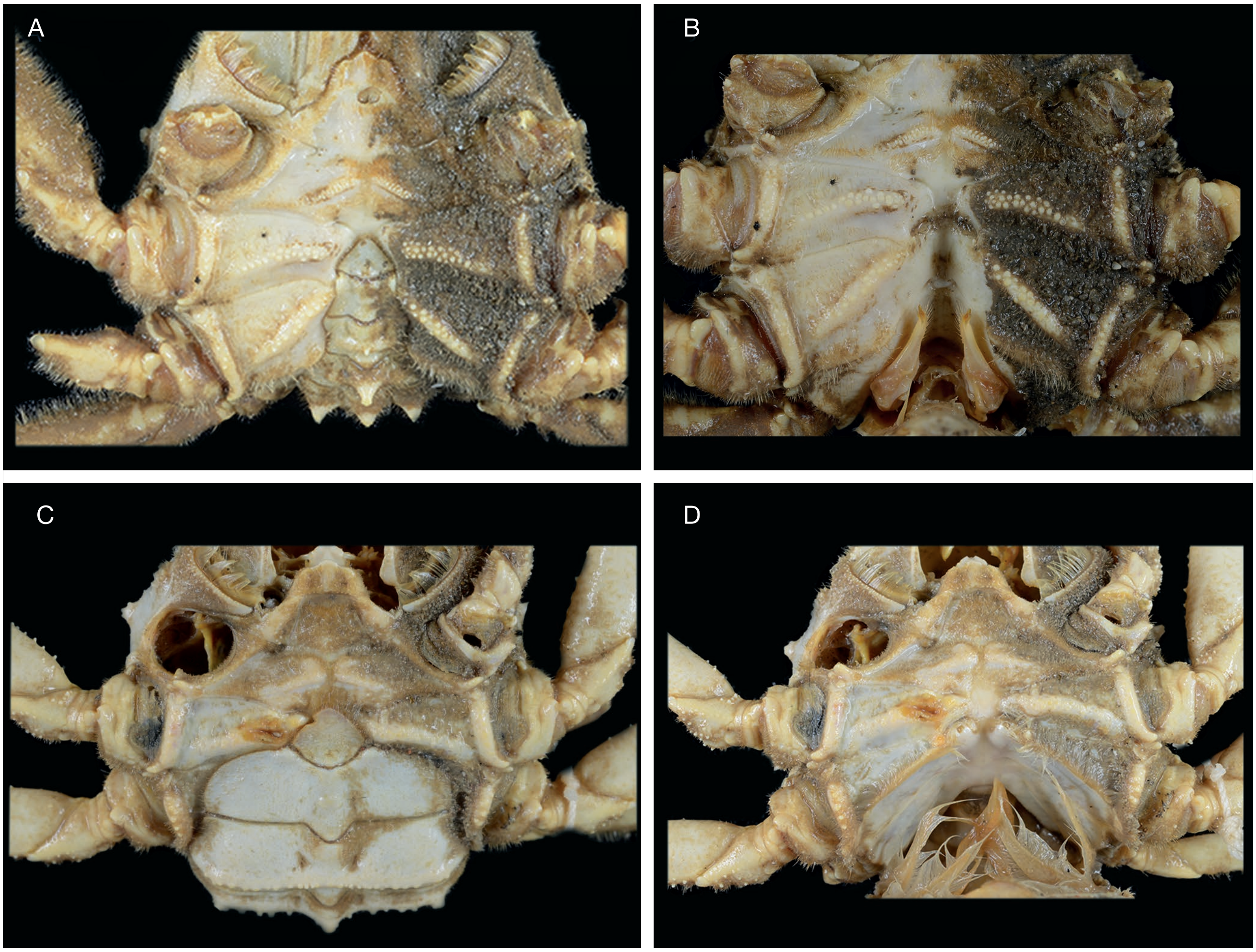

Fig. 13. — Dorippinae H. Milne Edwards, 1837 n. stat.. *Dorippe sinica* Chen, 1980: **A**, **B**, ♂ 36.2 × 39.5 mm, China, Guangdong, Nanao Island, ZRC 1999.0470: **A**, ventral view, thoracic sternum and pleon; **B**, thoracic sternum, G1 and G2; **C**, **D**, ♀ 34.8 × 38.9 mm, same data as **A**, **B**; **C**, thoracic sternum and pleon; **D**, thoracic sternum and vulvae.

et al. (2018), as *D. tenuipes* is known with certainty only from the abovementioned regions, the report of *D. tenuipes* from the Gulf of Mannar region, southeast coast of India by Vidhya *et al.* (2017) is most likely a misidentification with another *Dorippe* species.

Three species of *Dorippe* are so far only known from their type locality and have never been found since. Two are endemic to Australia: *D. glabra* from the Northern Territory on the north coast at 38 m, and *D. trilobata* from Western Australia (Admiralty Gulf) at 18 m depth (Manning 1993; Davie 2002). The third is *Dorippe irrorata* from the east Andaman Sea, at depths of 62 and 73 m (see below, *Remarks*).

Carrying behaviour

Dorippe quadridens has been observed carrying a sponge (Borradaile 1903: 439), the scutellid sea urchin *Echinodiscus* Leske, 1778 (Macnae & Kalk 1958; 1969: 44, 71; Kalk 1995) and starfish (McNeill 1923), pieces of shell or debris (Ng 1987: 15), broken or intact valves of lamellibranchs (Ng & Tan 1986), and accumulated amounts of silt and detritus (Guinot *et al.* 1995). The sculptured carapace with its different microstructures and dense setae likely assists the species to acquire a massive coat of detritus (Osman *et al.* 2021). According to Holthuis & Manning (1990: 33), it is not clear whether the species camouflaged under the umbrella of a jellyfish reported as *D. quadridens* by Estampador (1937: 514; 1959: 65, footnote) is really this species or rather represents *D. frascone* instead, since these authors reported a *D. frascone* from the Philippines "taken from a jellyfish". Several online field videos show amazing images of a crab on the sea floor holding the toxic 'fire urchin' *Asthenosoma varium* Grube, 1868 with its P4 and P5, running on the bottom and then burying forward until most of the body is covered by the sediment. The crab *in situ*, called 'sea urchin carrier crab' and alternatively identified with *D. frascone* or *D. quadridens*, is probably the latter because of the tuberculate carpus of the cheliped recognisable on the videos. Laboratory experiments on *D. quadridens* collected in Thailand (Rayong Province) and tested by Wisespongpand *et al.* (2014) provide some summary data: about 45% of the crabs tested selected the green urchin *Salmacis sphaeroides*

(Linnaeus, 1758) as the first item for carrying, whereas 60% selected the majoid *Chlorinoides* sp. as the first item from five crab species. According to Sakai (1937: 74, as *D. dorsipes*), *Dorippe sinica* was protected by a dead shell, but there is no other record of the species carrying a mollusc. According to Quintana (1987: 285, figs 3B-F, 5L, M, m, 7F, G, 24A, as *Dorippe frascone*), both the megalopa and the first crab stages of *D. sinica* observed in the laboratory normally used their P4 and P5 to carry small objects dorsally over the carapace, so they were not active swimmers.

Remarks

The subfamily Dorippinae n. stat. is monotypic, with the genus *Dorippe* known from seven species, of which three, very poorly known, are photographed here for the first time (see below).

Dorippe callida of White (1847: 54) (not Fabricius 1798), based on two specimens from the Philippine Islands, was assigned to *D. dorsipes*, actually *D. quadridens*, by Miers (1884: 258) despite the elongated legs and weakly sculptured carapace surface that distinguish it. Serène (1982: 1128, figs 1-3, pl. 1, figs 1, 2, pl. 2, figs 1-4) regarded this species as new and established it as *Dorippe miersi* (type locality: Vietnam, Nhatrang), unaware that Chen (1980: 156. fig. 2, pl. 2, figs 3, 5, 7, 8) had described one year earlier *Dorippe tenuipes* (type locality: South China Sea, off Guangdong Province), a specific name meaning ‘thin-legged’. Comparison of the descriptions provided by these two authors and examination of their type material convinced Holthuis & Manning (1990: 47) of their synonymy. They consider that *D. tenuipes* “is distinguished from all other species of *Dorippe* by the very long and slender legs” (a character already noted by Serène: “length of the merus of P2 six times its width”) and by the sculpture of the body surface, especially that of the pleon “far less pronounced” than in most other species of the genus. Serène (1982: 1129) speculated that *D. miersi* (in fact *D. tenuipes*) might be a much smaller species than *D. quadridens* (which he named *D. frascone*) and in which the shape of the adult cheliped would appear at a smaller size, e.g. 28 × 30 mm, with the conclusion that *D. miersi* in relation to *D. quadridens* seemed to be “in a similar situation to that of *Neodorippe taiwanensis* in relation to *Neodorippe japonica*”. *Dorippe tenuipes* is distinguished from all other *Dorippe* by the most developed callosity (Figs 9D; 33G, H).

The female of *Dorippe frascone* measuring 23.3 × 24.4 mm figured here (Fig. 14E, F) is prepubertal, as evidenced by its not yet enlarged triangular pleon (Fig. 14F), compared to the one shown by Chen (1980: pl. 2, fig. 4): the latter is characterised by the shape of somites 4-6 that differs from that of other *Dorippe*.

Remarks on *Dorippe irrorata* Manning & Holthuis, 1986

Dorippe irrorata, which has never been found since its description in the eastern Andaman Sea, is known from only two specimens (Manning & Holthuis 1986: 363, fig. 1a, b; Holthuis & Manning 1990: 9, 15-17, fig. 4), that are currently fragile: a male 21.5 × 22.0 mm, the holotype (Fig. 14H, I) (Andaman Sea, south of Mergui Archipelago; 09°54’N, 97°42’E, International Indian Ocean Expedition, *Anton Bruun Cruise 1*, stn AB-21, 73 m, 24.III.1963, USNM 172495); and a transparent female 17.0 × 17.5 mm, W of the Moscos Islands, 14°07’N, 97°05’E, *Anton Bruun Cruise 1*, stn AB-38, 62 m, 30 Mar 1963, USNM) that was incorrectly indicated as being a paratype (see *Subsequent erroneous designation of paratypes by* Holthuis & Manning [1990]). Both authors considered the species close to *D. quadridens* (Figs 10A, B; 11A-C) and *D. tenuipes* (Fig. 9D) but with some differences. Thanks to the photographs of the holotype kindly sent to us by Karen Reed and, before that, of the supposed ‘paratype’ by Rafael Lemaitre, we can confirm at least that the teeth of somites 2 and 3 of the male pleon are very low and distinctly granular in *D. irrorata* (Fig. 14H, I) (versus strong, acute and smooth in *D. quadridens*) and that the palm of the cheliped is granulated (versus smooth in *D. quadridens*).

The resemblance of *Dorippe irrorata* to *D. tenuipes* (Fig. 9D) is obvious. *Dorippe irrorata* (Fig. 14H, I) has a male pleon with only elevations on somites 2 and 3 (though much lower in *D. irrorata*), but the major cheliped has a granulated palm in *D. irrorata*, smooth in *D. tenuipes*. The main difference mentioned by Holthuis & Manning (1990: 17), i.e., the “far less elongated” P2 and P3 in *D. irrorata*, should be taken with caution as leg length is a highly variable character in some dorippids, such as *Heikeopsis japonica*. Nevertheless, the frontal teeth are slightly different in the two species. The major character that would have allowed us to settle the matter, namely the callosity on P3, which is highly developed in *D. tenuipes* (Figs 9D; 33G, H) and only as an elongated and thickened bulge in *D. quadridens* (Figs 10A; 33C), is unfortunately not detectable in the photographs of *D. irrorata* provided by the USNM (Fig. 14H). Not being able to make a clear decision, we consider *D. irrorata* to be valid, at least provisionally.

Remarks on *Dorippe trilobata* Manning, 1993 and *Dorippe glabra* Manning, 1993

Two *Dorippe* from Australia described by Manning (1993; see Davie 2002: 156), each known only by its type specimen and thus by a single sex, and never reported since, are problematic. The characters used to distinguish them from other known species are tenuous and mainly concern the more or less marked ornamentation and especially the setation and size of the legs. Previously, only two dorippids were known from Australia: *Dorippe quadridens* and *Paradorippe australiensis.* Thanks to photographs of the types of each of these species deposited in the AM, kindly sent to us by Shane Ahyong, some remarks can be provided.

Dorippe trilobata (Manning 1993: 3, 4, fig. 4; cited by Davie 2002: 156), described from Western Autralia (Admiralty Gulf) on the basis of the single holotype, a male 20.5 × 21.1 mm, was considered to be close to *D. tenuipes* Chen, 1980. Both species were regarded as “different from all other species of *Dorippe* in having elongate P2 and P3, with the P3 merus six or more times longer than high”, although to a lesser degree in *D. tenuipes*. In *D. trilobata* the P2 and P3 (Fig. 15A, B)

Fig. 14. — Dorippinae H. Milne Edwards, 1837 n. stat.: **A**-**G**: *Dorippe frascone* (Herbst, 1785), Philippines, Panglao Island, ZRC 2008.0076: **A**-**D**, ♂ 29.7 × 31.0 mm, **A**, habitus; **B**, ventral view; **C**, thoracic sternum with pleon; **D**, G1; **E**-**G**, prepubertal ♀ 23.3 × 24.4 mm: **E**, habitus; **F**, ventral view; **G**, vulvae; **H**, **I**, *Dorippe irrorata* Manning & Holthuis, 1986, holotype, ♂ 21.5 × 22.0 mm, Andaman Sea, south of Mergui Archipelago, USNM 172495: **H**, habitus; **I**, ventral surface.

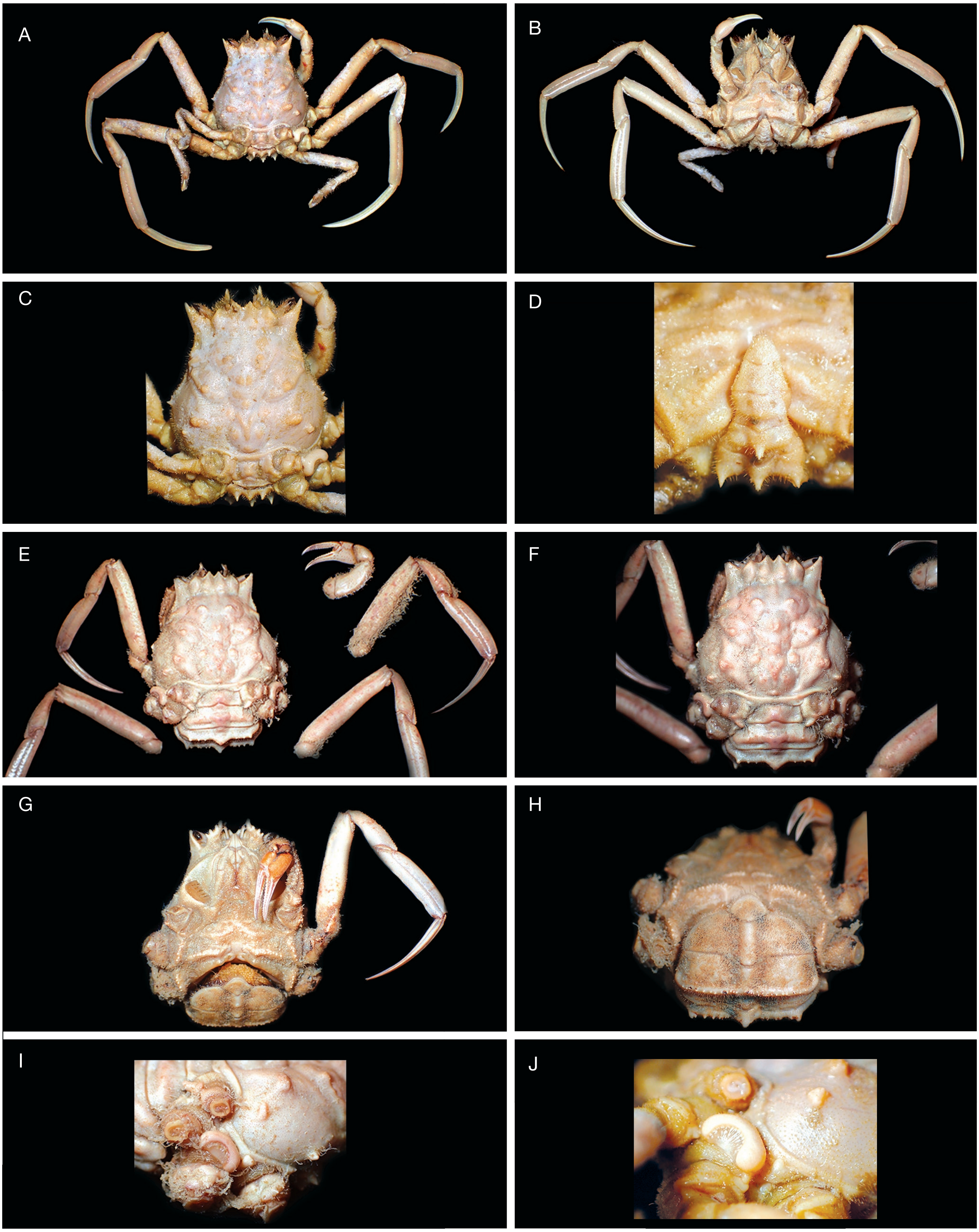

Fig. 15. — Dorippinae H. Milne Edwards, 1837 n. stat.: **A**-**D**, **J**, *Dorippe trilobata* Manning, 1993, holotype, ♂ 20.5 × 21.1 mm, off Mitchell River, Admiralty Gulf, AM P27124: **A**, habitus; **B**, ventral surface; **C**, carapace; **D**, pleon; **J**, callosity. **E**-**I**: *Dorippe glabra* Manning, 1993, holotype, ovigerous ♀ 24.3 × 26.7 mm, Chambers Bay, Australia, AM P13363: **E**, habitus with detached right cheliped, right P2 and P3, left P3; **F**, carapace; **G**, ventral surface; **H**, pleon; **I**, callosity.

are longer and thinner than those of most *Dorippe* (Fig. 10), thus quite similar to those of *D. tenuipes* (Fig. 9D) but not as thin and elongated as in the latter. The long meri of P2 and P3 of *D. trilobata* are naked and the dactyli of P2 and especially P3 are enlarged. A characteristic feature of *D. trilobata*, namely the pleonal somites 2 and 3 with three sharp teeth, is not found in *D. tenuipes* where there are only low rounded and granular elevations. In *D. trilobata*, the anterolateral margin is unarmed anterior to epibranchial region and then shows low tubercles, whereas in *D. tenuipes* it bears numerous denticles. Most significantly, the callosity of *D. trilobata* is simply hemicircular (Fig. 15A, C, J), contrasting with the complex callosity in the form of a double calcified bulge with a whitish central area in *D. tenuipes* (Figs 9D; 33G, H). The anterolateral margin of the carapace without spines, tubercles or denticles in front of the epibranchial region is as in *D. sinica* (Fig. 10C, D); but the three detached spines on the lower margin of the orbit contrast with the cluster in *D. sinica* and the higher number of teeth there in *D. quadridens* (Fig. 12B) and may approximate the 3-5 teeth of *D. frascone* (Fig. 14A-D). *Dorippe trilobata* (Fig. 15A-D) differs from all other species of *Dorippe* in having a short, triangular and straight-edged pleon, instead of the longer and irregular-edged pleon of other *Dorippe*; in addition, the three sharp tubercles on pleonal somites 2 and 3 are much more acute than in *D. quadridens* (Figs 10A; 11B), *D. sinica* (Figs 10C; 13A) and *D. frascone* (Fig. 14A-D). The relatively small size 20.5 × 21.1 mm of the holotype of *D. trilobata* cannot account for these differences, so until more material is available this species can be considered valid.

Dorippe glabra (see Manning 1993: 1, fig. 1; cited by Davie 2002: 156), from the north of the Northern Territory, known only by an ovigerous female measuring 24.3 × 26.7 mm (deposited in the AM, see Springthorpe & Lowry 1994) and found mixed in a large collection identified as *D. quadridens*, "could be distinguished on sight from all of the other specimens in that lot by the naked meri of its P2 and P3", the most significant feature according to Manning (1993: 2, 4). In photographs of the holotype, a male, the meri of the attached left P2, detached left P3 and detached right P3 are naked, but the merus of the detached right P2 (Fig. 15E) is covered with dense setae on the posterior margin. In *D. sinica* the meri of P2 and P3 are naked or barely pubescent in females (Fig. 10D) and setose in males (Fig. 10C), whereas they are covered with setae in both sexes of *D. quadridens* (Figs 10A, B; 12A). The P2, P3 of *D. glabra* (female) are sligthly longer and thinner than in most *Dorippe*, but not so elongated and thin than those of *D. trilobata* (Fig. 15A, B), and those of *D. tenuipes* (Fig. 9D) that are granular. In *D. glabra* the merus and carpus of the cheliped (Fig. 15E) is covered with dense granules, which eliminates *D. frascone* with a smooth carpus. In *D. glabra* the coxa of P3 is flanked by a high hemicircular calcified callosity (Fig. 15E, F, I) similar to that of *D. sinica* (Figs 9C; 10C, D; 33D, E), quite distinct from the double callosity of *D. tenuipes* (Figs 9D; 33G, H). A direct comparison between *D. glabra* and the other *Dorippe* would be most useful.

Subfamily Dorippoidinae n. subfam.

Type genus. — *Dorippoides* Serène & Romimohtarto, 1969 (type species by original designation and monotypy: *Cancer facchino* Herbst, 1785). Other included species: *Dorippoides nudipes* Manning & Holthuis, 1986.

Description

Carapace (Fig. 16)

Carapace wider than long, convex posteriorly, flattened anteriorly, appearing flatter in large individuals. Dorsal surface weakly sculptured, rather smooth, covered with pubescence; 'human face' distinctly delineated. Only a few grooves: precervical groove continuous, distinct in small specimens, with extreme lateral part behind orbit vaguely distinct, or not indicated at all medially in adult males; indistinct, medially interrupted in females; cervical and branchiocardiac grooves deep. Median area (urogastric region) circular or oval, flanked by large, rounded, convex branchial lobes. Meso-metagastric region with two small, oblique submedian gastric pits at the base. Front consisting of two distinct triangular teeth directed forward, or of blunter teeth directed outward, separated by rather deep emargination. Inner orbital angle triangular or blunt. Outer orbital tooth sharp, pointed, reaching as far forwards as or slightly beyond frontal teeth. Antero- and posterolateral margins devoid of spine or tooth, only demarcated by very faint angle. Exposed pleurites 5-7 as granulous sclerites; exposed pleurite 6 rather narrow, granular, separated from P3 coxa by thick, whitish membrane. Carapace posterior rim not extending laterally at all along inflated posterolateral margin and lined posteriorly by nearly rectangular strip, thinner medially in male *Dorippoides facchino* (Fig. 16A) and *D. nudipes* (Fig. 16C); strip with two developed lateral extensions and thus appearing much more hollowed medially in female *D. facchino* (Fig. 16B) and *D. nudipes* (Fig. 16D).

Illustrations: *Dorippoides facchino*: Herbst 1785: pl. 11, fig. 68, as *Cancer facchino* (reproduced by Holthuis & Manning 1990: fig. 23); H. Milne Edwards 1837: pl. 20, fig. 11, as *Dorippe sima* (reproduced by Holthuis & Manning 1990: fig. 24); Verrill 1869a: pl. 2, fig. 1, as *Dorippe facchino* (reproduced by Holthuis & Manning 1990: fig. 25a); Holthuis & Manning 1990: figs 19a-d, 22 (male syntype of *Dorippe astuta* Fabricius, 1785), 19b (reproduced by Sin *et al.* 2009: fig. 3B), 25b; Chen & Sun 2002: fig. 92.1; Naruse *et al.* 2014: fig. 2d; Wong *et al.* 2021: fig. 10a, pl. 2D. *Dorippoides nudipes*: Chen 1988: fig. 1a, pl. 1B, C; Holthuis & Manning 1990: fig. 26a-c.

Cephalic structures (Fig. 17A)

Eyestalk inclined, well protected in rather deep orbital hollow and along outer orbital tooth. Antennule almost entirely folded into fossa. Antenna: basal article exposed; articles 2+3 very developed, moveable, with salient setose external part; other articles directed forward; flagellum curved outwards.

Oxystomatous disposition

Opening of exhalant channels perceptible in dorsal view between rostral teeth, hardly visible in *Dorippoides nudipes*.

Pereiopods (Figs 16; 17A; 18C)
Chelipeds of females and most males of same size and shape; heterochely only in large adult males: major chela swollen, short, with short fingers; minor chela with slender and downwardly curved fingers, forming slight angle with axis of palm.

Illustrations: *Dorippoides facchino*: Holthuis & Manning 1990: fig. 19e; Chen & Sun 2002: fig. 92.2, 3; Wong *et al.* 2021: fig. 10b. *Dorippoides nudipes*: Holthuis & Manning 1990: fig. 26d.

P2 and P3 not very long, P3 longest, all articles rather short and wide, flattened, unarmed. Meri without spines on dorsal margins; sexual dimorphism of setation in *D. facchino* (Fig. 16A, B): males with dense setae only on posterior margins and females with entirely naked margins; dimorphism not marked in *D. nudipes*, with naked margins in both sexes (Fig. 16C, D). Dactyli flattened, twisted, without fringes of hair. P3 ischium of females with spur-like process on anterior margin; process may be present on ischium of P2 but smaller (Figs 9A; 18A, B); these processes completely absent in males.

Illustrations: *Dorippoides facchino*: Holthuis & Manning 1990: fig. 20. *Dorippoides nudipes*: Manning & Holthuis 1986: fig. 1c; Chen 1988: fig. 1d, e; Holthuis & Manning 1990: figs 26e, f, 27f; Chen & Sun 2002: fig. 92.2, 3; Wong *et al.* 2021: fig. 10c.

Thoracic sternum (Figs 17; 18)
Thoracic sternum almost smooth in males, minutely granular and eroded in females. Sternite 1 pointed; sternite 2 pentagonal, high, separated from sternite 3 by broad depression; sternite 3 large, extended laterally; sternite 4 with two raised submedian prominences protruding from pubescence; sternites 4 and 5 lacking sharp ridges, only with blunt, naked transverse ridge. Suture 3/4 rather long, ending in deep depression in males. In males, interruption points of sutures very close to each other at bottom of deep sterno-pleonal cavity, which may give the false impression of a median line. Female thoracic sternum extremely tilted backwards at level of ridge running through entire sternite 6.

Pleon and telson (Figs 17B; 18D)
Sterno-pleonal cavity very narrow and deep. On pleon no tubercles or spines, only low, blunt transverse elevations or indistinct grooves. Male pleon with articular membranes situated between all somites and across entire breadth of each somite. In males, somite 1 long, trapezoidal, widening posteriorly, with posterior margin deeply concave in middle; somite 2 long, widening posteriorly, lacking erect tubercles or spines; somite 4 short, wide; somite 5 distinctly narrowing; somite 6 elongate, very narrow, with concave lateral margins and produced posterolateral angles; telson triangular, with constricted base, its tip far exceeding level of suture 5/6.

Illustrations: *Dorippoides facchino*: Holthuis & Manning 1990: fig. 21g, f. *Dorippoides nudipes*: Chen 1988: fig. 1b, c.

Female pleon (Fig. 18A, E) wide and rounded, without tubercles or teeth; somites 2-5 with blunt but distinct transverse carina; somite 5 widest; somites 5 and 6 longest; telson small, with semicircular posterior margin.

Pleonal-locking mechanism by press-button (Figs 17C, D; 18B, C, F),
Press-button in deep curve of thoracic sternal suture 5/6.

Additional female pleonal-retention mechanism
In females of *D. facchino* (Fig. 16B), dorsally exposed part of sternite 8 with very small prominence that does not overhang pleonal somite 2 and seems not functional; in females of *D. nudipes* (Fig. 16C), the process of sternite 8 is quite developed but seems too distant to be able to overhang pleonal somite 2, thus also nonfunctional. Small telson engaged between raised slopes of sterno-pleonal cavity at level of sternite 5 (Fig. 18A, E).

Male gonopore and penis
Gonopore coxal; coxo-sternal condition with penial tube consisting of inclined portion, then vertical portion, without visible membrane between the two (sternites 7 and 8 in contact over very short distance); bulb more or less long.

Illustrations: *Dorippoides facchino*: Guinot *et al.* 2013: fig. 18A, B. *Dorippoides nudipes*: Guinot *et al.* 2013: fig. 19A, B.

Gonopods (Figs 17C; 31B)
G1 short, stubby, with very elongated coxa and well-developed basis encircling most of endopodite. Apical process twisted, ending in slender simple point, rolled-up in a spiral, triangular (*D. facchino*) or produced into long, thin whip-like appendage (*D. nudipes*); subdistal cluster of setae. Basal lobe rounded, covered with several setae.

Illustrations: *Dorippoides facchino*: Chen 1986a: fig. 4a, b; Holthuis & Manning 1990: fig. 21a-e (reproduced by Sin *et al.* 2009: fig. 4B); Dai & Yang 1991: fig. 22, as *Dorippe* (*Dorippoides*) *facchino*; Chen & Sun 2002: fig. 92.4; Guinot *et al.* 2013: fig. 18C, D; Vehof 2020: fig.12. *Dorippoides nudipes*: Stephensen 1946: fig. 4C, as *Dorippe facchino*?; Chen 1988: fig. 1f-h; Holthuis & Manning 1990: fig. 26g, h.

G2 shorter than G1, straight, with indistinct flagellum.

Illustrations: *Dorippoides nudipes*: Stephensen 1946: fig. 4D, as *Dorippe facchino*?; Chen 1988: fig. 1i; *Dorippoides facchino*: Vehof 2020: fig. 12A.

Vulvae (Figs 17D; 18B, C, F; 32B)
Vulvae on clearly raised, well delimited, globose, papillae-like whitish prominences on sternite 6, each very close to the other, almost joining on median axis, in prolongation of raised oblique setose ridge; opening relatively large, not recessed, near external margin of prominence. In the diagnosis of *Dorippoides* by Holthuis & Manning (1990: 48) the statement that the 'female gonopore' is on the third sternite is erroneous (a confusion with sternite of P3).

Illustrations: *Dorippoides facchino*: Holthuis & Manning 1990: fig. 21h, i; Vehof 2020: fig. 7A-C.

Female reproductive system
Studied in *Dorippoides facchino* by Vehof (2020: 55, figs 7E-G, 17, 20, 22). See Figure 37 and below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae.*

Fig. 16. — Dorippoidinae n. subfam.: **A**, **B**, *Dorippoides facchino* (Herbst, 1785): **A**, ♂ 25.3 × 32 mm, Malaysia, Johore, Pontian, ZRC 1991.66-72; **B**, ovigerous ♀ 20.3 × 26.2 mm, South China Sea, Hee Huat, ZRC 1984.5347; **C**, **D**, *Dorippoides nudipes* Manning & Holthuis, 1986: **C**, ♂ 16.2 × 19.4 mm, Iran, ZRC 2017.1227; **D**, ♀ 21.6 × 29.5 mm, South Africa, vicinity of Tugela River mouth, ZRC 2009.0885.

Callosities

In both sexes of *Dorippoides facchino* (Fig. 33A), on dorsal part of P3, between the coxa and the widely exposed pleurite 6, a large thick, movable, whitish membrane lined on pleural side by narrow calcified strip: structure considered here as a 'simple' callosity. A similar structure observed in females of *D. nudipes* but seemingly lacking in males (Fig. 33B).

Distribution and habitat

Dorippoides facchino is known from Sri Lanka and India (?Pillai & Nair 1970, 1976, as *Dorippe astuta*; Dev Roy 2008; Dev Roy & Nandi 2001, 2008; Venkataraman *et al.* 2004; Ravichandran & Kannupandi 2007; Vidhya *et al.* 2017; Trivedi *et al.* 2018: table 1; Bhat *et al.* 2021: table 1) eastward to Malaysia, Indonesia, Vietnam (André 1931: 639), Thailand, southern China, Hong Kong (Chen & Sun 2002; Wong *et al.* 2021), at depths between 2 and 80 m, most often between 10 and 30 m, usually in sandy mud, but also in soft clay, soft gray mud, and in stones and sand (Holthuis & Manning 1990; Ng & Davie 2002); there are no definite records from either Japan or the Philippines.

Dorippoides nudipes is known from various parts of the eastern Indian Ocean, including the southern Red Sea, the Persian Gulf (Apel 2001), the Gulf of Oman (Naderloo *et al.* 2015: table 2), Iran (Stephensen 1946), southern Madagascar, and probably reaches South Africa (Holthuis & Manning 1990; Chen 1988). And also from the western Indian Ocean: India (Devi & Kumar 2017: fig. 1E, F; Trivedi *et al.* 2018: table 1; Gosavi *et al.* 2021: table 3) and western Thailand (Davie *et al.* 2002; Ng & Davie 2002). Recent records of *Dorippoides nudipes* in the Middle East need to be reviewed. In Naderloo's 2017 *Atlas of crabs of the Persian Gulf*, although the keys to *Dorippe quadridens* and *Dorippoides nudipes*, their figures of the G1 and distribution maps (Naderloo 2017: 47, fig. 4.2.e and 4.2.f, respectively) are correct, the carapace assumed to be that of *Dorippoides nudipes* (Naderloo 2017: fig. 7.3) is actually that of *Dorippe quadridens*. In our opinion, the figures for the two species have been accidentally mixed. The correct representation of the carapace of *Dorippoides nudipes* is shown under *Dorippe quadridens* (Naderloo 2017: fig. 7.2). Subsequently, crabs from the northwestern Persian Gulf, Iraq, identified as

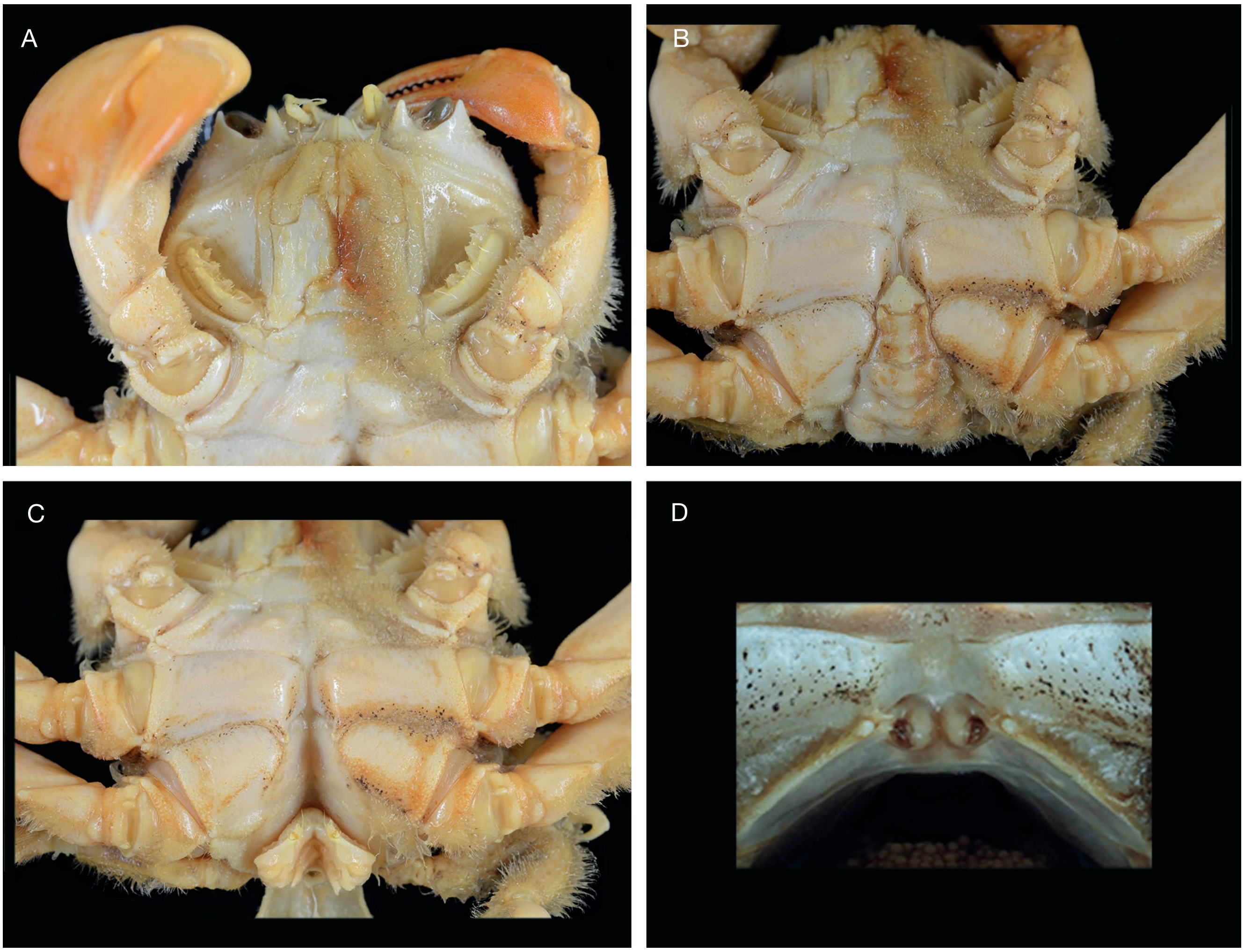

Fig. 17. — Dorippoidinae n. subfam. *Dorippoides facchino* (Herbst, 1785): **A**-**C**, ♂ 25.3 × 32 mm, Malaysia, Johore, Pontian, ZRC 1991.66-72: **A**, anterior ventral view; **B**, thoracic sternum with pleon; **C**, without pleon. **D**, ovigerous ♀ 21 × 25 mm, South China Sea, MNHN-IU-2018-5195 (= MNHN-B18802): vulvae.

Dorippe quadridens by the records of Yasser & Naser (2019: fig. 2) and Al-Khafaji *et al.* (2019: fig. 2a, table 2) are likewise *Dorippoides nudipes* and not *Dorippe quadridens* (see under *D. quadridens*).

Carrying behaviour

The association of *Dorippoides facchino*, the 'porter crab' or 'anemone-carrying crab', with another organism, in fact with a sea anemone, has long been recognised (Herbst 1796: 215, as *Cancer facchino*; Stimpson 1855: 37, as *Dorippe facchino*; Verrill 1869a: 58-60; 1869b: 249-250, pl. 2, fig. 1, as *D. facchino* [reproduced by Holthuis & Manning 1990: fig. 25a]; Henderson 1893: 405, as *D. facchino*; Alcock 1896: 279, as *D. granulata*; Lanchester 1900: 769; 1902: 55, as *D. facchino*; Shelford 1916: 299-300, as *D. facchino*; Hornell 1922: 934-935, fig. 5, as *D. dorsipes*; Verrill 1928: 16, as *D. facchino*; Hose 1929: 31, as *D. facchino*; Shen 1931: 101, as *D. facchino*; Gravely 1941: 81, as *D. facchino*; Chopra 1935, as *D. facchino*; Serène & Romimohtarto 1969: 11; Morton & Morton 1983: 187, fig. 10.4, 7, as *D. granulata*; Tan & Ng 1988: 149, unnumbered fig.; 1992: 149; Holthuis & Manning 1990: 60, 63, fig. 25a, b; Manning 1993: 114, fig. 3a, b; Guinot *et al.* 1995: fig. 4A, pl. 1B; Guinot & Wicksten 2015: 599, fig. 71-11.8B; Fautin *et al.* 2015: 47, fig. 5). The symbiosis between *Dorippoides facchino* and the actinid *Cancrisocia expansa* Stimpson, 1856 is very close and obligatory, with the young crab carrying a very small shell and holding with its P4 and P5 dactyli an ovoid to kidney-shaped platform on which the actinian is sitting and will grow. Most platforms consist of an eccentrically positioned bivalve shell around which the anemone had secreted chitinous material as it grows; in some cases, the shell extends the edge of the platform and gives the crab greater coverage (Fautin *et al.* 2015).

The carrying behaviour of *D. nudipes*, a species closely related to *D. facchino*, has not been documented (Manning & Holthuis 1986: 364, fig. 1c; Holthuis & Manning 1990: 70; Davie *et al.* 2002: 315; Devi & Kumar 2017: fig. 1E, F).

Remarks

The species known as *Medorippe lanata* in the Adriatic was actually described by James Plancus (Latinisation of Simon Giovanni Bianchi, 1693-1775), who gave it the Italian ver-

Fig. 18. — Dorippoidinae n. subfam.: **A**-**C**, *Dorippoides facchino* (Herbst, 1785), ovigerous ♀ 20.3 × 26.2 mm, South China Sea, Hee Huat, ZRC 1984.5347: **A**, thoracic sternum with pleon; **B**, without pleon, vulvae. **C**, ovigerous ♀ 21 × 25 mm, South China Sea, trawl, 37 m, Chen leg. 1987, MNHN-IU-2018-5195 (= MNHN-B18802). **D**-**F**, *Dorippoides nudipes* Manning & Holthuis 1986: **D**, ♂ 16.2 × 19.4 mm, Iran, ZRC 2017.1227; thoracic sternum with pleon; **E**, **F**, ♀ 21.6 × 29.5 mm, South Africa, vicinity of Tugela River mouth, ZRC 2009.0885: **E**, thoracic sternum with pleon; **F**, thoracic sternum without pleon; vulvae. See the spur-like process on P3 ischium of females on **A**, **B**.

nacular name 'facchino', which means 'porter', to the inhabitants of his hometown, Rimini, a famous city on the Adriatic coast of northern Italy. According to Holthuis & Manning (1990: 52), Plancus only referred to the fact that the carapace of this crab resembles an ugly human face, as supposedly often found among members of the porter profession, and without mentioning the possibility that the crabs can carry objects with their last two pairs of legs. The point is that, in originally establishing and figuring *Cancer facchino* for material from the East India, Herbst (1785) erroneously included in the description a reference to the description and figure by Plancus (1739, 1760) of the Mediterranean crab now known as *Medorippe lanata*, thus incorrectly assuming that *Cancer facchino* occurred in the Mediterranean. The specific name *facchino* is thus the result of the misidentification by Herbst (1785) of the pre-Linnean 'Cancer hirsutus personatus maris Superi, vulgo Facchino Ariminensibus dictus' by Plancus (1739; 1760: 36-38, pl. 5, fig. 1) with *Dorippoides facchino*. Plancus' specimen thus becomes a syntype of the Herbst's *Cancer facchino*. As Herbst's *Cancer facchino* was a composite species, Serène & Romimohtarto (1969: 4) selected as the lectotype the specimen represented by Herbst (1785: pl. 11, fig. 68) (reproduced by Holthuis & Manning 1990: fig. 23), thereby fixing the identity of Herbst's species and making *facchino* its valid name. Through this lectotype selection, the specific name *facchino* is now definitively linked to the Indo-West Pacific species of *Dorippoides* rather than to the Mediterranean *Medorippe lanata* (Holthuis & Manning 1990: 51-52, 63-64).

Dorippe astuta Fabricius, 1798, is actually a junior synonym of *Dorippoides facchino* (Ng *et al.* 2008: 59).

Dorippoides nudipes was established by Manning & Holthuis (1986: 364, fig. 1c) on a single male specimen, the holotype 17.0 × 19.0 mm, from Massawa, Ethiopia, Red Sea, and on the basis of the more granular carapace and the dactyli of P2 and P3 broadest in the distal fourth rather than at midlength, in contrast to the only other species of the genus, *D. facchino*. Later, Holthuis & Manning (1990: 66-68) designated as paratypes several specimens from the Red Sea and various samples from the Gulf of Aden, Gulf of Oman, Persian Gulf and Madagascar, deposited in various institutions. This was an unjustified act, and these paratypes are invalid (see above, *Subsequent erroneous designation of paratypes by* Holthuis & Manning 1990). Although Holthuis & Manning (1990: 49 key, 69, 70, fig. 26) have listed the characters distinguishing *D. nudipes* from *D. facchino*, it is useful to restate them here. In *D. nudipes*, the general granulation is more marked, as for example on the anterolateral margin behind the outer orbital tooth; the fingers of chelae are shorter in young males as well in males with inflated palm; the P2 and P3 are cylindrical, with longer and slender articles with naked margins, and with paddle-like dactyli (in *D. facchino* merus and propodus stout and wider, with a fringe of setae on posterior border in adult males, dactylus tapering distally.

When Chen (1988: 678, fig. 1, pl. 1B, C) assigned some specimens from Madagascar to *D. nudipes*, she found that the main differences between the two were related to the length and setation of P2 and P3. According to Devi & Kumar (2017: 626, fig. 1E, F), their specimen from southern India fits well with the characters previously mentioned for *D. nudipes*, and some of the older records of *D. facchino* may well refer to *D. nudipes* due to their close similarity. The sexual dimorphism of the setation of P2 and P3 meri is marked in *D. facchino*, with thick fringe of setae on the posterior margins in males instead of margins naked in females (Fig. 16A, B, respectively), but not marked in *D. nudipes* with naked margins in both sexes (Fig. 16C, D).

The Dorippoidinae n. subfam. is monotypic, with the genus *Dorippoides*, only known from two species.

Subfamily HEIKEOPSINAE n. subfam.

TYPE GENUS. — *Heikeopsis* Ng, Guinot & Davie, 2008 (replacement name for *Heikea* Holthuis & Manning, 1990; type species by original designation: *Dorippe japonica* von Siebold, 1824). Other included species: *Nobilum arachnoides* Manning & Holthuis, 1986.

OTHER INCLUDED GENERA. — *Neodorippe* Serène & Romimohtarto, 1969 (type species by subsequent designation by ICZN plenary powers: *Dorippe callida* Fabricius, 1798). Other included species: *Neodorippe simplex* Ng & Rahayu, 2002. *Nobilum* Serène & Romimohtarto, 1969 (type species by original designation: *Dorippe histrio* Nobili, 1903), monotypic.

DESCRIPTION

Carapace (Figs 1; 5C, D; 19A, B, E, F; 20A, B; 21A)

Carapace slightly or distinctly longer than wide and appearing elongated (*Neodorippe*), or slightly wider than long (*Heikeopsis, Nobilum*); convex (*Heikeopsis*, *Nobilum*) or flattened (*Neodorippe*). Dorsal surface moderately or deeply sculptured, with delineated human facies (*Heikeopsis*); smooth and bare (*Heikeopsis*, *Neodorippe*) or with some tubercles (*Nobilum*). Gastric regions more or less marked; branchial lobes variously developed or absent. Only a few grooves: precervical groove distinct (but shallow, just discernible in *Neodorippe simplex*); cervical and branchiocardiac grooves deep. Antero- and posterolateral margins not demarcated, lacking lateral branchial spine. Front consisting of two broad or sharply pointed triangular teeth separated by shallow, rather wide U-shaped emargination, and extending to or reaching slightly or well beyond outer orbital teeth. Inner orbital teeth practically absent, only as low lobes. Orbital fissure closed (*Heikeopsis*, *Neodorippe*) or open (*Nobilum*). Inner suborbital tooth or lobe far shorter than front. Outer orbital tooth extending to anterior margin of inner orbital lobe, falling far short of front. Exposed pleurite 6 rather narrow, separated from P3 coxa by thick, whitish membrane. Carapace posterior rim not at all extending at all laterally sideways along posterolateral margin and lined posteriorly by narrow strip, thinner medially than laterally, thus slightly concave, in males as in females.

Illustrations: *Heikeopsis arachnoides*: Holthuis & Manning 1990: figs 27a-d, 28a, b, as *Heikea arachnoides*; Ng & Huang 1997: fig. 3E, as *Heikea arachnoides*; Chen & Sun 2002: fig. 93.1, pl. 1.4, as *Heikea arachnoides*; Wong *et al.* 2021: fig. 11a, pl. 2E. *Heikeopsis japonica*: De Haan 1839: pl. 31, fig. 1, as *Dorippe callida*, but with the specific name of *japonica* in the Index p. 237 (reproduced by Holthuis & Manning 1990: fig. 34); Shen 1932: fig. 6 (reproduced by Holthuis & Manning 1990: fig. 35; by Sin *et al.* 2009: fig. 3D); Hothuis & Sakai 1970: 116, 309, pl. 8, fig. 3, as *Dorippe japonica*; Takeda 1983: 303, fig. p. 121, as *Neodorippe japonica*; Chen 1986b: fig. 5.23, as *Nobilum japonicum*; Quintana 1987: fig. 20B, as *Nobilum japonicum japonicum*; Holthuis & Manning 1990: figs 29a, 30a, b, 31a, b, 33a, as *Heikea japonica*; Ng & Huang 1997: fig. 3F, as *Heikea japonica*; Chen & Sun 2002: fig. 94.1, as *Heikea japonica*; Ng *et al.* 2017: fig 3a, as *Heikea japonicum*; Wong *et al.* 2021: fig. 12a, pl. 2F; *Neodorippe callida*: Chen 1986b: fig. 4.17; Holthuis & Manning 1990: figs 39 (reproduced by Sin *et al.*

Fig. 19. — Heikeopsinae n. subfam. **A**-**D**, *Heikeopsis japonica* (von Siebold, 1824): **A**, ♂ 22.5 × 24.3 mm, Japan, Tokushima, SMF 57856: habitus; **B**, ♀ 23.5 × 26.7 mm, Japan, Chaffanjon, MNHN-IU-2000-4091 (= MNHN-B4091): habitus; **C**, ♂ 25.0 × 27.3 mm, same data as B: ventral view; **D**, ♂ 24.2 × 25.4 mm, same data as **B** and **C**: thoracic sternum and pleon. **E**, **F**, ?*Heikeopsis* aff. *japonica*, China, seas off Qingdao, ZRC 2002.0491: habitus: **E**, ♂ 21.9 × 24 mm; **F**, ♀ 23.4 × 26.4 mm.

2009: fig. 3E), 40, 41a, 42a-c; Chen & Sun 2002: fig. 95.1; Wong *et al.* 2021: fig. 13a, pl. 3A. *Neodorippe simplex*: Ng & Rahayu 2002: figs 1, 2, 3A. *Nobilum histrio*: Chen 1986b: fig. 4.20; Holthuis & Manning 1990: fig. 43a (reproduced by Sin *et al.* 2009: fig. 3F); Chen & Sun 2002: fig. 96.1.

Cephalic structures (Figs 20F; 21B)

Eyes short and stout, widening distally; cornea ventrolateral. Antennule entirely folded into fossa, except in *Nobilum* in which distal part of article protrudes from fossa; in *Neodorippe callida*, antennule and antenna directed forwards. Antenna:

article 2 + 3 quadrate, hardly moveable; article 4 short, bent outwards; article 5 only slightly longer than preceding, bent outwards; both articles 4 and 5 widened and lying nearly horizontally on eyestalk; flagellum long.

Illustrations: *Heikeopsis arachnoides*: Holthuis & Manning 1990: figs 27b-d, 28b, as *Heikea arachnoides*. *Heikeopsis japonica*: Quintana 1987: fig. 20B-b, as *Nobilum japonicum japonicum*. *Neodorippe callida*: Holthuis & Manning 1990: fig. 42b, c. *Neodorippe simplex*: Ng & Rahayu 2002: fig. 3B.

Oxystomatous disposition (Figs 20F; 21B)
Openings of exhalant channels scarcely (*Heikeopsis* spp.) or not at all (*Neodorippe*, *Nobilum*) visible in dorsal view.

Pereiopods (Figs 1; 19; 20A, B, C, F, G; 21A, B)
Distinct heterochely in adult males: major chela much inflated, with short fingers; minor chela slender, with very long fingers bearing numerous teeth on cutting edges; dorsal margin of palm and proximal part of dactylus with fringe of hairs; male major chela greatly inflated, smooth, even as polished, with swollen lobe ventrally near base of fixed finger.

Illustrations: *Heikeopsis arachnoides*: Holthuis & Manning 1990: figs 27e, 28c, 29b, 30c, as *Heikea arachnoides*; Chen & Sun 2002: fig. 93.2, as *Heikea arachnoides*; Wong *et al.* 2021: fig. 11b, pl. 2E. *Heikeopsis japonica*: Chen 1986b: fig. 5.24, as *Nobilum japonicum*; Holthuis & Manning 1990: fig. 33b, c, *as Heikea japonica*; Chen & Sun 2002: fig. 94.2, 3, as *Heikea japonica*; Wong *et al.* 2021: fig. 12b, pl. 2E. *Neodorippe callida*: Holthuis & Manning 1990: figs 39, 42d; Chen & Sun 2002: fig. 95.2; Wong *et al.* 2021: fig. 13b. *Neodorippe simplex*: Ng & Rahayu 2002: fig. 3D, E. *Nobilum histrio*: Holthuis & Manning 1990: fig. 43b; Chen & Sun 2002: fig. 96.2, 3.

P2 and P3 varying from proportionally short and stout to long and slender, P3 longest; articles flattened, unarmed, with fringes of long setae (*Heikeopsis*, *Neodorippe*) or fringes of short setae (*Nobilum*); upper and lower margins of dactyli with fringe of setae, either long (*Heikeopsis*, *Neodorippe*) or short (*Nobilum*).

Illustrations: *Heikeopsis arachnoides*: Holthuis & Manning 1990: figs 27f, 28d, *as Heikea arachnoides*; Chen & Sun 2002: fig. 93.3, as *Heikea arachnoides*; Wong *et al.* 2021: fig. 11c, pl. 2E. *Heikeopsis japonica*: Holthuis & Manning 1990: figs 29c, 30d, e, 31c, 33d, *as Heikea japonica*; Wong *et al.* 2021: fig.12c, pl. 2E. *Neodorippe callida*: Holthuis & Manning 1990: fig. 42d; Wong *et al.* 2021: fig. 13c. *Neodorippe simplex*: Ng & Rahayu 2002: fig. 3F. *Nobilum histrio*: Holthuis & Manning 1990: fig. 43c, d.

P4, P5 reduced (Chen & Sun 2002: fig. 96.4).

Thoracic sternum (Figs 19C, D; 20C-H; 21B-F)
Thoracic sternum moderately wide. Sternite 1 with small portion may be dorsally visible. Sternite 2 salient, with marked external angles; sternite 3 extended, consisting of deep, smooth depression and salient curved margins. Sutures 4/5-7/8 interrupted. Suture 3/4 ending in closed boutonniere. Sternite 7 exposed as long, oblique plate along each side of pleon; suture 4/5 and 5/6 with short interruption points. Suture 5/6 slightly curved backwards. Suture 6/7 interrupted in males, but each end linked by low bridge; in females, interrupted and each end linked by sulcus, sometimes membranous. Female thoracic sternum progressively tilted backwards at level of weak ridge of sternite 6 (*Heikeopsis*, *Nobilum)* or only weakly tilted (*Neodorippe*); in females, sternite 8 (its fused portion) with erect axial spine (*Heikeopsis*), long and recurved (*Neodorippe*), or with tubercule (*Nobilum*).

Illustrations: *Heikeopsis japonica*: Holthuis & Manning 1990: fig. 29e, f, as *Heikea japonica*. *Neodorippe callida*: Holthuis & Manning 1990: fig. 41b. *Nobilum histrio*: Holthuis & Manning 1990: fig 43h, i.

Pleon and telson (Figs 19C, D; 20C, D; 21C, E, F)
Male pleon with somites 1, 2 and part of 3 dorsal; female pleon with somites 1-3 and part of 4 dorsaly exposed. All somites free (*Heikeopsis*) except in *Neodorippe simplex* with somites 3-5 fused, immovable but sutures still visible (according to Ng & Rahayu 2002: fig. 3C). Somite 1 trapezoidal, widening posteriorly, with longitudinal groove on either side; somite 2 with wide and blunt transverse ridge or protuberance; somite 3 with two large, blunt lateral swellings and one median less elevated (*Heikeopsis*), or trilobed (*Neodorippe*, *Nobilum*), lodging bulged protopodite of G1s; somite 4 small, narrowing posteriorly, smooth (*Heikeopsis*, *Neodorippe*), with tooth-like dorsal elevation in middle (*Nobilum*); somites 5, 6 smooth (*Heikeopsis*) or with elevations (*Nobilum*, *Neodorippe*); telson triangular, apex rounded, tip of telson not very far from suture 4/5.

Illustrations: *Heikeopsis arachnoides*: Holthuis & Manning 1990: figs 27g-i, 28e, f, as *Heikea arachnoides*; Chen & Sun 2002: fig. 93.4, as *Heikea arachnoides*; Ng *et al.* 2017. *Heikeopsis japonica*: Holthuis & Manning 1990: figs 29c, 30f, 31e, f, as *Heikea japonica*. *Neodorippe callida*: Holthuis & Manning 1990: fig. 42f. *Neodorippe* s*implex* Ng & Rahayu 2002: fig. 3C. *Nobilum histrio*: Holthuis & Manning 1990: fig. 43e; Chen & Sun 2002: fig. 96.5.

Female pleon with all somites free, somites increasingly broader posteriorly; somites 2-5 smooth, without sharp teeth or spines, each somite crossed by smooth submedian ridge; telson subtriangular to semicircular, tip of telson exceeding level of suture 5/6. (See below, *Additional female pleonal-retention mechanism*).

Illustrations: *Heikeopsis japonica*: Holthuis & Manning 1990: figs 29d, 31d, g, as *Heikea japonica*. *Neodorippe* s*implex*: Ng & Rahayu 2002: 747.

Pleonal locking mechanism by press-button (Figs 20E-H; 21D-F)
Locking buttons on posterior margins of sternite 5. Also effective in females as in all dorippids, locking prominences lying very close to vulvae. Despite thickness of egg mass and long pleopodal setae, locking mechanism remaining efficient: for example, firm closing with highly effective buttons and sockets found in ovigerous females of *Neodorippe* from Australia.

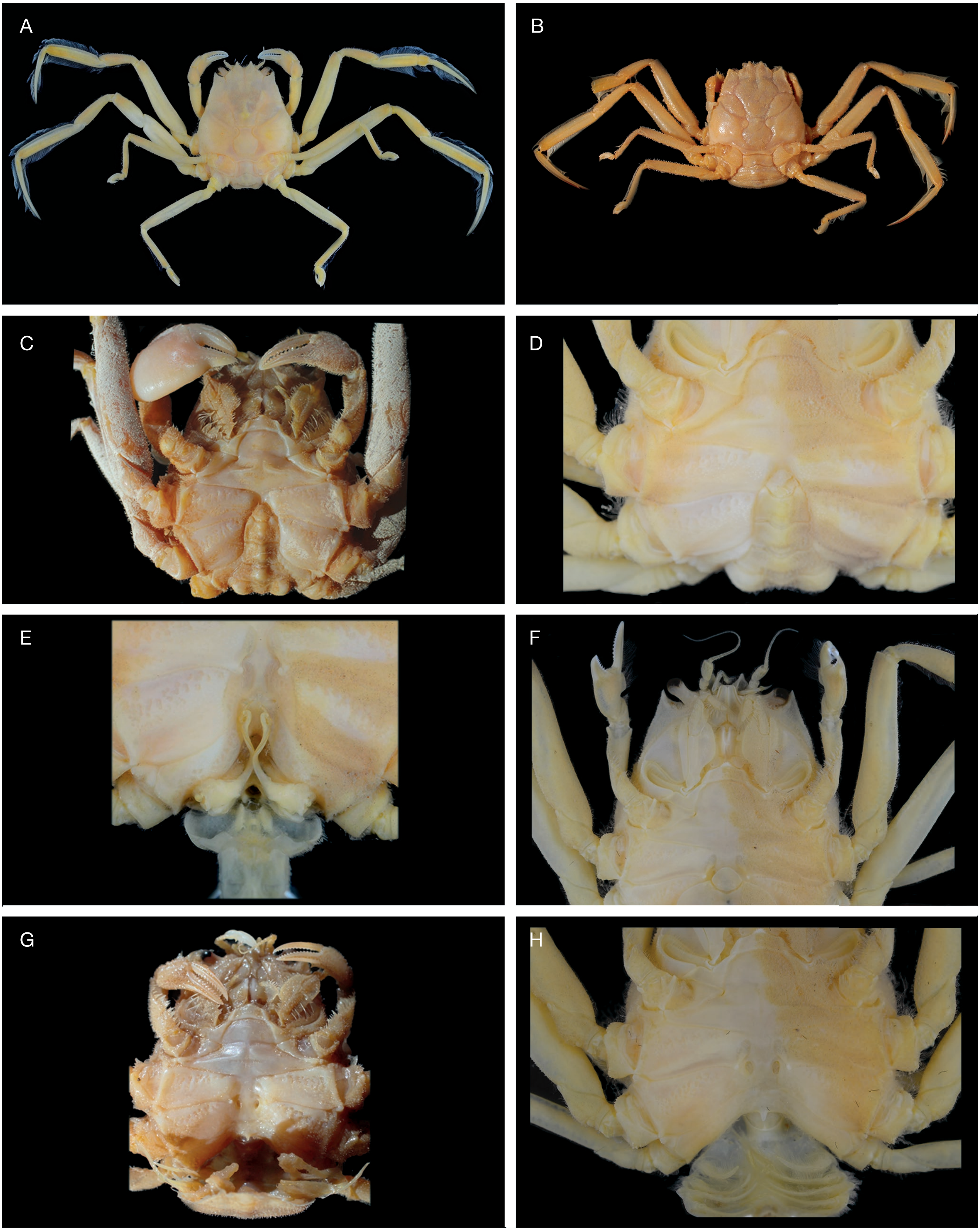

FIG. 20. — Heikeopsinae n. subfam. *Neodorippe callida* (Fabricius, 1798): **A**, young ♂ 10.1 × 10.3 mm, Singapore, Changi Point Beach, ZRC 2018.0445: habitus of young male; **B**, **C**, Andaman Sea, Phuket, Thailand, MNHN-IU-2016-10754 (ex ZRC 1998.1116): **B**, ♀ 14.0 × 15.0 mm, habitus; **C**, ♂ 13.5 × 14 mm: ventral view. **D**, **E**, ♂ 10.1 × 10.3 mm, same data as **A**, ZRC 2018.0445: **D**, thoracic sternum with pleon; **E**, without pleon, G1, press-buttons. **F**, ♀ 11.2 × 11.5 mm, same data as **A**, **D**, **E**, ZRC 2018.0445: anterior view. **G**, ♀ 11.2 × 11.5 mm, sama data as **B**, **C**, MNHN-IU-2016-10754: vulvae, press-buttons. **H**, ♀ 11.2 × 11.5 mm, same data as **A**, **D**, **E**, **F**, ZRC 2018.0445: vulvae.

Additional female pleonal-retention mechanism (Figs 19B, F; 21E, F)
In females, strong retention by wide process of sternite 8 overhanging pleonal somite 2 in *Heikeopsis* and *Nobilum*, whereas only a small non-functional tubercle in *Neodorippe callida* (Fig. 20B), and nothing in *N. simplex*. In addition, small telson engaged between raised slopes of sterno-pleonal cavity at level of sternite 5.

Male gonopore and penis
Male gonopore coxal. Coxo-sternal condition, the most elaborate of all dorippids and similar to that of ethusids. Sternites 7 and 8 close to one another for long distance (much longer than in any other dorippid), so penis very long, with elongated bulb prolonging into penis without clear demarcation, then long exposed inclined portion and shorter vertical portion covered by well-developed G1 protopodite; in *Heikeopis* and *Nobilum* penial bulb and proximal inclined portion of penis clearly visisible dorsally between sternite 7 and widely exposed sternite 8; similar arrangement but less easy to see in *Neodorippe*.

Illustrations: *Neodorippe callida*: Guinot *et al.* 2013: 104, fig. 19 (reproduced by Davie *et al.* 2015a: 41, fig. 72-2.19H).

Gonopods (Figs 20E; 21D; 31D-F)
G1 without basal lobe; inverted C-shaped (*in situ*), stout proximally, then slender and elongated, strongly bent and largely curved outward; apex tapering in single process (*Neodorippe simplex*) or more elaborate and ending in rounded lobe plus two sharp unequal distal processes (*N. callida*), or in three short, broad, rounded subequal processes (*Nobilum*), or in two elongate, blunt-toped unequal lobes plus two subdistal processes (*Heikeopsis*).

Illustrations: *Heikeopsis arachnoides*: Holthuis & Manning 1990: fig. 28g, h, as *Heikea arachnoides*; Dai & Yang 1991: fig. 24.1, as *Dorippe* (*Neodorippe*) *japonica*; Ng & Huang 1997: fig. 4A, as *Heikea arachnoides*; Chen & Sun 2002: fig. 93.5, as *Heikea arachnoides*. *Heikeopsis japonica*: Chen 1986b: fig. 5.25-27, as *Nobilum japonicum*; Holthuis & Manning 1990: figs 32, 33e-g (reproduced by Sin *et al.* 2009: fig. 4D; by Davie *et al.* 2015a: fig. 71-2.31E), as *Heikea japonica*; Ng & Huang 1997: fig. 4B, as *Heikea japonica*; Chen & Sun 2002: fig. 94.4.5, as *Heikea japonica*; Vehof 2020: fig. 11A, C, D. *Neodorippe callida*: Chen 1986b: fig. 4.19; Holthuis & Manning 1990: fig. 42g, h (reproduced by Sin *et al.* 2009: fig. 4E); Dai & Yang 1991: fig. 24.2, as *Dorippe* (*Neodorippe*) *callida*; Chen & Sun 2002: fig. 95.3. *Neodorippe simplex* Ng & Rahayu 2002: fig. 3G-I. *Nobilum histrio*: Chen 1986b: fig. 4.21, 22; Holthuis & Manning 1990: fig. 43d, g (reproduced by Sin *et al.* 2009: fig. 4F); Chen & Sun 2002: fig. 96.6.

G2 folded, bent (*Heikeopsis japonica*: Vehof 2020: fig. 11B. *Neodorippe simplex*: Ng & Rahayu 2002: fig. 3J); also bent in *Nobilum*.

Vulvae (Figs 20F-H; 21E, F; 32D-F)
In *Heikeopsis* and *Nobilum* vulva at internal part of conspicuous sternal prominence close to sternal bulge of sternite 6, showing as long, extremely narrow, curved, vertically oriented slits, overhung by prominence; opening not entirely exposed or slightly obliquely directed on submedian area of sternite 6. In *Neodorippe* vulva suboval, shorter, not sunken, completely exposed.

Illustrations: *Heikeopsis japonica*: Holthuis & Manning 1990: fig. 29e, f, as *Heikea japonica*. *Neodorippe callida*: Holthuis & Manning 1990: fig. 41b, c; Vehof 2020: fig. 5B, C. *Nobilum histrio*: Holthuis & Manning 1990: fig 43h, i; Chen & Sun 2002: fig. 96.6; Vehof 2020: fig. 5D.

Female reproductive system
Studied in *Heikeopsis japonica*, *Neodorippe callida* and *Nobilum histrio* by Vehof (2020: 52, fig. 6) the reproductive system is similar in the species of the three genera. Here, on each side of the body there is a single sperm storage organ, as in Medorippinae n. subfam. (Figs 35C; 37) and other Eubrachyura. See Figures 35E; 37 and below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae.*

DISTRIBUTION AND HABITAT
Heikeopsis japonica, native to Japan and abundant in the Inland Sea and also in Ariake Bay (Yokoya 1933, as *D. japonica*; Sakai 1937: 72, pl. 10, fig. 1, as *D. japonica*, material from 130 m; Sakai 1976, as *D. japonica*; Horikoshi *et al.* 1982, as *D. japonica*), is thought to inhabit the western Pacific: Korea (it is common on the Yellow Sea side) (Kim 1973; Koh & Lee 2013; Lee *et al.* 2021), north to south China (Shen 1937a, 1937b, as *D. japonica*; Dai & Song 1986, as *D. japonica*; Dai *et al.* 1986, as *D. japonica*; Dai & Yang 1991, as *D. japonica*; Chen & Sun 2002: 222; Wong *et al.* 2021: 11, fig. 12, pl. 2F), Taiwan (Ng *et al.* 2001, as *Heikea japonicum*; Ng *et al.* 2017, as *Heikeopsis japonicum*), and Nhatrang, Vietnam (Serène & Romimohtarto 1969, as *Dorippe japonica*). Other records of *Heikeopsis japonica* are: Doflein 1904: 292, as *D. japonica*; Chou *et al.* 1999, as *D. japonica*). But it is likely that two species are confused under the specific name of *japonica*: the typical *Heikeopsis japonica*, with rather long and slender P2 and P3, and another form with shorter and stouter P2 and P3, see below, *Status of non-Japanese* Heikeopsis japonica, H. taiwanensis *(Serène & Romimohtarto, 1969), and* H. arachnoides *(Manning & Holthuis, 1986): a major problem*.

The status of two other *Heikeopsis* with long and slim legs is also a problem: 1) *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis* established by Serène & Romimohtarto (1969) and whose holotype is preserved in ZRC (Yang 1979: 3, as *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis*), but judjed as falling within the range of variation of *H. japonica* by Holthuis & Manning (1990: 87); 2) *Heikeopsis arachnoides*, assumed to inhabit only the Inland Sea of Japan according to Holthuis & Manning (1990: 74, as *Heikea arachnoides*; see Miers 1886: L, 327, 328, as *Dorippe japonica*), but reported from China by Chen & Sun (2002: 220, fig. 94) and from Hong Kong by Wong *et al.* (2021: 11, fig. 12, pl. 2E), and also recorded from northeastern Taiwan (Ng & Huang 1997, as *Heikea arachnoides*; Ng *et al.* 2001, as *H. arachnoides*; Ng *et al.* 2017). According to Ng & Huang (1997: 267), “Whether any of the old records also represent *H. arachnoides* cannot

Fig. 21. — Heikeopsinae n. subfam. *Nobilum histrio* (Nobili, 1903), Malaysia, Johore, Pontian, ZRC 2002.0491: **A**-**D**, ♂ 21.0 × 22.4 mm: habitus; **B**, anterior ventral view; **C**, thoracic sternum with pleon; **D**, thoracic sternum without pleon, penis and G1. **E**, **F**, ovigerous ♀ 22.1 × 24.7 mm: thoracic sternum, pleon and vulvae.

be ascertained". Holthuis & Manning (1990: 72 and 75, respectively, as *Heikea arachnoides* and *H. japonica*) recognised two species: *Heikeopsis arachnoides* and *H. japonica*. See below, *Status of non-Japanese* Heikeopsis japonica, H. taiwanensis *(Serène & Romimohtarto, 1969), and* H. arachnoides *(Manning & Holthuis, 1986): a major problem.*

Neodorippe callida shows a wide distribution, ranging from Red Sea (Herklots 1861, as *Dorippe astuta*) to Southeast Asia and China and having been also reported from Pakistan, India and Bangladesh (Alcock 1896, as *Dorippe astuta*; Venkataraman *et al.* 2004, as *Dorippe astuta*; Dev Roy 2008; Roy & Nandi 2008; Trivedi *et al.* 2018: table 1; Akash *et al.* 2020), the

Philippines, Vietnam (Dai & Song 1986, as *Dorippe astuta*), Singapore (Ng & Tan 1986; Tan & Ng 1988, as *Neodorippe* (*Neodorippe*) *astuta*); Vietnam (Do Van Nhuong *et al.* 2021, as *Neodorippe callida*); Malaysia (Zakirah *et al.* 2022), western Indonesia, Thailand (Ng & Davie 2002) and South China (Chen 1986b; Chen & Sun 2002; Wong *et al.* 2021). For more references, see Holthuis & Manning (1990: 95-103). The species has been recorded in tide pools and shallow waters at depths from 3.6 to 46 m and is found on mud or sandy mud bottoms, being very common in mangrove swamps (Serène & Romimohtarto 1969, as *Neodorippe* (*Neodorippe*) *callida*; Ng 1987, as *Neodorippe* (*Neodorippe*) *callida*).

Neodorippe simplex is known from the shallow waters of the continental shelf of Irian Jaya and northern Australia (Ng & Rahayu 2002). The identity of the *N. callida* from the western continental margin of Australia (McEnnulty *et al.* 2011) would be interesting to check.

Nobilum histrio is only known from Malaysian and Singapore waters (Nobili 1903, as *Dorippe histrio*; Serène & Romimohtarto 1969, as *Neodorippe* (*Nobilum*) *histrio*; Holthuis & Manning 1990: 106), Vietnam (Dawydoff 1952, as '*Doryppe histrix*'), and China (Chen 1986b; Chen & Sun 2002). Its habitat and biology are not documented.

CARRYING BEHAVIOUR

All species of Heikeopsinae n. subfam. have reduced and subcheliform P4 and P5 but the carrying behaviour is only well documented in *Heikeopsis* and *Neodorippe*; almost nothing is known of the habitat or biology of *H. arachnoides* (if valid) and *Nobilum histrio*.

Heikeopsis japonica uses dead shell or other material such a sand dollar and is sometimes associated with a sea anemone or wooden-piece (Sakai 1937: 73; 1976: 61, as *Dorippe japonica*; Holthuis & Manning 1990: 86, as *Heikea japonica*) and with sea pens (Itani & Fujihara 2001). Laboratory experiments showed that both megalopa and first crab stages of *H. japonica* virtually do not swim and carry fragments of shells or rocks dorsally by using P4 and P5 (Quintana 1987: 253, figs 8, 10E, F, 12F, G, 24C, as *Nobilum japonicum japonicum*).

Species of *Neodorippe*, which are primarily inhabitants of mangrove area, differ from all other dorippids in having a leaf carrying habit. The association of *N. callida*, the 'leaf-porter crab', with mangrove leaves is very close and not just temporary (Rathbun 1910; Guinot *et al.* 1995; Guinot & Wicksten 2015: fig. 71-11.8C). Observations of *Neodorippe callida* in Singapore (Ng & Tan 1986: 45-46, fig. 1, table 1, as *Neodorippe* (*Neodorippe*) *callida*; Ng 1987: 14-15; Tan & Ng 1992: 102 as *Neodorippe* (*Neodorippe*) *callida*; Lim *et al.* 1994: 108, 127) point to a unique pattern of behaviour. "Even during the day when the individual is buried in the mud, it holds a leaf; at night, it is a slow but competent swimmer, reversing its orientation with the ventral sternal plate facing the water surface and the leaf downward" (Ng 1987: 14-15). The P4 and P5 grasp the four different corners of the leaf, the point of articulation between the carpus and propodus being equipped with opposable tufts of hairs providing an excellent hold to grip the leaf with the hooked dactylus (P. K. L. Ng, pers. comm.; see his sketch in Guinot & Wicksten 2015: fig. 71-11.9H, I). In the aquarium, individuals of *Neodorippe simplex* "carry leaves on their backs and swim upside down, with the leaf, when disturbed" (Ng & Rahayu 2002: 757, fig. 1). For further references, see Holthuis & Manning (1990: 101-103). The use of seaweeds as camouflage in brachyuran crabs with the legs is not very common, being observed occasionally only in some podotremes (dromiids, cyclodorippids, latreilliids) and eubrachyurans (palicids with their P5). In a completely different way, it is widespread in majoids, which use specialised setae on the body and legs (Guinot & Wicksten 2015; McLay 2020).

REMARKS

Dorippe japonica, collected in Japan by local fishermen for Ph. F. von Siebold in 1823 and described by von Siebold (1824: 15, as *Doripe* [sic] *japonica*; 1826: 18; 1850: xiii), was studied and represented by De Haan in *Fauna Japonica* (1839: pl. 31, fig. 1, as *Dorippe callida*; 1841: 122 and in Index p. 227, as *Dorippe. japonica*) (Fig. 1A). In the collections of pictures of crabs and shrimps (*Kai-ka Rui Siya-sin*), prepared by the well-known naturalist Kurimoto Suiken (1756-1834) and donated to Von Siebold in 1826, figures 41 and 42 of plate 6 of volume 1 show a long-legged crab (dorsal and ventral views) with two vernacular names: 'Kimen-gani', i.e., ogre-faced crab, and 'Heike-gani' in reference to the famous Japanese legend that crabs of this species are the spirits of deceased members of the Heike family with human traits engraved on their carapaces (Figs 2; 39; Appendix 1). They are accompanied by two mentions: Von Siebold's name in ink: *Dorippe japonica* n. sp., and De Haan's name in pencil: *Dorippe japonica* F. J., by reference to *Fauna Japonica* (Yamaguchi & Holthuis 2001: 30, 31). Von Siebold (1824: 14; 1850: xiii, footnote) and De Haan (1841: 122), who quotes the figures of Suiken, gave *Dorippe japonica* the vernacular names 'Heike-gani', 'Heike-Kani' and 'Feike-Gani'. In fact, 'Heike-gani' is the only vernacular name that corresponds with certainty to the Japanese crab of von Siebold and De Haan. Much later, the genus was given the name *Heikea* by Holthuis & Manning (1990), replaced by *Heikeopsis* by Ng *et al.* (2008: 59, 60).

A total of 31 specimens had been collected and deposited at the RMNH (RMNH.CRUS.D.822) (see Fransen *et al.* 1997: 83, as *Heikea japonica*). A lectotype (see Fig. 1B) and several paralectotypes were designated from the type series by Yamaguchi & Baba (1993: 300, figs 90a.a-1, a-2, b, d-f, 90-B, as *Heikea japonica*). The type locality mentioned by Von Siebold (1824) is Shimonoseki, the one in the *Fauna Japonica* is Nagasaki, but according to Yamaguchi & Baba (1993: 300, as *Heikea japonica*) such a locality record is absent from the labels of all the type series material. Holthuis & Manning (1990: 77) considered the provenance to be more likely from "near Nagasaki". A dry specimen deposited at the MNHN, MNHN-IU-2000-34 (= MNHN-B34), considered non-type according to Yamaguchi & Baba (1993: fig. 90B.g, as *Heikea japonica*), could be part of the type series. Another Japanese sample from the historical collection, with a male and a female in dry condition MNHN-IU-2000-4091 (= MNHN-B4091), probably belongs to the type series (Fig. 1C).

Nobilum and *Heikeopsis* are closely related genera but differ primarily in the G1, with three petaloid lobes in *Nobilum*, with two subdistal processes and two elongated, unequal distal lobes in *Heikea*, and by a spine on the orbital margin in *Nobilum*, absent in *Heikea*. Note that the G1 of *Neodorippe callida* ends in two processes, one sharp, one rounded, and that of *Neodorippe simplex* is simple, with a single tapering process.

In *Neodorippe* the elongation and shape of the penis as well as other features, such as the small size and the smooth, flattened and elongated carapace (Figs 5D; 20A, B), are somewhat suggestive of an ethusid, but it is a true dorippid.

Status of non-Japanese *Heikeopsis japonica*, *H. taiwanensis* (Serène & Romimohtarto, 1969), and *H. arachnoides* (Manning & Holthuis, 1986): a major problem

While the present revision was in progress, we noted that the syntype specimen of *Dorippe japonica* described by De Haan (1839: pl. 31, fig. 1; 1841: 122; reproduced by Holthuis & Sakai 1970: pl. 8 fig. 3, and by Holthuis & Manning 1990: fig. 34, as *Heikea japonica*), and the crabs of the type series figured by Yamaguchi & Baba (1993: 304, fig. 90A, B, as *Heikea japonica*), have all invariably very long and thin P2 and P3. A long-legged crab is also shown in the picture of *Dorippe japonica* represented by Suiken (pl. 6, figs 41, 42), see above. De Haan's illustration (Fig. 1A) indeed shows very long and slender legs in accordance with the text (*Pedes secundi 3” 4”’, tertii 3” 8”’ vix quater thorace longiores*, i.e., “legs barely four times as long as carapace”). Likewise, the three dry specimens from Japan in the MNHN historical collection (Fig. 1C) have very slim and long P2 and P3. Typical *japonica* was depicted by Miyake (1983: 17, pl. 6, fig. 1, as *Nobilum japonicum japonicum*) and by Takeda (1983: fig. p. 121, as *Neodorippe japonica*). The crabs figured as *japonica* by Takeda (1982b: 93, coloured fig., as *Neodorippe japonica)* are typical *Heikeopsis japonica.* There is no figure in Yamaguchi *et al.* (1976: 34, as *Neodorippe* (*Neodorippe*) *japonica*), whereas the crab from the Amakusa Islands in Yamaguchi *et al.* (1987: 8, pl. 1, fig. 10, as *Nobilum japonicum*) is a typical *Heikea japonica.* Note that figures in various papers of Sakai show either a crab with long, slender P2, P3 (e.g. Sakai 1937: 72, pl. 10, fig. 1, as *Dorippe japonica*, from Omoniti), or others that are not significant (Sakai 1976: 61, pl. 22, fig. 1, as *Neodorippe* (*Neodorippe*) *japonica*), but this can be attributed to a bias. Sakai (1956: 6, 24, fig. 7, as *Dorippe japonica*) reproduces De Haan's figure of *Dorippe japonica*.

In his key paper ‘Heike-gani, its Prosperity and Fossils’, Sakai (1985: 330, as *Neodorippe japonica*) reproduces in his fig. 1 a typical *Heikea japonica* with long, slender P2 and P3; his fig. 2 shows the carapace of ‘Heikegani’ in Japan: from top left to right, *Dorippe frascone*, *Paradorippe granulata*, *Heikeopsis japonica*, and below *Ethusa izuensis*, *E. minuta*, *E. quadrata*, and *Tymolus japonicus*. His fig. 3 reproduces at the top a sketch taken from Shen (1932: fig. 6, as *Dorippe japonica*; the indicated date 1835 is erroneous) and showing a crab with short, stout P2 and P3, from northern China: Sakai was thus quite conscious that this was a species distinct from the typical *japonica*; the middle photo is listed as representing *Dorippe polita* from Shen (1932: fig. 4) (T. Naruse, pers. comm.).

Holthuis & Manning (1990: 80) note in their specific description of *Heikeopsis japonica* “Second and third legs slender, long, both reaching beyond front [of carapace] with distal end of merus” but, at the same time, they do not distinguish between the Japanese syntype specimen of De Haan (1839: pl. 31, fig. 1) and a North Chinese specimen with short, robust P2 and P3 by Shen (1932: fig. 6), whose figure they reproduce (Holthuis & Manning 1990: fig. 35). In fact, the *Heikea japonica* of Holthuis & Manning (1990) indiscriminately includes crabs from Japan, China, Korea, Vietnam, Paracels Islands and Taiwan, whether long- or short- legged.

Yet, earlier, Serène & Romimohtarto (1969: 13, as *Neodorippe* (*Neodorippe*) *japonica*) had recognised Chen's Chinese crab as a doubtful *japonica*, arguing that its P3 was less than 3 times the carapace length, unlike their specimens from Nagasaki and Vietnam that have the merus of P3 much longer than the carapace length, and just like the Japanese specimens with ‘slender legs’ “more than 3.4 times the length of the carapace” of Sakai (1937: 72, pl. 10, fig. 1, as *Dorippe japonica*). Consequently, Serène & Romimohtarto (1969: 14, figs 21, 22, pI. 5A, B, D) established a variety of *japonica* as *Neodorippe (Neodorippe) japonica* var. *taiwanensis*, based on two specimens from Keelung, Taiwan, with the P3 having a total length (coxa and basis-ischium excluded) 3.2 times the carapace length, thus much longer and slimmer than the *japonica* from China and almost similar to the typical *japonica* from Japan. However, Holthuis & Manning (1990: 87) concluded that the features used to distinguish *H. japonica taiwanensis* from *H. japonica* fell within the range of variation of this character in *H. japonica*, including Chinese representatives, and that the two species were synonymous. Furthermore, it is rather incomprehensible that Manning & Holthuis (1986: 364, fig. 1d, as *Nobilum arachnoides*) at the same time described a new species, now *Heikeopsis arachnoides*, collected by the *Challenger* in 1875 from the same provenance (Japan, Inland Sea) as *H. japonica*, and characterised by very long legs. Holthuis & Manning (1990: 72, figs 27, 28, as *Heikea arachnoides*) continued in the same vein, separating the two species only by the size of P2 and P3 without mentioning any other substantial distinguishing features. *H. arachnoides* is clearly synonymous with *H. japonica*.

Subsequent carcinologists followed suit, but with some variations. Ng & Huang (1997: 267, figs 3E, 4A) identify a male from northeastern Taiwan as *H. arachnoides*, but regard three males and two females collected at the same site as *H. japonica* on the basis of a lower length of P3. In their *Fauna Sinica*, Chen & Sun (2002) distinguish two species: *Heikea japonica* (Chen & Sun 2002: 222, fig. 94), with *taiwanensis* as synonym; and *Heikea arachnoides* (Chen & Sun 2002: 220, fig. 93, pl. 1.4). In the Catalogue of crabs from Taiwan, Ng *et al.* (2017: 36), as previously in 2001 (p. 8), list two species: *H. arachnoides* and *H. japonicum* [*sic*], the latter being considered a senior synonym of *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis*, all with long, slender legs and none with short, stout legs. In Hong Kong seas two species are recognised: one, along the Tolo Channel, identified with *Heikeopsis arachnoides* by its ambulatory legs with long meri, notably P3 meri 6.6 to 7.3 times longer than high; and a second, in western waters, as *H. japonica*, with shorter P3 meri, less than 6.3 times longer than high (Wong *et al.* 2021: 10, fig. 11, pl. 2E and fig. 12, pl. 2F, respectively). The *Heikeopsis japonica* from Korea in Koh & Lee (2013: 19, pls 10-12) has P2 and P3 that are more or less long and slender.

The discrepancies in the use of ambulatory leg length by Holthuis & Manning (1990) is an issue that will require detailed study, also taking into account changes during the growth and possible sexual dimorphism. The use of the ambulatory leg length has been followed by other reserchers since then, but there are clearly problems. We have examined a large number of range specimens as well as the types, and it is clear that all specimens from Japan, Korea, Taiwan, Hong Kong and Vietnam have long to very long P2 and P3. However, those from northern mainland China (Shen 1932: 11, figs. 6, 7a-e, as *Dorippe japonica*; Chen 1986b: 123, fig. 5. 23-27, as *Nobilum japonicum*) (see ?*Heikeopsis* aff. *japonica* in our Material examined) have consistently shorter legs, but comparisons of their carapaces, pereopods and gonopods have so far not uncovered any significant differences; and initial genetic studies also do not show any patterns. The issue will have to be addressed separately (Guinot D., Ng P. K. L. & Naruse T., in progress).

Subfamily MEDORIPPINAE n. subfam.

TYPE GENUS. — *Medorippe* Manning & Holthuis, 1981 (type species by original designation: *Cancer lanatus* Linnaeus, 1767). Other included species: ?*Medorippe crosnieri* Chen, 1988 (see *Remarks about the validity of* Medorippe crosnieri *Chen, 1988* and Fig. 23A, B, D).

DESCRIPTION

Carapace (Figs 22A, B; 23A, B)
Carapace wider than long, hexagonal. Dorsal surface without large tubercles or spines, and only with numerous small tubercles and relatively low ridges. Meso-, meta-, urogastric regions clearly defined. Cardiac region usually with distinct V-or Y-shaped ridge. Precervical groove indistinct; cervical groove more marked but shallow; branchiocardiac groove moderately deep. Gastric pits as two quite distant small slits on depression separating meso-meta gastric regions from urogastric regions. Antero- and posterolateral margins demarcated by distinct but short epibranchial tooth. Front narrow, bidentate, consisting of two very close triangular teeth, separated by narrow emargination. Inner orbital teeth very low, at a much lower level. Superior margin of orbit with fissure. Lower infraorbital margin smooth. Inner suborbital tooth slender, reaching to level of outer orbital tooth. Supraorbital lobe present. Exposure of pleurites 5-7, with smooth texture; margin of carapace lying in small gutter at this level. Carapace posterior rim extending laterally sideways along posterolateral margin, passing behind exposed pleurite 6, and tapering further to reach arthrodial cavity of P2; lined posteriorly by thin strip that is slightly thicker on each lateral side, more concave and elongated in females.

Illustrations: *Medorippe lanata*: Monod 1933b: 39, fig. 5A, as *Dorippe lanata* (reproduced by Monod 1956: fig. 103, erroneously as *D. armata*; by Manning & Holthuis 1981: fig. 4a; by Holthuis & Manning 1990: fig. 36; by Sin *et al.* 2009: fig. 3c); Zariquiey Alvarez 1968: fig. 106d, as *D. lanata*; Holthuis & Manning 1990: fig. 37a; Henriksen 2009: fig. 11; Guinot *et al.* 2013: 219, figs 46A, B, 47A, B; Emmerson 2016: 332. ?*M. crosnieri* Chen, 1988: fig. 2a (reproduced by Holthuis & Manning 1990: fig. 38a), pl. 1D.

Cephalic structures (Figs 22A-C; 23A, B)
Eyestalks elongated but stout and not reaching beyond outer orbital teeth. Antennule not completely folded into fossa. Antenna entirely directed anteriorly: articles 2+3 rather wide, moveable, with external portion elevated; following articles setose; article 4 short, bent inwards; article 5 slightly elongate.

Illustrations: *Medorippe lanata*: Bouvier 1940: 199, fig. 140, as *Dorippe lanata*; Zariquiey Alvarez 1968: fig. 2f, as *D. lanata*; Guinot *et al.* 2013: figs 42C, 46A, 47A, B.

Oxystomatous disposition (Figs 4; 22C)
Exposed portion of mxp1 endopod protruding beyond extent of mxp3 being very long. Opening of exhalant channels clearly visible in dorsal view between rostral teeth.

Illustrations: *Medorippe lanata*: Bouvier 1940: 199, fig. 140, as *Dorippe lanata*; Guinot *et al.* 2013: fig. 42C (reproduced by Davie *et al.* 2015a: 41, fig. 72-2.14A).

Pereiopods (Figs 22A, B; 23A, B)
Left and right chelipeds equal, similar in both sexes and in young adult males; heterochely in large males (from 18 to 29 mm carapace width), with male major chela swollen and setiferous, remaining setiferous even when it becomes larger

Illustrations: *Medorippe lanata*: A. Milne-Edwards & Bouvier 1900: 33, as *Dorippe lanata*; Mori 1986: 81, figs 3, 4; Rossetti *et al.* 2006: fig. 7.

P2, P3 meri with dorsal margin carrying row of spines (*M. lanata*, see Figs 22A, B; 23C) or unarmed if ?*M. crosnieri* (see Fig. 23A, B, D) is confirmed as valid. Dactyli narrow and slightly twisted, mostly not fringed with setae. Both P4, P5 reduced and setose; P5 being much thinner and shorter than P4.

Illustrations: *Medorippe lanata*: Monod 1933b: figs 3C-E, *as Dorippe lanata*; Monod 1956: fig. 103, erroneously as *D. armata*; Manning & Holthuis 1981: fig. 4a-f; Holthuis & Manning 1990: fig. 36.

Thoracic sternum (Figs 4; 22C-F)
Thoracic sternum rather wide. Sternites 1 and 2 forming fairly pentagonal, broad shield, separated from sternite 3 by slight lateral notch, extending medially into depressed sulcus; sternite 1 visible dorsally as blunt tip but extending ventrally by large, concealed piece; sternite 3 broad, connected to pterygostome by wide extension; sternite 8 of female without median spine. Sutures 3/4 short but deep, ending in marked boutonniere;

sutures 4/5-7/8 interrupted; suture 4/5 straight; suture 5/6 deep, abruptely curved backwards, with conspicuous curve lodging press-button; suture 6/7 oblique; suture 7/8 shorter. Female thoracic sternum extremely tilted backwards at level of ridge crossing whole sternite 6.

Illustrations: *Medorippe lanata*: Guinot 1979a: fig. 28A, as *Dorippe lanata* (reproduced by Davie *et al.* 2015a: fig. 71-2.18A); Holthuis & Manning 1990: figs 37c; Guinot & Bouchard 1998: figs 15C, D, 16A, B; Guinot *et al.* 2013: figs 46, 47A, B.

Pleon and telson

Male pleon (Fig. 22D, F) with all somites free and dorsal first somites; articular membranes being situated between all somites and on complete breadth of each somite; somite 1 trapezoidal, widening posteriorly, posterior margin concave; somite 2 longer and wider than somite 1; somite 3 widest of all and without teeth in both sexes; pleon regularly narrowing from somite 4 to telson; tip of telson exceeding level of suture 5/6.

Illustrations: *Medorippe lanata*: Guinot 1979a: fig. 28A, B, as *Dorippe lanata*; Guinot & Bouchard 1998: figs 15D, 16B; Guinot *et al.* 2013: fig. 51G.

Female pleon (Fig. 22B) with dorsal first somites, very wide, unarmed, with conspicuous transverse ridges on somites 2-5; telson about as long as wide, suboval, with rounded apex.

Illustrations: *Medorippe lanata* (Guinot & Bouchard 1998: fig. 16A).

Pleonal-locking mechanism by press-button (Figs 4; 22C-E)

Press-button located in abruptely curved sternal suture 5/6, effective in both sexes.

Illustrations: *Medorippe lanata*: Holthuis & Manning 1990: fig. 37c; Guinot & Bouchard 1998: figs 15C, 16A, B.

Male gonopore and penis

Male gonopore coxal, oriented vertically and unprotected by thoracic sternum, i.e., nearly coxal condition. Penis lying on steep slope formed by sternite 7; sternites 7 and 8 laterally expanded at level of bulb, just leaving gap for penis passage, thus sternites 7 and 8 not joined proximally; bulb and small portion of penial tube (hidden by setae) being the only exposed portions; remaining portion being concealed by pleon.

Illustrations: *Medorippe lanata*: Guinot 1979a: figs 28, 46F; 1979b: fig. 2A, B1, B2, as *Dorippe lanata*; Guinot *et al.* 2013: fig. 15A.

Gonopods (Figs 4A; 22D, E; 31C)

G1 short, stout, abruptly turned outward, setiferous, with long, very acute, sharp apex, angled at nearly 90°; basal lobe with pappose setae and small denticles.

Illustrations: *Medorippe lanata*: Brocchi 1875: 102, fig. 194, as *Dorippe lanata*; Monod 1933b: fig. 3F, as *D. lanata* (reproduced by Manning & Holthuis 1981: fig. 4j; by Sin *et al.* 2009: fig. 4C; by Davie *et al.* 2015a: fig. 71-2.31B); Zariquiey Alvarez 1968: fig. 14b, as *D. lanata*; Guinot *et al.* 2013: fig. 15B, D; Vehof 2020: fig. 9.

G2 rather long, straight, with indistinct partition (Guinot *et al.* 2013: fig. 15B, C; Vehof 2020: fig. 9A).

Illustrations: *Medorippe lanata*: Brocchi 1875: 102, fig. 195, as *Dorippe lanata*; Guinot *et al.* 2013: fig. 15C.

Vulvae (Figs 4A; 32C)

Vulva placed anteriorly and medially on sternite 6, recessed at internal margin of very salient sternal prominence in prolongation of sternal ridge; opening small, of oval shape, partially roofed by anterolateral sternal projection; histologically, opening enclosed by protruding parts of vagina. Operculum stiff. Numerous and very small eggs.

Illustrations: *Medorippe lanata*: Hartnoll 1968: 293, as *Dorippe lanata*; Mori 1986: 78; Holthuis & Manning 1990: 89, fig. 37c, d; Guinot *et al.* 2013: fig. 42C; Vehof *et al.* 2017: figs 1B-E, 2B.

Female reproductive system

Studied in *Medorippe lanata* by Vehof *et al.* (2017) and Vehof (2020) (Figs 35C; 37). See below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae.*

DISTRIBUTION AND HABITAT

Medorippe lanata inhabits the Eastern Atlantic, from Portugal to Angola (Crosnier 1970; Muñoz *et al.* 2012) and South Africa, and the Mediterranean Sea (Modena *et al.* 2001; Abelló *et al.* 2002; Biagi *et al.* 2002; Pipitone & Arculeo 2003; Zenetos *et al.* 2005; Fanelli *et al.* 2007; El Lakhrach *et al.* 2012), including the Israel Coast (Galil & Shlagman 2010) and the Adriatic Sea (d'Udekem d'Acoz 1994; Artüz 2007; Çelik *et al.* 2007; Kocataş & Katağan 2007, Ungaro *et al.* 2005). It is a neritic species that may be found in rather deep waters to about 100 m, even 112 m in Mauritania (De Matos-Pita *et al.* 2017), the depth of 952-1038 m off Morocco given by Türkay (1976: 36) being far in excess (Manning & Holthuis 1981: 34); preferently on soft sandy bottoms (Balss 1921: 49; Monod 1956: 92; Manning & Holthuis 1981: 34; Forest & Guinot 1966: 50; d'Udekem d'Acoz 1999: 203; Mori 1986: 78; Rossetti *et al.* 2006: 21); a wide bathymetrical distribution over muddy bottoms, but with peak abundance on the shelf off the Catalan coast (North-West Mediterranean) (Abelló *et al.* 1988: 47, tables 2, 3, 5). In the western Mediterranean, *M. lanata* is one of the most abundant and frequent brachyurans on the West coast of Central Italy, with a depth range of 15-306 m (Fanelli *et al.* 2007).

Medorippe lanata cohabits with *Phyllodorippe armata* along the West-African coast, in Dahomey (Crosnier coll. et det., MNHN-IU-2009-2004 (= MNHN-B16380), Ghana (in the same station 24, see Forest & Guinot 1966: 36, 50), Gulf of Guinea (Henriksen 2009), Sierra Leone, and Ivory Coast (Forest & Guinot 1966: 36, 50; Manning & Holthuis 1981: 36).

CARRYING BEHAVIOUR

Medorippe lanata carries living organisms, but studies on its biology do not mention the carried objects. Marine experiments in Mediterranean aquaria showed that *M. lanata* preferred large tunicates (Pesta 1918; Mori 1986; Bedini *et al.* 2003: figs 2, 7; Rossetti *et al.* 2006).

Fig. 22. — Medorippinae n. subfam. *Medorippe lanata* (Linnaeus, 1767): **A**, ♂ 18.5 × 23.2 mm, Dahomey Coasts, ZRC 2009.0411: habitus; **B**, ovigerous ♀ 21.2 × 27.7 mm, Israel, ZRC 1999.0632: habitus; **C**-**E**, ♂ 18.5 × 23.2 mm, same data as **A**: **C**, anterior ventral view; **D**, thoracic sternum, press-button and G1; **E**, G1 and G2. **F**, ♂ 23.2 × 28.9 mm, no data, ZRC 2009.0412 (ex MNHN): thoracic sternum with pleon.

Remarks

Dorippe facchino, originally described by Herbst (1785) while including a reference to the Mediterranean *Dorippe lanata* of Plancus (1739), is now definitely related to the Indo-West Pacific *Dorippoides facchino* rather than the Mediterranean *Medorippe lanata* (see *Remarks under Dorippoides facchino*).

As *Phyllodorippe armata* cohabits with *Medorippe lanata* in some places, their main distinguishing characteristics,

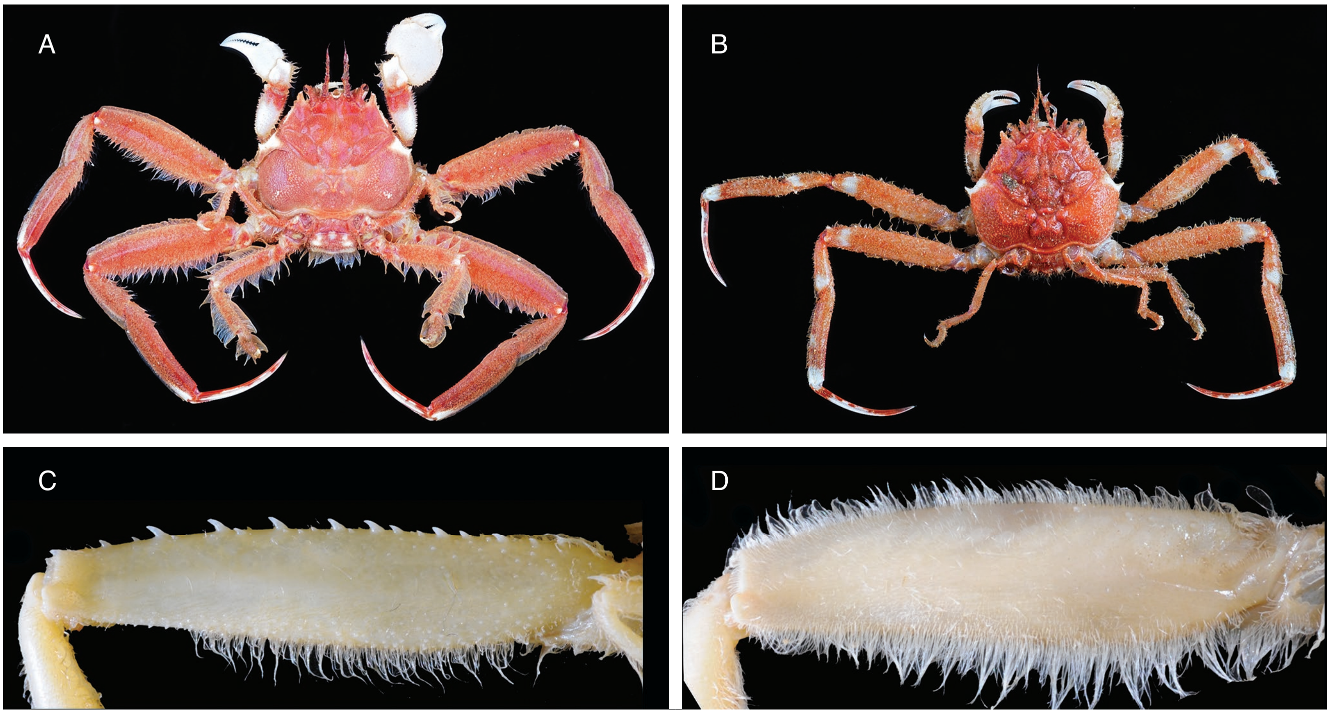

Fig. 23. — Medorippinae n. subfam.: **A**, **B**, ?*Medorippe crosnieri* Chen, 1988. Mozambique Channel, MAINBAZA Expedition: **A**, ♂ 21.1 × 25.9 mm, CP 3132, MNHN-IU-2009-1998, with dimorphic chelipeds; **B**, young ♂ 12.0 × 15.0 mm, CP 3130, MNHN-IU-2009-1999, with symmetrical chelipeds. Photos courtesy of T.-Y. Chan. **C**, *Medorippe lanata* (Linnaeus, 1767), ♂ 23.2 × 28.9 mm, no data, ZRC 2009.0412 (ex MNHN): P2 merus with spinulated dorsal margin; **D**, ?*Medorippe crosnieri* Chen, 1988, ♂ 21.1 × 25.9 mm, same data as in **A** (MNHN-IU-2009-1998): P2 merus with smooth dorsal margin. Photographs made by S. Soubzmaigne.

which are also those that separate the two subfamilies Phyllodorippinae n. subfam. and Medorippinae n. subfam., are listed below: in *Phyllodorippe*, carapace dorsal surface without V-shaped ridge (present on cardiac region in *Medorippe*); distinct, sometimes strong epibranchial tooth (variably marked in *Medorippe* but never as long); no supra-orbital lobe (present in *Medorippe*); short exposed portion of mxp1 endopod exceeding extent of mxp3 (long in *Medorippe*), thus opening of exhalant channels barely visible in dorsal view (clearly visible in *Medorippe*); antennule partially folded, distal part of antennular article out the fossa (unable to be retracted into fossa and directed anteriorly as antenna in *Medorippe*); male pleon with low, blunt elevations (more pronounced in *Medorippe*); articular membranes between pleonal somites very poorly developed or even absent (present between all pleonal somites in *Medorippe*, see Guinot *et al.* 2013: fig. 51G); telson short (longer in *Medorippe*); dorsal exposure of a large part of sternite 8 (of a smaller part in *Medorippe*); G1 long, very slender, S-shaped, with two short, lobiform distal appendages, and ending in narrow corneous point (short, stout, subdistally abruptly turned outward, setiferous, with long, acute, sharp apex in *Medorippe*); vulva submedian and elongate (recessed on external border of salient bulge in *Medorippe*); females with erect median spine on sternite 8 (without sternal spine in *Medorippe*); suture 6/7 practically continuous medially (interrupted in *Medorippe*); marked sexual dimorphism, strong heterochely, with palm of right cheliped strongly swollen and glabrous in males, even in young adults 20 mm width (right chela becoming larger only in large-sized males, about over 30 mm width, but palm never as swollen as in *M. lanata*; palm surface setiferous in *M. lanata*, even when the right chela becomes larger).

The question of the validity of *Medorippe crosnieri* described from Madagascar and synonymised with *Medorippe lanata* by Holthuis & Manning (1990: 89, 93, fig. 38) is not resolved (see below).

Remarks about the validity of *Medorippe crosnieri* Chen, 1988

A few years ago around 2010-2012, we had a project with J. C. Y. Lai (ZRC) to revise the status of *Medorippe crosnieri* Chen, 1988 by re-examining the Malagasy Chen's type material: holotype: MNHN-IU-2009-1995 (= MNHN-B18269); paratypes: MNHN-IU-2009-1996 (= MNHN-B18269) and MNHN-IU-2009-1997 (= MNHN-B18365). The main issue was to compare it with specimens in the MNHN and ZRC collections assigned to *M. lanata* but collected outside of its typical occurrence (the Mediterranean Sea and the West African coast), for example in the Mozambique Channel and in South Africa, by also including records in the literature. To test the hypothesis based on morphological characters that *M. crosnieri* could be a valid species, molecular analyses of COI gene of dorippids from West Africa and the Indian Ocean were undertaken. Unfortunately, this study could not be carried out due to inconclusive gene sequence results, awaiting further molecular analyses. The data summarised below are from an advanced draft in collaboration with J. C. Y Lai but is currently on hold.

A second species of *Medorippe*, *M. crosnieri*, from the northwest coast of Madagascar, was established by Chen (1988: 681, fig. 2, pl. 1D, E, table 2; paper often erroneously reported from 1987), based mainly on the smooth dorsal margins of P2 and P3 meri, as opposed to the spinulated margins in *M. lanata*. But *M. crosnieri* was immediately synonymised with *M. lanata* by Holthuis & Manning (1990: 89, 93), who argued that Chen's description was "based upon juveniles" and who reproduced (1990: fig. 38) all Chen's (1988) figures as *M. lanata*. Examination of the Chen's material, deposited in the MNHN, shows that the male holotype MNHN-IU-2009-1995 of *M. crosnieri* is a pre-adult with full-grown but slender gonopods and still symmetrical chelipeds; the two young paratype males MNHN-IU-2009-1997 (instead of females as mentioned by Chen [1988]) both have undifferentiated gonopods; another paratype MNHN-IU-2009-1996 is an immature female without opened vulvae. All these specimens have cylindrical, slender and rather long P2 and P3 meri, and evidently smooth (Chen 1988: fig. 2c, pl. 1D, E).

While the stout G1 ending in triangular apex in the Chen's species is similar to that of *M. lanata*, the main distinguishing feature of *M. crosnieri* was related to the smooth dorsal margins of the P2 and P3 meri, except for a few low teeth on the basal part of the P2 merus and one or two on the P3 merus (Fig. 23A, B, D), instead of the distinctly spinulated meri of *M. lanata* (Figs 22A, B; 23C). Additional differences were: in *M. crosnieri* body with short thin hairs (versus with club hairs in *M. lanata*); carapace surface with less prominent granules and tubercles in *M. crosnieri* than in *M. lanata*; and the surface of the male pleon not densely covered with short hairs (versus densely covered with rather long hairs in *M. lanata*).

Two specimens of *Medorippe* from the Mozambique Channel were collected by the MAINBAZA Expedition in 2009 (MNHN-IU-2016-1335 and MNHN-IU-2016-1336), a male 21.1 × 25.9 mm with dimorphic chelipeds and a young male 12.0 × 15.0 mm with symmetrical chelipeds, both having smooth meri on P2 and P3, which are long and cylindrical in the young (Fig. 23B), shorter and more robust in the adult (Fig. 23A). Both are related to *M. crosnieri* by their smooth P2 and P3 meri. Our Figure 23C, D seems to show that the merus is proportionally more elongated in *M. lanata* than in *M. crosnieri* but this criterion must be used with prudence as the size of the merus varies with age, becoming wider and stouter when the individual grows. It seemed possible that this material from Mozambique belonged to *M. crosnieri* and that the refutation by Holthuis & Manning (1990) of the characters used by Chen (1988) to distinguish it from *M. lanata* needs to be re-evaluated.

It should be noted that Holthuis & Manning (1990: 89, fig. 37b) assigned to *M. lanata* a male from Mozambique and several South African specimens, the latter being figured with spinulated meri. Chen (1988) added as possible synonyms of her *M. crosnieri* some *Dorippe lanata* of the literature, including that of Barnard (1950: 389, fig. 73d; 1955: 4) from South Africa (Natal). The material from Spanish Sahara, Sierra Leone, Gabon, Cabinda and Congo reported by Capart (1951b: fig. 6, as *Dorippe lanata*) has spines on the P2, P3 meri, a V-shaped cardiac region, and a G1 distally curved at right angle. As the southern limit of *Medorippe lanata* along the West African coast includes Angola with a reasonable certainty (Crosnier 1970), it is relevant to consider the material recorded in South Atlantic waters. Barnard (1950: 389) does indicate that P2 and P3 have spinulose meri. We have examined a few specimens from South Africa (ZRC 2012.0158 and MNHN-IU-2016-1336): they have spinulose meri and are most likely *M. lanata*.

Dorippoides nudipes Manning & Holthuis, 1986 (Manning & Holthuis 1986: 364, fig. 1c; Holthuis & Manning 1990: 66, fig. 26) is another dorippid with unarmed P2 and P3 meri, which occurs in South Africa (see under Dorippoidinae n. subfam.): it cannot be confused with a *Medorippe* species on account of its short G1 ending in horn-coloured projection with a twisted whip-like appendage, the carapace margin lacking epibranchial spine and the cardiac region without a V-shaped ridge (Fig. 16C, D). Similarly, *Medorippe crosnieri* cannot be confused with the West-African *Phyllodorippe armata*, known from the Spanish Sahara to Angola and never recorded further south, which also has unarmed P2 and P3 meri (Fig. 29A, B) and a slender, S-shaped G1 ending in a prominent subdistal lobe (Fig. 30C, D) (Monod 1933b: fig. 3H; Manning & Holthuis 1981: fig. 4k, l), contrasting with the typical short, stout G1 of *Medorippe*, abruptly turned outward and ending in a long, sharp setiferous apex (Chen 1988: fig. 2f; reproduced by Holthuis & Manning 1990: fig. 38g).

It proved difficult to conclude the value of the small differences reported by Chen (1988: table 2) due to insufficient material in hand assignable to *M. crosnieri*. In addition, examination of *M. lanata* revealed a range of morphological variation (variations that also exist in the Mediterranean form), including spinulation of meri P2 and P3 that was more pronounced in smaller individuals and tended to decrease in larger adult males, particularly in the proximal half of the merus. Spinulation may also occasionally be missing completely, e.g. in a sample from the north of mouth of Congo River, MNHN-IU-2009-2001 (= MNHN-B13583), a large male 26.0 × 30.0 mm (with markedly asymmetrical chelae) that has abnormally smooth meri P2, P3; in contrast, another adult male of 28.2 mm cw (with less asymmetrical chelas) has spinulated meri, both specimens showing the typical G1 of *Medorippe*. For more details on the spinulation of P2, P3 meri of *M. lanata*, see Monod (1933b: fig. 3C, D; 1956: 84, fig. 103, as *D. armata*); Manning & Holthuis (1981: 32, figs 4a, c-f, table 1) and Holthuis & Manning (1990: 89, figs 36, 37).

An ovigerous female collected in southern Madagascar - thus in proximity to Chen's (1988) type series – by the ATIMO VATAE expedition in 2010 (MNHN-IU-2010-4307), which we had not previously examined, shows smooth meri P2, P3, which undermines Holthuis & Manning's (1990) argument that the smoothness of P2 and P3 is a juvenile character, and leads us to believe that *M. crosnieri* is a valid species.

Molecular analyses based on the COI carried on by J. C. Y. Lai were inconclusive, showing that the *M. lanata* from South Africa, with spinulated meri, was genetically almost identical to the *M. crosnieri* of the MAINBAZA Expedition in 2009, with smooth meri. The genetic evidence supported that *M. lanata* and *M. crosnieri* were closely related with little divergence (< 3% divergence), insufficient to revalidate *M. crosnieri*, so the planned paper was not published, pending further research.

Subfamily PARADORIPPINAE n. subfam.

TYPE GENUS. — *Paradorippe* Serène & Romimohtarto, 1969 (type species by original designation: *Dorippe granulata* De Haan, 1841). Other included species by Holthuis & Manning (1990: 108, 109): *Dorippe australiensis* Miers, 1884; *Paradorippe cathayana* Manning & Holthuis, 1986; *Dorippe polita* Alcock & Anderson, 1894.

PRELIMINARY NOTE

We were able to examine only the type species *Paradorippe granulata* (De Haan, 1841), so in this paper all our following descriptions, figures and mentions refer only to this one species. We believe that the genus *Paradorippe sensu* Holthuis & Manning (1990) and subsequent authors may not be monophyletic, with at least two groups of species (with possibly misidentified species): one, i.e., the genus *Paradorippe sensu stricto*, with *P. granulata* and *P. australiensis*, namely with a G1 bearing unequal processes, one being longer and hammer-shaped, and with a wide vulva on a slightly marked prominence; a second, i.e., a new genus, with *P. polita* (and probably also *P. cathayana*), with a G1 bearing shorter processes of equal length and with a smaller, possibly recessed vulva. Genetic analyses of two of the four known species of *Paradorippe*, *P. granulata* and *P. polita*, support such a distinction as they indicate that they form a distinct clade "with high bootstrap and posterior probability support, with intrageneric divergence being 12.5% in 16S", the latter being the highest recorded in the study of seven genera and 12 dorippid species by Sin *et al.* (2009: 229, tables 1; 2) (see our Figure 10). This problem still needs to be improved. However, the presumed distinctive generic characters do not affect the recognition of the subfamily Paradorippinae n. subfam.

DESCRIPTION (BASED ON *PARADORIPPE GRANULATA* ONLY)

Carapace (Fig. 24A, B)

Carapace wider than long in adults, widening considerably in posterior part, flat. Dorsal surface sparsely sculptured but with distinct grooves and visible human facies, often naked, only with low, rare pubescence, lacking erect spines, coarsely granular or appearing smooth, at most slightly granular on magnification. Regions with well-delinated mesogastric region; metagastric region indistinct, urogastric region defined; generally, branchial lobes relatively large. Precervical and cervical grooves more or less distinct, maybe shallow across midline; precervical groove may be deeper than cervical, deepest at lateral margins; branchiocardiac groove quite distinct. A pair of oblique submedian gastric pits visible just at base of meso-metagastric region. Antero- and posterolateral margins not demarcated, epibranchial spine absent. Front consisting of two sharp or bluntly triangular teeth, not extending beyond outer orbital spines and separated by broadly U-shaped emargination revealing exhalant channels. Inner orbital teeth low and blunt or as rounded, lobes scarcely marked. Orbit small. Orbital fissure narrow, closed or open anteriorly. Inner suborbital tooth short, much smaller than outer orbital tooth, sometimes rudimentary. Carapace posterior rim not extending laterally at all along posterolateral margin, thus interrupted on each side, and lined posteriorly by well-defined strip, much more delineated in females (Fig. 24B) than in males where it is straight (Fig. 24A), often even appearing as separate sclerite.

Illustrations: *Paradorippe australiensis*: Miers 1884: pl. 26, fig. D, as *Dorippe australiensis* (reproduced by Holthuis & Manning 1990: fig. 44; by Davie *et al.* 2015a: fig. 71-2.2D); Holthuis & Manning 1990: fig. 45a; Davie 2002: fig. p. 154; Poore 2004: fig. 95. *P. cathayana*: Shen 1932: fig. 4, as *Dorippe polita* (reproduced by Holthuis & Manning 1990: fig. 46; by Sin *et al.* 2009: fig. 3G), pl. 1, fig. 11; Chen 1986b: fig. 7.33, as *P. polita*; Holthuis & Manning 1990: fig. 47a; Chen & Sun 2002: fig. 98.1. *P. granulata*: De Haan 1839: pl. 3, fig. 2, as *Dorippe granulata* (reproduced by Holthuis & Manning 1990: fig. 48); Shen 1931: pl. 6, fig. 3, as *D. granulata*; 1932: fig. 8, as *D. granulata* (reproduced by Holthuis & Manning 1990: fig. 49), pl. 1, fig. 12; Takeda 1982b: pl. p. 94; Takeda 1983: 247, fig. p. 121; Miyake 1983: pl. 6, fig. 3; Chen 1986b: fig. 6.28; Holthuis & Manning 1990: fig. 50a; Chen & Sun 2002: fig. 97.1; Ng *et al.* 2008: fig. 44; Wong *et al.* 2021: fig. 14a, pl. 3B. *P. polita*: Alcock & Anderson 1894: pl. 24, fig. 4, as *D. polita* (reproduced by Holthuis & Manning 1990: fig. 53); Holthuis & Manning 1990: figs 54a, 55a-c, 56.

Cephalic structures (Figs 24A, B; 25A; 26A)

Eyes short, distally tapering; cornea ventrolateral; eye slightly extruded from orbit. Antennula retractable into fossa, directed anteriorly like antenna. Antenna well developed: articles 2+3 quadrangular; article 4 short but wide; article 5 much developed, foliaceous, fringed with dense setae, bent outwards nearly horizontally, extending along most of orbit and lying along eyestalk; flagellum bent inwards.

Illustrations: *Paradorippe cathayana*: Holthuis & Manning 1990: fig. 46. *P. granulata*: Quintana 1987: fig. 20C-c; Holthuis & Manning 1990: fig. 49. *P. polita*: Holthuis & Manning 1990: figs 53, 54.

Oxystomatous disposition (Fig. 26A)

Large development of endostomal roof, thus opening of exhalant channels clearly visible in dorsal view between rostral teeth.

Illustrations: *Paradorippe cathayana*: Shen 1932: fig. 5a, b, as *D. polita*; Holthuis & Manning 1990: fig. 46. *P. granulata*: Shen 1932: fig. 9a, *as D. granulata*; Holthuis & Manning 1990: figs 48, 49. *P. polita*: Holthuis & Manning 1990: figs 53, 54.

Pereiopods (Figs 24; 25A)

Chelipeds of females and non-adult males of same size and shape; marked heterochely in adult males, with globular palm having bulbous ventral protuberance, and short fingers. Carpus and merus smooth or granular, often with larger granules on upper and lower margins. Outer surface of palm smooth, punctate, or granular, with or without short hairs; dorsal margin of palm and proximal part of dactylus with fringe of long hairs; lower margin of palm, except in inflated chelae, variously fringed; lower margin of fixed finger without setae. In smaller specimens fingers very long, bent downwards, with teeth of equal size, more pointed and triangular at smaller size.

Illustrations: *Paradorippe australiensis*: Holthuis & Manning 1990: figs 44, 45b, c. *P. cathayana*: Manning 1986: fig. 1e; Chen 1986b: fig. 7.34, as *P. polita*; Holthuis & Manning 1990: figs 46, 47; Chen & Sun 2002: fig. 98.2, 3. *P. granulata*: Chen 1986b: fig. 6.29; Yamaguchi *et al.* 1987: pl. 1, fig. 8; Holthuis & Manning 1990: figs 48, 49; Chen & Sun 2002: fig. 97.2, 3; Wong *et al.* 2021: fig. 14c. *P. polita*: Holthuis & Manning 1990: fig. 53.

P2, P3 not very long and may be rather stout in both males and females, or longer and slender. P3 slightly longer, with flattened unarmed articles, smooth or granular; dactyli flattened, slightly twisted, with well-developed carinae on anterior and posterior surfaces and with at least a sparse layer of short setae in both sexes. Both P4, P5 reduced, with subeheliform apparatus.

Illustrations: *Paradorippe australiensis*: Holthuis & Manning 1990: figs 44, 45d, e. *P. cathayana*: Holthuis & Manning 1990: figs 46, 47c; Chen & Sun 2002: fig. 98.4. *P. granulata*: Holthuis & Manning 1990: figs 48, 49, 50c; Wong *et al.* 2021: fig. 14b. *P. polita*: Holthuis & Manning 1990: figs 53, 54, 55f, g, 56c.

Thoracic sternum (Figs 25; 26)

Thoracic sternum narrow, narrowing distinctly posteriorly, finely or coarsely granular. Sternite 1 with only a small portion visible dorsally; sternite 2 forming short, rectangular, sharply delineated shield with thick vertical margins, separated from sternite 3 by well-marked, straight depression. Lateral margin of sternite 2 straight, directed vertically, with slightly pointed anterior angles; lateral margin of sternite 4 slightly concave, directed obliquely; lateral margin of sternite 5 almost straight, directed vertically; lateral margin of sternite 6 clearly concave. Suture 3/4 short, curved into closed boutonniere in both sexes. Sternite 3 with distinct quadrate process bearing gynglyme for articulation of mxp3 sterno-coxal condyle close to edge of Milne Edwards opening; sternite 4 thickened on each side, with longitudinal median depression; sternites 4 and 5 with narrow extensions, i.e., laterally expanded between P1/P2 and P2/P3. Sutures 4/5-7/8 interrupted. Suture 4/5 horizontal, almost parallel to suture 5/6, only slightly oblique and weakly curved posteriorly; both sutures 4/5 and 5/6 with short interruption points; suture 6/7 interrupted in males but variable in females, being medially interrupted. Female thoracic sternum tilted backwards at level of raised ridge crossing whole sternite 6; sternite 8 lacking axial spine.

Illustrations: *Paradorippe australiensis*: Holthuis & Manning 1990: fig. 45i. *P. granulata*: Shen 1931: pl. 6, fig. 2; Holthuis & Manning 1990: fig. 50h; Vehof *et al.* 2018b: fig. 2A; 3. *P. polita*: Holthuis & Manning 1990: fig. 56i.

Pleon and telson (Figs 24A; 25B)

Male pleon with all somites free; with articular membranes, especially at sutures 4/5 and 5/6; surface without strong tubercles or spines but often with distinctly granular ridges and bumps. Somites 1, 2 exposed dorsally in males; somites 1-3 and part of 4 exposed dorsally in adult females. Somite 1 trapezoidal, widening posteriorly, posterior margin excavated in middle; somite 2 widening posteriorly, with low transverse ridge, often appearing trilobed in dorsal view; somite 3 with swollen lateral parts; somites 4 and 5 short, each with low, transverse ridge; somite 6 with posterolateral angles produced; telson triangulary blunt, telson extending over much of sternite 5, with tip far exceeding level of suture 5/6.

Illustrations: *Paradorippe australiensis*: Serène & Rohmimohtarto 1969: fig. 14. *P. cathayana*: Shen 1932: fig. 5d, *as D. polita*; Holthuis & Manning 1990: fig. 47d; Chen & Sun 2002: fig. 98.5. *P. granulata*: Shen 1932: fig. 9b, as *D. granulata*; Holthuis & Manning 1990: figs 48, 50e. *P. polita*: Holthuis & Manning 1990: figs 53, 54a, 56d.

Female pleon wide and rounded, smooth or variously granular. Somites 2-5 usually with blunt but distinct transverse carina; somites 4 and 5 widest, 5 and 6 longest; telson small, with semicircular or subtriangular posterior margin (Figs 24B; 26B).

Illustrations: *Paradorippe cathayana*: Shen 1932: fig. 5e, as *D. polita*; Holthuis & Manning 1990: fig. 47e. *P. granulata*: Shen 1932: fig. 9c, as *D. granulata*; Holthuis & Manning 1990: figs 48, 50d. *P. polita*: Holthuis & Manning 1990: figs 53, 54a, 55h.

Pleonal locking mechanism by press-button (Figs 25C-E; 26B-D)

Press-button quite large, located on suture 5/6 weakly curved backwards and situated far from G1 tip in males, very close (almost contiguous) to vulvae. Location of sockets clearly discernible dorsally on pleonal somite 6 by swollen lateral areas. No additional pleonal retention in females, unlike many other dorippids (see below). Sternite 8 only slightly enlarged posteriorly and, together with narrow sternite 7, only flanking the base of the pleon.

Additional female pleonal-retention mechanism

Unlike some genera (*Dorippe*, *Heikeopsis*, *Nobilum*, *Philippidorippe* and *Phyllodorippe*), in females the process emanating from the dorsally exposed sternite 8 not actually overhanging the pleonal somite 2. Here, sternite 8 only slightly enlarged posteriorly, with a square projection that just abuts the edge of the female pleon and, together with narrow sternite 7, merely flanking the base of the pleon (Fig. 24B).

Male gonopore and penis

Coxo-sternal condition: penis overhung over a rather long distance by sternites 7 and 8, close or not in contact; penis with inclined portion weakly sclerotised; vertical portion rather short, with long soft papilla.

Illustrations: *Paradorippe granulata*: Guinot *et al.* 2013: fig. 17C; Vehof *et al.* 2018a: fig. 1B, G.

FIG. 24. — Paradorippinae n. subfam. *Paradorippe granulata* (De Haan, 1841): habitus: **A**, ♂ 23.6 × 27.3 mm, NE Taiwan, I-Lan county, ZRC 2001.0014; **B**, ovigerous ♀ 23. 2 × 25.7 mm, Japan, off Hota, ZRC 1999.0082.

FIG. 25. — Paradorippinae n. subfam. *Paradorippe granulata* (De Haan, 1841): **A**, **C**, **E**, ♂ 24.0 × 26.0 mm, China, Tuandao, off Quingdao, MNHN-IU-2016-10753. **B**, **D**, ♂ 23.6 × 27.3 mm, NE Taiwan, I-Lan county, ZRC 2001.0014; **A**, chelae; **B**, thoracic sternum and pleon; **C**, **D**, thoracic sternum without pleon, with G1, G2 and press-buttons; **E**, G1 and G2 *in situ*.

Gonopods (Figs 25C-E; 31G)

G1 stout throughout, short, filling most of sterno-pleonal cavity; shaft strongly swollen, abruptly constricted and angularly bent at obtuse angle towards about three-quarters of its length; bent portion wider, possibly flattened dorso-ventrally; terminal part swollen, elaborate with two distinct bulbs bearing several apical processes; these processes rather elongated, one of which being longer and hammer-shaped; no basal lobe.

Illustrations: *Paradorippe australiensis*: Serène & Romimohtarto 1969: figs 26-28; Holthuis & Manning 1990:

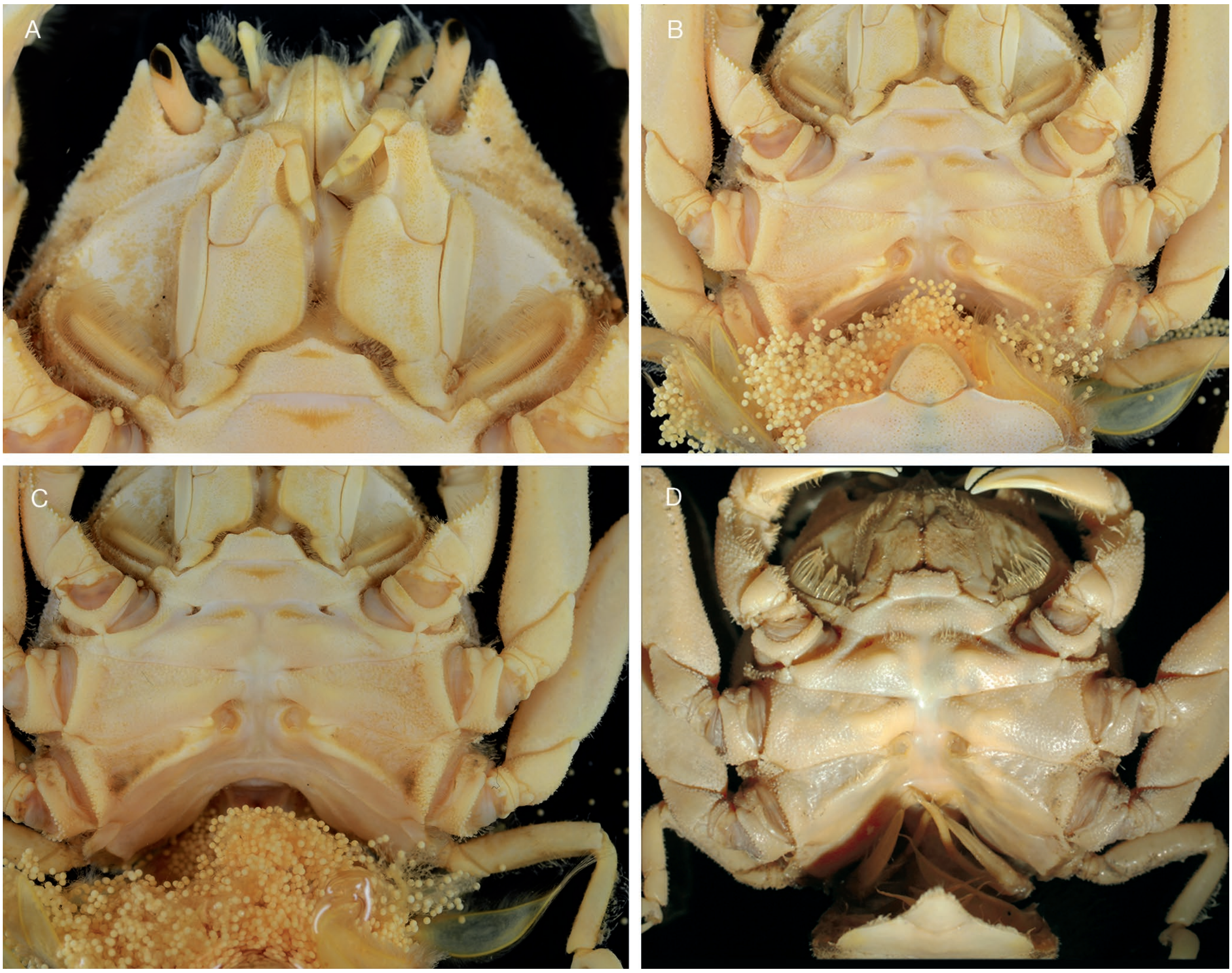

Fig. 26. — Paradorippinae n. subfam. *Paradorippe granulata* (De Haan, 1841): **A**-**C**, ovigerous ♀ 23.2 × 25.7 mm, Japan, off Hota, ZRC 1999.0082. **D**, ♀ 22.7 × 24, 7 mm, China, Tuandao, off Quingdao, MNHN-IU-2016-10753. **A**, anterior ventral view; **B**, **C**, thoracic sternum and pleon; **D**, vulvae.

fig. 45f, g. *P. cathayana*: Chen 1986b: fig. 7.35, as *P. polita*; Holthuis & Manning 1990: fig. 47f, g (reproduced by Sin *et al.* 2009: fig. 4G); Chen & Sun 2002: fig. 98.6. *P. granulata* Serène & Romimohtarto 1969: figs 23-25; Chen 1986b: fig. 6.30, 31; Holthuis & Manning 1990: fig. 50f, g (reproduced by Davie *et al.* 2015a: fig. 71-2.22D); Dai & Yang 1991: fig. 23.1, as *Dorippe* (*Paradorippe*) *granulata*; Chen & Sun 2002: fig. 97.4-6; Vehof *et al.* 2018a: fig. 1. *P. polita*: Holthuis & Manning 1990: fig. 56e-h; Dai & Yang 1991: fig. 23.2, as *Dorippe* (*Paradorippe*) *polita*.

G2 straight, rather long

Illustrations: *Paradorippe granulata*: Chen 1986b: fig. 6.32; Serène & Romimohtarto 1969: fig. 29; Chen & Sun 2002: fig. 97.7; Vehof *et al.* 2018a: fig. 1.

Vulvae (Figs 26B-D; 32C)

Vulvae not juxtaposed, close to suture 5/6, and near distal part of raised ridge; opening large to very large, rounded, surrounded by numerous setae, clusters of setae projecting to some extent above vulva opening; vulva located on more or less prominent part of sternite 6; wider and on slightly marked prominence. Histologically, lateral margin bulging in median direction, forming a muscle-operated vulvar cover that partially roofs vulva opening, so that the opening actually visible externally is crescent-shaped.

Illustrations: *Paradorippe australiensis*: Holthuis & Manning 1990: fig. 45h, i. *P. granulata*: Holthuis & Manning 1990: fig. 50h, i; Vehof *et al.* 2018a: fig. 2. *P. polita*: Holthuis & Manning 1990: figs 55i, 56i-k.

Female reproductive system

Studied in *Paradorippe granulata* by Vehof *et al.* (2018a: 68; 2018b: 82, figs 1-5; Vehof 2020: 78, 86, figs 17, 20, 22) (Figs 35D; 37). See below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae.*

DISTRIBUTION AND HABITAT

(see *Preliminary note*, p. 279)

Paradorippe australiensis, known from Australia (Western Australia, Queensland), is a shallow water species, caught under stones on reef flat at 22 m, on mud at 18 m, on sand and occasional sponges and corals at 15 m (Holthuis & Manning 1990; McEnnulty *et al.* 2011).

Paradorippe cathayana is known mainly from many localities in China (Shen 1932, 1937a, 1940b, as *Dorippe polita*; Yang 1986, as *D. polita*; Chen 1986b, as *P. polita*; Chen & Sun 2002); found in tidepools on sandy beaches (Shen 1932, as *D. polita*) and shallow pools of clear water, along sand beach (Shen 1937a, as *D. polita*), Gulf of Tonkin (Dai & Song 1986, as *D. polita*) and from Vietnam (Serène 1937, as *D. polita*); also from India, Gulf of Mannar (Rajan *et al.* 2017: 3, 11; Zoological Survey of India 2018 fig. p. 73).

Paradorippe granulata lives much further north than any of the Indo-West Pacific dorippids, occurring as far east in Russia as Vladivostock and Peter the Great Gulf, as well as in the Sakhalin Island (Balss 1922; Urita 1942; Kobjakova 1955, 1966; Vinogradov 1950; Levin 1976, all as *Dorippe granulata*). It is abundant in many localities of Japan (De Haan 1841; Herklots 1861; Bouvier 1899; Parisi 1914; Sakai *c.* 1930, 1936, 1940, 1956; Nishimura & Suzuki 1971; Yang 1986, all as *Dorippe granulata*; Sakai 1976, 1985; Takeda 1975, 1982a, b, 1983; Yamaguchi *et al.* 1976; Muraoka 1982; Miyake 1983; Sakai *et al.* 1983; K. Sakai & Nakano 1983; Minemizu 2000); of Korea (Kim 1970, as *D. granulata*; Kim 1973; Koh & Lee 2013; Lee *et al.* 2021); and of China, Hong Kong (Shen 1932, 1940a, b, as *D. granulata*; Takeda & Miyake 1970; Huang 1994; Chen 1986b; Dai *et al.* 1986; Chen & Sun 2002; Wang 2005, 2009; Wong *et al.* 2021) and Taiwan (Ng *et al.* 2017). For complete and recent distribution of *P. granulata*, see Holthuis & Manning 1990; Wang *et al.* 2013, 2017; Ng *et al.* 2001, 2017.

Paradorippe polita is known from a few localities: southeast India (Alcock & Anderson 1894; Alcock 1896; Sankarankutty 1966; all as *Dorippe polita*; Dev Roy 2008; Venkataraman *et al.* 2004, as *D. polita*; Krishnamoorthy 2007: 90, as *Paradorippe granulata*; Trivedi *et al.* 2018: table 1) and Malaysia (Holthuis & Manning 1990). The figure by Jeyabaskaran *et al.* (2000: pl. 32a) of a *P. granulata* from the Gulf of Mannar is too small to be sure that it is *P. polita* instead of *P. granulata*. The *Paradorippe polita* from the Gulf of Tonkin (Zarenkov 1972: 250) should be confirmed.

CARRYING BEHAVIOUR

Paradorippine crabs are known to exclusively select valves of bivalve molluscs, often intimately associated with sea anemones in cases of symbioses (Castro 2015). This long-recognised behaviour has been widely documented (for full literature, see Holthuis & Manning 1990). Nevertheless, the question of how and to what extent the P4 and P5 subcheliform device is specialised to grasp the valve of lamellibranchs rather than a sponge or leaf like in other dorippids has apparently not been studied. A small male of *Paradorippe australiensis* was found carrying on its back a 16 mm long valve of the venerid genus *Antigona* Schumacher, 1819 (Rathbun 1924: 27, as *Dorippe australiensis*). *Paradorippe cathayana* is always found carrying a bivalve shell, which is thrown away when it buries itself (André 1937, as *Dorippe polita*; Shen 1937a, as *D. polita*). For *P. granulata* (see Döderlein 1883: 109, as *D. sima*; Patton 1967, as *Dorippe*; Levin 1976: fig. 106a, as *D. granulata*), the carried shells seem to belong mainly to the tellinid lamellibranch genus *Macoma* Leach, 1819, on which one and sometimes two or three sea anemones are fastened; a dead shell of *Macoma* with three longitudinally striped anemones of the actinarian *Carcinactis ichikawai* Uchida, 1960 has been found carried (Uchida 1960: 595, pl. 1, fig. 1, as *Dorippe granulata*); the crab disappears completely under the shell (Kobjakova 1966: pl. 49: fig. 1a; Minemizu 2000: fig. p. 189; Koh & Lee 2013: pl. 15). According to Quintana (1987: figs 15C-H, 17E, F, 19F, 24B), in laboratory the megalopa and first crab stages of *P. granulata* did not swim, had benthic habits like adults, and carried dorsally over the carapace fragments of shells or small rocks provided in rearing vessels: the dorippid early-carrying behaviour is the unique case known within the Brachyura (the homolid megalopa has a P5 that may be held in a dorsal position and bears a recurved ending with long setae corresponding to a 'feeler', not functional for carrying; see Rice 1964: figs 4, 8f; Williamson 1965: fig. 2).

Illustrations and data: *Paradorippe australiensis*: Rathbun 1924: 27, as *Dorippe australiensis*; Davie 2002: 156; Thoma 2007: 301. *Paradorippe cathayana*: Shen 1932: 11; 1937a: 171, as *D. polita*; André 1937: 79, as *D. polita*. *P. granulata*: Döderlein 1883: 109, as *D. sima*; Sakai 1956: 26, fig. 9, as *D. granulata*; Uchida 1960: 595, 600, pl. 1, fig. 1, as *D. granulata*; Kobjakova 1955: 155, pl. 49, fig. 1a, as *D. granulata* (reproduced by Holthuis & Manning 1990: fig. 51); 1966: pl. 49, fig. 1a, as *D. granulata*; Patton 1967: 1232, as *Dorippe*; Burton 1969: fig. p. 64, as Japanese crab (redrawn by Holthuis & Manning 1990: fig. 62); Levin 1976: fig. 106a, as *D. granulata*; Sakai *et al.* 1983: fig. p. 29; Tan & Ng 1988; 1992: 149; Guinot *et al.* 1995: fig. 5B; Ng *et al.* 2008: fig. 44; Guinot & Wicksten 2015: 599, fig. 77-11.9.J.

REMARKS

Von Siebold had collected a total of 38 specimens of *Dorippe granulata*, described a little later in the *Fauna Japonica* by De Haan (1839: pl. 31, fig. 2; 1841: 122) and which became the type species of *Paradorippe* Serène & Romimohtarto, 1969. The holotype and many paralectotypes are deposited at RMNH (Fransen *et al.* 1997), and a dry paralectotype is deposited at MNHN (MNHN-IU-2000-11383, ex MNHN-B11383) (Yamaguchi & Baba 1993: 304, fig. 90A, B; Yamaguchi 1993: 586).

Paradorippinae n. subfam. is monotypic, with the genus *Paradorippe* known from four species (see *Preliminary note* p. 279). We agree with Alcock & Anderson (1894) that the flattish, smooth and naked carapace of *P. polita* resembles more that of an ethusid than that of a dorippid.

Subfamily PHILIPPIDORIPPINAE n. subfam.

TYPE GENUS. — *Philippidorippe* Chen, 1986 (type species by original designation: *P. philippinensis* Chen, 1986 (Chen 1986a: 183, fig. 3a-g, pl. 1, fig 3, pl. 2, fig. 4). Genus monotypic.

DESCRIPTION

Carapace (Fig. 27A, B)
Carapace wider than long, greatly enlarged and swollen at level of branchial regions. Dorsal surface slightly inflated, finely granular, especially on prominences, without spines. Regions well defined, especially proto-, meso- and urogastric regions. Precervical groove distinct but irregular; cervical groove deep. Branchial lobes low, convex. Gastric pits as two slits just at limit between meso-metagastric and urogastric regions (thus not on cervical groove as indicated by Holthuis & Manning 1990: 132). Front with two pointed submedian teeth separated by narrow, V-shaped median emargination, exposing exhalant channels. Posterior margin of orbit with fissure. Outer orbital tooth triangular, slender, acute, very long and overreaching frontal teeth. Lower orbital margin unarmed, deeply depressed. Inner suborbital tooth large, sharp, not overreaching outer suborbital tooth. Carapace posterior rim thin, rather narrow, not extending sideways along posterolateral margins and lined by weakly developed strip, only thickened laterally, especially in females.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: pl. 1, fig. 3, pl. 2, fig. 4; Holthuis & Manning 1990: fig. 57a (reproduced by Sin *et al.* 2009: fig. 3H); Chen & Xu 1991: fig. 8.1; Chen & Sun 2002: fig. 99.1, pl. 2, fig. 2; Takeda & Manuel-Santos 2006: 96, fig. 6A; Ng *et al.* 2008: fig. 45.

Cephalic structures (Figs 27A, B; 28A, B)
Eyes short and stout, cornea ventrolateral. Antennule obliquely folded and may be completely retracted into fossa; articles short. Antenna entirely directed forward, all along fringed with dense setae: articles 2+3 quadrangular; article 4 short; article 5 slitghly longer; flagellum long.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: fig. 3a (reproduced by Holthuis & Manning 1990: fig. 58a); Holthuis & Manning 1990: fig. 57b; Chen & Xu 1991: fig. 8.1; Chen & Sun 2002: fig. 99.1.

Oxystomatous disposition (Fig. 28A-C)
Opening of exhalant channels visible in dorsal view between rostral teeth. Mxp3 narrow (especially merus) and long, reaching level of eyes.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: fig. 3a (reproduced by Holthuis & Manning 1990: fig. 58a); Chen & Xu 1991: fig. 8.1; Holthuis & Manning 1990: fig. 57c; Chen & Sun 2002: fig. 99.1.

Pereiopods (Figs 27A, B; 28A, B, E)
Chelipeds of females and young males equal in size and shape; marked heterochely in adult males, with smooth outer surface of palm inflated; dorsal margin and outer surface covered with granules and fringed with short hairs.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: fig. 3b (reproduced by Holthuis & Manning 1990: fig. 58b, c), pl. 1, fig. 3, pl. 2, fig. 4; Chen & Xu 1991: fig. 8.2; Chen & Sun 2002: fig. 99.2, 3.

P2, P3 of males extra-long, P2 longest, slender; meri very long, longer on P2, flattened, with distal spine basally erect; dactyli without fringes of hair. P2, P3 shorter and proportionally stouter in females. P4, P5 very slender; P5 with very long ischio-merus; both ischio-merus and merus of P5 clearly curved, applying on convex sides of carapace.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: pl. 1, fig. 3, pl. 2, fig. 4; Holthuis & Manning 1990: fig. 57e.

Thoracic sternum (Figs. 27C, D; 28)
Thoracic sternum wide, granular, tomentose. Sternites 1 and 2 forming a regular triangle (instead of pentagonal shield); very small portion of sternite 1 visible dorsally; sternite 2 separated from sternite 3 by depression; suture 3/4 short, not ending in boutonniere. Sutures 4/5-7/8 interrupted; median longitudinal furrow at level of sternite 4; suture 5/6 moderately curved backwards. Sternal extensions between P2/P3, P3/P4, shorter betwen P4/P5. Female thoracic sternum only obliquely tilted backwards from middle of sternite 6 (Fig. 27C, D).

Illustrations: *Philippidorippe philippinensis*: Holthuis & Manning 1990: fig. 57f.

Pleon and telson (Figs 27; 28)
Male pleon short, not completely filling sterno-pleonal cavity; all somites free, without strong tubercles or spines, only with granules on some somites. Somites 1-3 exposed dorsally; somite 1 rather broad and short, widening slightly posteriorly, posterior margin excavated in middle; somite 2 widening posteriorly; somite 3 with distinctly swollen lateral parts highly visible in dorsal view; somites 4-6 regularly narrowing; telson short, bluntly triangular, slightly exceeding suture 5/6.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: fig. 3c (reproduced by Holthuis & Manning 1990: fig. 58d); Holthuis & Manning 1990: fig. 57d; Chen & Xu 1991: fig. 8.3; Chen & Sun 2002: fig. 99.4.

Female pleon very wide, with tomentose, granular surface. In adult females somites 1-3 and part of 4 exposed dorsally (Fig. 27B-D) (see below, *Additional female pleonal-retention mechanism*).

Pleonal-locking mechanism by press-button
(Figs 27C, D; 28D, E)
Press-button located on moderately curved backwards suture 5/6.

Additional female pleonal-retention mechanism (Fig. 27B)
In females, strong retention by wide, quadrate process of sternite 8 overhanging pleonal somite 2; small telson engaged between slightly raised slopes of sterno-pleonal cavity at level of sternite 5.

Fig. 27. — Philippidorippinae n. subfam. *Philippidorippe philippinensis* Chen, 1986, Philippines, Bohol Province, ZRC 2016.0240: **A**, ♂ 23.0 × 29.3 mm: habitus; **B**-**D**, ovigerous ♀ 25.2 × 33.2 mm; **B**, habitus; **C**, thoracic sternum with pleon, press-button; **D**, vulvae.

FIG. 28. — Philippidorippinae n. subfam. *Philippidorippe philippinensis* Chen, 1986: **A**-**D**, ♂ 23.0 × 29.3 mm, Philippines, Bohol Province, ZRC 2016.0240: **A**, ventral view; **B**, anterior region; **C**, thoracic sternum with pleon; **D**, thoracic sternum, G1. **E**, ♂ 25.0 × 30.0 mm, Philippines, MUSORSTOM 3, MNHN-IU-2018-5201 (= MNHN-B18913): thoracic sternum, G1 and G2.

Male gonopore and penis
Coxo sternal condition. Sternites 7 and 8 expanded over penis for quite long distance, close together but not completely joined, thus a condition similar to that of *Dorippe quadridens*, but penial bulb shorter, poorly demarcated from thick, long, sclerotised subsequent portion that is exposed between sternites 7 and 8.

Illustrations: *Philippidorippe philippinensis*: Guinot *et al.* 2013: 102, fig. 17D.

Gonopods (Figs 28D, E; 31H)
G1 short, extremely stout, tapering distally; basal half very thick and broad, with rounded basal lobe at outer margin; distal third curved outwards, tip with two auricular processes.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: fig. 3d, e (reproduced by Holthuis & Manning 1990: fig. 58e-h; by Sin *et al.* 2009: fig. 4H); Chen & Xu 1991: fig. 8.4; Chen & Sun 2002: fig. 99.5, 6.

G2 straight.

Illustrations: *Philippidorippe philippinensis*: Chen 1986a: fig 3f, g.

Vulvae (Figs 27D; 32H)
Vulva rather distant from distal part of sternal ridge, not located on sternal prominence but situated on obliquely directed flank of flared sterno-pleonal cavity; opening not recessed, quite large, elongated, crescent-shaped.

Illustrations: *Philippidorippe philippinensis*: Holthuis & Manning 1990: fig. 57f, g; Vehof 2020: fig. 8A.

Female reproductive system
Studied in *Philippidorippe philippinensis* by Vehof (2020: 51, 57, 70, 73, 86, figs 4, 8, 17, tables 2, 5), unfortunately on a specimen in a very poor state of preservation so that the histological results are fragmentary. See Figure 37 and below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae*.

Distribution and habitat
Known only from localities in and around the Philippine Islands and from South China Sea (Chen & Sun 2002). Found at depths betwen 96-107 m and 193-200 m, *Philippidorippe philippinensis* is the only deep-sea dorippid species (Chen 1986a; Holthuis & Manning 1990; Chen & Xu 1991; Chen & Sun 2002; Takeda & Manuel-Santos 2006: 96).

Carrying behaviour
Unknown.

Remarks
The genus *Philippidorippe* is a deep-water genus and the only dorippid in this case. In a combined analysis using three genes, it has been interpreted as basal in the clade *Dorippe-Dorippoides-Medorippe* (Sin *et al.* 2009).

Subfamily Phyllodorippinae n. subfam.

Type genus. — *Phyllodorippe* Manning & Holthuis, 1981 (type species by original designation: *Dorippe armata* Miers, 1881). Monotypic.

Description
Carapace (Fig. 29A, B)
Carapace short, clearly wider than long. Dorsal surface without large tubercles, spines or elevations (only granules), but with raised tripartite ridge on swollen branchial region. Meso-, meta-, urogastric regions weakly demarcated. Precervical groove shallow; cervical groove well defined; branchiocardiac groove moderately deep. Antero- and posterolateral margins delimited by marked epibranchial tooth, very developed in large specimens. Front bidentate, consisting of two low obtuse teeth; median emargination wide, flat. No inner orbital teeth or lobes. Outer orbital teeth reaching slightly further forward than front. Lower margin of orbit between extra- and infraorbital teeth smooth, large U-shaped. Superior margin of orbit with fissure. Partial and weak exposure of pleurites 5-7 with smooth texture; margin of carapace lying in small guter at this level. Carapace posterior rim not extending laterally along posterolateral margin and lined posteriorly by narrow, straight, integrated strip in males and females.

Illustrations: *Phyllodorippe armata*: Monod 1933b: fig. 4A, as *Dorippe armata* (reproduced by Manning & Holthuis 1981: fig. 4j); Capart 1951b, as *D. armata*; Monod 1956: fig. 102, erroneously as *D. lanata* (reproduced by Manning & Holthuis 1981: fig. 4i; by Sin *et al.* 2009: fig. 3I); Capart 1951b: fig. 7, as *D. armata.*

Cephalic structures (Figs 29A; 30A)
Eyestalks rather short, not reaching beyond outer orbital teeth. Antennule partly folded, distal part of antennular article being out fossa. Antenna directed entirely forward; articles 2+3 rather narrow; article 4 slightly enlarged; article 5 elongate; flagellum rather long.

Oxystomatous disposition (Fig. 30A-C)
Exposed portion of mxp1 endopod beyond extent of mxp3 short. Opening of exhalant channels barely reaching frontal margin, thus not visible in dorsal view.

Illustrations: *Phyllodorippe armata*: Monod 1933b: fig. 4A, B, as *Dorippe armata*; 1956: figs 102, erroneously as *D. lanata* (reproduced by Manning & Holthuis 1981: fig. 4i), 104.

Pereiopods (Figs 29A, B; 30A,C)
Left and right chelipeds equal and similar in both sexes at small size; strong sexual dimorphism: pronounced heterochely in young adult males of 20 mm carapace width, with glabrous major chela becoming enormous.

Illustrations: *Phyllodorippe armata*: Miers 1881: fig. 4, 4a, as *Dorippe armata*; Monod 1956: fig. 105, as *D. armata*; Manning & Holthuis 1981: fig. 4a.

Fig. 29. — Phyllodorippinae n. subfam. *Phyllodorippe armata* (Miers, 1881), Guinean Trawling Survey, ZRC 2009.0413 (ex MNHN-B24202). **A**, ♂ 12.3 × 16.2 mm, habitus; **B**-**D**, ovigerous ♀ 11.9 × 16.6 mm. **B**, habitus; **C**, thoracic sternum and pleon; **D**, thoracic sternum, vulvae and spine on sternite 8.

P2, P3 meri without spines on dorsal margin, only with several striated rows on raised ridges, resulting in a keeled appearance; dactyli narrow and slightly twisted, fringed with short hairs in basal half of upper margin in both sexes.

Both P4, P5 reduced, narrow and much setose; P5 thinner and shorter than P4.

Illustrations: *Phyllodorippe armata*: Monod 1933b: fig. 3A, B, as *Dorippe armata*.

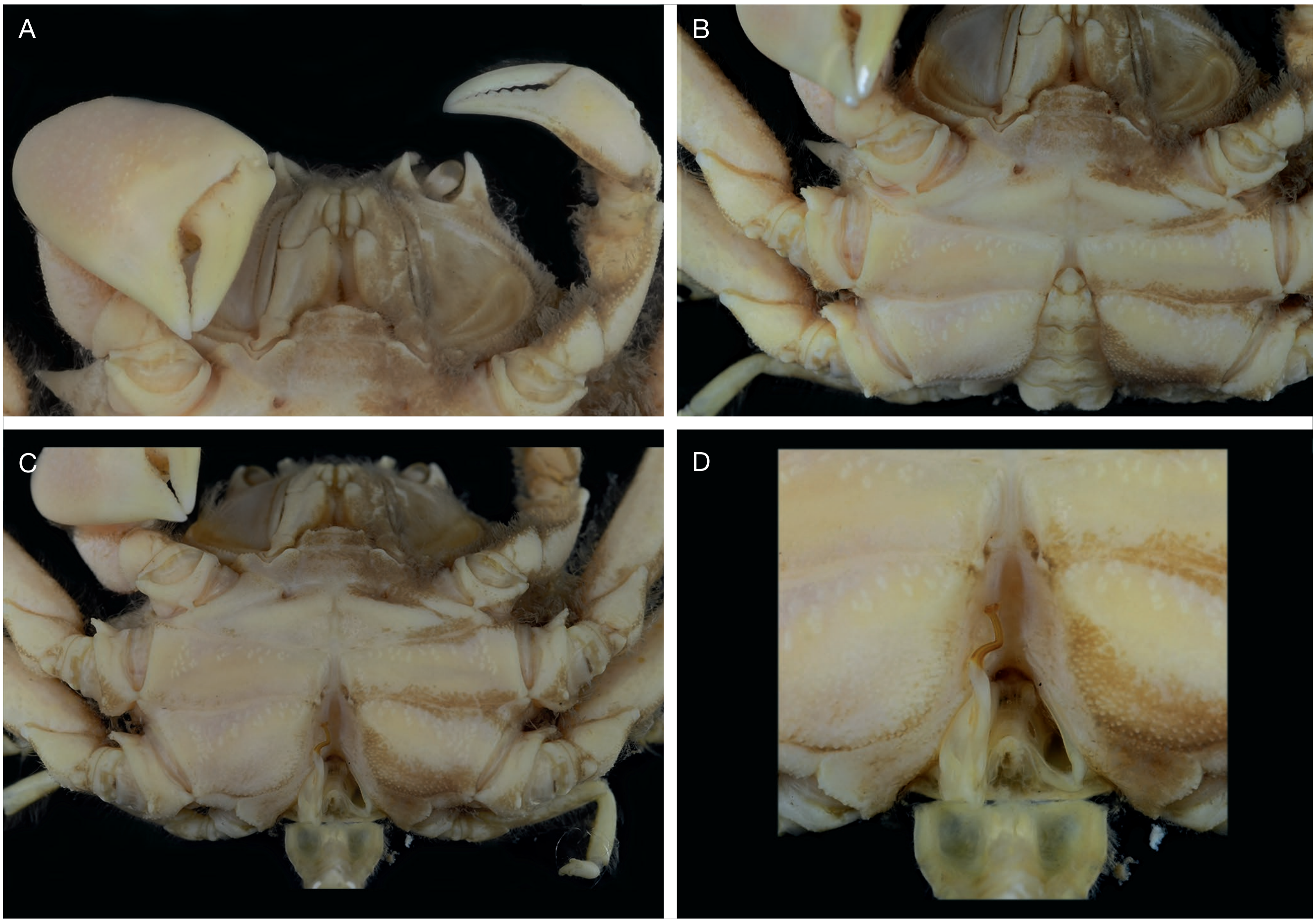

Fig. 30. — Phyllodorippinae n. subfam. *Phyllodorippe armata* (Miers, 1881), ♂ 12.3 × 16.2 mm, Guinean Trawling Survey, ZRC 2009.0413 (ex MNHN-B24202): **A**, both chelae; **B**, thoracic sternum and pleon; **C**, thoracic sternum without pleon; **D**, G1 and press-buttons.

Thoracic sternum (Figs 29C, D; 30)
Thoracic sternum extremely wide. Sternites 1 and 2 forming short pentagonal shield, with thickened lateral margins; sternite 1 with small blunt median portion visible dorsally, remaining part passing under mxp3 and being concealed; sternite 2 separated from sternite 3 by lateral notch and median depression; sternite 3 very broad, with two extended lateral portions: a foliaceous lobe connected to pterygostome, the other extending along arthrodial cavity of P1; sternite 4 with thick oblique ridge on each part. Sutures 4/5-7/8 interrupted; suture 3/4 only lateral, deep, ending in marked boutonniere; sutures 4/5 and 5/6 with short interruption points; suture 5/6 abruptely curved backwards, with narrow curve accommodating press-button. Female thoracic sternum almost vertically tilted backwards at level of ridge crossing whole sternite 6, which marks delimitation between the two distinct parts of thoracic sternum; sternite 8 with erect axial spine (Fig. 29D).

Pleon and telson (Figs 29A-C; 30B)
Sterno-pleonal cavity short and very narrow. Male pleon with all somites free, first three somites exposed dorsally; first three and part of 4 exposed in females; surface with only low, very blunt elevations especially on male somite 3; somites 2 and 3 granular; telson very short, exceeding suture 5/6. Female pleon as on Figure 29C, D.

Illustrations: *Phyllodorippe armata*: Monod 1933b: 36, as *Dorippe armata*; 1956: figs 106, 107, as *D. armata*.

Pleonal-locking mechanism by press-button (Figs 29C, D; 30C, D)
Press-button prominent, located in abruptely curved sternal suture 5/6, effective in both sexes, even in mature females.

Additional female pleonal-retention mechanism (Fig. 29B)
In females, strong retention by small spine of exposed dorsal portion of sternite 8 overhanging pleonal somite 2; small telson wedged between abrupt slopes of sterno-pleonal cavity at level of sternite 5.

Male gonopore and penis
Male gonopore coxal. Penis rather short (Monod 1933b: fig. 5C, as *Dorippe armata*). Note that the penial region figured by Guinot *et al.* (2013: fig. 15E) was based on a misidentified specimen and thus represents the condition of *Medorippe lanata* as shown in fig. 15B, D of the same paper.

Gonopods (Figs 30C, D; 31H)
G1 long, basally twisted, very slender, S-curved, second half horny-looking, with large, lobiform inverted triangular subdistal appendage, and ending in narrow acute point; no basal lobe.

Illustrations: *Phyllodorippe armata*: Monod 1933b: fig. 3H, as *Dorippe armata* (reproduced by Manning & Holthuis 1981: fig. 4k-l; by Sin *et al.* 2009: fig. 4I).

G2 rather long, straight, with indistinct partition.

Vulvae (Figs 29C, D; 32I)
Females already ovigerous at size of 7.0 × 10.0 mm. Vulvae (hitherto unknown and shown here for the first time) rather distant from distal part of setose sternal ridge, situated on raised slopes of narrow sterno-pleonal cavity, rather close to each other, in the shape of narrow slit.

Female reproductive system
Not known.

Distribution and habitat

Phyllodorippe armata lives in shallow waters on sand, mud or shell bottoms (Zariquiey Alvarez 1968: 313, as *Dorippe armata*; Monod 1956: 96; Manning & Holthuis 1981: 34, 35), being able to tolerate low salinities (Balss 1921: 48; Voss 1966: 37; Sourie 1954, all as *D. armata*). Tropical and subtropical eastern Atlantic, off West Africa, from many localities between Spanish Sahara and Angola (Capart 1951b, as *D. armata*; Le Loeuff *et al.* 2000); from Cape Verde Islands (A. Milne-Edwards & Bouvier 1900, as *D. armata*; Gonzáles 2018: 421, table 3), the Canary Islands (García-Isarch & Muñoz 2015) and islands off the Gulf of Guinea, São Tomé and Principe (Forest & Guinot 1966: 50, as *D. armata*). Also off Nigeria and Gabon (Henriksen 2009: 38; Dessouassi *et al.* 2018). *Phyllodorippe armata* cohabits with *Medorippe lanata* along the West-African coast, in Dahomey (Crosnier coll. et det., MNHN-IU-2018-5196 (= MNHN-B16380 *pro parte*), Ghana (in the same station 24, see Forest & Guinot 1966: 36, 50, as *Dorippe armata*), Sierra Leone, off the Ivory Coast (Forest & Guinot 1966: 50, as *D. armata*; Manning & Holthuis 1981: 36, 338; Le Loeuff & Intès 1999: 547), Nigeria (Manning & Holthuis 1981: 36) and Angola (Guinot & Ribeiro 1962, as *D. armata*). The *Phyllodorippe armata* from Dahomey recorded as *Dorippe armata* by Crosnier (1964: 32, 38) actually contains both species *M. lanata* and *P. armata* [fig. on pl. A is *M. lanata*, apparently taken from Monod (1956)].

Carrying behaviour

The carrying behaviour of a dorippid that is probably *Phyllodorippe armata* is only documented by the report of a crab from the mangrove of Crique Banjia, Gabon, described with a leaf held on its back with the last legs (Pechüel-Loesche 1882: 288), a habit somewhat similat to that found in *Neodorippe* Serène & Romimohtarto, 1969.

Remarks

Examination of numerous specimens in the MNHN, which holds large number of both *Medorippe lanata* (Medorippinae n. subfam.) and *Phyllodorippe armata* (Phyllodorippinae n. subfam.), confirms that *P. armata* is a much smaller species than *M. lanata*: it reaches only a small size, with an ovigerous female 10 mm in width (A. Milne-Edwards & Bouvier 1900: 33, as *Dorippe armata*).

STATUS OF ATLANTIC AND MEDITERRANEAN DORIPPIDS, WITH PARTICULAR REFERENCE TO MONOD (1933b)

The figures of the carapaces of *Phyllodorippe armata* (Miers, 1881) and *Medorippe lanata* in Monod (1956: figs 102, 103) have been inverted: correctly, *P. armata* is shown in Monod's figure 102, whereas *M. lanata* is shown in Monod's figure 103 (see Forest & Guinot 1966: 5; Manning & Holthuis 1981: 34). Being all copies of Monod's (1956), the figures (figures only, not text) of *P. armata* by Crosnier (1964: fig. on pl. A) and by Maurin (1968: figs 5D.a, 7D.a) do not represent *P. armata*, but *M. lanata*. Formerly, material from Morocco (Monod 1933b: figs 3C-E, F, 5A, D; see also Monod 1933a, as *Dorippe lanata*), also correctly identified, is *Medorippe lanata*; material from Mauritania and Guinea (Monod 1933b: figs 3H, 4A, B, 5C, as *D. armata*), also correctly identified, is *Phyllodorippe armata*.

The dorippid species from Syria studied as *Dorippe lanata* by Monod (1933b: 35, 37, figs 3G, 4C, D, 5B) and reproduced by Manning & Holthuis (1981: 34, fig. 4b, h) as *Medorippe lanata* deserves discussion. The material is unfortunately lost. Monod (1933b: 37) did notice the numerous differences separating his 'apparently adult' Syrian material from *M. lanata* (as well from *Phyllodorippe armata*) from the Atlantic Ocean, notably the ornamentation of P2, P3, the penial disposition, the male pleon and mxp3. The sculpture of the dorsal surface with the Y-shaped cardiac region, the frontal lobes, the long outer orbital spines, the three teeth of the pleonal somite 3 are characteristic of *Dorippe quadridens* (see Holthuis & Manning 1990: 18, figs 5-12). The particularly accurate remark of Monod (1933b: 37, fig. 5B) that the penial disposition of the Syrian dorippid differs from those of *Dorippe armata* (now *Phyllodorippe*) and *D. lanata* (now *Medorippe*) (Monod 1933b: 37, fig. 5C, D) indicates a distinct genus, namely *Dorippe*. In *Dorippe* (Guinot *et al.* 2013: fig. 16) the dorsally exposed proximal portion of the penis is indeed longer than in *Medorippe* and *Phyllodorippe* (Guinot *et al.* 2013: fig. 15A-D and 15E, respectively). While the carapace of the dorippid figured by Monod (1933b: fig. 4C) can be considered roughly drawn (anterolateral margin represented too short, epibranchial spine too strong), it can be speculated that it could possibly correspond to *Dorippe quadridens,* which however has a longer and much narrower anteriorly carapace than *Medorippe lanata*. Although dissimilar, the V-shaped ridge on the cardiac region, the frontal lobes, the long outer orbital spines, the three teeth of the pleonal somite 3 are shared by both species. The *Phyllodorippe armata* from Dahomey recorded as *D. armata* by Crosnier (1964: 32, 38) in fact contains the two cohabiting species, *M. lanata* and *P. armata* [fig. on pl. A is *Medorippe lanata*].

In addition, Monod (1933b: 37, fig. 3G) noted that the G1 of the Syrian material did not correspond to that of *Medorippe lanata* and hypothesised that the eastern Mediterranean population of *M. lanata* might be subspecifically distinct from those in the western Mediterranean and the Atlantic Ocean. Manning & Holthuis (1981: 34) rejected such a hypothesis, arguing that Monod's Syrian specimens were juveniles, without fully developed gonopods. In fact, the G1 of the Syrian dorippid (Monod 1933b: fig. 3G) is neither that of *Medorippe lanata* (Figs 22E; 31C) nor that of *P. armata* (Figs 30C, D; 31I). And it does not completely correspond to that of *Dorippe quadridens* (Figs 11C, D; 31A). However, the figures by Manning & Holthuis (1981: fig. 4b, h) of the carapace and the G1, respectively (which reproduce those of Monod's Syrian material) would actually represent *D. quadridens*, a Lessespian species introduced from the Red Sea into the Mediterranean, especially to the Levant (see Galil 2005; Hasan 2008: 344; Galil 2011: table 1 p. 382, 391). The assumption of Hasan (2008: 57, 344) that *D. quadridens* is probably widespread in the Levant Basin and in particular in Syria is supported by the fact that this alien dorippid could have been recorded in the Mediterranean Sea since Monod (1933b). *Dorippe quadridens* is an alien species also introduced into Australia (Brockerhoff & McLay 2011: 50, tables 1-3).

Théodore Monod (1933b: 35, figs 3C-E, F, 5A, D; see also Monod 1933a) highlighted some features of the Moroccan material assigned to *Medorippe lanata.* Manning & Holthuis (1981: 32) agreed that, despite close resemblance (spinulate P2 and P3 meri, similar G1), the *Medorippe* specimens from northern localities (such as Morocco) and specimens from the Gulf of Guinea show some dissimilarity. Manning & Holthuis (1981: 32, fig. 4c, d, table 1) also questioned the status of Mediterranean populations, e.g. the Tunisian one with a more pubescent carapace, longer and much thinner pereiopods, and larger, perhaps fewer spines on P2 and P3 meri. The question of whether these Mediterranean and North Atlantic populations merit nomenclatural separation is beyond the scope of the present paper. Detailed molecular analysis could provide new insight into the identity of the two Atlantic and Mediterranean populations of *M. lanata*.

RELATIONSHIPS BETWEEN DORIPPIDAE AND ORITHYIIDAE

The family Orithyiidae Dana, 1852, monogeneric with *Orithyia* Fabricius, 1798, monospecific with the commercially valuable *O. sinica* (Linnaeus, 1771), has sometimes been considered a potential third member of the Dorippoidea. Previously included in the Calappidae De Haan, 1833, it was given a familial status within the Calappinea De Haan, 1833 thanks to Ortmann (1892: 555, 559). Alcock (1896: 138) subdivided the Calappinae De Haan, 1833 into two alliances, Calappoida De Haan, 1833 and Orithyioida Dana, 1852. The Orithyiidae as a separate family was resurrected by Guinot (1978: 254), and the recognition of its own superfamily, Orithyioidea, was accepted by Števčić (2005: 102), Ng *et al.* (2008: 125, figs 93-95), De Grave *et al.* (2009: 37) and Davie *et al.* (2015b: 949).

For a long time, carcinologists continued to recognise its affinities with Calappidae (within the former Oxystomata) or with Calappoidea De Haan, 1833 (Balss 1957: 1611; Kim 1973; Sakai 1976: 127, 143; Guinot 1978; Dai & Yang 1991: 101, 113; Chen & Sun 2002), or have envisaged relationships with Dorippoidea (Ihle 1918; Guinot 1979a; Bellwood 1996, 2002; Schweitzer & Feldmann 2000; Martin & Davis 2001; Schweitzer *et al.* 2010). Bellwood (1996: 185, 186, fig. 4) defined a *Dorippe* + Orithyiinae clade supported by nine synapomorphies, and considered Orithyiidae to be the possible sister group to Dorippidae, thus placing Orithyiidae in Dorippoidea, but without taking into account many characters, such as those of pleon and vulvae. The approach of Bellwood (1996) was followed in genetic studies of the complete mitochondrial genome of *Orithyia sinica* by Zhong *et al.* (2018: fig. 1) and by Wang *et al.* (2021: fig. 3, with *Orithyia* being included in Dorippoidea), which did not, however, contain any dorippid or ethusid species. A similar analysis by Liu *et al.* (2013), with an insufficient sampling of genera, showed a close relationship with the Portunidae Rafinesque, 1815. Morphological characters shared by Orithyiidae and Matutidae De Haan, 1835 were discussed by Guinot *et al.* (2013: 199) as possibly resulting from a common ancestry, with an elaborate respiratory system, albeit much more specialised in Orithyiidae.

The pattern of special characters of *Orithyia* has been described in detail by Guinot (1979a: pl. 14, figs 7, 8) and Guinot *et al.* (2013: figs 31A, F, 56K, table 4): thoracic sternum very wide and circular, remaining narrow posteriorly; all sutures interrupted, with relatively close interruption points, and a medial line along sternites 7 and 8 (pattern 5, subpattern e); large part of sternite 8 exposed (Guinot & Bouchard 1998: fig. 15A); high median plate at sternite 7 level, partially at sternite 8 level, before connecting to a rather wide sella turcica; endosternites 5/6, 6/7 with invaginated extremities like glove fingers; sterno-pleonal cavity long, reaching sternite 3 in both sexes; first two pleonal somites clasped between strong coxae of P5, and somite 1 apparently not mobile; male pleon very short and filling only the middle of the sterno-pleonal cavity, its tip not reaching suture 6/7, and pleonal somite 6 being very far from sternite 5; vestigial pleopods on male pleonal somite 5; at least in the large-sized males examined, absence of buttons or sockets for pleonal locking (Guinot & Bouchard 1998: fig. 15A); male gonopore coxal; penis emerging from extremity or anterior margin of coxo-sternal P5 condyle (condylar protection) and covered by sclerotised sheath, followed by soft papilla after emergence; G1 short, widely opened along its subdistal and distal portions (Dai & Yang 1991: fig. 57), completely sheltered by pleon; G2 with rather long and thin flagellum; female pleon longer and filling slightly larger part of sterno-pleonal cavity (thus extremities of pleopods exposed); vulva (with surrounding inflated sternal cover) completely external on sternite 6 and exposed outside the sterno-pleonal cavity (Shen 1931: pl. 9, fig. 3; Guinot 1979a: pl. 14, fig. 9; Guinot & Bouchard 1998: fig. 15B; Ng *et al.* 2008: fig. 95), not due to the pleon shortness but as a result of its lateral location outside the cavity. It is also noteworthy that in Orithyiidae, the mxp3 exopodite lacks a flagellum (Bellwood 1996: fig. 3D), P2-P4 have thick, sharp, carinate dactyli (for digging and burying), P4 and P5 have a short, flattened carpus, and P5 has a paddle-like dactylus (for swimming). Furthermore, in *Orithyia*, unlike in the Dorippidae, pleurites 5-7 are not exposed and the carapace is not housed in a gutter, the coxa of P1-P5 are not complex, P4 and P5 are normal, and the mode of life is completely different.

The zoeal morphology of *Orithyia sinica* (cf. Hong 1976) shows a combination of characters that has not been reported in any other brachyuran. Although the zoeae bear a general resemblance to those of the Dorippidae, they differ in so many important details that they cannot be very closely related (see Rice 1980: 317). The megalopa also differs from those of all other eubrachyurans (Kim *et al.* 2014), setting the family Orithyiidae apart. On the basis of the larval stages described by Hong (1976), Rice (1980: 316-317, 356-357; 1981: 293) indicated the presence of a unique combination of characters, with the larval stages of *Orithyia* being so distinct from those of all other crabs (including the Calappidae) that they "suggest an isolated position that should be recognised by separate family status, at least": as a result, the "extant dorippid zoeae have several advanced features that exclude them from the possible ancestry of *Orithyia*".

The phylogenetic relationships of the family Matutidae remain still conflicting (Lin *et al.* 2018), but the result of the genetic studies by Kim *et al.* (2019: fig. 1) and Huang *et al.* (2021: fig. 1, with *Orithyia* being included in Dorippoidea) clearly suggested that Matutidae form a group within the Calappoidea. According to the genetic data of Tsang *et al.* (2014: 5, figs 1B, 2), the primary freshwater family Trichodactylidae H. Milne Edwards, 1853, distantly related to the other primary freshwater crabs (albeit with low nodal support), surprisingly aligned with Orithyiidae with strong nodal support. This study positioned Trichodactylidae clearly within the clade for Heterotremata as sister to the marine Orithyiidae (see Cumberlidge *et al.* 2021). According to the genetic data of Wolfe *et al.* (2022, pers. comm.), Orithyiidae was again recovered as sister to freshwater crabs, in this case to Pseudothelphusidae Ortmann, 1893, i.e., *Epilobocera sinuatifrons* (A. Milne-Edwards, 1966) and *Ptychophallus* sp. Smalley, 1964.

The first reported occurrence of Orithyiidae in the fossil record, with *Orithyia eikii* Karasawa, 2020 from Japan, a male showing a well-preserved rostrum with three well-developed spines, lateral margins of carapace with two spines, laterally flattened P2-P5, and lanceolate P5 propodus, but a poorly preserved thoracic sternum and pleon (Karasawa 2020: figs 1-3), expands the geologic range of both family and genus into the Early Miocene.

The inclusion of the Orithyiidae in the Dorippoidea is not supported by most of the morphological characters, and the superfamily rank Orithyioidea is fully justified.

REVIEW OF EXTERNAL MORPHOLOGICAL CHARACTERS IN THE SEVEN SUBFAMILIES OF DORIPPIDAE

According to Guinot *et al.* (2013: 184), evidence for monophyly of the Dorippidae is inferred from several putative synapomorphies: (1) similar arrangement of cephalic appendages, at least in main features: absence of orbits and disposition of cephalic appendages, e.g. antennule and antenna both close to the eyestalks, all three being housed in the one and only fossa (Ihle 1916: fig. 41); antennules long; (2) thoracic sternum/pterygostome junction complete and involving sternite 3, a disposition leading to a specialised respiratory system, in relation with burying activities; prechelipedal afferent branchial openings receiving developed, calcified mxp3 coxa; oval and elongated Milne Edwards openings as pterygostomial slits, separated from chelipeds (Figs 4; 7C) (H. Milne Edwards 1834-1840, Atlas: pl. 20, fig. 12; Ihle 1916: fig. 45, as *Dorippe dorsipes*; Guinot *et al.* 2013: fig. 42C); (3) closure of endostomal gutter by mxp1, with calcified endopods forming floor of gutter, the efferent openings at the extremity of the endostome being produced anteriorly; (4) presence of sternal extensions (lateral outgrowths of sternites) joining the thoracic sternum to the carapace at sutures 4/5-6/7 levels (formed each time by two consecutive sternites, thus being double) and inserted respectively between P1 and P2 as well as between P2 and P3, and between P3 and P4, respectively, so that their arthrodial cavities are encircled by these sclerites (Guinot 1979a: 103; Guinot *et al.* 2013: figs 42C, 46A, B, 47A, B); (5) posterior thoracic curvature, with thoracic sternites 7 and 8 more or less tilted, perpendicular to the preceding sternites in females; (6) P4, P5 arthrodial cavities not aligned with the preceding arthrodial cavities; (7) P4 and P5 greatly reduced, positioned dorsally over carapace, and subchelate for carrying behaviour, a behaviour already performed by the megalopae in at least three species: *Dorippe sinica*, *Heikeopsis japonica* and *Paradorippe granulata* (Quintana 1987: 234, 245, 253 as *Dorippe frascone, Nobilum japonicum japonicum*, and *Paradorippe granulata*, respectively), a trait probably generalised within the family; (8) first two somites of male pleon dorsal, thus pleon not folded under cephalothorax; (9) G1 and G2 with a long protopodite; (10) presence of long penial tube; (11) shape of the first thoracic sternites, that form a developed shield (especially sternite 3); sternal suture 3/4 short but very deep (corresponding to a thick endosternal phragma), ending by a marked depression, even showing as a perforation (boutonniere) (Guinot 1979a: 103, fig. 28A; Guinot *et al.* 2013: fig. 42C), already visible in the first juvenile crab (Quintana 1987: fig. 8E); (12) press-button located in variously deep curve of sternal suture 5/6, a character already present in the first larval stages of e.g. *Dorippe sinica* (Quintana 1987: fig. 3F, as *Dorippe frascone*); pleonal locking persisting in mature females; (13) skeleton regularly compartmentalised (Guinot *et al.* 2013: figs 46, 47A, B); (14) sperm ultrastructure (Jamieson & Tudge 2000: 52, fig. 11B, C); and (15) female reproductive system, with multistate characters (Figs 35; 37).

New traits identified in the course of this work can be considered new synapomorphies of the Dorippidae: exposure of lateral portions of pleurites 5-7 (Fig. 7A, B), in particular the distal end of pleurite 6 that is largely exposed at level of P3; pattern of grooves on dorsal carapace (Fig. 5B-D), the interpretation of which is debatable; posterior margin of carapace strongly protruding (rim) and bordered posteriorly by a strip (Figs 8A-C; 9C, D); dorsal exposure of sternites 7 and 8 to varying degrees on each side of the carapace (Figs 8C; 9C); persistence of a functional pleonal-locking mechanism by press-button in mature, even sometimes ovigerous, females; additional female pleonal retention mechanism by a process on dorsal sternite 8 overhanging pleonal somite 2 (Figs 8C; 9C), coupled with the telson clasped at level of sternite 5 (Fig. 8D).

All major dorippid features are examined below and discussed as they are allocated to the new subfamilies.

CEPHALOTHORAX

Ventrally, the anterior margin of the dorippid carapace disappears beneath the forward extension of the buccal frame, with the extension of the endostome covering the region below the front (downwards process of the rostrum not visible), so the anterior cephalic region is not externally visible, making it not possible to recognise the proepistome and epistome.

The incomplete folding of the pleon, with its first somites (usually the first two in males, more in females) positioned dorsally, the dorsal exposure of thoracic sternites 7 and 8, and the posterior thoracic curvature of the body lead to a dramatic change in the alignment of the P1-P5 arthrodial cavities, resulting in a dorsal location of both P4 and P5, allowing for carrying behaviour. The first pleonal somites in the prolongation of the carapace, narrow and wedged between the P4, P5 coxae in males, are dorsally visible in both sexes of all subfamilies (see below, *Sterno-pleonal cavity and pleon*). All these conditions are shared by all dorippid subfamilies (also by ethusids) and are not found together in other heterotreme families. The arrangement in two other heterotreme families, though probably quite close, is different. In Palicidae, thoracic sternites 7 and 8 have a particular, sexually dimorphic arrangement and only the highly mobile, thin P5 are capable of carrying (Guinot *et al.* 2013: figs 32A, B, 44A, 54). In Retroplumidae, only a very small portion of sternite 8 and a large part of the expanded sternite 7 are exposed dorsally, but a carrying by thin, horizontal P5 has not yet been recorded (Saint Laurent 1989: fig. 22; Guinot *et al.* 2013: figs 34, 44C). An important consequence of the posterior thoracic curvature is that there is a dorsal exposure of thoracic sternites 7 and 8: this unique dorippid (and ethusid) feature leads to the development of an additional pleonal-locking mechanism in females of some subfamilies, i.e., the emergence of a process on the dorsally exposed part of sternite 8, which will have the function of maintaining the female pleon at the level of somite 2 (Figs 8C; 9C).

CARAPACE

The dorippid carapace, characterised by dorsal exposure of the latero-external parts of some pleurites as well as by diverse reduction of the branchiostegite, varies in shape and proportions, pattern of dorsal carapace grooves, dorsal surface ornamentation, lateral and posterior margins, frontal and lateral teeth, and protection of the orbit.

Proportions

The carapace is wider than long (becoming wider in larger specimens) in the Dorippinae n. stat. but there is a marked anterior narrowing, longer than wide in the genus *Neodorippe* within the Heikeopsinae n. subfam., and slightly longer than wide in other Heikeopsinae (*Heikeopsis* and *Nobilum*); proportionally very wide and short in the Phyllodorippinae n. subfam.; distinctly wider than long in the Medorippinae n. subfam. and in the other subfamilies. It is very inflated laterally at level of the branchial regions in the Philippidorippinae n. subfam.

The lateral margins bear an epibranchial tooth or spine (more or less developed and constant) in Dorippinae n. stat., Medorippinae n. subfam. and Phyllodorippinae n. subfam. or lack a demarcation between the antero- and posterolateral parts in Dorippoidinae n. subfam. (sometimes at an angle), Heikeopsinae n. subfam., Paradorippinae n. subfam., and Philippidorippinae n. subfam.

The dorsal surface of the carapace is strongly sculptured by several grooves, uneven and tuberculate in Dorippinae n. stat., slightly sculptured and with low, small tubercles or granules in Medorippinae n. subfam., Philippidorippinae n. subfam. and Phyllodorippinae n. subfam., whereas only finely and uniformly granulate or naked and smooth in Dorippoidinae n. subfam., Heikeopsinae n. subfam. (carapace moderately sculptured in *Heikeopsis*, more sculptured in *Nobilum*, smooth in *Neodorippe*), and Paradorippinae n. subfam. (see below, *Key to dorippid subfamilies based on morphological characters other than G1 and vulva*).

The groove pattern, with two main grooves including the precervical groove (see above, *Interpretation of grooves on the carapace dorsal surface in Dorippidae*) is similar in all subfamilies, being obviously more obvious in the poorly ornamented dorippids (e.g. Dorippoidinae n. subfam., Heikeopsinae n. subfam., Paradorippinae n. subfam., Philippidorippinae n. subfam., Figs 3B, D-I; 5C, D) than in others (e.g. Dorippinae n. stat., Medorippinae n. subfam., Figs 3A, C; 5A, B).

The gastric pits are located in the same place in all dorippid subfamilies at the base of the meso-metagastric region, at the boundary with the urogastric region.

The structure of the frontal region appears quite diverse on close examination. Dorippinae n. stat. and Dorippoidinae n. subfam. are the only subfamilies to have distinct inner orbital teeth, although they are shorter and less advanced less advanced than the submedian teeth. In Dorippinae n. stat., the two triangular, closely submedian teeth are separated by a more or less deep V-shaped emargination, not revealing the openings of the exhalant channels in dorsal view. In the Dorippoidinae n. subfam. the inner orbital teeth are small, triangular, and the two distinct triangular or blunt submedian teeth are separated by a fairly deep emargination, revealing just the openings of the exhalant channels. In the other subfamilies, the internal orbital teeth are very small, most ofen only as angles or lobes. In Paradorippinae n. subfam., the inner orbital teeth may be small, but more usually they are lobe-shaped, with the two triangular sharp or blunt submedian teeth separated by a broad U-shaped emargination revealing the openings of the exhalant channels. In Heikeopsinae n. subfam., the inner orbital teeth are only low or nearly absent lobes, and the two broad or pointed triangular submedian teeth are separated by a shallow and rather wide U-shaped emargination, with the openings of the exhalant channels barely or not all visible. In Phyllodorippinae n. subfam., there is no inner orbital teeth or lobes, and the two low obtuse submedian teeth are separated by a wide, shallow median emargination not revealing the openings of the exhalant channels. In Medorippinae n. subfam., the inner orbital teeth are slightly swollen lobes at a low level, and the two very narrow closely spaced submedian teeth are separated by a narrow emargination exposing the openings of the exhalant channels. In Philippidorippinae n. subfam., there is no inner orbital teeth or lobes, and the two sharp submedian teeth are separated by a narrow V-shaped median emargination, exposing the openings of the exhalant channels. The Medorippinae n. subfam. and Philippidorippinae n. subfam. are the only cases where the closely spaced submedian teeth appear almost as a single rostrum, with the exhalant channels exposed; but they differ in that the inner orbital tooth is present in Medorippinae n. subfam. but absent in Philippidorippinae n. subfam.

RIM OF CARAPACE POSTERIOR MARGIN AND THE POSTERIOR STRIP (Figs 8A, B; 9C, D)

The morphology of the variously protruding, extended and variably shaped strip is described below in alphabetical order of subfamilies. It is clearly a subfamilial character, as follows.

Dorippinae n. stat.

The carapace rim extends laterally along the posterolateral margin. It is lined posteriorly by a rather long, narrow, straight strip overlapping the P5 coxae, similar in both sexes of all species: *Dorippe frascone*, male (Fig. 14A, E) (Holthuis & Manning 1990: fig. 2a); *D. glabra*, female (Fig. 15E, F): *D. irrorata*, male (Fig. 14H) (Holthuis & Manning 1990: fig. 4a); *D. quadridens*, male (Fig. 10A) (Holthuis & Manning 1990: figs 7a, 8, 11b, reproduced from Borradaile 1903: pl. 22, fig. 1) and female (Figs 10B; 12A) (Holthuis & Manning 1990: figs 5a, 6a); *D. sinica*, male (Fig. 10C) (Holthuis & Manning 1990: fig. 13a; Wong *et al.* 2021: fig. 9a) and female (Figs 9C; 10C) (Holthuis & Manning 1990: fig. 13a); *D. tenuipes*, male (Figs 9D; 33H) and female (Fig. 33G) (Holthuis & Manning 1990: fig. 17a; Chen & Sun 2002: fig. 91.1); *D. trilobata*, male (Fig. 15A, C). No sexual dimorphism exists for the rim and strip.

Dorippoidinae n. subfam.

The posterior rim does not extend at all laterally along the swollen posterolateral margins of the carapace, is interrupted at the level of the P5 coxae, and is lined posteriorly by a fairly well-developed strip. In male *Dorippoides facchino* (Fig. 16A), the rim expands as a nearly rectangular strip, though thinner medially (drawn as a separate plate by Holthuis & Manning 1990: fig. 19a, b; Chen & Sun 2002: fig. 92.1; and Wong *et al.* 2021: fig. 10a); in females (Figs 8A; 16B) it is much more hollow medially and has two lateral expansions (overlapping the P5 coxae), giving the appearance of two separate plates, as drawn by Chen (1993: fig. 1a), when it is only the extension of the rim. The pattern is the same in *D. nudipes*, both in males (Fig. 16C) and females (Fig. 16D). The apparently detached strip is actually included in the rim, as it is particularly evident in the figure of a female by Holthuis & Manning (1990: fig. 26i, erroneously untittled “sternum and gonopores”). Sexual dimorphism of the strip is well marked.

Heikeopsinae n. subfam.

In *Heikeopsis*, *Nobilum* and *Nedorippe*, the carapace posterior rim does not extend laterally along the posterolateral margins (it is drawn in *‘Heikea arachnoides*’ by Holthuis & Manning 1990 as not extended in their fig. 27a but extended in their fig. 28a); it is interrupted at the level of P5 coxa, and is particularly thick and raised in males. It appears to be lined posteriorly by a narrow strip, thinner medially than laterally, resulting in an apparently concave posterior margin in males and females of *Heikeopsis japonica* (Fig. 5C), *H.* aff. *japonica* (Figs 1; 19A, B, E, F) and of *Nobilum histrio* (Fig. 21A). This is illustrated in drawings of *Heikea arachnoides* (Holthuis & Manning 1990: figs 27a, 28a; Chen & Sun 2002: fig. 93.1), of *H. japonica* (Holthuis & Manning 1990: figs 29a, 30b, 33a; Wong *et al.* 2021: fig. 12a), and of *Nobilum histrio* (Holthuis & Manning 1990: fig. 43a). A separate strip is drawn in *H. japonica* from Japan (Holthuis & Manning 1990: fig. 30a, as *Heikea japonica*) and in what we suspect to be a different species from the typical *H. japonica* from Japan (Holthuis & Manning 1990: fig. 35 as *Heikea japonica*, which is a reproduction of Shen 1932: fig. 6), thus the possible new species, *H.* aff. *japonica*, from China (see earlier discussion on the species). In *Neodorippe callida*, similarly, the posterior rim does not extend laterally along the posterolateral margins, but is medially concave, short, rather thick and appears to include the strip in females (Fig. 20A, B), as drawn by Holthuis & Manning (1990: fig. 41a). But a strip is not drawn in the male *N. callida* by Holthuis & Manning (1990: fig. 42a), Ng & Rahayu (2002: figs 2B, 4A) and Wong *et al.* (2021: fig. 13a). In contrast, a visible strip is shown in male *N. simplex* by Ng & Rahayu (2002: figs 2A, 3A), whereas it appears thinner in females (Ng & Rahayu 2002: figs 1, 2). It is noteworthy that “a broad ridge [that] bounds the deeply sinuous posterior margin” is described and well represented in the fossil *Heikeopsis tuberculata* (Morris & Collins, 1991), from the Miocene Sarawak (Morris & Collins 1991: 5, fig. 1, as *Dorippe* (*Dorippe*) *frascone* (Herbst) *tuberculata*), with an arrangement very similar to that of extant *H. japonica* (see *Appendix 2*).

Medorippinae n. subfam.

In *Medorippe lanata*, the posterior rim extends laterally along the posterolateral margins, passing behind the exposed pleurite 6 and tapering further to reach arthrodial cavity of P2. It is lined posteriorly by a very narrow strip, only slightly thicker on each lateral side in females, where it is also more concave and elongated (Fig. 22B) (Monod 1933b: fig. 4C, as *Dorippe lanata*, reproduced by Manning & Holthuis 1981: fig. 4b) than in males (Fig. 22A) (Monod 1956: fig. 103, as *Dorippe armata*; reproduced by Manning & Holthuis 1981: fig. 4a and by Holthuis & Manning 1990: fig. 36; Guinot *et al.* 2013: fig. 46A, B).

Paradorippinae n. subfam.

The posterior rim does not extend at all laterally along the swollen posterolateral margins and is interrupted at the level of P5 coxae. It is bordered posteriorly by a well-defined strip, which is much more distinct in males than in females and sometimes even resembles a separate sclerite. In male *Paradorippe granulata* (Figs 8B; 24A), especially in larger individuals, the rim, which is strongly hollowed at the level of P5 coxae, is lined posteriorly by a short, straight but slightly axially thinner strip, and thus appears as a separate part; in females (Fig. 24B), the rim is lined by a much wider strip integrated with the rim; both of which extend slightly laterally. The male of *P. granulata* is a rare case in the Dorippidae where a truly separate strip appears inserted between the carapace and the first pleonal somite (Fig. 8B), but, however, there is no doubt that this strip is an extension of the carapace. In the sketches by Shen (1932: fig. 8, as *Dorippe granulata*; reproduced by Holthuis & Manning 1990: fig. 49) and by Wong *et al.* (2021: fig. 14a), the male of *P. granulata* is indeed shown with a separate strip; the female figured by De Haan (1839: pl. 3, fig. 2; reproduced by Holthuis & Manning 1990: fig. 48) and the original sketch by Holthuis & Manning (1990: fig. 50a) also shows a separate strip. The sketch of the female of *P. cathayana* by Shen (1932: fig. 4, as *Dorippe polita*; reproduced by Holthuis & Manning 1990: fig. 46) shows an integrated strip, whereas the original sketch of a female by Holthuis & Manning (1990: fig. 47a) shows a separate strip, as in the male. For *P. polita*, figures of the female by Alcock & Anderson (1896: pl. 24, fig. 4; reproduced by Holthuis & Manning 1990: fig. 53) and the original sketches by Holthuis & Manning (1990: figs 54a, 55a) show an integrated strip, as in the males (Holthuis & Manning 1990: fig. 56a). In the male *P. australiensis* depicted by Holthuis & Manning (1990: fig. 45a) the strip is integrated. The disposition is not clear in the female *P. australiensis* (Miers 1884: pl. 26, fig. D, as *Dorippe australiensis*, reproduced by Holthuis & Manning 1990: fig. 44; by Davie 2002: unnumbered fig. p. 154; Poore 2004: fig. 95). Sexual dimorphism of the rim/strip is well marked.

Philippidorippinae n. subfam.

In *Philippidorippe philippinensis*, in both males (Fig. 27A) (Chen 1986a: pl. 1, fig. 3; Holthuis & Manning 1990: fig. 57a, d) and females (Fig. 27B) (Chen 1986a: pl. 2, fig. 4), the posterior rim does not extend along the posterolateral margins and is lined by a weakly developed strip, only thickened laterally in females. Sexual dimorphism of the rim/strip is not marked.

Phyllodorippinae n. subfam.

In *Phyllodorippe armata*, the posterior rim does not extend laterally along the posterolateral margins and is lined posteriorly by an indistinct, regular, integrated strip, similar in males (Fig. 29A) (Monod 1933b: fig. 4A, as *Dorippe armata*; 1956: fig. 102, as *D. lanata*) and females (Fig. 29B).

In conclusion, only two subfamilies, Dorippinae n. status and Medorippinae n. subfam., are characterised by a long rim that extends laterally with the same thickness, instead of becoming thinner along the posterolateral margins. Dorippinae n. stat. has a rather long, narrow, straight strip that does not show sexual dimorphism. Medorippinae n. subfam. and Phyllodorippinae n. subfam. share a straight, narrow or even indistinct strip, also without sexual dimorphism. Philippidorippinae n. subfam. also has a weakly developed strip and shows slight sexual dimorphism. In contrast, Heikeopsinae n. subfam. has a more or less thick, raised, medially concave strip that is sexually dimorphic. The Dorippoidinae n. subfam. displays a fairly developed, almost rectangular strip, thinner medially in males, much hollowed medially and with two lateral expansions in females, giving the appearance of two separate plates; sexual dimorphism is thus quite pronounced. In Paradorippinae n. subfam., there is a peculiar pattern: the strip, which is well marked and straight but slightly thinner axially, sometimes appears to be like a separate sclerite; in females, the much wider and more delineated strip seems to be integrated with the rim.

According to the above observations, the strip can be considered a subfamilial character. Based on our investigations, we believe that such a rim-plus-strip is a unique structure in Eubrachyura, where it is true, however, that this region may not have been examined in detail. It can only be compared with the structure found along the posterior margin of the carapace in Palicidae (but not in the Crossotonotidae Moosa & Serène, 1981), a structure not documented but often well figured by Castro (2000: fig. 1 et *sqq*.). All palicids have posteriorly a more or less wide rim and, below, a long and keeled strip, similar in both sexes, which runs only along the carapace posterior margin of the carapace to reach the arthrodial cavity of the small P5 and extends to the arthrodial cavity of P4. Its shape is very different from that of the dorippid strip: the palicid strip is completely detached, independent, located between the posterior rim and the first pleonal somite, and constitutes a distinct sclerite. It has nothing to do with the 'episternal process', as Castro (2000) correctly termed it, which is merely a lamellar sternal extension (sternite 7). It is difficult to identify the strip in the palicoids presented in Takeda & Tachikawa (2015) as the posterior margin of the carapace bears several lobes that conceal the eventual strip. Although dissimilar in shape, could these structures of Dorippidae and Palicidae, whose affinities we have shown (Guinot *et al.* 2013: 212), be homologous? Is the strip homologous to the wide and barely concave posterior margin provided with a tuberculated carina found in the fossil palicoid *Montemagrellus denticulatus* De Angeli & Ceccon, 2014 (De Angeli & Ceccon 2014: 84, fig. 4.1-3), from the Early Eocene of Monte Magrè (Vicenza, northern Italy)?

Another crown group of crabs, the Hymenosomatoidea, shows, in some species, thoracic projections. They are erroneously named 'abdominal projections' by Hill & Forbes (1979: fig. 6) (who mention as 'abdomen variation': 'no projection', 'rudimentary projections', or 'two flattened posterior projections'), by Edkins *et al.* (2007: 669, 674, 680, fig. 2, table 1), and by Dawson & Griffiths (2012: 16, 27, 28, figs 3, 6A, B, table 1), who make the 'abdominal projections' a specific, sexually dimorphic criterion. All these authors have shown that the South African crab, *Hymenosoma orbiculare* Desmarest, 1823 in fact represents several distinct species, including one, *Hymenosoma projectum* Dawson & Griffiths, 2012, named by allusion to this character. Naruse & Guinot (2023) attribute these structures to the thoraric sternum and correct this terminology to 'posterior thoracic lobes'. Lucas (1980: fig. 2E) represented these thoracic expansions, notably in *Hymenosoma hodgkini* Lucas, 1980, but did not document this arrangement. This question deserves special attention, and first of all a detailed comparison of the various arrangements encountered in Hymenosomatidae, to identfy whether these similarities between the latter and the Dorippidae are homologies, i.e., are inherited from common ancestor.

Such a rim all along the wide, concave posterior margin of the carapace is present in podotreme crabs, namely in the extant Cyclodorippoidea Ortmann, 1892, but this without lateral extension: for example, in the cyclodorippine *Tymolus japonicus* Stimpson, 1858 and in the xeinostomine *Xeinostoma eucheir* Stebbing, 1920, *Krangalangia rostrata* (Ihle, 1916), and *Ketamia depressa* (Ihle, 1916) (Tavares 1993: fig. 2a, c, e, f, respectively). A modified posterior region, not separated from the rest of the carapace, is clearly visible in several extant Est Asian Cymonomidae species: a portion of a different nature is well shown in the sketches of e.g. *Cymonomus chani* Ahyong & Ng, 2017, *C. cognatus* Ahyong & Ng, 2017, *C. deforgesi* Ahyong & Ng, 2009, *C. japonicus* Balss, 1922 (Ahyong & Ng 2017: figs 1A, 7A, 2A, 7C, 4A, 7E and 5A, respectively). A similar disposition, although not commented, exists in living cymonomids from New Zealand and Australia (Ahyong 2019). The special arrangement of the posterior region of the carapace, with a medially concave posterior margin, is also well described in fossil Cymonomidae from the Late Eocene (Priabonian) of Monti Berici (Vicenza, northeastern Italy): a wide, medially concave and superficially keeled posterior area replaces the dorippid rim in cymonomids such as *Spathanomus felicianensis* De Angeli, 2016 (De Angeli 2016: 28, fig. 4, pl. 1, figs 1-4) and *Caporiondolus bericus* De Angeli, 2016 (De Angeli 2016: 28, 30, fig. 5, pl. 1, figs 5, 6).

The dorippid strip is unrelated to the flange present in various fossils, notably in the Cretaceous Archaeochiapasidae Guinot, Carbot-Chanona & Vega, 2019 (Guinot *et al.* 2019: figs 6-8, 9B, 12C), in which the lateroposterior and posterior regions of the carapace are expanded, forming a flange all around, i.e., a narrow, continuous, undivided, channel-like depressed area, bordered by a deeply concave, strongly rimmed and raised posterior margin. It seems premature to recognise as homologous all the rims and flanges found in various Jurassic and Cretaceous families. In the monotypic extinct Bucculentidae Schweitzer & Feldmann, 2009 from Upper Jurassic localities in Europe, a family that was hypothetically considered a putative eubrachyuran (Guinot 2019: 757, fig. 2A-D), the posterior margin of the carapace has only a short, variously thickened rim, which is represented by an ostensibly straight bulge in the carapace reconstructions of Starzyk *et al.* (2011: fig. 1), Krzemińska *et al.* (2019: fig. 1C, D) and Krzemińska *et al.* (2021: fig. 1A, C, E, G). Whether this arrangement has similarities with the rim + strip of Dorippidae should be carefully examined. In contrast, in the Lecythocaridae from the Upper Jurasssic and Early Cretaceous of Europe, a family that is an eligible candidate to be eubrachyuran (near to or in the Majoidea) instead of podotreme (Guinot *et al.* 2019: 295; Guinot 2019: fig. 10), the strongly rimmed posterior margin of the carapace is complemented by a flange, which is not present in Dorippidae.

It is also worth mentioning here a peculiarity of certain species of Hymenosomatidae that show a strip located at the same place as in Dorippidae, which correspond to our hypothesis of links which we have already noted between this family and Dorippidae (Guinot 2011; Guinot *et al.* 2013). A structure apparently similar to the dorippid strip is seen in the genus *Hymenicoides* Kemp, 1917: *H. carteri* Kemp, 1917 (Kemp 1917: fig. 17), *H. naiyanetri* (Chuang & Ng, 1991) (Ng & Chuang 1996: fig. 21A), and *H. robertsi* Naruse & Ng, 2007 (Naruse & Ng 2007: fig. 4A) where it is more projected laterally. A strip is shown in some species of *Halicarcinus* White, 1846, such as in *H. rostratus* (Haswell, 1882), *H. afecundus* Lucas, 1980 and *H. hondai* (Takeda & Miyake, 1973), by Lucas (1980: fig. 3F, G, H, respectively). It will be very interesting to review in this context what Melrose (1975) calls 'true rim' (p. 92, 93, 111, fig. 58D, E), 'false rim' (p. 69, 73) and 'second false rim' (p. 87) in New Zealand Hymenosomatidae.

Dorsal exposure of lateral portions of pleurites 5-7 (Fig. 7A, B)

In the Dorippidae, expansion of pleurites 5-7 beyond each side of the carapace results in exposure of their latero-external portions, which are inserted in a short, shallow setting gutter that remains concealed. This was recently documented for the first time in *Medorippe lanata* through a dissection (Guinot *et al.* 2013: 219, 221, figs 46A, B, 47A, B). The gutter marks the separation between the covered inner portion of pleurites 5-7 and their narrow uncovered latero-outer portion that is calcified in the same manner as the dorsal surface, so that it appears to be part of the carapace due to similar ornamentation. Pleurite 4 is entirely covered by the carapace at the P1 level, unlike pleurites 5-7; pleurite 5 is partially exposed at the P2 level, with its exposed posterior portion forming a conspicuous sclerite 5; exposed pleurite 6, the most complete and forming a wide sclerite 6, is crossed by the gutter in which the carapace margin lies; exposed pleurite 7, at the P4 level, is obliquely oriented and also receives the carapace margin; pleurite 8 is not exposed at P5, which, like P4, is dorsally oriented and serves for carrying. There are different subtle arrangements within the Dorippidae (with only more or less developed and prominent or differently ornamented sclerites), but, as far as can be examined, it is broadly the same pattern in each subfamily. For example, in Dorippoidinae n. subfam., Paradorippinae n. subfam. and Philippidorippinae n. subfam. pleurite 5 is more developed than in Medorippinae n. subfam. and clearly encroaches on the carapace. We were unable to further investigate variations within the family as a thorough examination would have required dissection, which was not possible given the available material.

Such an arrangement is unique to Dorippoidea and therefore represents a synapomorphy of the superfamily. There are different subtle arrangements within the Dorippidae (with only more or less developed and prominent or differently ornamented sclerites), but, as far as can be examined, it is broadly the same pattern in each subfamily. For example, in Dorippoidinae n. subfam., Paradorippinae n. subfam. and Philippidorippinae n. subfam., pleurite 5 is more developed than in Medorippinae n. subfam. and clearly encroaches on the carapace. We were unable to investigate the variations within the family further, as a thorough examination would have required dissection, which was not possible given the available material.

Such an arrangement is unique to Dorippoidea and therefore represents a synapomorphy of the superfamily. In Ethusidae pleurites 5-7 also extend beyond the carapace, with their latero-external portions exposed like in Dorippidae but with differences in the morphology of the exposed parts. As far as a very brief examination allows, the exposure appears to differentiate *Ethusa* (sclerite 6 exposed about the entire beadth of the P3 coxa; sclerite 7 forming a very salient quadrangular plate) from *Ethusina* (sclerite 6 smaller; sclerite 7 exposed over the whole of the P4 coxa), all of which require confirmation. It seems that the short, shallow setting gutter remains concealed.

In the Inachoididae Dana, 1851 (Majoidea), by a similar process some pleurites have their latero-external portions widely exposed and ornamented like the carapace. But several major features differentiate them from the Dorippidae: in inachoidids all pleurites 5-8 are exposed with a much larger portion exposed, leading to the development of a wide and longer collar around the posterolateral margins of the carapace; pleurite 8 is exposed (unlike Dorippidae); all pleurites 5-8 as well as the first pleonal somite are 'integrated' into the carapace; the semicircular groove in the lateral part of the pleural walls forms a regular setting gutter in the form of a continuous collar; and, as the carapace margin fits perfectly and invisibly into the setting gutter, the dorsal cover of the crab includes not only the carapace *sensu stricto* but also the lateral portions of the pleurites 5-8 and, in addition, the first pleonal somite (Drach & Guinot 1982, 1983; Guinot 1984; Guinot 2012: fig. 2A, B; Guinot *et al.* 2013: fig. 47G-I; Guinot *et al.* 2019: fig. 16A; Guinot & Van Bakel 2020a: figs 1, 2A; 2020b).

In Inachidae MacLeay, 1838, a weak dorsal exposure of the latero-external parts of some pleurites in the form of small sclerites, but without constituting a 'setting gutter' (Guinot *et al.* 2013: 219), proceeds from a similar process. However, the exposed sclerites are tiny, triangular, differently oriented. In Macrocheiridae Dana, 1851, the latero-external part of pleurite 7 is exposed at level of P4 (Guinot *et al.* 2022: fig. 9E, F).

BRANCHIOSTEGITE

In Dorippidae, the carapace does not extend ventrally, or only slightly, and does not even overhang a more or less flat body depending on the species. The condition of the branchiostegite varies, from being present only at the level of first pereiopods in crabs with an inflated branchial region (so the carapace simply rests on the bases of P1-P3, which are inserted laterally) (e.g. Dorippoidinae n. subfam., Paradorippinae n. subfam.) to being reduced and even almost absent posteriorly (e.g. Dorippinae n. stat., Medorippinae n. subfam., Phyllodorippinae n. subfam.). When the branchiostegite is reduced, there is close proximity between the carapace and the thoracic sternum (in fact between the carapace and the exposed pleurite 6 at the level of P3), the two being separated only by the arthrodial by the arthrodial cavity of the pereiopod.

CEPHALIC APPENDAGES

Two main trends can be observed in Brachyura: one for the protection of the eye at the expense of its motion capabilities, the other that tends to increase the contact of the eye with the external environment while reducing the protective structures. In the plesiomorphic brachyuran state, the eyes have no protective structures or are weakly protected.

The eyes and cephalic appendages of dorippids were represented by Holthuis & Manning (1990) who did not, however, document the diversity of antennules and antennae.

In Dorippidae, the orbit is absent or poorly developed, and the eye is found unprotected, except by outer orbital and infraorbital teeth of various sizes, sometimes by spines of the orbital margin (Holthuis & Manning 1990: fig. 42). However, in some dorippids such as Heikeopsinae n. subfam. (Figs 20F; 21B), Paradorippinae n. subfam. (Figs 24; 26A) (Holthuis & Manning 1990: figs 46, 49) and Philippidorippinae n. subfam. (Figs 27A, B; 28A, B) (Chen & Sun 2002: fig. 99.1), the eyestalk is obliquely to horizontally inclined and covered by the small foliaceous antennal articles 4 and 5, and is thus better protected.

The eyestalks are short and stout or slightly elongated. The cornea may rest only on a shallow excavation of the outer orbital spine; the visual part of the cornea is not terminal but ventrolateral (Pichod-Viale 1966: 1266, as *Dorippe lanata*; Holthuis & Manning 1990: figs 1, 4c, 5c, 6c, 13c, 16b, 17c, 18b, 27b-d, 55c, 57b).

The eyestalk, antennule and antenna, all visible dorsally, are inserted close together and housed in a single fossa ('orbito-antennular Grube' of Ihle 1916: 99), which receives the thick, weakly mobile or immobile basal antennal article in the middle. Dissections of *Medorippe lanata* have shown that the antennular somite forms an ophthalmic sheath around the eye, not fully enclosing the eyestalk that remains free from the basophthalmite/podopthalmite articulation; the eye is very mobile, and the antennal tergite is invaginated (Pichod-Viale 1966: 1266, as *Dorippe lanata*).

The long antennule shows three configurations: either it cannot be completely retracted into the fossa (long second article) and is directed forward, like the antenna (Medorippinae n. subfam.: Fig. 22A-C); or it is partially folded, with the distal part of the second article outside the fossa: (Phyllodorippinae n. subfam.: Fig; 29A, B; 30A; Dorippoidinae n. subfam.: Figs 16; 17A; 18A; Paradorippinae n. subfam.: Figs 24; 26A); or it is obliquely folded and may be (more or less) completely retracted into the fossa (Dorippinae n. stat.: Figs 10; 12A, B; 14A, B, E-I; 15A-C, E-G; Heikeopsinae n. subfam.: Figs 20F; 21B; Philippidorippinae n. subfam.: Figs 27A, B; 28A, B). In their diagnoses of the Dorippidae, Dev Roy & Bhadra (2011: 115) wrote about *Dorippe quadridens*: "Antennules usually too large to fold inside their fossettes. Antennae large".

The basal article (articles 2 + 3) of the antenna occupies the orbital hiatus. The following articles 4, 5 are of two types: either they are entirely directed forward (Dorippinae n. stat., Dorippoidinae n. subfam., Medorippinae n. subfam., Philippidorippinae n. subfam., Phyllodorippinae n. subfam.); or they are (more or less) horizontally inclined, variously foliaceous, and cover the eyestalk (Heikeopsinae n. subfam., Paradorippinae n. subfam.).

The condition of the eystalk and antenna reveals two main dorippid groups: one with Dorippinae n. stat., Dorippoidinae n. subfam., Medorippinae n. subfam., Philippidorippinae n. subfam., and Phyllodorippinae n. subfam.; and another with Heikeopsinae n. subfam. and Paradorippinae n. subfam.

Oxystomatous condition (Fig. 7C)

The oxystomatous condition is complete. The elongated endostome projects anteriorly to form a gutter, with its extremity not reaching or passing as far as or even beyond the anterior end of the front; it is covered distally by the enlarged and elongated endopodite of mxp1; the mxp3 does not cover the anterior part of the buccal cavern (Bouvier 1940: fig. 140). Depending on the subfamily, the anterior border of the endostome reaches different levels relative to the posterior border of the antennular fossae, and the openings of the exhalant channels are visible or not in dorsal view.

The openings of the exhalant channels are just or barely visible dorsally between the rostral teeth in Dorippoidinae n. subfam. (Figs 16; 17A; 18A) and clearly visible in Medorippinae n. subfam. (Fig. 22C, D, F), Paradorippinae n. subfam. (Figs 24A, B; 26A), and Philippidorippinae n. subfam. (Figs 27A, B; 28A, B). They are not visible in Dorippinae n. stat. (Figs 10; 12A, B; 14B, F, I; 15A-C, E-G); Heikeopsinae (Figs 20F; 21B), and Phyllodorippinae n. subfam. (Fig. 29A, B). The arrangement with visible openings is not related to a narrow front (Medorippinae n. subfam.: Fig. 22A, C), Philippidorippinae n. subfam.: Fig. 27A, B) as it exists in dorippids with a wider front and a developed median emargination (Paradorippinae n. subfam.: Figs 24; 26A).

Pereiopods

As usual in other Brachyura, both chelipeds of female and small male individuals are equal in size and shape. Heterochely/heterodonty resulting in sexual dimorphism occurs in males at puberty moult, and only from a certain size onwards depending on the species with the timing of appearance and rate of development occurring at different stages. The change reflecting a high level of positive allometry of the male chelae ('size allometry' of Hartnoll 1974, 2015; McLay 2015) leads to a strong right cheliped, a palm greatly inflated and much higher than long, often with a swollen lobe near the base of the fixed finger, as e.g. in Heikeopsinae n. subfam. (*Heikeopsis japonica*: Figs 1A, below; 19D, *Neodorippe callida*: Fig. 20C; *Nobilum histrio*: Fig. 21B), and in *Paradorippe granulata* (Figs 25A; 26A).

Usually in Brachyura, at each articulation of the pereiopods with the thorax, the area between the thorax and coxa, i.e., the arthrodial cavity, contains a narrow, soft and flexible arthrodial membrane; and another membrane separates the coxa from the basis-ischium (Bellwood 1996: fig. 1A-C). The articulation point is the location at which the condyle of each article (or podomere) inserts into a corresponding socket hollowed out of the thoracic sternum or adjacent article, i.e., the gynglyme, as named by H. Milne Edwards (1851: 52, see Guinot & Tavares 2003: 47; Guinot *et al.* 2013: 14; sometimes referred to as the glenoid cavity). The joint is bicondylar, meaning that it has two articulation points, limiting the article to movement in a single plane (Hessler 1982).

The coxal area has special characteristics in the Dorippoidea (Dorippidae and Ethusidae). In all dorippoids, the coxa of the pereiopods is separated from the thorax by an exceptionally wide arthrodial cavity containing a thick whitish membrane (broad 'ligamentous sheet' of Bellwood 1996), particularly developed on P4 and P5; similarly, the basis-ischium is not directly articulated with the coxa, and the two articles are connected by a wide membrane (Figs 7B; 33). The only exception to this arrangement in the Eubrachyura seems to be the Orithyiidae, in which the large complex coxa bears a conspicuous membrane on each side, wider between the coxa and basis-ischium (Bellwood 1996: fig. 1D) (see above *Relationships between Dorippidae and Orithyiidae*).

Another singularity in both sexes of the Dorippidae (and Ethusidae) is the coxa itself. In dorsal view of the crab, the coxa of P2-P5 is highly developed, often very prominent, usually wide (width varying in size, e.g. very wide in *Heikeopsis*, narrower in *Medorippe*), and has two different parts: a more or less prominent dorsal part, medially sulcated; and a lateroventral part as a single undivided area, all of which being more visible on the larger coxae, namely P2, P3 (Figs 9C; 33). On P2, the coxa joins the thoracic sternum since at this level the pleurite 5 is only partially exposed and is represented externally only by a small but salient posterior sclerite; on P3, the coxa articulates with the widely exposed (and usually granular) pleurite 6 (Fig. 7B).

The ornamentation of the coxa is a specific character, varying as follows: smooth (e.g. in *Heikeopsis*), fringed with setae (e.g. in *Dorippe quadridens*, Fig. 33C), granular (e.g. in *Medorippe lanata*), spinulous (e.g. in *Dorippoides nudipes*, Fig. 33B), or with three spinules dorsally and numerous spinules on the lateroventral one-piece portion (e.g. in *Dorippe tenuipes*, Fig. 33G, H), or with numerous to very numerous tubercles over the entire surface (e.g. in *Paradorippe granulata*); the one-piece portion may be completely covered with tubercles (e.g. in *Philippidorippe philippinensis*, *Phyllodorippe armata*).

The simultaneous presence of long/thin and short/stout legs observed in adults of the same species may indicate the presence of a puberty (terminal) moult, as in majoids. Within a species or even a population, terminal moult may be achieved by individuals that have gone through a variable number of moult instars. If this is the case, the difference in size at morphometric maturity may be explained by a different number of moult instars in the populations across the range of the species.

The pereiopods P2 and P3 are relatively long in dorippids, but relative length of the merus can be a reliable specific character in some cases. For example, in the genus *Dorippe*, the short-legged species *D. sinica* (Figs 9C; 10C, D) and *D. quadridens* (Figs 8C; 10A, B) have in both sexes a P3 merus 4 to 4.5 times as long as high, whereas the long-legged species *D. tenuipes* (Fig. 9D) has a P3 merus almost 7 times as long as high. P2 and P3 may not be sexually dimorphic in size as e.g. in Dorippoidinae n. subfam. (Fig. 16) and Paradorippinae n. subfam. (Fig. 24A, B). But sexual dimorphism in leg length, especially of the merus, occurs in *Philippidorippe philippinensis*, where P2, P3 are proportionally shorter and stouter in females than in males (Fig. 27A, B). Regarding *Heikeopsis*, see above *Status of non-Japanese* Heikeopsis japonica, H. taiwanensis *(Serène & Romimohtarto, 1969), and* H. arachnoides *(Manning & Holthuis, 1986): a major problem.*

A sexual dimorphism in the setation of the P2 and P3 merus characterises *Dorippe frascone* where the merus is naked in males and hairy in females (Fig. 14A, B and E, F, respectively), and much more so *D. sinica* where the merus is almost completely naked in females but covered with dense pubescence in adult males (Fig. 10A, B and C, D, respectively).

Pereiopods P4 and P5 are reduced, mobile, carried over the carapace, and with subchelate ending (see *Carrying behaviour*).

Strange structures showing as callosities are present at the base of the coxae of P3 in Dorippinae n. stat. and Dorippoidinae n. subfam., with various patterns (see below, *Callosities*).

THORACIC STERNUM AND PRESS-BUTTON

The basic plan of the dorippid thoracic sternum is rather uniform in the different subfamilies, apart from the ornamentation. The thoracic sternum, exemplified by that of the male and female of *Medorippe lanata* (Fig. 4A, B) (Guinot 1979a: fig. 25), is very wide, except for the anterior sternites. Sternite 1, which extends between the mxp3, is not visible externally. Anterior sternites 2-3 form a clearly individualised shield, with sternite 3 widening. Sternite 4 is very wide. The suture 1/2 is not visible. The location of suture 2/3 is detectable by a slight depression. Suture 3/4 is only visible laterally where it is deep; it very often ends in a boutonniere ('boutonnière' in French) marked by a perforation (already present in the first juvenile crab of e.g. *Heikeopsis japonica*, see Quintana 1987: fig. 8E, as *Nobilum japonicum japonicum*). The suture 4/5 is not covered by the short pleon and is therefore fully visible.

An interesting difference (especially in males) is the shield formed by the sternites 1-3. In Dorippoidinae n. subfam. (Figs 17A-C; 18), Paradorippinae n. subfam. (Figs 25A-D; 26), Heikeopsinae n. subfam. (Figs 19C, D; 20C, D, F-H; 21B, C) and Phyllodorippinae n. subfam. (Figs 29C, D; 30A-C), the short, wide shield is pentagonal, with parallel margins and a rectangular sternite 2. In Dorippinae n. stat. (Figs 11; 12B-E; 13; 14B, C, F, I; 15B), it is proportionally longer, narrower and with oblique margins. In Medorippinae n. subfam. (Figs 4; 22C, D), the pentagonal shape is present, with a small portion of sternite 1 visible and a rather long sternite 2 with oblique margins. In Philippidorippinae n. subfam. (Figs 27C, D; 28), the shape tends to become almost triangular.

In Dorippidae, suture 5/6 has a curve that includes the hooked press-button of the pleonal-locking mechanism, in males (Fig. 4A) (as in *Medorippe lanata*, see Guinot 1979a: fig. 28; Guinot & Bouchard 1998: figs 15C, D, 16B) as well as in females, where the button is positioned close to the vulva (Figs 4B; 7C). This curve is very pronounced in e.g. Medorippinae n. subfam. (Figs 4; 22C-E) (see Holthuis & Manning 1990: fig. 37c: *M. lanata*; Guinot & Bouchard 1998: fig. 16A: *M. lanata*), Dorippoidinae n. subfam. (Figs 17B, C, E; 18B-F) and Phyllodorippinae n. subfam. (Fig. 30B, C). It is less marked in Heikeopsinae n. subfam. (Figs 19D; 20C, D, F-H), Paradorippinae n. subfam. (*Paradorippe*, see Figs 25B-D; 26B-D) and Philippidorippinae n. subfam. (*Philippidorippe*, see Figs 27C, D; 28). Suture 6/7 is long, with relatively close interruption points and, sometimes, with a more or less low bridge below (e.g. in Heikeopsinae n. subfam., Fig. 20F). Suture 6/7, which is shown continuous in the sketches of Holthuis & Manning (1990: figs 29e, 41b for females of *Heikeopsis* and *Neodorippe*, respectively), may be replaced medially by a membrane as in a female individual of *Heikeopsis*, but is interrupted medially in all Heikeopsine species. The figures 45i, 50h, 55i, 56i of Holthuis & Manning (1990) inaccurately show continuous sutures 6/7 and/or 7/8 in the female *Paradorippe*. The interruption points are variously located, being very close to each other, e.g. in males of Dorippoidinae n. subfam. (Fig. 17C), in which the sterno-pleonal cavity is paticularly narrow and deep. The suture 7/8 is shorter and obliquely oriented.

A curve of the suture 5/6 that includes the press-button in both sexes as in the Dorippidae is rare in Eubrachyura. It is present, but to a lesser degree, in *Macrocheira kaempferi* (Temminck, 1836) (Macrocheiridae) (Guinot *et al.* 2022: figs 9B, D, 11C, E). In the genus *Achelous* De Haan, 1833 (Portunidae Portuninae Rafinesque, 1815), the suture 5/6 is strongly curved, with a similarly located press-button. In the related portunine *Cavoportunus dubius* Nguyen & Ng, 2010 (see Nguyen & Ng 2010: fig. 3D), the press-button is placed in a conspicuous curve of the suture 5/6, the male pleon does not entirely fill the sterno-pleonal cavity and is positioned posteriorly, suggesting that a posterior displacement of the complete pleon had occurred (Guinot *et al.* 2013: fig. 55).

Sternite 8 presents two features in females: 1) it bears medially an erect spine in only two subfamilies, i.e., Heikeopsinae n. subfam. (in the three genera, Figs 9B; 20G, H) and in Phyllodorippinae n. subfam. (in the only genus and species *Phyllodorippe armata* Fig. 29D) (see below, *Erect spine on sternite 8*); and 2) its dorsally exposed part at the level of P5 coxa bears a tubular process that overhangs the proximal part of pleonal somite 2. This more or less developed structure is an additional modality of female pleon retention in Dorippinae n. status (Figs 8C; 9C; 10B, D; 12A; 15E, F; 33G), in Heikopsinae n. subfam. (Fig. 19B, F) (except in *Neodorippe*) and in Phyllodorippinae n. subfam. (Fig. 27B). In the other subfamilies, the structure does not appear to be functional or is completely absent (See below, *Additional pleonal-retention mechanism in females by process on sternite 8*). In Dorippoidinae n. subfam., the dorsally exposed sternite 8 of female *Dorippoides facchino* (Fig. 16B) bears an obscure prominence that is too raised (like the sternite 7, which forms a granular carina) to overhang pleonal somite 2, whereas in *D. nudipes* from diverse localities sternite 8 bears only a low tubercle without any potential role (Fig. 16D) (P. K. L. Ng, pers. comm.).

Of the many suture arrangement patterns we have recognised in Eubrachyura, the wide dorippid thoracic sternum, with the interruption of the main sternal sutures (4/5-7/8) in both sexes and the absence of a median line, belongs to pattern 5, subpattern 5a (Guinot *et al.* 2013: fig. 56G). This subpattern 5a without median line includes Dorippoidea, Palicoidea, Retroplumoidea, Majoidea, Hymenosomatoidea, and Hexapodoidea Miers, 1886, i.e., clades of eubrachyuras that we also considered among the most basal (Guinot *et al.* 2013), as follows:

Palicoidea, with a re-entrant P5 and carrying behaviour (Guinot 1979a: figs 30G, 31, pl. 19, fig. 5; Guinot *et al.* 2013: figs 32, 34, 45A, 54);

Retroplumoidea, with parallel and interrupted sutures 4/5-7/8, in both extant and fossil representatives, with the first pleonal somites exposed dorsally and only P5 being dorsal (Guinot 1979a: fig. 30C-F; Saint Laurent 1989: figs 4, 5, 22; Guinot *et al.* 2013: figs 5D, 34, 45B);

Majoidea, which should also be a deeply rooted clade, with extant inachoidids, oregoniids, inachids, and macrocheirids (Guinot *et al.* 2013: 196, 197). Based on a molecular estimate of decapod phylogeny, Majoidea was recovered as the oldest brachyuran lineage, with a divergence time from other brachyurans of approximately 254 million years, i.e., Late Permian (Porter *et al.* 2005: fig. 2; Crandall *et al.* 2009: fig. 2) (however, their two figures 2 show that it is Middle Triassic; see Wolfe *et al.* 2019; Colavite *et al.* 2019); and with all data, spermatozoal (Jamieson & Tudge 2000; Tudge *et al.* 2014), larval (Rice 1980, 1981, 1983, 1988; Clark & Webber 1991; Pohle 1991; Marques & Pohle 1998, 2003; Pohle & Marques 2000) and genetic (Ahyong *et al.* 2007; Hultgren *et al.* 2009; Guinot *et al.* 2022: fig. 16), which are congruent in substantiating the Majoidea as a deeply rooted lineage;

Hexapodoidea, with vestigial P5 (only a coxa), with modified sternite 8 and pleurite 8 (Guinot 1979a: figs 32, 33; Guinot *et al.* 2013: figs 5A-C, 48C);

Hymenosomatoidea, which has the widest known thoracic sternum, including a very wide sternite 8, and the most widely interrupted 4/5-7/8 sutures of all Brachyura (Guinot 1979a: fig. 30A, B; Guinot *et al.* 2013: figs 43C, 48C). These features were discussed by Guinot *et al.* (2013, *Affinities between Palicoidea, Retroplumoidea and Hexapodoidea; Affinities between Dorippoidea and Hymenosomatoidea*). See also below, *The female reproductive system in Brachyura, its evolution and unique disposition in Dorippidae*.

Note that the thoracic sternum of Cryptochiroidea Paulson, 1875 (for the incorrect spelling Paul'son, see Evans 2018; Spiridonov 2020), cryptic crabs that are obligate symbionts of living scleractinian corals and have sternal gonopores (thus considered thoracotremes), offers several character states, the plate varying from narrow to wide, and various suture patterns. And *Hapalocarcinus marsupialis* Stimpson, 1859 and *Pseudohapalocarcinus ransoni* Fize & Serène, 1956 belong to the cryptochiroid group having a broad thoracic sternum and with (in the females) largely interrupted sutures (Guinot & Bouchard 1998: 662; Guinot *et al.* 2013: 234, fig. 48E). Beyond 'a species-level diagnostic character' as recently stated by Wong *et al.* (2023: 30), the morphology of the cryptochiroid thoracic sternum is promising to be an important criterium at a higher rank.

A very broad thoracic sternum with interrupted sutures 4/5-7/8 (Fig. 4) is, in some respects, an unexpected structure for a family (Dorippidae) and superfamily (Dorippoidea) considered to be among the most basal and earliest representatives of the Eubrachyura (Guinot *et al.* 2013; Luque 2015; Van Bakel *et al.* 2020). In other words, how can a thoracic sternum as wide as that of the Dorippidae be present in basal Eubrachyura? This raises a crucial question: is the development of a very wide thoracic sternum the expression of an ancestral arrangement (plesiomorphy) or can it be interpreted as the result of an already existing evolutionary process of carcinisation. Carcinisation, which is an emergent potentiality of the Brachyura (and Anomura), is "an underlying synapomorphy […] compatible with both neodarwinian and structuralist conceptions of phylogenesis" (Sternberg 1996). In the evolution of Brachyura, carcinisation is assumed to include a reduction and folding of the pleon, an enlargement and shortening of the cephalothorax, with a posterior expansion of the thoracic sternum, thus intercalating a large sternal portion between the legs, which will favour the displacement of the female and male coxal gonopores towards the sternum, while invariably the two pairs of gonopods remain close to each other, in the axis of the body. In a logical sequence, the evolutionary process would first be a podotreme arrangement (coxal gonopores in both sexes), then heterotreme (female gonopores becoming sternal, formation of vulvae), then thoracotreme (male gonopores becoming sternal). Should this polarity be questioned? According to the consensus view, the palaeontological data follows more or less the same scheme: podotremes appeared in the Jurassic and have persisted to the present day, but with far fewer Recent representatives than in the Jurassic and Cretaceous (podotremes recovered as the earliest diverging brachyuran clade, see Davis *et al.* 2022); contrary to the currently widespread view, some Late Jurassic families will certainly turn out to be in fact heterotreme eubrachyurans (Guinot 2019; see *Palaeontological data* in *Appendix 2*) and then flourished in the Early Cretaceous; thoracotremes did not appear until the Tertiary.

We addressed this issue with the discovery in southeastern Mexico (Chiapas) of the small Lower Cenomanian (Upper Cretaceous) crab *Archaeochiapasa mardoqueoi* Guinot, Carbot-Chanona & Vega, 2019, which displayed exceptional three-dimensional preservation of nearly all its structures, including a very wide thoracic sternum (Guinot *et al.* 2019: fig. 11). Investigations have shown that the Cretaceous, the period when brachyurans flourished and diversified, is in fact the time when two stocks of eubrachyurans seem to have coexisted. One stock including e.g. Dorippoidea, Majoidea, Retroplumoidea, all with a wide thoracic sternum; and a more 'modern' stock, almost contemporary or even older, with a narrow thoracic sternum, including e.g. Componocancroidea Feldmann, Schweitzer & Green, 2008 (thought to have reduced and dorsal P4 and P5), Marocarcinidae Guinot, De Angeli & Garassino, 2008 (normal P4 and P5), Eogeryonidae Ossó, 2016 (P5 probably smaller and subdorsal), and some basal Portunoidea Rafinesque, 1815 (P5 variously modified).

Interestingly, the thoracic sternum of these basal heterotremes (Dorippoidea, Hymenosomatoidea, Palicoidea, Retroplumoidea) is wider than that of several thoracotreme crabs, considered the most derived (see Guinot 1979a: fig. 24D; Guinot *et al.* 2018: figs 5, 8, 9), with the exceptions, however, of the varunids (N. K. Ng 2006; Ferratges *et al.* 2022), the mictyrids (Guinot 1979a: fig. 29), the macrophthalmid ilyograpsines (see Komai & Fujita 2018: fig. 2K), and all the Aphanodactylidae Ahyong & Ng, 2009, which display a wide thoracic sternum (see Ahyong & Ng 2009: fig. 1F). What is the phylogenetic significance of all these discrepancies? This is more so if we also take into account that some podotremes, such as the Dynomenidae (Guinot 2008: fig. 2) and Cyclodorippoidea (Tavares 1993: figs 6b, 7c, 16C), have a relatively developed thoracic sternum, with incomplete or almost absent sutures. It would seem that the evolutionary history of brachyurans is much earlier than previously believed and that the knowledge already acquired should be the starting point for new research directions.

A very wide thoracic sternum is also found in heterotreme families such as the chasmocarcinids (Ng & Castro 2016) or scalopidiids (Ng & Castro 2013; Ng & Rahayu 2014).

Erect spine on sternite 8

An erect axial spine is present on sternite 8 of females of Heikeopsinae n. subfam. (in all three genera) and Phyllodorippinae n. subfam., and is absent in the other subfamilies. The spine is long and straight in *Heikeopsis*, long and recurved in *Neodorippe* (Figs 9B; 20G, H), apparently less developed in *Nobilum*, and triangular in *Phyllodorippe* (Fig. 29D).

Sternum/pterygostome junction at level of sternite 3

Dorippidae shows extensions of the thoracic sternum between the first pereiopods. A sternum/pterygostome junction involves sternite 3 and leads to the formation of highly specialised Milne Edwards openings, which is a synapomorphy of the family (Figs 4; 7C). The dorippid sternum/pterygostome junction is unique in Eubrachyura in that it involves sternite 3. The only other exception appears to be the Palicidae, the only other eubrachyuran family to share this sternal junction via episternite 3, but the latter is only slightly projected, and the Milne Edwards openings are 'normal' in palicids (Guinot *et al.* 2013: fig. 32A). In Dorippidae, the sternite 3 is so extended and the thoracic sternum/pterygostome junction so considerable that the Milne Edwards openings (inhalant or afferent branchial openings) are markedly modified and become separate structures in front of the chelipeds, namely two independent, deep slits excavated in the pterygostome, each receiving the elongated, lamelliform, largely exposed and calcified mxp3 coxa, prolonged by a non-articulated epipodite (A. Milne-Edwards & Bouvier 1902: 39; Ihle 1916: 103, figs 45, 51, 54, 58, 59, 61, as *Dorippe dorsipes*; Bouvier 1940: 199, fig. 140; Guinot *et al.* 2013: fig. 42C). This particular arrangement already appears in the first juvenile crab (Quintana 1987: figs 3F, 8E, 15G). In contrast to the Dorippidae, the Ethusidae has typical Milne Edwards openings (Guinot *et al.* 2013: fig. 42A).

A sternum/pterygostome junction involves another sternite, namely sternite 4, to varying degrees, in some other brachyurans. It leads to the development of respiratory adaptations and manifests itself in two extreme arrangements: either the separation of the Milne Edwards openings from the chelipeds (pre-chelipedal afferent branchial openings) as in the Dorippidae; or their loss at this level. This latter case of sternum/pterygostome junction, varying from narrow to wide, occurs in the Raninoidea De Haan, 1839 (Van Bakel *et al.* 2012a: 133, figs 44D, 47A, 48; Guinot *et al.* 2013: figs 38B, C, 42E) in which the Milne Edwards openings (afferent openings) are replaced by inhalant posterior openings. In Leucosioidea Samouelle, 1819 *pro parte*, the sternum/pterygostome junction is markedly developed and the Milne Edwards openings are absent (Guinot *et al.* 2013: fig. 42D), but a pterygostomial gutter ('exostegal canal') provides a respiratory flow below the junction site allowing respiratory water to enter the branchial chamber (Garstang 1897; Davie *et al.* 2015a).

Some eubrachyuran families develop a sternum/pterygostome junction (at the level of sternite 4) to the extent of isolating the Milne Edwards openings from the arthrodial cavity of the cheliped, but retain the Milne Edwards orifices in their normal position, as e.g. in Retroplumoidea and Hexapodoidea (Guinot *et al.* 2013: figs 5A-C and 5D, respectively). Different modalities are present in Hymenosomatoidea (Guinot *et al.* 2013: fig. 48C), leading to "Milne Edwards apertures fused laterally for more than half their length" (Lucas 1980: 186, fig. 5I), and in some cryptochiroid genera (Guinot *et al.* 2013: fig. 48D, E). A complete loss is achieved in the Leucosiidae (see above).

Different states of the thoracic sternum/pterygostome junction are found in Inachoididae, depending on the extension of sternite 4, and, as a result, the Milne Edwards opening is varied in shape, with the developed mxp3 coxa differently exposed (Guinot *et al.* 2013: figs 48A, 49C, E). The junction is incomplete, as e.g. in *Paradasygyius depressu* (Bell, 1835), *Collodes leptocheles* Rathbun, 1894, *Pyromaia tuberculata* Lockington, 1877, and *Leurocyclus* Rathbun, 1897. The resemblance to the Dorippidae is significant when the junction is complete, although not identically, with entirely separated Milne Edwards openings in other species, as e.g., *Paulita tuberculata* (Lemos de Castro, 1949) (Guinot 2012: figs 2C, D, 3A, B), *Batrachonotus fragosus* Stimpson, 1871, *Arachnopsis filipes* Stimpson, 1871, *Euprognatha rastellifera* Stimpson, 1871, *E. bifida* Rathbun, 1893, and *Anasimus latus* Rathbun, 1894 (Guinot & Richer de Forges 1997: 488, figs 11C, 12C, D, 13A, B, 14A, B). Therefore, in the Inachoididae some subfamilies are diagnosed by a complete sternum/pterygostome junction: Esopinae Guinot & Van Bakel, 2020 (Guinot & Van Bakel 2020a, with type genus by monotypy: *Esopus* A. Milne-Edwards, 1875); Paradasygyiinae Guinot & Van Bakel, 2020 (= Dasygyiinae Holmes, 1900) (Guinot & Van Bakel 2020b, with type genus by original designation: *Dasygyius* Rathbun, 1897, replaced by *Paradasygyius* Garth, 1958); Paulitinae Guinot & Van Bakel, 2020 (Guinot 2012; Guinot & Van Bakel 2020b, with type genus by monotypy: *Paulita* Guinot, 2012); and Stenorhynchinae Dana, 1851, with type genus: *Stenorhynchus* Lamarck, 1815; see Guinot 2012). Other subfamilies such as e.g. Salaciinae Dana, 1851 (type genus: *Leurocyclus* Rathbun, 1897), have no sternum/pterygostome junction.

Sterno-pleonal cavity and pleon

The sterno-pleonal cavity is excavated posteriorly. It consists of a distinctly inclined posterior portion covered by pleonal somites 1-6 and a very narrow anterior portion, often covered only by the telson. Both the male and female pleons have a posterior position. The male pleon is short and may leave an empty space in front of the telson.

In relation to the incomplete folding of the pleon, in males the first two somites, which are clasped between the P4, P5 coxae, are exposed dorsally; in females, the somites show a greater dorsal exposure, at least the first three. The presence of articular membranes that are situated between all pleonal somites across the full width of each somite, as shown here in *Medorippe lanata* (Fig. 7D), does not correspond to a particular curvature of the tergites.

All pleonal somites are free in both sexes of all subfamilies except for Heikeopsinae n. subfam. *pro parte*, in which males of *Neodorippe simplex* have somites 3-5 fused, though with sutures still visible (Ng & Rahayu 2002: 757, fig. 3C), but with all somites free in females, interestingly with the same arrangement as in the Ethusidae.

The Dorippinae n. stat. is notable for the male pleon with somites 2, 3 bearing three conspicuous teeth and somites 4, 5 with a single median tooth, as in *Dorippe frascone* (Fig. 14A-D), *D. quadridens* (Figs 10A; 11B), *D. sinica* (Figs 10C; 13A), *D. trilobata* (Fig. 15A-C); or with somites 2, 3 bearing blunt granular elevations and somites 4 and 5 with low granular elevations as in *D. irrorata* (Fig. 14H, I) and *D. tenuipes* (Fig. 9D). In other subfamilies, distinct teeth are missing on pleonal somites 2 and 3, these somites being with low elevations or more or less undulating elevations. Male pleonal somite 3 shows two swollen lateral parts in Paradorippinae n. subfam. (Fig. 25B) and two large projections in Philippidorippinae n. subfam. (Figs 27A; 28A, C).

In all subfamilies, the enlarged female pleon with the first somites exposed dorsally forms a pouch posteriorly, providing a semi-brood cavity (Guinot 1979a: pl. 25, figs 8, 9), which allows somite 6 with its sockets to face sternite 5 with its press-buttons in the backward curve of the suture 5/6, facilitating the preservation of a pleonal locking in females. The hypothesis (the first one that comes to mind) of a shortening of the dorippid pleon during carcinisation is supported by the fact that the sternal suture 5/6 curves sharply backwards so that it might accommodate the press-buttons of the pleonal-locking mechanism in both sexes (Fig. 4). This remarkable adaptation between the sternal structures and the pleonal sockets, i.e., between two different and originally independent parts of the body, is a perfect example of 'coaptation by assemblage' (Guinot & Bouchard 1998).

Pleonal-locking mechanism by press-button in males and females

A typical and functional press-button is present in both male and female dorippids, positioned in a marked curve (though to a greater or lesser extent depending on the subfamily) of the sternal suture 5/6 that includes it perfectly and consistently throughout the family without exception. All dorippids show a consistent pattern similar to that of the male *Medorippe lanata* (Fig. 4A), with acute prominences and deep sockets providing an efficient locking mechanism. A functional pleonal-locking mechanism by press-button persits in mature females (Fig. 4B), even in those carrying eggs in their brood chamber (Guinot 1979a: fig. 28; Guinot & Bouchard 1998: fig. 15C, D). This pattern is a synapomorphy of Dorippidae. In the Ethusidae, the sternal suture 5/6 is straight, and the press-button is normally located.

A pattern such as that of the Dorippidae is rare in Eubrachyura. It is occurring, but to a lesser degree, in the basal majoid *Macrocheira kaempferi*, in which the sternal suture 5/6 forms a clear curvature (Guinot *et al.* 2022: figs 9B, D, 11C, E). The portunine genus *Achelous* with *A. tumidulus* Stimpson, 1871 (see Mantellato *et al.* 2009), and the related genus *Cavoportunus* with *C. dubius* (Laurie, 1906) (see Nguyen & Ng 2010: fig. 3D) have a press-button located in a substantial curve of the suture 5/6.

In postpubertal dorippid females, the press-buttons and vulvae are positioned very close together, side by side (Kollmann 1937: fig. 68; Guinot 1979a: 183; Holthuis & Manning 1990: figs 6g, 21h, 29e, 37c, 41c, b, 43h, i, 45h, i, 50h, i, 55i, 56i-k, 57f; Guinot & Bouchard 1998: fig. 16A; Guinot *et al.* 2013: fig. 42C; Köhnk *et al.* 2017: 40; 2018: 102). The extremely enlarged and domed female pleon, with developed setose pleopods, forming a large brood chamber, does not completely lie within the sterno-pleonal cavity but occupies a posterior location against the almost vertical sternites 7 and 8. According to Guinot & Bouchard (1998: 650), the positive allometric growth essentially involves the female pleon at the back, thus without any significant modification of the spacing between the different locking structures (sockets on pleonal somite 6 facing the press-buttons on sternite 5), and thus does not affect the holding system after the puberty moult. The domed pleon above the wide brood chamber solves the problem of interfering pleopods. We examined a female *Dorippe quadridens* (MNHN-IU-2018-5198 = MNHN-B11172) in which the thickness of the egg mass and the long pleopodal setae prevented locking, but, on the opposite, an ovigerous female *Neodorippe callida* in which efficient buttons and sockets ensured a firm closure. Significantly, even in Ethusidae in which the sterno-pleonal cavity is normally hollow, mature females possess both well-developed components of the apparatus allowing effective locking. Accordingly, the retention of an effective locking mechanism in mature dorippoid females is not dependent on the pleon and holding components.

Dorippoidea is one of those exceptional lineages of eubrachyurans that retain a functional locking mechanism in mature females, as noted by Guinot (1979a). Although rather rare, the functionality of the locking mechanism in mature females is fully present and functional in adult females of some other eubrachyuran families, e.g. Hexapodoidea (Guinot & Bouchard 1998: fig. 17E; Guinot & Quenette 2005: fig. 29B; Guinot *et al.* 2013: fig. 5A-C), extant as fossil (Guinot *et al.* 2010: 300, figs 3B, 4C); Retroplumoidea (Guinot 1979a: 148, fig. 30C, E; Guinot & Bouchard 1998: fig. 17D; Guinot *et al.* 2013: fig. 5D), extant as fossil. In Palicoidea Bouvier, 1898 (see Castro 2010), whose adult and larval traits support the division into two families, Palicidae and Crossotonotidae A. Milne-Edwards, 1873 (see Clark *et al.* 2012), developed press-buttons and sockets persist in adult females (Guinot & Bouchard 1998: fig. 17C), but the functionality of the mechanism should be verified. In Parthenopidae MacLeay, 1838 (in both subfamilies Parthenopinae MacLeay, 1838 and Daldorfiinae Ng & Rodríguez, 1986), mature females (and even females holding large egg masses) display an effective locking mechanism (Tan & Ng 2007a: 96; 2007b: 127). In most Calappidae, the thoracic sternum and pleon of females are relatively narrow (as in males) compared to those of other eubrachyurans, and the pleon of females does not show conspicuous enlargement at puberty moult; a functional mechanism occurs in mature females (Köhnk *et al.* 2018). The weak sexual dimorphism as well as the absence of marked morphometric changes (allometry) at puberty moult may explain the persistence of the functionality of this mechanism.

In other Eubrachyura, the press-button for pleonal holding may persist only as non-functional scar, for example in the Majoidea, e.g. in *Libinia spinosa* Guérin, 1832 (Sal Moyano *et al.* 2011: fig. 4E, F), and more often it is lost entirely in mature females. The loss in pubertal females should be related to the pronounced change in pleon linked to its positive allometric growth (Hartnoll 1969, 1974). Compared to the chelae in males, which can continue to grow at puberty, the female pleon is not an independent effector but can only operate together with the thoracic sternum, its large increase in size at the puberty moult preventing the fitting (coaptation) between the two parts, the sternal press-buttons and the pleonal sockets.

Additional pleonal-retention mechanism in females by a process on sternite 8

A female feature documented here for the first time in the Dorippidae and apparently never reported in other Brachyura, appears to be exclusive to all but four subfamilies. Sternite 8, in its dorsally exposed portion at the level of the P5 coxa, bears a tubular process that overhangs the pleon base, i.e., the proximal part of somite 2 (Figs 8C; 9C). This device constitutes an additional modality of retention of the female pleon (in its proximal part), which is already retained by the press-button system that persists in postpubertal females (see above). This additional female pleonal retention modality is a subfamilial character and is found in the following subfamilies:

Dorippinae n. stat.
A conspicuous process on sternite 8 in e.g. *Dorippe quadridens* (Figs 8C; 10B; 12A), *D. sinica* (Figs 9C; 10D), *D. frascone*, *D. glabra* (Fig. 15E, F), and *D. tenuipes* (Fig. 33G), where there is a rather low tubercle in a prepubertal female (Fig. 14E) but robust in a larger female 26.8 × 24.3 mm (ZRC 2001.0389) (P. K. L.Ng, pers. comm.). The disposition could not be confirmed either in *Dorippe trilobata* known from the single male holotype, or in *D. irrorata* known only from one male.

Heikopsinae n. subfam.
A rather large, thick process with a blunt tip in female *Heikeopsis japonica* (Fig. 19B), *H.* aff. *japonica* (Fig. 19F) and *Nobilum histrio*, but absent in female *Neodorippe* (Fig. 20B).

Phyllodorippinae n. subfam.
A small spine in the females of *Phyllodorippe armata* (Fig. 29B).

Dorippoidinae n. subfam.
The dorsally exposed sternite 8 of female *Dorippoides facchino* (Fig. 16B) bearing an obscure prominence that is too elevated (as is sternite 7 that forms a granular carina) to be able to overhang pleonal somite 2; in *D. nudipes* (Fig. 16D) the tubercle-shaped process seems also non-functional.

Such a functional device of thoracic sternite 8 is absent in Medorippinae n. subfam. (*Medorippe lanata*: Fig. 22B) and Paradorippinae n. subfam. (*Paradorippe granulata*: Fig. 25B), in which the first two pleonal somites are slightly contained between the raised margins of sternites 7 and 8. In Philippidorippinae n. subfam., the rather large process in *Philippidorippe philippinensis* (Fig. 27B) just reaches the margin of the pleon and does not seem functional.

The telson of all dorippid females is wedged between the steep slopes of the sterno-pleonal cavity between the more or less raised edges of sternite 5, so that the pleon is gently secured at this level. The level reached by the telson, when properly positioned on the thoracic sternum, varies in Dorippidae. In females of Dorippinae n. stat. (*Dorippe quadridens* and *D. sinica*: Figs 12C; 13C, respectively), Heikeopsinae n. subfam. (Figs 20H; 21E, F) and Medorippinae n. subfam. (*Medorippe lanata*), the tip of the telson extends beyond the level of suture 4/5. It just reaches suture 4/5 in Dorippoidinae n. subfam. (*Dorippoides facchino* and *D. nudipes*: Fig. 18A, E, respectively), Paradorippinae n. subfam. (*Paradorippe granulata*), Philippidorippinae n. subfam. (*Philippidorippe philippinensis*: Fig. 27C), and Phyllodorippinae n. subfam. (*Phyllodorippe armata*: Fig. 29C).

Penis and coxo-sternal condition

The dorippid penis typically consists of four portions: a proximal sclerotised and moveable penial bulb that is (together with a small portion of the penial tube) the only exposed part of the penis (Guinot *et al.* 2013: figs 15A, B, E, 16A, B, C, 17A-C, 18A-C, 19A-C); a membranous portion of variable length, which may be partially covered by the bulb; a long penial tube, typically angled, and a soft terminal papilla, which may be rather long when fully everted. The bulb provides protection at the emergence of the penis. The penial tube, which varies from vertical and unprotected by the thoracic sternum (then being only covered by the pleon) to inclined or angled and variously covered by sternal portions, runs along a deep groove on the lateral side of the G1 basipodite, its distal end extending into a soft papilla inserted into a lateral foramen located at the base of the G1 endopodite.

Dorippidae offers multistate characters of penis protection not found elsewhere in Eubrachyura. There are numerous patterns of the coxo-sternal condition in Dorippidae (Guinot *et al.* 2013: 99-105, figs 15-19), compared to only one (though to be verified) in Ethusidae. Dorippids show a distinct sclerotised bulb whereas in Ethusidae the proximal portion of the penis is sclerotised but without forming a distinct structure (Guinot *et al.* 2013: figs 20A, B, 21B, 22A-C). The dorippid bulb has no relevance to a condylar location of the penis, as the penis emerges above the coxo-sternal condyle. On the opposite, an arrangement with the penis emerging from the extremity of the condyle (condylar protection of the penis) is shared by e.g. Orithyioidea Dana, 1852, Palicoidea, Retroplumoidea, Inachoididae *pro parte* (e.g. in Stenorhynchinae Dana, 1851, see Guinot 2012) (Guinot *et al.* 2013: 87, table 4), and probably in Hexapodidae.

In the leaf-porter crab *Neodorippe* (Heikeopsinae n. subfam.), the lengthening of the penis as well as other features (relatively small size; smooth, flattened and elongated carapace) are reminiscent of an ethusid. But in ethusids the penis is for the most part located along sternal suture 7/8 and is never angled, whereas in *Neodorippe* there are, like in dorippids, two distinct portions: a proximal portion inclined and a distal portion vertical to the body axis (Guinot *et al.* 2013: fig. 19C: *N. callida*; and fig. 20A: *Ethusa mascarone* (Herbst, 1785)).

The dorippid disposition varies: from a coxal gonopore, with a proportionally short vertical penis, unprotected by sternites 7 and 8, i.e., a (nearly) coxal condition, in Medorippinae n. subfam. to a long and even very long penis, variously inclined and covered by the thoracic sternum, reflecting different character states of the coxo-sternal condition in other subfamilies, the Heikeopsinae n. subfam. having the longest penis, with the longest inclined part. This unique disposition, which is a synapomorphy of Dorippidae, differs from the penis protection arrangements found in other eubrachyurans, in which the penis usually runs along the suture 7/8 and is protected within an invagination of sternite 8 that forms a gutter, together with a varied juxtaposition of sternites 7 and 8 (Guinot *et al.* 2013: figs 8I-K, 24, 32A-E, 44B).

G1

The morphology of the penis, G1 and G2, and their interactions are strongly related to both the incomplete folding of the pleon and the dorsal position of its first somites that implies long G1 and G2 protopodites. As a result, the dorippid G1 has a long protopodite that consists of an elongated coxopodite and a well-developed basipodite, which encircles most of the twisted endopodite.

The dorippid G1 is a highly diverse structure (Fig. 31) (Holthuis & Manning 1990: 6, key to genera based on G1s; Sin *et al.* 2009: fig. 4; present paper, *Key to dorippid subfamilies based on G1 and vulva*). The presence of a basal lobe characterises the Dorippinae n. stat., Dorippoidinae n. subfam., Medorippinae n. subfam., and Philippidorippinae n. subfam. The G1 is variable in proportion, narrow or robust, straight and simple or curved (regular or C- or S-shaped), and with subdistal and distal parts of various shapes, provided with one to four or more lobes that are rounded, auricular or pointed, and end in a sharp or twisted tip or in an irregular, spiniform or hook- or hammer-shaped process, sometimes with setae. The G1 is very similar in genera comprising several species (e.g. Dorippinae n. status, Paradorippinae n. subfam.), and it is fairly uniform in subfamilies comprising several genera (e.g. the Heikeopsinae n. subfam.). In total, seven main types of G1s can be recognised, corresponding to the seven subfamilies we distinguish, as follows.

Dorippinae n. stat.
G1 uniform in all species, relatively simple, straight, proportionally slender, gradually tapering to a single apex, with subdistal setae; distal part relatively short, gently curved, with a tongue-shaped corneous process, tip bluntly rounded; basal lobe present, covered with numerous small denticles and with a prominent cluster of pappose setae on its tip (Figs 11C, D; 13B; 31A).

Dorippoidinae n. subfam.
G1 relatively simple, straight, with a simple, twisted apical process, ending either in a slender, long, spiral-shaped point (*Dorippoides facchino*) or in a flattened, rectangular, horn-coloured projection produced into a narrow whip-like appendage (*D. nudipes*); basal lobe present, covered with several setae (Figs 17C; 31B).

Medorippinae n. subfam.
G1 short, stout, abruptly turned outward and almost at right angles for nearly three-fourths of length; tip simple, setiferous, directed laterally, with a very acute apex, without distal or subdistal lobe; basal lobe present, covered with numerous denticles and a row of pappose setae (Figs 4A; 22D, E; 31C).

Heikeopsinae n. subfam.
G1 long, stout proximally, then slender and elongate, inverted C-shaped, strongly bent and largely curved outward; apex tapering into a single process (*Neodorippe simplex*) or ending in three or four lobes: rounded lobe plus two unequal sharp distal processes in *N. callida* (Fig. 20E); three short, broad, petaloid subequal processes in *Nobilum* (Fig. 21D); several elongated, blunt-toped, unequal lobes plus subdistal and distal processes in *Heikeopsis*; no basal lobe.

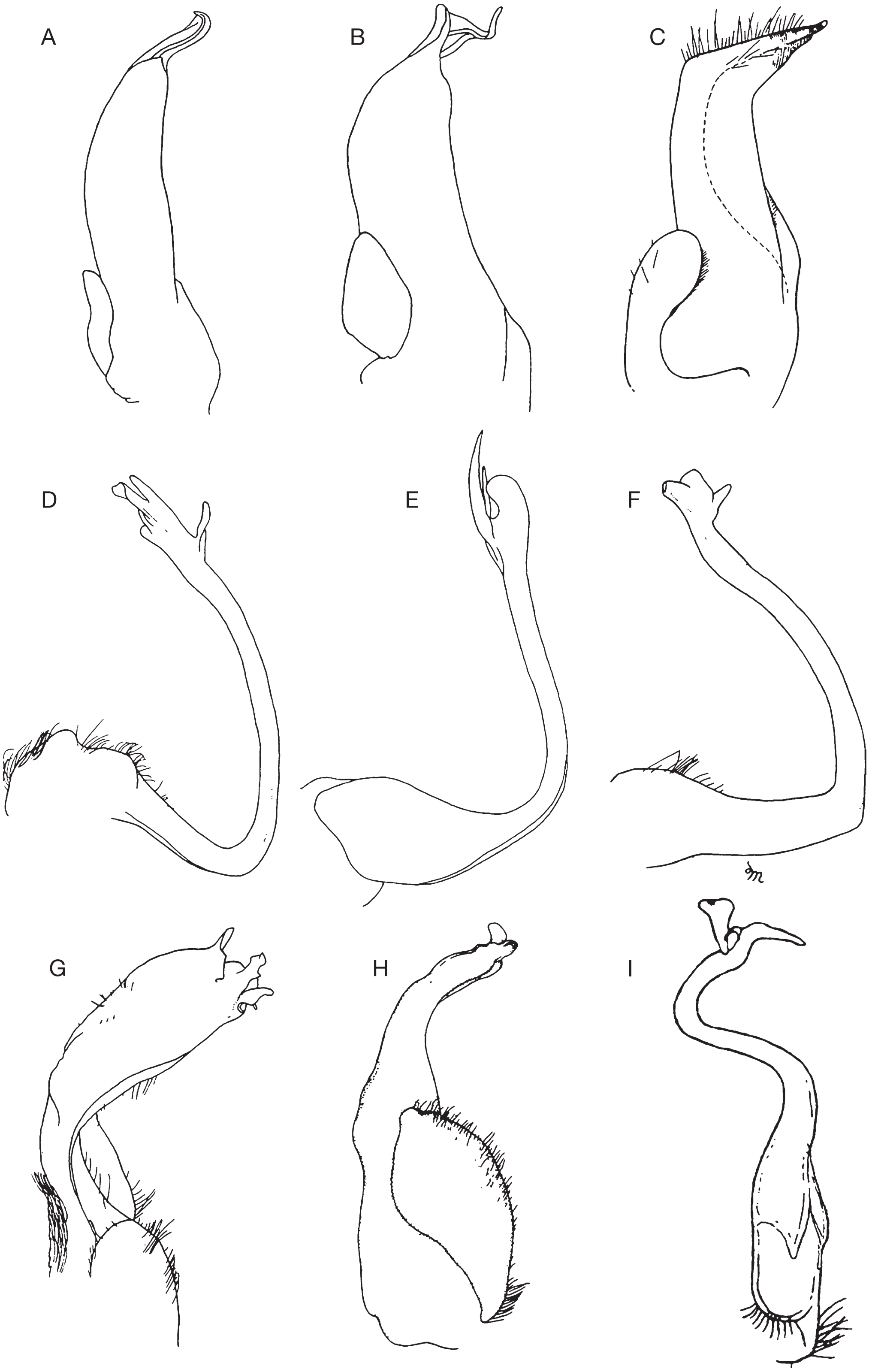

Fig. 31. — Diversity of G1s in the seven dorippid subfamilies (schematic drawings): **A**, Dorippinae n. stat. (*Dorippe quadridens*); **B**, Dorippoidinae n. subfam. (*Dorippoides facchino*); **C**, Medorippinae n. subfam. (*Medorippe lanata*); **D**-**F**, Heikeopsinae n. subfam.: **D**, *Heikeopsis ?japonica*; **E**, *Neodorippe callida*; **F**, *Nobilum histrio*; **G**, Paradorippinae n. subfam. (*Paradorippe cathayana*); **H**, Philippidorippinae n. subfam. (*Philippidorippe philippinensis*); **I**, Phyllodorippinae n. subfam. (*Phyllodorippe armata*). (A-H, after Holthuis & Manning 1990; I, after Manning & Holthuis 1981). From Sin *et al.* (2009: fig. 4). Setae not always figured.

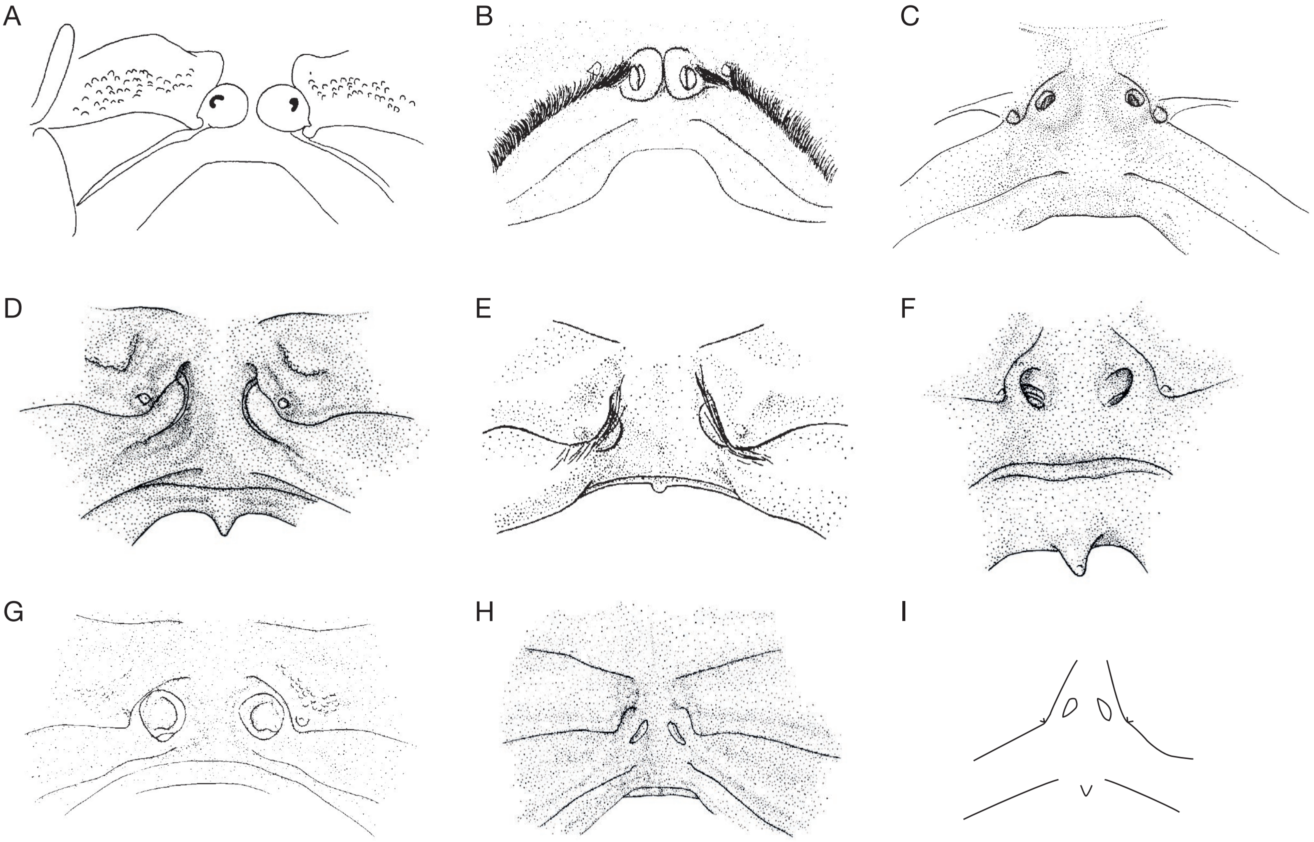

Fig. 32. — Diversity of vulvae in the seven dorippid subfamilies (schematic drawings): **A**, Dorippinae n. stat. (*Dorippe quadridens*); **B**, Dorippoidinae n. subfam. (*Dorippoides facchino*); **C**, Medorippinae n. subfam. (*Medorippe lanata)*; **D**-**F**, Heikeopsinae n. subfam.; **D**, *Heikeopsis ?japonica*; **E**, *Neodorippe callida*; **F**, *Nobilum histrio*; **G**, Paradorippinae n. subfam. (*Paradorippe cathayana*); **H**, Philippidorippinae n. subfam. (*Philippidorippe philippinensis*); **I**, Phyllodorippinae n. subfam. (*Phyllodorippe armata*, ♀ 13.0 × 19.0 mm, Guinean Trawling Survey, MNHN-IU-2021-8731 [= MNHN-B24199]). Setae represented only on **B**. A-H, modified from Holthuis & Manning (1990).

Paradorippinae n. subfam. (see *Preliminary note*, p. 279*).*
G1 very short, stout throughout, filling most anterior part of sterno-pleonal cavity, abruptly constricted to about mid-length, then bent; second part very swollen, elaborate with distinct bulbs bearing several more or less elongated, unequal apical processes, one of which may be hook- or hammer-shaped; no basal lobe (Figs 25C-E; 31G).

Philippidorippinae n. subfam.
G1 short, thick basally, then regularly curved, distal third bent outwards; tip with a finger-shaped process and an auricular, inwardly directed ventral lobe; basal lobe present, thick, broad (Figs 28D, E; 31H).

Phyllodorippinae n. subfam.
G1 long, very slender, twisted at base, S-shaped, with a rather large inverse triangular main appendage, and ending in a narrow recurved subdistal spine; no basal lobe (Figs 30C, D; 31I).

Likewise, the Dorippidae displays a rather substantial morphological diversification of the vulvae (see below, *Vulvae*). How is the diversely ornamented distal portion of the eubrachyuran G1 distinctively conformed to fit the vulva and what degree of compatibility between the gonopods and the vulvae is necessary for mating? Very often, in Brachyura the vulvae and G1 require exact matching to each other for mechanical coupling, at most a simple adjustment between the gonopod and the vulva, and sometimes a 'lock-and-key' mechanism. These adjustments should include the size, thickness, orientation and twist of the G1 as well as modification of its tip to facilitate its insertion into the vulvar opening and hold the gonopod and vulva in place. It is clear that the dorippid G1 fits the vulva of the corresponding species, and there is evidence for coevolution between male and female external genitalia. For example, in Paradorippinae n. subfam., the large, exposed opening of the vulva must match the swollen, bulbous and elaborate distal part of the G1; in Heikeopsinae n. subfam., the narrow, vertically oriented or suboval, exposed vulva (Figs 20G, H; 21E, F; 32D-F) is adapted to receive the long, inverted C-shaped and strongly bent G1 (Figs 20E; 21D; 31D-F).

In summary, the Dorippidae shows considerable morphological diversification of male and female external reproductive structures, with also a highly varied arrangement of the penial region. This diversification may have contributed to a rapid and divergent evolution of this lineage.

G2

The dorippid G2, like G1, has a long protopodite (long coxopodite + basipodite). It is uniform in all the family, with a size approximately half the length of G1 (thus of 'intermediate length'), straight-shaped, without a delimited or folded flagellum.

VULVA (Fig. 32)

The dorippid vulva is located on thoracic sternite 6 as usual: it is never displaced forward, unlike the cases of the displaced vulvae of some Eubrachyura such as Inachoididae, Palicoidea, Hymenosomatoidea (compare with anteriorly displaced spermathecal apertures in podotremes, e.g. of family Dromiidae, see Guinot & Tavares 2001: fig. 10; 2003; Tavares & Franco 2004). The dorippid vulva lies very close to the press-button providing firm pleonal locking and, when the pleon is closed, it is uniformly covered by the posterior part of the pleonal somite 6 and, to a variable extent, by the telson as e.g. in *Dorippe*, *Medorippe*, *Heikeopsis*, *Nobilum*, *Paradorippe*, *Phyllodorippe* (Guinot *et al.* 2013: 44). All dorippid vulvae have immobile opercula. Hartnoll (1968: 293, as *Dorippe lanata*) observed in *Medorippe lanata* that ovulation is possible in mid-intermoult because the vulvar region has undergone local decalcification shortly before egg-laying, rendering the operculum mobile, and that recalcification occurs shortly thereafter. It would be worthwhile to investigate if this was the case for all dorippids.

The dorippid vulva is highly diverse (Fig. 32). It varies greatly in location and position on thoracic sternite 6 (in a depression or on a prominence), in shape of the opening, and is more or less or not at all associated with a sternal ridge. The vulva of *Phyllodorippe armata* is pictured here for the first time (Figs 29D; 32I). In total, seven main types of vulvae can be recognised, corresponding to the seven subfamilies we distinguish, as follows:

Dorippinae n. stat.

The vulva has a uniform pattern in all species, i.e., it is located at the apex of the elevated portion of sternite 6 at the tip of a setose raised sternal ridge; opening rather large, rounded, not recessed (Figs 4B; 12D, E; 13D; 32A).

Dorippoidinae n. subfam.

Vulva medially, on outer side of clearly delimited globular whitish prominences ('on raised, papilla-like tubercles', see Holthuis & Manning 1990: 48, fig. 21h, i, *Dorippoides facchino*), each very close to the other, in continuation of an oblique setose raised ridge; opening comparatively large, not recessed (Figs 17D; 18B, C, F; 32B).

Medorippinae n. subfam.

Vulva situated on sternite 6 at outer margin of salient sternal prominence, in continuation of a setose sternal ridge; opening very small, oval-shaped, recessed, barely roofed by sternal projection; histologically, opening enclosed by protruding parts of vagina (Hartnoll 1968: 293, as *Dorippe lanata*; Mori 1986: 78; Holthuis & Manning 1990: 89, fig. 37c, d; Guinot *et al.* 2013: fig. 42C; Vehof *et al.* 2017: figs 1B, C, 2B) (Figs 4B; 32C).

Heikeopsinae n. subfam.

A single pattern in *Heikeopsis* and *Nobilum* (Figs 21E, F; 32D, E). Vulva, each clearly separated from the other, at inner part of sternal prominence that may form a rounded ridge; opening as long, extremely narrow, curved, vertically oriented slits, thus not entirely exposed (Holthuis & Manning 1990: figs 29e, f, as *Heikea japonica*; 43h, i, *Nobilum histrio*). In *Neodorippe* (Figs 20F-H; 32F), slightly oblique on submedian area of sternite 6, not sunken, thus completely exposed; opening suboval (Holthuis & Manning 1990: fig. 41b, c, *Neodorippe callida*).

*Paradorippinae n. subfam. (*see *Preliminary note*, p. 279*)*

Vulva below distal part of suture 5/6, situated on more or less marked prominent part of sternite 6 and at end of a raised sternal ridge; opening large or even very large, rounded or crescent-shaped, widely exposed, completely visible on surface (Holthuis & Manning 1990: figs 45h, i, *P. australiensis*; 50h, i, *P. granulata*; 55i, 56i-k, *P. polita*; Vehof *et al.* 2018b: figs 2, 3, *P. granulata*) (Figs 26C, D; 32G).

Philippidorippinae n. subfam.

Vulva quite distant from distal part of sternal ridge, situated on obliquely directed flank of flaired sterno-pleonal cavity, not very close to each other; opening not recessed, quite large, elongated, crescent-shaped (Holthuis & Manning 1990: fig. 57f, g) (Figs 27C, D; 32H).

Phyllodorippinae n. subfam.

Vulva quite distant from distal part of setose sternal ridge, situated on raised flanks of narrow sterno-pleonal cavity, quite close together, and narrowly slit-shaped. (Figs 29C, D; 32I).

Based on the vulvae, the subfamilies can be roughly classified in three main groups, as follows: one group with Dorippinae n. stat., Dorippoidinae n. subfam., Medorippinae n. subfam. and perhaps Phyllodorippinae n. subfam.; one group with Heikeopsinae n. subfam.; and one group with Paradorippinae n. subfam.; the position of Philippidorippinae n. subfam. is enigmatic. But a more refined categorisation requires us to distinguish seven distinct types of vulvae, corresponding to the seven subfamilies recognised here and more particularly to the seven types of gonopods observed (Fig. 31) (see above).

AXIAL SKELETON

The axial skeleton of the Dorippidae is poorly known and was only briefly and partially discussed in *Medorippe lanata* by Guinot *et al.* (2013: 216, 217, 272, figs 46C, 47A) as exhibiting a plesiomorphic disposition, i.e., a regular longitudinal compartmentalisation, with phragmata extending further than the junction plate and reaching the median axis. A median line was considered absent in both sexes of *Medorippe lanata*, whereas a peculiar configuration was observed internally (invaginations of the sternal floor, which could be assimilated to a particular median plate), with a sexually dimorphic arrangement: phragmata connected medially in males, but separated medially in females.

Hazerli *et al.* (2022: 9, fig. 1A) give an interesting interpretation of the raised laminae and infoldings issued from the sternal floor, present only in males: they are not homologous to the median plate found in other hetrotreme taxa: we agree that a median plate, similar to that of other Eubrachyura, is effectively absent in *Medorippe lanata*. Hazerli *et al.* (2022) concur with Guinot *et al.* (2013: table 8) that the interosternite 7/8 is directly connected to the sella turcica and the intertagmal phragma is connected to the interopleurite 7/8, with these authors adding that the latter is confluent with the sella turcica. Hazerli *et al.* (2022: 44, fig. 33) conclude in their phylogenetic analysis that, regarding this character, *Medorippe lanata* is "positioned as sister to a clade comprising Heterotremata and Thoracotremata (not as a heterotrematan taxon as suggested by Jamieson & Tudge, 1990)". This is a further argument in favour of the very special place occupied by the Dorippidae within the Eubrachyura. The study of the axial skeleton is not known for the different subfamilies recognised here: it would be interesting to see if the internal features also support the external differences observed in this paper.

CALLOSITIES, UNIQUE STRUCTURES AT THE BASE OF P3 IN DORIPPINAE N. STAT. AND DORIPPOIDINAE N. SUBFAM.

Serène (1982: 1130) described and figured a whitish, cup-shaped outgrowth at the base of P3 in two species of *Dorippe*. He figured (pl. 1, fig. 1, pl. 2, figs 1, 4) a large structure in his *D. miersi* (now *D. tenuipes*) and (pl. 1, fig. 3) a smaller one in his *D. frascone* (now *D. quadridens*). In their introduction, Holthuis & Manning (1990: 2) referred the structure found dorsally on P3 coxae in 'members of *Dorippe*' and in 'females of *Dorippoides*' to a 'sausage-like callosity', without giving a figure. Their generic diagnosis of *Dorippe* (Holthuis & Manning 1990: 8) indicates the presence in both males and females of a "swollen, sausage-shaped, often whitish callosity, fused with posterolateral margin of carapace", but no details are given in their specific descriptions of the five species of the genus. Their generic diagnosis of *Dorippoides* (Holthuis & Manning 1990: 48) refers to a "dorsal, often whitish, sausage-like callosity, fused to posterolateral margin of carapace" on the P3 coxa of females, but no details are given in the specific descriptions of *D. facchino* and *D. nudipes*. Such a callosity has escaped the attention of other carcinologists, probably because it is hidden by the dorsally carried P4 and P5. Serène (1982) and Holthuis & Manning (1990) are credited with the detection of these enigmatic structure, whose function could, according to the first author, be related to the type of camouflage and of unknown function for the other two.

The callosities are actually found only in two genera, *Dorippe* and *Dorippoides*, at the base of P3, and are absent in other dorippids. In fact, different modalities can be recognised and distinguished. A simple pattern is found in both species of *Dorippoides*, being present in both sexes of *Dorippoides facchino*. The narrow shape of this pattern bears little resemblance to what Holthuis & Manning (1990) have termed a 'sausage-shaped callosity'. Three more complex patterns are found in species of *Dorippe* (Figs 9C; 33C-H), the most elaborate being that of *D. tenuipes* (Figs 9D; 33G, H). Our examination reveals that these callosities represent a unique novelty of the Dorippidae, more diverse and complex than expected, and which would require per se study and histological analysis. Only a brief description of the external morphology will be given here, as follows.

Dorippoidinae n. subfam.

The pattern is very simple, occurring as a small, thin structure in both sexes of *Dorippoides facchino* and, apparently, only in females of *D. nudipes.* Although this so-called callosity is hardly indurated and scarcely deserves the name of callosity, it can nevertheless be assimilated to a callosity, which can only be demonstrated by dissection. In *D. facchino* (Fig. 33A), the large coxa of P3 is articulated to the partially granular pleurite 6, which is widely exposed across the width of the coxa; between the two, there is a thick, movable membrane that is lined on the pleural side by a narrow calcified portion. This structure, reduced to a thin calcified band, which seems to be merely a continuation of the softer and more flexible articular membrane, is however different from the articular membrane of the other legs and may termed a callosity, even if it is not really hard, indurated. The 'callosity' is already present at the size of 13 mm carapace length. On P2 (at this level, pleurite 5 is only partially exposed as a small but salient posterior sclerite), the coxa joins the thoracic sternum through a narrow membrane, and it is impossible to discern a thin calcified portion present on the thoracic side. At P4 and P5, there is only a wide, very soft membrane.

In *Dorippoides nudipes*, a callosity seems absent in males (Fig. 33B), whereas in females, on the thoracic side, between the heavily calcified pleurite 6 and the membrane, there is a thin indurated portion.

Dorippinae n. stat.

In the genus *Dorippe*, P3 has a callosity at its base, which is apparently similar in both sexes but varies according to species. (On P2, there is no callosity, only a rather wide, whitish movable membrane). Three patterns can be recognised, as follows.

In *Dorippe frascone* (Fig. 33F), *D. glabra* (Fig. 15E, F, I), *D. sinica* (Figs 9C; 10C, D; 33D, E), and *D. trilobata* (Fig. 15A, C, J), P3 bears a callosity that appears as a prominent, high, immobile, hemicircular structure, articulated on the pleural side (i.e., on the exposed pleurite 6); this calcified part bears short setae; a whiter area of peculiar histological texture lines the inner part of the callosity facing the coxa. Located at a lower level, the piece that articulates laterally (without a membranous zone) on the exposed pleurite 6 by a very strong condyle that is difficult to identify without dissection. The callosity is similar in both sexes.

In *Dorippe quadridens* (Figs 10A; 33C), instead of being hemicircular, the callosity, covered by some setae, has the appearance of an elongated and thickened bulge (perhaps more calcified in females, a condition to be verified on more abundant material), only concave on the side of the coxa where a whiter area with a peculiar histological texture is found.

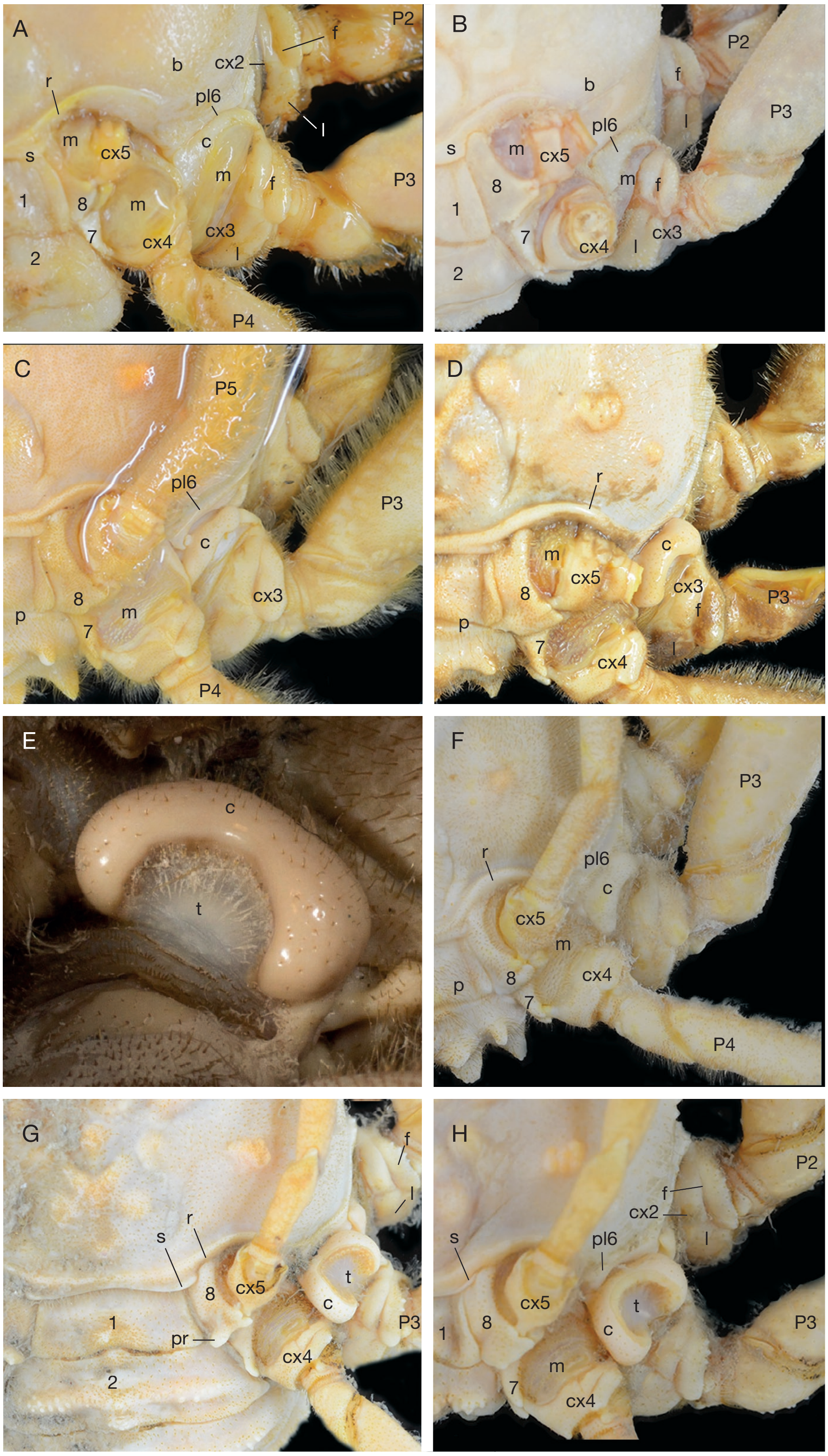

Fig. 33. — Callosities in Dorippoidinae n. subfam. (*Dorippoides*) and Dorippinae n. stat. (*Dorippe*): **A**, callosity reduced to a thin calcified band: *Dorippoides facchino* (Herbst, 1785), ♂ 25.3 × 32.0 mm, Malaysia, Johore, Pontian, ZRC 1991.6672. **B**, no apparent callosity in male *Dorippoides nudipes* Manning & Holthuis, 1986, ♂ 16.2 × 19.4 mm, Iran, ZRC 2017.1227. **C**, callosity as a thick, elongated bulge: *Dorippe quadridens* (Fabricius, 1793), ♂ 39.0 × 41.4 mm, Thailand, Pattani Province, ZRC 2003.0126. **D**-**F**, callosity as a hemicircular structure: close-up views from different angles: **D**, **E**. *Dorippe sinica* Chen, 1980. **D**, ♀ 36.2 × 39.5 mm, China, Guangdong, Nanao Island, ZRC 1999.0470; **E**, ♂ 36.6 × 38.6 mm, Japan, Kochi, Shikoku, SMF 57855. **F**, *D. frascone* (Herbst, 1785), ♂ 29.7 × 31.0 mm, Philippines, Exp. Panglao 2004, ZRC 2008.0076. **G**, **H**, callosity as an arched double cup: *D. tenuipes* Chen, 1980, South China Sea, ZRC 1999.0009: **G**, ovigerous ♀ 17.3 × 19.6 mm; **H**, ♂ 13.2 × 14.2 mm. Abbreviations: **b**, branchiostegite; **c**, callosity; **cx2**-**cx5**, P2-P5 coxae; **f**, sulcated part of coxa; **l**, one-piece lateroventral part of coxa; **m**, membrane; **p**, pleon; **pr**, process of retention of female pleonal somite 2; **pl6**, exposed pleurite 6; **P2**-**P5**, pereiopods 2-5; **r**, rim of carapace posterior margin; **s**, strip along posterior rim; **1**, **2**, pleonal somites 1, 2; **t**, bottom of callosity with special texture; **7**, **8**, thoracic sternites 7, 8.

In *Dorippe tenuipes* (Figs 9D; 33G, H), a more complex structure is present on P3 than in the above species. Between the coxa and the exposed pleurite 6 is interposed, without an intermediate membrane, an arched double cup, covered with short, stiff setae, showing a hollow laterointernal part, showing a characteristic soft histological texture and a white bottom. In contrast, the P2 coxa is separated from the carapace rim only by a completely soft movable membrane. The double arched cup of P3 corresponds to the protruding structure of other *Dorippe* species, but, in addition to being more developed, it has a very different shape; furthermore, the soft-textured area is not restricted to the inner part but extends along the entire length of the lateral parts of the cup. The nature of its tissues, with apparent cells, needs to be investigated histologically. Note that a small callosity, externally similar to that of larger individuals, is already present in a small specimen of 7.6 mm carapace length, from the Philippines, MUSORSTOM Exp., stn 73, Chen det. MNHN-IU-2018-5202 (MNHN-B18927). The callosity of *D. tenuipes* best fits the structure that Holthuis & Manning (1990) called 'sausage-like callosity', although in our opinion the resemblance to a sausage shape does not actually apply to any of them. We have not been able to find out what the callosities of *D. irrorata* are like.

Interestingly, the narrow and weakly calcified structure of *Dorippoides facchino* and in females of *D. nudipes* (Dorippoidinae n. subfam.), which is initially only a small calcified band of the articular membrane of the P3 coxa, appears to have thickened and hardened into a prominent bulge (*Dorippe quadridens*) or into a hemicircular structure (other *Dorippe* species) located at the same site. A greater complexity is achieved in only one species of the genus, *D. tenuipes*, a species whose behaviour and in particular the type of camouflage are unfortunately not known.

The fact that these structures, whose homology does not seem to be in doubt, offer four distinct modalities in only two genera of Dorippidae and is absent in the other genera, is a new example of biodiversity within the family. The function of these callosities remains unknown, but, as the most developed are found in species of *Dorippe* that carry toxic animals (such as the toxic 'fire urchin' *Asthenosoma varium* and jellyfish) for camouflage, a plausible hypothesis would be that it is a gland that can secrete mucus for protection? In the species of *Dorippoides*, which carry sea anemones capable of producing neurotoxins, the callosities are less developed. Other dorippid species, which, as far as we know, camouflage themselves with more harmless animals, do not possess such callosities. However, in contradiction with this hypothesis, there is the case of *Dorippoides nudipes* where, it seems, a callosity would be only present in the females.

The female reproductive system: its evolution and unique disposition in Dorippidae

A recently discovered novel organisation in the two families of Dorippoidea, Dorippidae and Ethusidae (Hayer *et al.* 2016a, b; Vehof *et al.* 2017; 2018a, b; Vehof 2020), using both histology and magnetic resonance imaging (MRI) and microcomputed tomography (μCT) analyses, presents a new challenge by revealing that the female reproductive system of Dorippidae not only shows an amazing diversity across genera but also deviates from known types in the Brachyura. It is surprising to find such a variety of fundamentally different sperm storage organs in a family as small as the Dorippidae. Similar studies in other eubrachyuran groups show that their reproductive systems, whose variability was probably underestimated, reveal characters that may be of considerable importance for understanding the phylogeny and evolution of Brachyura, hence the need to investigate the female sperm storage organs in all Eubrachyura. We can now state that in no other eubrachyuran family does the female reproductive system show such a strikingly diverse structural morphology as in the Dorippidae, nor a range of fertilisation from external to internal fertilisation.

As a preliminary, some general data will be reminded. The morphology of females related to sperm transfer and storage, as well as the male copulatory system, all leading to reproductive strategies and ultimately to fertilisation, show a high degree of modification in decapods. The histology of reproductive systems in a phylogenetic context discloses how internal organs, external structures, mating behaviour and fertilisation mechanisms have co-evolved. We agree with Bauer (1986) that the reproductive organs have considerable phylogenetic value, because the type of sperm storage reflects a range of related fundamental and conservative reproductive traits, such as female moulting patterns, ovarian growth, egg laying and embryo hatching. The anatomical diversity of seminal receptacles has a profound impact on the evolution of mating strategies that are adopted to minimise or avoid the risk of sperm competition. According to Bauer (1986, 1994), the degree of complexity of the female sperm storage organ is a measure of phylogenetic distance from the ancestral state, with the lowest level of complexity demonstrated by a spermatophoric mass that simply adheres to the chitinous surface around the female gonopore and then to the ventral cephalothorax, thus with little modification in this body region. The evolution of the genital area is enhanced by the invagination of sternite 6 to form an open, then closed, receptacle, offering better protection to the spermatophores.

The study of the reproductive system is particularly appropriate for Brachyura since the gonopores are not uniformly situated in the group, with a radical change in their location (i.e., trajectories of the genital ducts and their connections) occurring in both females and males. The shift from an appendicular position (as in other decapods) to a more central, sternal body position has been considered an evolutionary process (Guinot 1977, 1978, 1979a; Guinot *et al.* 2013). The following conditions are observed (Figs 34A *left*; 36D): only perforation of the coxae, and both female and male gonopores being appendicular (podotreme crabs); female gonopores being the first to abandon their appendicular location on P3 coxae and (presumably) substituted by vulvae on thoracic sternite 6 (Eubrachyura), with the oviduct connection being performed with a sternal chamber rather than with the P3 gonopore (Heterotremata); male gonopores abandoning their appendicular location on P5 coxa and substituted by their

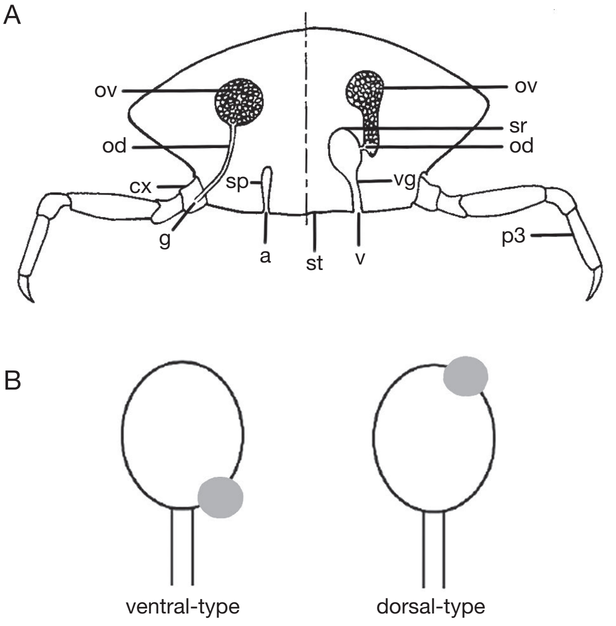

FIG. 34. — **A**, schematic cross-section of thoracic region at level of P3 to show in one diagram the two distinctive arrangements of female organs in Brachyura. *On left*, a typical podotreme, with coxal openings; *on right*, a typical eubrachyuran, with sternal openings or vulvae; **B**, schematic representation of the two types of brachyuran seminal receptacles, either of ventral type (*left*), or of dorsal type (*right*), and their connection to the oviduct (see Diesel 1991). Abbreviations: **a**, spermathecal aperture; **cx**, coxa; **g**, coxal female gonopore; **od**, oviduct; **ov**, ovary; **sp**, spermatheca; **sr**, seminal receptacle; **st**, thoracic sternum; **v**, vulva; **vg**, vagina. Modified from Hartnoll (1968: fig. 1), Guinot (1978: fig. 1; 1979a: fig. 38) and Vehof (2020: fig. 19).

emergence on sternite 8 (Thoracotremata). The heterotreme-thoracotreme distinction results from two different trajectories of the ejaculatory duct, either through the P5 coxa (Heterotremata) or through the thoracic sternum (Thoracotremata), with in both cases a perforation of the thoracic sternum by the oviduct via the vagina and vulva (Guinot *et al.* 2013: fig. 1B-E). It was quite logical to attribute these changes to the intercalation of a large sternal part between the legs, more properly to a posterior expansion of the thoracic sternum. Is this interpretation correct, was it a carcinisation event? McLay & López Greco (2011) followed Guinot's hypothesis that the shift of the female and male gonopores towards the thoracic sternum was a consequence of carcinisation, with the main changes in body shape during carcinisation being a progressive widening and shortening of the cephalothorax. With coxal female gonopores and a narrow thoracic sternum in both sexes, males can use the gonopods to deposit spermatophores around each gonopore and carry out fertilisation. But when the cephalothorax shortens and widens, the space between the gonopods has not the potential to widen, and all the more so as the male sternopleonal cavity remains narrow: the gonopods cannot therefore reach the female gonopores, and spermatophores can no longer be deposited (Guinot & Quenette 2005). Males are adapted to transfer spermatophores to a central position on the thoracic sternum, so that no sudden change is required on their part. Female sternal gonopores were favoured, and carcinisation made the female pleon wider and shorter, with the advantage of developing a large brood chamber where external fertilisation can take place; the male pleon (enclosing the gonopods) became shorter and folded, but remained narrow like in the ancestor. Many questions remain unanswered, including the perennial problem of the origin of crab gonopores, the ontogeny of the female thoracic sternum, the reproductive apparatus and the like, which, in short, concerns the polarity of characters during evolution, the polarity of the carcinisation process.

Controversies have arisen regarding the monophyly of the three brachyuran subsections in their current compositions and their interrelationships. In opposition to a fairly broad consensus since these taxa, although debated, are widely (presumably reluctantly) used, many studies have argued that Podotremata and Heterotremata were paraphyletic and Thoracotremata nested within Heterotremata (e.g. Sternberg *et al.* 1999; Sternberg & Cumberlidge 2001a, b; Ahyong *et al.* 2007; Ji *et al.* 2014; Shi *et al.* 2015, 2016, Shih *et al.* 2015, 2016a, b; Chen *et al.* 2018; Davis *et al.* 2022). Molecular analyses by Yuhui *et al.* (2017: 50) showed a strongly or weakly supported monophyletic Podotremata based on two different datasets and, in both cases, Podotremata as a sister group to the eubrachyurans with a relatively high nodal support. The first expanded mitochondrial phylogenetic tree of Thoracotremata including four superfamilies (Grapsoidea, Ocypodoidea, Pinnotheroidea, and Cryptochiroidea) by Sun *et al.* (2022: fig. 5) provided some new information on phylogenetic relationships, with Pinnotheroidea forming a basal and monophyletic group. According to Sun *et al.* (2022: 1), the symbiotic groups, the cryptochiroids and pinnotheroids, display variable mitochondrial gene orders, providing evidence for possible correlations of rearranged mitochondrial gene orders to the adaptations to specialised lifestyles. Recently, the interfamilial relationships of Thoracotremata, using 10 molecular markers and exemplars from all nominal families have been resolved to prepare a new taxonomy consistent with phylogenetic relationships (Tsang *et al.* 2022). In the genetic study of thoracotremes by Kobayashi *et al.* (2023: 7), the phylogenetic placements of Pinnotheridae and Cryptochiridae were not resolved in the ML phylogenies, whereas Pinnotheridae + Ocypodidae and Cryptochiridae + Grapsidae MacLeay, 1838 were highly supported in the Bayesian phylogenies.

In any case, there are three major groups of crabs: podotremes, with spermathecae, with P3 and P5 bearing the female and male gonopores respectively, and with, for most of them, a carrying behaviour implying P4 and P5; heterotremes, with vulvae, with only P5 bearing the male gonopores; and thoracotremes, with vulvae and where the legs are freed from any reproductive role. It is beyond the realm of possibility (especially for a taxonomist who has worked for over 50 years on all extant crabs and more recently has become fully involved in the palaeontological data) to comment here on 'decarcinized crabs' defined as the result of evolution away from the carcinised body plan, the secondary loss of the crab-like habitus (Scholtz 2014: 97, 101; Keiler *et al.* 2017; Luque *et al.* 2019: figs 1, 2A-D; Wolfe *et al.* 2021), some statements of these authors being inconsistent with our view.

Before discussing the specific case of fertilisation in the Dorippidae, it is worth recalling the prevailing concepts on the evolution of sperm storage in Brachyura. In decapods, Bauer (1986: 314; 1994: 716) defined the 'thelycum' as "any external modification of the female posterior thoracic sternites or coxae related to sperm transfer and storage", whereas the 'spermatheca' was defined as "any exoskeletan invagination for sperm storage", both of which are not fertilisation sites. The female genital duct opens into the gonopore, and the seminal receptacle opens separately. A higher level of complexity could be demonstrated by the development of protuberances, depressions, evaginations or invaginations of the female exoskeleton, the most highly modified set of genitalia culminating in Brachyura (Bauer 1986). Before the 1990s, the same term 'spermatheca' was used for all brachyurans (Hartnoll 1968, 1969). After the separation of the podotreme crabs from the rest of the Brachyura (Guinot 1977, 1978), the distinction between the two reproductive systems within the Brachyura began to be considered. Diesel (1991) distinguished the 'thelycum' of Podotremata from the 'seminal receptacle' of Eubrachyura. Tavares & Secretan (1993) suggested restricting the application of the term 'spermatheca' to the sperm storage structure derived from phragmata 7/8, i.e., only for the intersegmental cuticular invagination found in podotreme crabs, and using the term 'seminal receptacle' for the sperm-storage structure associated with the ovary found in Eubrachyura. Bauer (1994) argued that the term 'spermatheca' (considered synonymous with 'seminal receptacle') should be retained in its general sense, i.e., any enclosed space related to extended storage of sperm; accordingly, the same term could be considered appropriate to describe the function of the organs holding sperm, all the more so as 'spermatheca' is a general term used in many animal groups without any further consideration. However, since the two structures encountered in Brachyura involve two different parts of the thoracic sternum and are therefore not homologous, and in order to avoid confusion, the definition that suits the two distinctive conditions has begun to take precedence. Most recent authors (except some, e.g. as Sal Moyano *et al.* 2010; Lautenschlager *et al.* 2010; Rodgers *et al.* 2011; Jensen & Bentzen 2012) currently distinguish between the two brachyuran oganisations by using 'seminal receptacle' for Eubrachyura, as opposed to the spermatheca of podotremes. Whether the spermathecae of all podotreme lineages are homologous is another issue.

Thus, it was the discovery of two fundamentally different types of female reproductive systems and mechanisms of sperm storage and fertilisation in Brachyura that revealed two independent solutions for sperm storage and insemination. In the podotreme condition (Figs 34A *left*; 36A), the female genital apparatus consists of two completely independent structures: a gonad comprising the ovary and the oviduct opening through a gonopore on P3 coxa; and a separate spermatheca, i.e., the storage chamber, derived from a split between the plates of the intersegmental phragma 7/8, without any connection to the gonad and opening through an independent aperture at the end of sternal suture 7/8, often far from the coxal gonopore (Hartnoll 1968: fig. 1 *left*; 1975; Guinot 1978: fig. 1 *left*; Tavares & Secretan 1993: fig. 1E-G; Bauer 1986: table 1; 1994; Guinot & Tavares 2001; Guinot & Quenette 2005; McLay & López Greco 2011; Guinot *et al.* 2013: fig. 1; López Greco 2013: fig. 15.4A; McLay & Becker 2015: fig. 71-4.2 *left*; Davie *et al.* 2015a: fig. 71-2.19A, 71-2.20A; Becker & Scholtz 2017; Becker & Bauer 2020). As the sperm storage chamber is separate from the oviduct and coxal gonopore, the gametes meet outside the female's body, fertilisation is external, with egg release from the gonopores coordinated with sperm expulsion from the spermatheca. The podotreme reproductive system shows a complete spatial division into two structures: the storage site chamber (the spermatheca), entirely cuticular, lined with chitin, of ectodermal origin; and the genital ducts of mesodermal origin. The duration of sperm storage is short, since at moult, during the process of exuviation (ecdysis), the spermatheca is shed like the old exoskeleton, and all stored sperm is lost (Vernet-Cornubert 1957; Hartnoll 1975). Until now, the podotreme reproductive system has been described only in terms of gross morphology and macroscopic structures, and the mechanism of fertilisation is poorly known. But new data have been recently published on the reproductive anatomy of podotremes and on the spermatozoal ultrastructure of Dromiidae leading to a molecular analysis (Garcia Bento *et al.* 2019a, b).

The eubrachyuran condition (Figs 34A *right*, D) has hitherto been considered to follow the same common arrangement, with internal fertilisation (i.e., outside the vulva) being an apomorphy for the group. The pouch-like seminal receptacle, which corresponds to an enlargment of the genital tract, is part of the gonad, is directly connected to the ovary via the oviduct and opens via the vagina (i.e., a cuticle-lined duct) into the vulva (i.e., a cuticular invagination of the thoracic sternite 6). The first contact of oocytes and sperm occurs internally, this internal fertilisation being in complete contrast to the external fertilisation of podotreme crabs (Gordon 1950; Hartnoll 1968, 1979; Guinot 1977, 1978: fig. 1; Bauer 1986; Diesel 1991; Tavares & Secretan 1993; Guinot & Tavares 2001; Tavares & Franco 2004; Guinot & Quenette 2005; Sal Moyano *et al.* 2010; McLay & López Greco 2011; Becker *et al.* 2011: fig. 1; Guinot *et al.* 2013; López Greco 2013; Zara *et al.* 2014; Hayer *et al.* 2015; McLay & Becker 2015: fig. 71-4.2 *right*; Antunes *et al.* 2016; Becker & Scholtz 2017; Souza *et al.* 2017; Garcia Bento *et al.* 2022). Typically, the seminal receptacle, which serves as a site of reception and storage, spermatophore dehiscence and sperm maintenance, consists of an ectodermal and a mesodermal part (see López Greco 2013: fig. 15.5B for more details). Only the cuticular portion is shed at moult, and the sperm material stored in glandular epithelia can be retained for extended periods beyond moult for fertilisation of consecutive broods without copulation.

The evolution from podotreme to eubrachyuran condition is considered to be the result of several changes: loss of the coxal gonopore on the pereiopod coxa of sternite 6 (P3); invagination of the surface of sternite 6 (vulva); loss of the spermatheca; and formation of an internalised chamber, the seminal receptacle, which is partly ectodermal, partly mesodermal. The seminal receptacle is incorporated into the genital structure, sometimes apparently without morphological division, and only the different nature of the precise portions is indicative of their functions, either as a sperm storage area or as a chamber for insemination or fertilisation. The pathway by which the podotreme spermatheca might evolve into eubrachyuran vulvae was discussed by Hartnoll (1979: 82, fig. 5) in searching how the raninid spermathecal apertures on sternite 7, lying in endosternite 7/8, could 'capture the oviducts' and move to sternite 6. This hypothesis has not been supported by dissection on fossil raninoids (Van Bakel *et al.* 2012a: 160, fig. 60). Similarly, Guinot & Quenette (2005) researched by which process the podotreme spermathecae with secondary openings on sternite 7 may have come to open on sternite 6 and become eubrachyuran vulvae; they concluded (2005: 332) that "the pathways of change for the female condition are unknown, and there is no evidence for a transition between the podotreme and eubrachyuran organisation". Scholtz & McLay (2009: 4) also questioned how the sternal eubrachyuran vulvae might be derived from spermathecae found in podotreme groups. McLay & López Greco (2011) agreed with Guinot & Quenette (2005), stating that the eubrachyuran connection between the oviduct and a sternal chamber, with the consequent elaboration of seminal receptacles, has the advantage of allowing a reproductive autonomy for females through trans-moult sperm retention, a major evolutionary advance. Vehof (2020: 93) came to the same conclusion as Guinot & Quenette (2005), but referring only to McLay & López Greco (2011). The question of Becker & Scholtz (2017: 103) "Have eubrachyurans lost spermathecae and replaced them with more efficient sperm storage systems, that is, seminal receptacles?" requires an explanation of the loss of spermathecae and the origin of seminal receptacles. The underlying issue that is ultimately addressed: is the vulva a neoformation?

Of particular interest is the sperm storage condition in the Cyclodorippoidea (or Cyclodorippiformia Guinot, Tavares & Castro, 2013), which has long been grouped with the Dorippidae (Guinot 1977; Guinot *et al.* 2013) and, together with the Raninoidea, forms the Archaeobrachyura *sensu* Guinot & Tavares, 2001 as opposed to the Podotremata *sensu stricto*. Since some carcinologists suspected Cyclodorippoidea as a potential sister group to Eubrachyura, could a transition between Cyclodorippoidea and Dorippidae be possible? Guinot & Quenette (2005: 309, fig. 23) showed that the arrangement in both Cyclodorippidae and Cymonomidae is typically podotreme, with paired spermathecae formed by the forwardly extended and anteriorly modified sutures 7/8 and with gonopores on the P3 coxae. The histology of spermatheca studied by Vehof (2020) in several species shows no relationship to the seminal receptacles of Dorippidae and other Eubrachyura.

Regarding the P3 coxal gonopore, one observation should be noted. According to Becker & Scholtz (2017: 94, figs 9A-D, 10A-C), the gonopore of the homolids *Paromola cuvieri* (Risso, 1816) and *Homologenus malayensis* Ihle, 1912 is closed by a mobile muscular operculum so that the opening is actually narrower. A similar but smaller closing mechanism of the gonopore is found in two cyclodorippoids: the bulge in the cuticular protrusion that prevents direct access to the oviduct is retractable by means of muscular attachments (Vehof 2020: figs 15DF, 16A-C). This is reminiscent of the integument, i.e., the operculum, that blocks the lumen of the vagina and more or less occludes the entrance of the vulva in many eubrachyurans, notably in dorippids (but operculum absent in ethusids). There are several types of opercula in Brachyura, present or not in Heterotremata, seemingly constant in Thoracotremata (Souza *et al.* 2017) but diverse: soft, calcified, hard, freely movable, fixed, immovable, temporarily decalcified or pushed by a terminal hook of the G1 (Guinot *et al.* 2013: 26, 39, 41, 65, figs 6, 36).

The situation for the Dorippidae

It has recently been discovered that species of the family Dorippidae show an amazing variety of female reproductive systems that differ from those of other eubrachyurans and even deviate from the known types in Brachyura. This is not really unexpected given the diversity already encountered in other morphological characters, in particular sexual ones, in particular sexual ones. It is further evidence of the diversity of Dorippidae, albeit on a completely different scale (internal anatomy) than the morphological features used so far. Due to the relatively high number of species of Dorippidae analysed histologically to date, this is an additional feature supporting the subfamilies recognised here.

Five dorippid species studied (*Dorippe quadridens*, *D. sinica*, *Dorippoides facchino*, *Medorippe lanata*, *Paradorippe granulata*) have prominent cuticular structures flanking the oviduct orifice. Not identified by Hayer *et al.* (2016a) and represented only in *D. sinica*, they are referred to as 'valve-like structures' or simply 'valves' by Vehof *et al.* (2017: figs 2, 3, 5, 6A-G) and Vehof (2020: figs 7D, F, G, table 2). These valves seem to be restricted to dorippids. However, instead of valves, the oviduct entrance is separated from the seminal receptacle by several cuticle folds in *Heikeopsis*, *Neodorippe* and *Nobilum* (Vehof 2020: figs 6A, C, D, 17; table 2); the condition is not described in *Philippidorippe philippinensis*.

In podotremes, the openings of the oviducts, i.e., the gonopores, open at the P3 coxae (Figs 34A *left*; 36A), whereas typically in eubrachyurans the oviducts, which are internally connected to the sperm storage organs, open in the sperm storage organ itself. But the Dorippidae is an exception, as the oviducts are not directly connected to the sperm storage organs but rather to the vaginae or even vulvae (see Fig. 36B) (at least, in the Paradorippinae n. subfam., where a vagina is missing).

According to Hayer *et al.* (2016a: 455-463, figs 1-6), in *Dorippe sinica* the seminal receptacle is an invagination of thoracic sternite 6, a separate structure not connected to the oviduct, and there is, typically as in all Eubrachyura, a vulva (Fig. 35A). But this vulva differs by an extension located next to the vagina, which is the continuation of the oviduct; the vulvar extension and the vagina open simultaneously in the vulva site; lined by cuticle and therefore of ectodermal origin, this vulvar extension is considered an invagination of the vulva. The contemporary histological study by Vehof

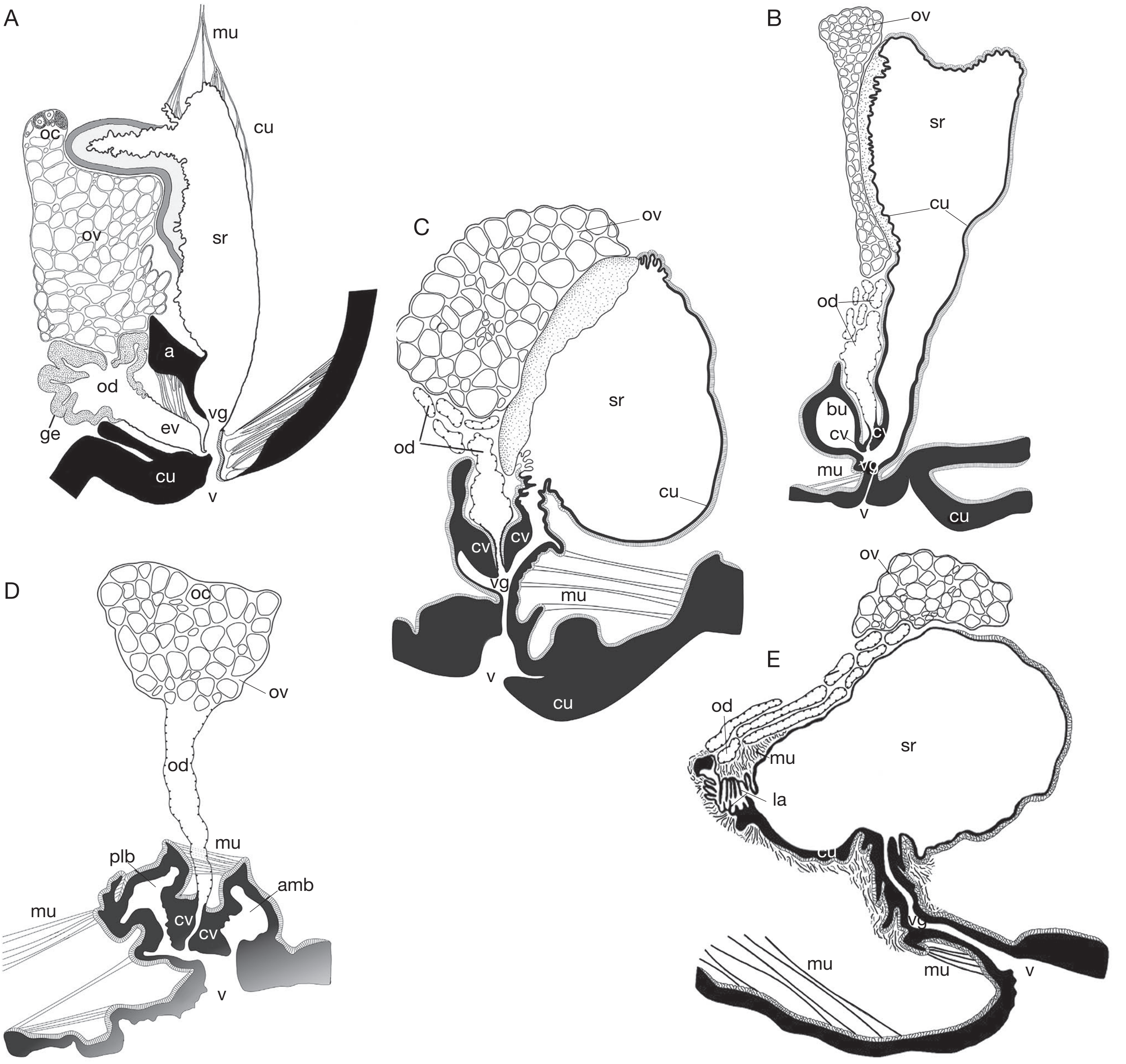

Fig. 35. — Schematic illustrations of female reproductive systems in representatives of four dorippid subfamilies: **A**, **B**, Dorippinae n. stat.: **A**, *Dorippe sinica* Chen, 1980, as interpreted by Hayer *et al.* (2016a: fig. 2); **B**, *Dorippe quadridens* (Fabricius, 1793) and *D. sinica*, as interpreted by Vehof *et al.* (2017: fig. 2A); **C**, Medorippinae n. subfam.: *Medorippe lanata* (Linnaeus, 1767), as interpreted by Vehof *et al.* (2017: fig. 2B); **D**, Paradorippinae n. subfam.: *Paradorippe granulata* (De Haan, 1841), as interpreted by Vehof *et al.* (2018b: fig. 3). **E**, Heikeopsinae n. subfam.: *Heikeopsis japonica* (von Siebold, 1824), with the same pattern shared by *Neodorippe callida* (Fabricius, 1798) and *Nobilum histrio* (Nobili, 1903), as interpreted by Vehof (2020: fig. 4). Abbreviations: **a**, apodeme; **amb**, anteromedian bursa; **bu**, bursa; **cu**, cuticle; **cv**, cuticular valves; **bu**, bursa; **ev**, extension of vulva; **ge**, glandular epithelium; **mu**, musculature; **oc**, oocyte; **od**, oviduct; **ov**, ovary; **plb**, posterolateral bursa; **sr**, seminal receptacle; **vg**, vagina; **v**, vulva.

et al. (2017: figs 1E, 2A, 6, 7) of *Dorippe quadridens* and *D. sinica* (Figs 35A, B; 37) showed full conformity of the reproductive systems in both species, making this a generic character and, even more so, a subfamily criterion of the Dorippinae n. stat.. Hayer *et al.* (2016a: fig. 6) suggested that in *Dorippe sinica* the contact of the oviduct with the thoracic sternum occurred independently of the invagination at the initial sperm storage site, with the lack of connection between the ovary and the seminal receptacle enabling only external fertilisation at the vulva opening. However, this organisation of the ventral part of the female reproductive was interpreted differently by Vehof *et al.* (2017: 281) who argued that Hayer *et al.* (2016a: fig. 2) defined the entire ventral part of the dorippid vagina as a vulva and who postulated a clear separation of the female reproductive system into the seminal receptacle and vagina on the one hand, and the oviduct and ovary on the other. It is true that the vulva is only the outermost structure of the vagina, and that the vagina is situated between the vulva and the oviduct orifice. According to Vehof *et al.* (2017, 2018b; Vehof 2020: figs 17, 20, 22), this division into two distinct units was apparently overestimated by Hayer *et al.* (2016a), and there are actually two twin bursae near the oviduct orifice that should be considered accessory sperm storage structures; the vaginae of *D. quadridens* and *D. sinica* are so short that the first contact of spermatozoa and oocytes would occur somewhat deeper inside the body. This raises the question of the initiation of fertilisation, which is in fact 'neither internal nor external' in these species.

In summary, several characters substantially distinguish the reproductive system of the Dorippinae n. stat.: presence of two separate structures, both opening directly and independently into the vulva site; direct connection of the endodermal oviduct to the vulva via a highly specialised concave vagina; a seminal receptacle of ventral type (Fig. 34B), of ectodermal origin, completely cuticle-lined, and with additional sperm storage structures, the bursae, at the transition between the seminal receptacle and the vagina; ovary and oviduct not connected to the seminal receptacle, thus representing an independent part of the reproductive system; connection between oviduct and ovary via a single distinct opening to the vulvar extension.

The female reproductive system of the Dorippoidinae n. subfam., based on *Dorippoides facchino* studied by Vehof (2020: 55, figs 7E-G, 17, 20, 22), consists of paired ovaries and twin sperm storage organs (bursae) that open through the vaginae and vulvae onto the thoracic sternite 6. The sperm is stored in the bursae, which are completely cuticle-lined and very unequal in size and shape; the oviduct presumably opens directly into the vulva, the vagina being very short and the entrance to the bursae being close to the oviduct orifice and the vulvar aperture (Fig. 37). The initiation of fertilisation is as in the Dorippinae n. stat..

The quite distinct female reproductive system of *Medorippe lanata* (Figs 35C; 36B; 37), thoroughly investigated by Vehof *et al.* (2017: figs 1A, 2B, 3-5) and Vehof (2020: 72, 73, figs 17, 20, 22), supports the separate status of Medorippinae n. subfam. A single sperm storage organ occurs on each side of the body (as in Heikeopsinae n. subfam. and other Eubrachyura). The seminal receptacle, partly not cuticle-lined but glandular-lined, is secretory. The relatively small glandular area possesses a somewhat different tissue composition: multilayered, this secretory tissue slightly differs from those of other heterotremes. Medorippinae n. subfam. is the only dorippid subfamily with a glandular-lined sperm storage organ. Fertilisation is internal. All this implies that the medorippine system would have evolved independently of those of other eubrachyuran groups; in addition, the accessory sperm storage structure, the bursa, is missing.

Species of the three genera *Heikeopsis*, *Neodorippe* and *Nobilum*, which form the subfamily Heikeopsinae n. subfam., have a similar female reproductive system according to Vehof (2020: figs 4-6, 17, 20, 22, table 2), who, based on this character, recognised a '*Heikeopsis*-clade'. There are two ovaries and two seminal receptacles that open through the vagina and vulva onto thoracic sternite 6 (Figs 35E; 37). These two sperm storage chambers (e.g. a single sperm storage organ on each side of the body, as in Medorippinae n. subfam.) and their direct connection to the oviducts (instead of cuticular valves, cuticle lamellae shield the oviduct orifice from the lumen of the seminal receptacle, a character considered an apomorphy of the group) resemble the condition in other Eubrachyura, as does internal fertilisation.

Another kind of sperm storage organ, an entirely new type, studied in *Paradorippe granulata* (from China Shandong, Tiaozhou Bay) by Vehof *et al.* (2018a: 68, 2018b: 82, figs 1-5; Vehof 2020: 78, 86, figs 17, 20, 22), characterises Paradorippinae n. subfam. (Figs 35D; 37) (see *Preliminary note*, p. 279). Significantly different from those of all other eubrachyurans studied to date, it exhibits the following characters: absence of a seminal receptacle and vagina (a truly unique case); sperm stored in four cuticle-lined bursae ('twin bursae'), two on each side of the paired oviducts (twin sperm storage systems, equal in size); bulbous male gonopod with several terminal processes adapted to transfer sperm into the twin female bursae. *Paradorippe granulata*, which deviates from all other dorippids, is the first known eubrachyuran crab lacking a seminal receptacle and vagina, the presence of a seminal receptacle having been considered to date a synapomorphy of Eubrachyura. Since the oviducts and bursae have no internal connection and open into the vulva through separate pores, the first contact of spermatozoa and oocytes would only take place when the gametes pass into the vulva, i.e., would occur outside, in the vulva opening. Thus, already initiated in Dorippinae n. stat. (as postulated by Hayer *et al.* 2016a in *Dorippe sinica*), a totally external fertilisation would take place in Paradorippinae n. subfam., challenging the commonly held concept of internal fertilisation in eubrachyurans, a mode so far considered an apomorphy of the Eubrachyura (often referred to as 'true crabs') as opposed to podotremes whose fertilisation is external. Given the morphology and orientation of the bursa and seminal receptacle in *Dorippe* on the one hand, and the twin bursae in *Paradorippe granulata* on the other, it is questionable whether the seminal receptacle of *Dorippe* is homologous to one of the twin bursae of *P. granulata*, implying that the condition in *P. granulata* would either be the result of the reduction of a well-developed seminal receptacle and bursa or the plesiomorphic character state of the dorippid reproductive system (Vehof *et al.* 2018b: 89).

In the Philippidorippinae n. subfam., studied by Vehof (2020: 51, 57, 70, figs 8, 17, 20, 22, table 2) based on *Philippidorippe philippinensis* (poorly preserved, so histological results are fragmentary), the female reproductive system consists of paired ovaries and large, fully cuticle-lined and sac-like twin bursae of equal size (Fig. 37).

The Dorippidae is unique in the Eubrachyura in its great diversity of sperm storage organs and its various fertilisation sites. According to Vehof (2020: 70, 74), identifying patterns of sperm storage organs in the Dorippidae is difficult because all characters differ fundamentally within the family, with each species “marching to a different drummer”, so that “a continuous spectrum from external to internal fertilisation is developed”.

Are the podotreme spermatheca (Fig. 36A) and the dorippid seminal receptacle (Fig. 36B) homologous or convergent? Is the separate ectodermal sperm-storage chamber of some dorippids a spermatheca, as in podotreme crabs? It is in fact, as in podotremes, an independent cuticular structure, outside the rest of the reproductive system (which leads to external fertilisation); but, unlike podotremes where it derives from a split between the plates of the intersegmental phragmata 7/8, in dorippids there is, instead, a cuticular invagination of sternite 6, a vulva. On the other hand, it does not conform to the sperm storage organ of typical Eubrachyura (Figs 36D; 37) since it is not directly connected to the oviduct, thus is not integrated into the gonad; furthermore, the fertilisation pattern is different. According to Garcia Bento *et al.* (2019b), the spermatheca of dromiids and the reminiscent seminal receptacle of dorippids seem to be convergent: it is quite obvious that even a homology cannot be established since the organs, their positions on the body and connections are different.

To the questions that arise, Vehof *et al.* (2017: 286; 2018b: 89) answered the following. The occurrence of concave vaginae and ventrally located oviduct orifices in Dorippidae and other representatives of early diverging heterotreme lineages, such as Majoidea (González-Pisani *et al.* 2011), supports the possibility that a ventrally located oviduct orifice and a concave vagina may in fact be plesiomorphic characters. Given the complete cuticle lining of the seminal receptacle in dorippids, if complete cuticularisation of the seminal receptacle is ancestral to eubrachyurans including Dorippidae, the situation in *Medorippe lanata* (with a relatively small glandular area) and in other eubrachyurans (with a non-cuticle glandular region) must be the product of convergent evolution, under the likely assumption that Dorippidae is monophyletic. [In our opinion, there is no doubt that Dorippidae is monophyletic]. Are the seminal receptacles associated with internally initiated fertilisation really apomorphies of Eubrachyura or may they have developed later or even evolved independently several times within that group? We will not attempt to make interpretations of the scenarios and are reticent to conjecture how the female reproductive system of the dorippids and that of other eubrachyurans may have evolved. The simplest observation is that some dorippids exhibit ancestral sperm storage, with a plesiomophic characer state of their female reproductive system, and the only evidence is that arrangements among the Dorippidae show several character states. All this corroborates the high diversity of the Dorippidae and also its uniqueness among the Eubrachyura.

In conclusion, the diversification of the female reproductive system of the Dorippidae, which differs fundamentally from that of other Eubrachyura, is reflected in the shape of the seminal receptacle (but absent in Paradorippinae n. subfam.), the occurrence and shape of the bursae, the location of the oviduct orifice, and the fertilisation sites (Vehof 2020: 70, fig. 17). Admittedly, it has not been possible for histologists to retrieve a ground pattern for the Dorippidae nor to determine whether a twin system as in Dorippinae n. status, Dorippoidinae n. subfam., and Paradorippinae n. subfam., or a single system as in Heikeopsinae n. subfam and Medorippinae n. subfam. represents the plesiomophic state in the family.

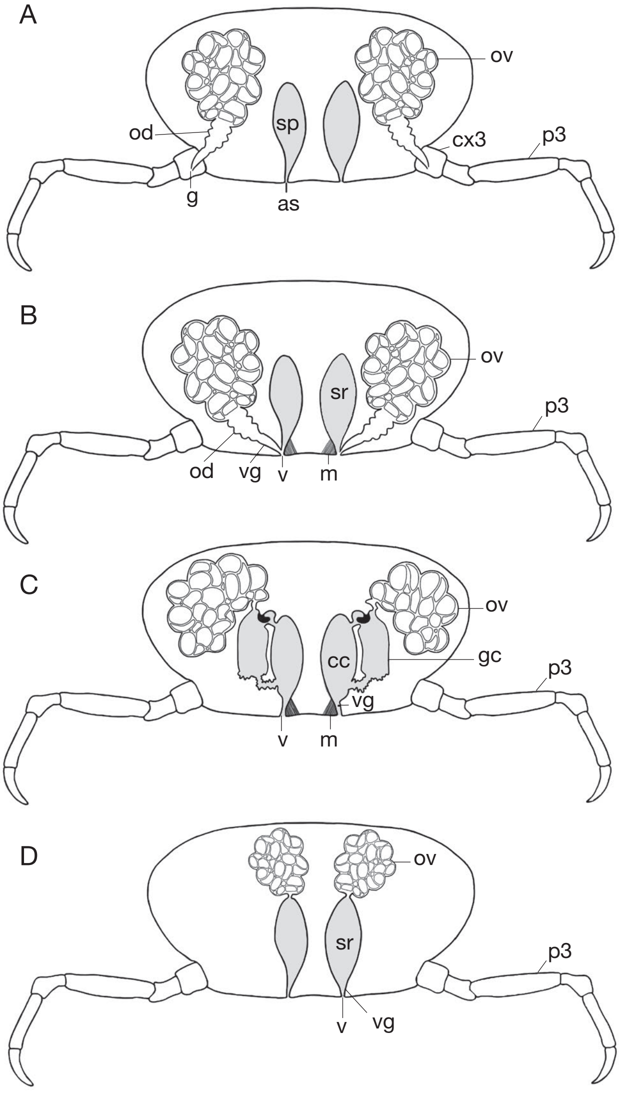

Fig. 36. — Schematic reconstructions of some female reproductive systems in Brachyura: **A**, in a podotreme crab, with spermatheca as cuticular invagination derived from a split between plates of intersegmental phragma 7/8, independent of the rest of reproductive system (gonopore on P3 coxa), and with external fertilisation; **B**, in *Dorippe sinica* (Dorippinae n. stat.), with glandular and cuticle chambers independent of seminal receptacle (not connected to ovary) and extension of vulva where fertilisation can take place (from Hayer *et al.* 2016a: fig. 8A). In Paradorippinae n. subfam. (not shown, but see Fig. 35D), without seminal receptacle, the fertilisation occurs externally in vulva opening (according to Vehof *et al.* 2018b: fig. 3; Vehof 2020); **C**, in *Ethusa mascarone* (Ethusidae), with glandular and cuticle chambers largely independent of the seminal receptacle (according to Hayer *et al.* 2016b: fig. 8); **D**, in a generalised eubrachyuran (one of several patterns), with seminal receptacle directly connected to ovary via oviduct, with vulvar opening on sternite 6 and with internal fertilisation. Abbreviations: **as**, spermathecal aperture; **cc**, cuticule chamber; **cx3**, coxa of P3 with coxal gonopore; **gc**, glandular chamber; **m**, musculature; **od**, oviduct; **ov**, ovary; **P3**, third pereiopod; **sp**, spermatheca; **sr**, seminal receptacle; **vg**, vagina; **v**, vulva.

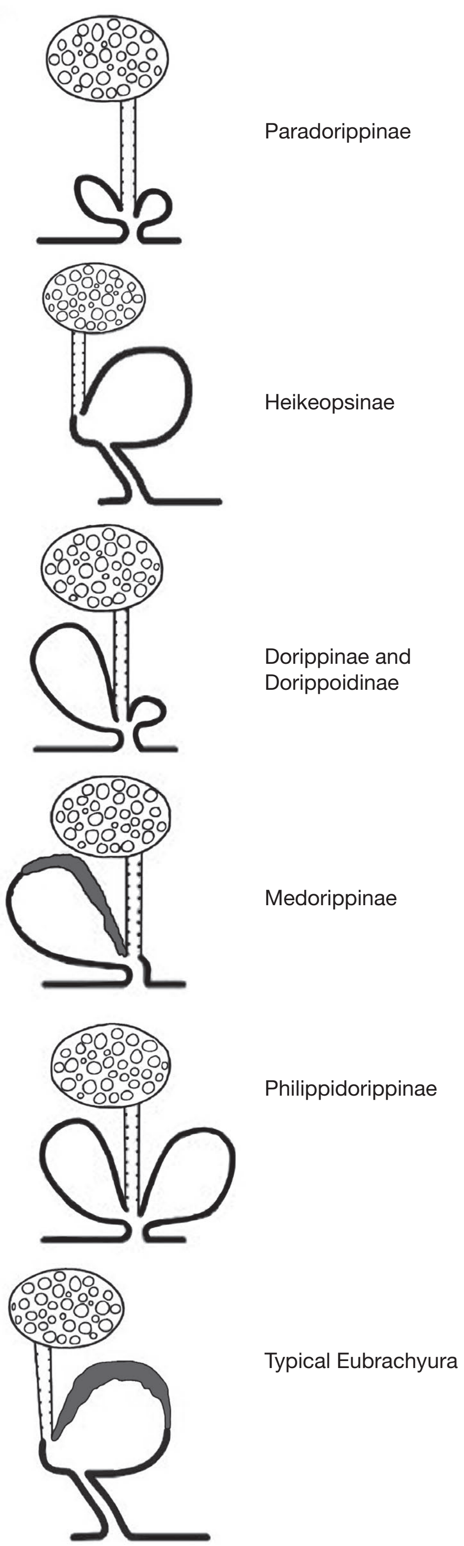

Fig. 37. — Schematic representation of character mapping of sperm storage organs in the different dorippid subfamilies recognised here (except Phyllodorippinae n. subfam. not studied) and in a typical eubrachyuran: ovary with oocytes; oviduct; cuticular bursae (**thin black line**), of equal or unequal size; seminal receptacle either bilateral twin- or bilateral single, and either completely cuticular (**thin black line**) or partially glandular (**thick black line**). The twin system occurs in Dorippinae n. stat., Dorippoidinae n. subfam., Paradorippinae n. subfam. and Philippidorippinae n. subfam.; the single system occurs in Heikeopsinae n. subfam., Medorippinae n. subfam. and in the typical Eubrachyura (most, see e.g. Ethusidae). Modified from Vehof 2020: figs 20-22).

At least, five/six distinct sperm storage chambers can be distinguished (Fig. 37):

– Dorippinae n. stat. and Dorippoidinae n. subfam.: bilateral twin sperm storage system (large, elongated main sperm storage organs accompanied by small, round bursae, unequal in size in Dorippoidinae n. subfam.); oviduct separate from sperm storage organ; fertlisation near vagina/vulva area.

– Paradorippinae n. subfam.: bilateral twin sperm storage system (equal-sized, small, thick-walled sperm storage organs); oviduct separate from sperm storage organ; external fertilisation.

– Philippidorippinae n. subfam.: like Paradorippinae n. subfam., but sperm storage organs larger and more sac-like.

– Medorippinae n. subfam.: single sperm storage organ, partly not cuticle-lined and partly with glandular tissue; oviduct separate from sperm storage organ; internal fertilisation.

– Heikeopsinae n. subfam.: single sperm storage organ; oviduct connected to sperm storage organ; internal fertilisation.

The situation for the Ethusidae

The Ethusidae, the sister family to the Dorippidae, exhibits another new type of female reproductive system, exemplified by *Ethusa mascarone* (Fig. 36C) (Hayer *et al.* 2016b: 1497-1508, figs l-7, 8B). The seminal receptacle is separated into two largely independent, laterally positioned chambers: a cuticular chamber that opens via a concave vagina through the vulva onto the cuticle of sternite 6; and a glandular chamber, interpreted as the modified portion of the oviduct. The two chambers are connected by two distinct openings: a ventro-lateral opening via a connective duct, lined by a strongly folded cuticle; and, secondly, a dorsolateral opening connecting the two chambers to the oviduct orifice. A distinct hook-shaped projection is located between the connection of the two chambers and the oviduct opening. Fertilisation is internal, like in other eubrachyurans, with the long G2 inserted into the cuticular chamber of the seminal receptacle via the vagina and vulva (Hendrickx 1989; Castro 2005; McLay & Becker 2015: fig. 7). According to the functional model proposed by Hayer *et al.* (2016b: 1506), spermatophores, first stored in the cuticular chamber and then relocated to the glandular chamber via the dorsolateral opening, can be retained at moult process, allowing trans-moult retention. An external sperm plug, located at the opening of the vagina to the seminal receptacle and blocking the vaginal lumen, has been found in *E. mascarone* (Hayer *et al.* 2016b).

One important feature distinguishes the female reproductive systems of ethusids and dorippids such as *Dorippe sinica*. The ethusid seminal receptacle consists of two connected chambers in addition to the ovary + oviduct, instead of the dorippid seminal structure + vagina independent of the ovary + oviduct. The topographic arrangement of ethusids deviates from all other currently known patterns in eubrachyurans, and is reported as apparently derived from that of dorippids (Hayer *et al.* 2016b, 2017). In a molecular phylogeny for the order Decapoda combining nuclear and mitochondrial sequences, a close affiliation of the Majoidea and Ethusidae has been suggested (Bracken *et al.* 2009: fig. 2).

The situation for the other Eubrachyura

The histology of the female reproductive system in Eubrachyura, typically with a seminal receptacle directly connected to the ovary by the oviduct opening through the vagina into the vulva, and with external fertilisation, has been described in various genera and species. The seminal receptacles show a rather wide variability in the heterotremes, but there is no known case leading to external fertilisation as in the Dorippidae. The apparently rather uniform pattern in thoracotremes turns out to be more diverse than expected. Here we will review the main types found in eubrachyurans, which will help to highlight the uniqueness of the female reproductive system of the Dorippidae.

The connection between the seminal receptacle and the oviduct, always located in the glandular chamber, varies considerably in its position, as already shown by Cano (1891: pl. 17). Two main morphological types have been distinguished in eubrachyurans (Diesel 1991). In the ventral type (Fig. 34B, *left*), the most common in heterotremes and frequently observed in "soft mating system species", the oviduct opens ventrally close to the vagina, as for example in Belliidae Dana, 1852, Calappidae, Cancridae Latreille, 1802, Corystidae, Goneplacidae MacLeay, 1838, Hymenosomatidae, Inachidae, Inachoididae, Leucosiidae, Majidae, Oregoniidae Garth, 1958, Parthenopidae, as well as in various primary freshwater families (Parathelphusidae Alcock, 1910, Potamidae Ortmann, 1896); it occurs also in various thoracotremes (Dotillidae Stimpson, 1858, Gecarcinidae H. Milne Edwards, 1837, Macrophthalmidae Dana, 1851, Pinnotheridae, Sesarmidae Dana, 1851, Varunidae H. Milne Edwards, 1853, Ucididae Števčić, 2005, Ocypodidae Rafinesque, 1815). In the dorsal type (Fig. 34B, *right*), more related to "hard mating system species", the oviduct enters the seminal receptacle more or less dorsally, with the oviduct opposite the vagina, as for example in Cheiragonidae Ortmann, 1893, Matutidae, Menippidae Ortmann, 1893, Pilumnidae Samouelle, 1819, Portunidae, Xanthidae MacLeay, 1838 (McLay & López Greco 2011: tables 1-3).

The ventral chamber, an ectoderm-derived region, has been termed the 'ventral insemination chamber', while the dorsal chamber, a mesoderm-derived region, has been referred to as the 'sperm storage chamber' by Diesel (1989) in *Inachus phalangium* (Fabricius, 1775) (Inachidae). In the oregoniid *Chionoecetes opilio* (Fabricius, 1790), the storage chamber was called the 'proper spermatheca', and the cuticle lined portion the 'intermediate chamber' (Beninger *et al.* 1988; Sainte-Marie & Sainte-Marie 1998; see also Elner & Beninger 1992: fig. 1B, C). An additional type, with an intermediate seminal receptacle in which the oviduct connection to the seminal receptacle occurs between the dorsal and ventral regions (McLay & López Greco 2011; McLay & Becker 2015: fig. 71-4.13), characterises Majoidea such as *Leurocyclus tuberculosus* (Inachoididae), *Macrocoeloma trispinosum* (Latreille, 1825) (Pisidae Dana, 1851 or Epialtidae MacLeay, 1838, see Windsor & Felder 2014; Colavite *et al.* 2016), *Libinia spinosa* (González-Pisani *et al.* 2011; López Greco 2013: fig. 15.5D, F), and the Portunidae (Spalding 1942; Ryan 1968; Pardo *et al.* 2013).

The sites of sperm storage and fertilisation appear to be highly variable in Eubrachyura. The dorsal chamber has been considered to have both functions in *Libinia spinosa* and *Leurocyclus tuberculosus* (Sal Moyano *et al.* 2010; González-Pisani *et al.* 2011), whereas sperm storage and fertilisation probably likely occur in the ventral chamber in *Chaceon chilensis* Chirino-Gálvez & Manning, 1989 (Geryonidae Colosi, 1923) (Pardo *et al.* 2017). The study of sexual differentiation in *Leurocyclus tuberculosus* (H. Milne Edwards & Lucas, 1842) (Inachoididae) and *Libinia spinosa* (Epialtidae) showed that the first ontogenic step in the female tract was the differentiation of the vulva, followed by invagination of the ectoderm to form the vagina and seminal receptacle, then differentiation of the ovary nearing puberty moult, and finally at puberty moult the connection between vagina and ovary (González-Pisani & López Greco 2007; González-Pisani *et al.* 2007a, b, 2011; McLay & López Greco 2011).

A spatial division into two chambers as two morphological and functional units characterises species of various families, with the dorsal and ventral parts separated by a muscular diaphragm or velum, e.g. in oregoniids (Beninger *et al.* 1988), majoids (Diesel 1991; Sal Moyano *et al.* 2010: fig. 3a, d), geryonids (Pardo *et al.* 2017); by an epithelial sheet, e.g. in portunids (Johnson 1980; Xuan *et al.* 2009); by folds, e.g. in spider crabs (González-Pisani *et al.* 2011); in ocypodids (López-Greco *et al.* 2009; McLay & López Greco 2011: 381). However, the two majoids *Mithraculus sculptus* (Lamarck, 1818) (Mithracidae MacLeay, 1838) and *Stenorhynchus seticornis* (Herbst, 1788) (Inachoididae Stenorhynchinae) investigated by Kienbaum *et al.* (2017: figs 4-7) show no anatomical or functional division of the seminal receptacle into two chambers separated by a muscular diaphragm; instead, there is a spatially restricted invagination of the seminal receptacle that, according to these authors, may have been misinterpreted as a velum. Hence the need to re-study and re-evaluate in majoids the division of the seminal receptacle separated into two chambers by a velum (Antunes *et al.* 2016). According to the results of Assugeni & Zara (2022), the presence of folds seems to be as common as the velum in Mithracidae such as *Mithrax hispidus* (Herbst, 1790), *Omalacantha bicornuta* (Latreille, 1825), and *Mithraculus forceps* A. Milne- Edwards, 1875. Seminal receptacles can be undivided: in cancrids (Orensanz *et al.* 1995; Jensen *et al.* 1996; Pardo *et al.* 2013) and pinnotherids (Becker *et al.* 2011).

The shape of the seminal receptacle varies from a simple elongated sac-like as e.g. in portunids (*Carcinus maenas*: see Spalding 1942; Hartnoll 1968; *Callinectes sapidus* Rathbun, 1896: see Ryan 1968; Johnson 1980) and cancrids (Jensen *et al.* 1996; Pardo *et al.* 2013), or kidney-shaped as in *Stenorhynchus seticornis* (Inachoididae Stenorhynchinae) in which the shape of the seminal receptacles and of ovaries appears to be associated with the elongated shape of the crab (Antunes *et al.* 2016: fig. 1, table 2).

The seminal receptacle of *Ebalia tumefacta* (Montagu, 1808) (Leucosiidae Ebaliinae), also referred to as a 'new type' of eubrachyuran seminal receptacle (Hayer *et al.* 2015: 517-525, figs 2-5), contrasts with that of other eubrachyurans by its anterior-posterior orientation, instead of a dorso-ventral orientation. The seminal receptacle is divided into two chambers placed side by side: a larger chamber, covered by a thin cuticle, is connected to the vagina ventrally; the smaller chamber, covered by a holocrine glandular epithelium, bears at its basal region, near the concave vagina, the oviduct connected to the ovary. A similar arrangement, but with laterally oriented chambers, found in the ebaliine *Ilia nucleus* (Linnaeus, 1758) and in the other leucosiid *Persephona mediterranea* (Herbst, 1794), was considered to represent the next derived step following that of the Ethusidae (Hayer *et al.* 2017: 274-286, figs 1-7). The conclusion of these authors regarding the evolution of seminal receptacles is that, while it is fair to assume that the seminal receptacles of Dorippoidea are the most basal states known, those of Leucosiidae may be the 'missing link' between Dorippoidea and other eubrachyuran families with a classical dorsal or ventral seminal-type receptacle (Hayer *et al.* 2017: 280).

In many eubrachyurans, the seminal receptacle, when known, has a dorso-ventral orientation. In the Calappidae, with two species of *Calappa* Weber, 1795 studied, the seminal receptacle is oriented anteroposteriorly and consists of two chambers connected by a small opening. The large ventral chamber of both ectodermal and mesodermal origin is the site of egg fertilisation, whereas the smaller ectodermal dorsal chamber is the site of spermatophore reception during copulation, via the long G2, and the site of egg fertilisation. The ventral chamber has openings to both the oviduct and genital duct, with the long G2 passing into the ventral chamber to enter the dorsal chamber through the small opening (Ewers-Saucedo *et al.* 2015: fig. 9A, B; 2017: figs 1-4).

A sclerotised bursa was first recorded in *Metacarcinus magister* (Dana, 1852) (Cancridae): located near the vulva and opening into the vagina, containing both free spermatozoa and spermatophores, and lacking a muscular sheet and glandular epithelium. The sperm plug found in the vagina and consisting of two sections, the distal one extending slightly outside the vulva but not occluding it, did not block access or prevent subsequent copulation by other males (Jensen *et al.* 1996: figs 3, 5-12; Oh & Hankin 2004: figs 1-6; Jensen & Bentzen 2012: fig. 1). Jensen *et al.* (1996: 347) interpreted the bursa of *M. magister* as an 'archaic structure', 'a type of thelycum': this bursa has lost its function, as sperm in the bursa is not used for fertilisation. Fertilisation may occur externally, with the female releasing its eggs in a pocket formed in the sand (Jensen & Bentzen 2012). A bursa is absent in other species of *Metacarcinus* A. Milne-Edwards, 1862, *M. edwardsii* (Bell, 1863) and *M. gracilis* (Dana, 1852) (Jensen & Bentzen 2012: 347; Pardo *et al.* 2013). While it appears that the proposed fertilisation for *Metacarcinus magister* is indeed external (Jensen & Bentzen 2012), this is another case of external fertilisation, albeit quite different from that of the Paradorippinae n. subfam. (Figs 35D; 37)

In *Danielethus crenulatus* (A. Milne-Edwards, 1879) (Platyxanthidae Guinot, 1977), a remarkable feature is the relative storage capacity and extensibility of the seminal receptacles, which show as a pair of simple sacs lacking internal structures dividing the internal lumen; and the vulva, with a mobile operculum that remains flexible and folds inwards, allowing penetration of the G1, irrespective of the carapace hardness of the female (Farias *et al.* 2017).

The distinct type of reproductive system described in the hydrothermal crab *Austinograea williamsi* Hessler & Martin, 1989 (Bythograeoidea Williams, 1980) is characterised by the remarkable size of the ovary, the shape and orientation (so far unique in Brachyura) of the (rotated) seminal receptacle that consists of a single chamber, apparently lacking a cuticular chamber, all unusual features for Brachyura (Köhnk *et al.* 2017: fig. 7; see also Hayer *et al.* 2018, abstract).

Analogous bursae to those found in dorippids, such as *Dorippe sinica*, *D. quadridens* (Vehof *et al.* 2017; Vehof 2020), *Paradorippe granulata* (Vehof *et al.* 2018b; Vehof 2020), have been described in few eubrachyuran species, e.g. in some Cancridae, as e.g. *Metacarcinus* (see above) and in certain Hymenosomatidae, as e.g. *Limnopilos naiyanetri* Chuang & Ng, 1991. However, with the emergence of an increasing number of studies describing bursae as accessory (Jensen *et al.* 1996; Klaus *et al.* 2014) or as sole sperm storage structures (Vehof *et al.* 2017; 2018b), the question arises whether those bursae are actually homologous and may represent the primary sperm storage structures of Eubrachyura.

As observed by Klaus *et al.* (2014: 1, figs 1, 2C) in the freshwater hymenosomatid *Limnopilos naiyanetri*, the bursa, a "secondary, additional sperm storage organ between the sclerotized ventral and the un-sclerotized dorsal part of the vagina", was described as cuticular and lacking glandular epithelium; in contrast, the seminal receptacle, lined only with a strongly thickened epithelium, apparently not divided into two chambers and containing only free spermatozoa, was distinct from the remaining tract. Kienbaum *et al.* (2018b: 513-520, figs 1-4), dealing with the same species, expressed opposite observations: seminal receptacle lined by a very thin cuticle, greatly capable of stretching according to the amount of sperm masses and fluids in the seminal receptacle, and by a monolayered glandular epithelium; vagina of the concave type fully lined by cuticle; bursa located on the anteromedial side of the seminal receptacle and without secretory activity. They concluded that Hymenosomatidae was most probably a member of the Thoracotremata. Such a bursa was not reported in *Halicarcinus cookii* Filhol, 1885 nor by Van den Brink & McLay (2009: 63, pl. 3.8), who described a seminal receptacle of "ventral-type with the oviduct and vaginal opening positioned close together", nor by Van den Brink & McLay (2009: fig. 1).

The general morphology of the reproductive systems of the Cryptochiridae Paulson, 1875 (for the incorrect spelling Paul'son, see Evans 2018; Spiridonov 2020), uniform across the three genera investigated (Vehof *et al.* 2016: 117-126, see fig. 2), has been interpreted as conforming to that of the thoracotremes: seminal receptacle for sperm storage lined internally by distinct types of epithelia; concave-type muscular vagina leading to the vulva. Whereas ovaries are normally restricted to the cephalothorax in brachyuran crabs, ovaries were found to extend into the last somites of the greatly enlarged pleon of the cryptochiroid species studied, as is the case in pinnotherids (Becker *et al.* 2011).

Studied in many species, the seminal reeceptacle of thoracotremes, initially assumed to be rather uniform, is more diverse than expected, appearing as a rounded or oval pouch, with the dorsal part always lined by a monolayered secretory epithelium, and the oviduct entrance consistently located ventrally (Sant'Anna *et al.* 2007; López Greco *et al.* 1999: figs 1, 2; López Greco 2013; McLay & Becker 2015). Kienbaum (2019) concurred, stating that the reproductive systems of Thoracotremata reveal great diversity. Based on several investigations (Souza & Silva 2009; Souza *et al.* 2013), Souza *et al.* (2017) concluded that thoracotremes shared similarities: a concave vagina in all analysed crabs (versus both simple and concave vaginae in Heterotremata), a seminal receptacle with connections of the ventral type (Fig. 34B); and similar histological components in thoracotreme species (versus variable in heterotremes).

According to Becker *et al.* 2011: fig. 2), the division of the seminal receptacle is primarily functional in the three species of Pinnotheridae studied: dorsally, a sperm storage area lined with glandular epithelium and, ventrally, a fertilisation area that includes connections to the vagina and oviduct.

In three species of *Uca* Leach, 1814 (Ocypodinae Rafinesque, 1815) studied by Lautenschlager *et al.* (2010: figs 1, 2), i.e., *Uca ecuadoriensis* Maccagno, 1928, *U. forcipata* (Adams & White, 1849) and *Uca tangeri* (Eydoux, 1835), the seminal receptacle is a sac-like organ, the inner wall of which consists of three distinct types of epithelium. The differences observed in the distribution of epithelia as well as the two kinds of glandular histology and ultrastructure were found to be in fact generic characters, with these species belonging in fact to three fully recognised genera, and even subfamilial features, since these taxa were later distributed in two distinct subfamilies according to a recent molecular analysis (Shih *et al.* 2016a): *Tubuca* Bott, 1973 (with *T. forcipata* (Adams & White, 1849)), *Minuca* Bott, 1954 (with *M. ecuadoriensis* (Maccagno, 1928)) in the Gelasiminae Miers, 1886; and *Afruca* Crane, 1975 (with *A. tangeri* (Eydoux, 1835)) in the Ocypodinae. *Ocypode quadrata* (Fabricius, 1787) has no macroscopically differentiated zones, and only histological zones are recognised: the larger dorsal part is mesodermal and the ventral part ectodermal (López-Greco *et al.* 2009: fig. 1).

The female reproductive system of *Percnon gibbesi* (H. Milne Edwards, 1853) (Percnidae Števčić, 2005) studied by Kienbaum *et al.* (2018a: 883-894) exhibits a combination of characters hitherto unknown in thoracotremes, namely: paired oviducts not leading into seminal receptacles but running into separate cuticular ducts connected to the vaginae; accessory sperm storage organs, the bursae, at the junction of seminal receptacle, cuticular duct and vagina. The unusual position of the oviduct connection has implications for copulation and fertilisation, the most important being that the seminal receptacle is not the site of fertilisation, the initiation of fertilisation likely occurring in the relatively long vagina.

In conclusion, the female reproductive system of Dorippoidea (Dorippidae, Ethusidae), which is evidence of two evolutionary states, sheds new light on the origin of the reproductive organisation of eubrachyurans. It effectively confirms the plesiomorphic condition of the group, apparently linked to its ancestral origin and early diversification. In addition, a significant item is the marked difference between the dorippid and ethusid systems. All this corroborates the high diversity of the Dorippoidea.

Larval and postlarval features

Rice (1980: 318-319, fig. 22) stated that "dorippid zoeae were so distinctive that it was difficult to see a close relationship between them and the larvae of any other group of crabs". He concluded that their "high degree of advancement" was somewhat reminiscent of thoracotreme larvae, but that they also shared some similarities with the 'higher majoids'. On the basis of its unique combination of zoeal characters (Rice 1980: 319), Dorippidae had "an evolutionary history distinct from that of all the brachyuran families", and its origin may be closer to those of the majoids than of any of the other crab group. According to Rice (1981: 291), who admits his inability to place the Dorippidae and Leucosiidae into its scheme, "dorippids are simply highly evolved Heterotremata in which the zoeal morphology has advanced beyond the general level for this group [Heterotremata] and in a number of features, has approached the thoracotrematous condition". This contradicts the current view that the Dorippidae is among the most basal crabs but is consistent with the special place of the family, its uniqueness among the Brachyura.

The larval characters of the Ethusidae, which are different but do not conflict with its grouping in the superfamily Dorippoidea, are thought to be less advanced than those of the Dorippidae (Aikawa 1937; Gilet 1952; Kurata 1964; Terada 1981; Quintana 1987; Paula 1991), supporting the hypothesis of an ancient, carcinised Dorippidae and a more recently evolved Ethusidae. Paula (1987a, b; 1991: table 1, as Ethusinae and Dorippinae, respectively) postulated that *Ethusa* might represent a link between ancestral dorippid larvae and those of *Medorippe* (see also Martin & Truesdale 1989; Paula 1996).

A distinction between the zoeae of Dorippinae n. status (*Dorippe frascone*) and Medorippinae n. subfam. (*Medorippe lanata*) is made by Bento & Paula (2018: key).

Our knowledge of the larval and postlarval development of the Dorippidae was improved by Quintana (1987), who reared three species in the laboratory: *Dorippe sinica* (as *Dorippe frascone*), *Heikeopis japonica* (as *Nobilum japonicum japonicum*, from Japan, thus the typical *H. japonica*), and *Paradorippe granulata*. He observed that some characters appear precociously, i.e., in the megalopa, and that characters of the adults already appear in the first juvenile crab, as follows:

– the rather benthic and weak swimmer megalopa displays carrying behaviour with small pieces of rocks held dorsally by the subchelate endings of P4 and P5 (Quintana 1987: figs 3B, 8C, l5H, 23); it does not differ much in its morphology from the first crab, except in the structure of the pleopods. The posterior sternites and the first pleonal somites of the megalopa of *Paradorippe granulata* are exposed dorsally as in the adult (Quintana 1987: 257). The possible hypothesis that the large zoea had moulted into a first crab instead of to a megalopa (as is plausible in the Hymenosomatidae), especially because of the absence of sensory setae ('brachyuran feelers', see Felder *et al.* 1985) on the P5 dactylus, was not adopted (Quintana 1987: 267);

– the first crab stage has separate Milne Edwards openings, a wide thoracic sternum with developed and dorsal first sternites, a well marked suture 3/4, and incomplete sutures 3/4 and 4/5 as in the adults, except in *Paradorippe granulata* where the suture 4/5 is complete (Quintana 1987: figs 3F, 8E, 15G);

– in the first juvenile crab a considerable sternum/pterygostome junction appears, so that the Milne Edwards openings become two independent and deep slits excavated into the pterygostome (Quintana 1987: figs 3F, 8E, 15G);

– the location of the dorippid press-button in a more or less marked curve of suture 5/6 is already present at the first larval stage (Quintana 1987: fig. 3D).

It is important to note that the existence of several morphologically distinct lineages can be recognised already in the megalopae and the early juvenile stages of the three species studied (Quintana 1987: tables 1; 2), corresponding to three dorippid subfamilies recognised here. Several characters strongly distinguish Dorippinae n. stat. (with *D. sinica*) from the two other subfamilies, Heikeopsinae n. subfam. (with *Heikeopis japonica*) and Paradorippinae n. subfam. (with *Paradorippe granulata*). According to Quintana (1987: 270, tables 1; 2), they can be easily differentiated at megalopal and first crab stages, and, among other characters, by the morphology of the dorsal and vental sides of the carapace, the structure of the maxillule, maxilla, the epipods of the three maxillipeds, and the setation of the P2 and P3 dactyli.

Moult, growth and reproduction

According to Mori (1986) and McLay (2015: table 4), Dorippidae is assumed to have a terminal moult of puberty, meaning that it the last moult of life, and thus has a determinate growth, as also do most majoids (Hartnoll 2015) and a few other eubrachyuran families that cease moulting after their puberty moult, hence the name 'terminal moult'. Although Hartnoll (2001, 2015) concluded that there was little correlation between growth format and phylogenetic level, it must be agreed that these brachyuran families with a determined growth format, e.g. Homolidae, Oregoniidae Garth, 1958, Macrocheiridae Dana, 1851, Inachoididae, Inachidae (Majoidea), are among the most basal.

Medorippe lanata has two overlapping growth phases, with both sexes showing positive allometric growth until maturity and allometric growth of the male chelae (heterochely) at the puberty moult, followed by reduced allometry in the second and final phases (Rossetti *et al.* 2006; McLay 2015: fig. 71-5.11). No post-puberty individuals have been observed in pro-ecdysis, indicating that the largest instar is terminal (Mori 1986; Rossetti *et al.* 2006): therefore, crabs cease growing at sexual maturity (determinate growth) in favour of reproduction. Observing the simultaneous presence of isochelid and strongly heterochelid males in *Ethusa sexdentata* Stimpson, 1858 and in other ethusid species, a terminal pubertal moult was proposed by Spiridonov & Türkay (2007) in the Ethusidae. When the puberty moult has been recognised as the last, ultimate, such a terminal moult implies that both sexes are hard-shelled at the time of mating. A determinate growth without post-puberty moult charaterises all Majoidea and some eubrachyuran groups, including Cryptochiroidea, Corystidae, Matutidae, and Leucosiidae (McLay & López Greco 2011: tables 2; 3; McLay 2015: fig. 75.5.11, tables 3; 4; Hartnoll 2015: 375, table 1). Is there a correlation between growth pattern and phylogeny? Could indeterminate growth be the ancestral pattern since it specialises all macrurans, occurs in dromiids but is also the commonest format in Brachyura, being general in cancroids and xanthoids as well as in grapsoids and ocypodoids? Can determinate growth be accepted as the evolved pattern when it is established in families recognised as basal within Brachyura such as the Homolidae (podotreme), Dorippidae and Ethusidae (Dorippoidea), Oregoniidae, Macrocheiridae, Inachoididae, and Inachidae (Majoidea)? The issue is well discussed by Hartnoll (2015: 376, 382, table 1).

The condition in which mating is restricted to the moulting period (when soft-shell females become receptive) has been considered 'ancestral': a post-moult mating is observed in Cancridae and most Portunidae (Jivoff *et al.* 2007). Conversely, in the 'derived' condition, moulting and reproduction would be delinked, with mating occurring during the intermoult period, when both sexes have hard-shelled exoskeletons, as in ocypodids, grapsoids and varunids (Sal Moyano *et al.* 2017).

Carrying behaviour

Non-morphological characters such as behaviour tend to be currently analysed in a phylogenetic context. The connection between morphology and behaviour is clearly evident in Brachyura, and in particular in basal crabs where there is a strong correlation, with severe constraints, between morphological characters and behavioural features. In Dorippidae, the carrying behaviour combined with burying is a concealment strategy to avoid detection and predation.

Indeed, dorippoids are specialised by their simultaneous behaviour of carrying and rapid burial. The Dorippidae and Ethusidae are the only carrier crabs within the Eubrachyura whose carrying involves the last two pereiopods. In Palicoidea, and only in Palicidae, carrying is performed exclusively by the P5. These crabs also belong to the oldest stock of heterotreme eubrachyurans. Similar elaborate carrying behaviour is absent in other decapods, with the exception of podotremes where it is largely the rule. In most anomurans, P4 and P5 are reduced and may be subchelate, even chelate. In paguroids the propodi usually bear broad rasps that are used to hold onto the shell (Tudge *et al.* 2012) but these propodal rasps tend to be reduced or lost in carcinised anomuran lineages, coinciding with the abandonment of gastropod domiciles. *Patagurus rex* Anker & Paulay, 2013, with P4 and P5 in dorsal position, the P4 propodal rasp modified to a single row of spines, the P5 propodus with no discernible rasp, and the short, strongly curved P5 dactylus, which much more closely resembles that of the carrier podotremes, is a remarkable example of changes that appear to be related to carrying rather than wearing domicile (Anker & Paulay 2013).

Cases of animals that camouflage themselves with foreign material are very rare in nature and, unlike dorippids, do not rely on specialised morphological structures: sea urchins using shells, rocks and pieces of algae; polychaetes incorporating large bits of material on their tubes. The only carriers, but in a very different way, are found in Arthropoda, i.e., in the 'lacewing' insects (family Chrysopidae Schneider, 1851), called 'trash carriers', which use a variety of vegetal and animal remains (Eisner 2003). The earliest evidence of insect camouflage is in a predatory larva of a green lacewing, covered by plant remains, discovered in a piece of amber from the Early Cretaceous of Spain, about 110 million years ago (Pérez-de la Fuente *et al.* 2012a, b). According to Wicksten (1986b), carrying is a conservative behavioural pattern in brachyuran crabs. Carrying behaviour is considered a relict behaviour (Guinot & Wicksten 2015).

Dorippid P4 and P5 are both reduced, subdorsal/dorsal and provided with a specialised subchelate ending, in a manner that resembles the organisation and behaviour of podotreme crabs (Dromiidae, Homolodromiidae, Cyclodorippoidea). In their extensive study of 3D-patterns of the fifth pereiopod in a wide range of swimming crabs compared to other crabs, Schmidt *et al.* (2020) showed that in the dromiid *Sternodromia monodi* (Forest & Guinot, 1966), whose P5 used for carrying behaviour cannot be moved in an anteromedial direction over the carapace, the total range of motion of all the joints of the P5 as a whole was the lowest of all Brachyura studied. The Dorippidae is probably in the same category.

Dorippids carry shells of lamellibranch mollusks, such as the dromiids *Hypoconcha* Guérin-Méneville, 1854 (Hypoconchinae Guinot & Tavares, 2003) and *Conchoecetes* Stimpson, 1858 (Dromiinae De Haan, 1833) that are, with their highly-specialised P4 and P5 (Guinot & Tavares 2000: figs 4, 5), by far the best known podotreme examples of permanent and elaborate shell-carrying behaviour (Guinot & Tavares 2003; McLay & Naruse 2019: figs 10, 19A, B, 21). The discovery in Early Cretaceous of podotremes with specialised last pereiopods demonstrates that this complex behaviour has not changed, probably since the Jurassic. Various modalities occur in Dorippidae, concerning the dimensions of P4 and P5 in relation to the size of the preceding legs, the shape of the basal extension of the propodus opposed to the dactylus, and the orientation of the dactylus.

Unlike podotremes, the dorippid megalopae already display carrying behaviour with their subcheliform P4 and P5, which are devoid of 'brachyuran feelers' (Quintana 1987: 267, figs 5L, M, 10E, F, 17E, F, 23B, C) (see *Larval and postlarval features*). Both the megalopa and the first crab stages of three species (*Dorippe sinica*, *Heikopsis japonica*, *Paradorippe granulata*) reared in the laboratory normally used their P4 and P5 to carry small objects dorsally over the carapace, so they were not active swimmers or did not swim at all; postlarval stages of *Paradorippe granulata* already carry fragments of shells or small rocks dorsally on the carapace, as do the adults. This early carrying behaviour is the only known case in Brachyura, including the podotremes, which are primarily carrier crabs and are known to carry fragile objects only in their juvenile stages.

In this paper, the carrying behaviour, where known, has been reported in a special paragraph for each subfamily, and only a few considerations will be made. A very particular case is that of the very close association of *Neodorippe callida* with mangrove leaves, which has been extensively described by Ng & Tan (1986: 45-46).

Some carrying behaviours in Dorippidae constitute instances of symbiosis *sensu* Castro (2015) as a strategy to escape predators by camouflage and defense. Cases with a close specificity between the crab and a living organism are those of dorippids associated with sea anemones fastened to shells attached on the carapaces. According to Verrill (1869a: 58-60; b: 249-250, pl. 2, fig. 1, as *Dorippe facchino*), who extensively studied these associations, "the sea anemone was never found except on the crab's back and the crab was never found without it". *Dorippoides facchino* is an obligate symbiont of *Cancrisocia expansa* Stimpson, 1856 (Fautin *et al.* 2015: 47, fig. 5; Guinot & Wicksten 2015: 599, fig. 71-11.8B), *Paradorippe granulata* of *Carcinactis ichikawai* Uchida, 1960 (Uchida 1960: 595, pl. 1, fig. 1, as *Dorippe granulata*). Paradorippine crabs, also known to exclusively select valves of bivalve molluscs often intimately associated with sea anemones, are also obligate symbionts of these animals. *Heikeopsis japonica* seems eclectic: it carries shells accompanied by sea anemones or sea pens but also dead shells or wood. *Dorippe quadridens* carries various materials: jellyfishes, stalked barnacles, scutellid sea urchins (Holthuis & Manning 1990; Shen 2006; Wisespongpand *et al.* 2014).

The identity of the crab shown in field videos holding the toxic 'fire urchin' *Asthenosoma varium* Grube, 1868 (and other species) with its P4 and P5, running along the bottom and then burying itself forwards, is difficult to identify with certainty. The 'carrier crab' or 'sea urchin carrier crab' is alternately identified with *D. frascone* and *D. quadridens*. The sea urchins prefer a solitary existence but seem to passively undergo this association that is clearly a defence for the carrier crab that is very creative in finding such protection. Another poorly documented association, only known from field videos, that of a dorippid carrying a jellyfish with its last legs, requires scientific information: indeed, as pointed out by Holthuis & Manning (1990: 33), it is not clear whether the crab reported by Estampador (1937: 514; 1959: 65) hidden under a jellyfish's umbrella is *D. quadridens* or *D. frascone*. The dorippid carrying a nudibranch shown in a field video could not been identified either, perhaps *D. frascone* because of the smooth carpus of the cheliped.

Forward locomotion and forward burying

The burying activity (not to be confused with burrowing, see Guinot *et al.* 2013: 250) of Dorippidae is not well documented and, for example, the family was not included among burying taxa by Bellwood (2002: fig. 1). Dorippids practise forward fast burying, i.e., they actively move through the substrate and dig into the sediment with their bodies and first legs. The combination of both carrying and burying behaviours had already been pointed out by Lamarck (1801). In the Dorippidae, the long P2 and P3 have a similar position to those of Dromiidae, i.e., they are oriented forward and can be positioned along the sides of the body, their dorsal margins being oriented in the same way as the dorsal surface of the carapace. The relative position between the sternal and pleural gynglymes determines the orientation and angle of movement of the pereiopod coxae, these positions being key to the locomotor characters of the crab. Field videos clearly show dorippids (with a sea-urchin, jellyfish, nudibranch, or other organisms covering most of the back and carried by P4 and P5) running forward, also using their P1 to walk, and then burying forward until the sediment covers most of the crab. According to Bedini *et al.* (2003: fig. 2), *Medorippe lanata* in rearing moves quite fast and leaps by pushing with its long P3, whereas the P2 are useful for balancing the weight of the carried object in relation to its body.

Forward locomotion (as opposed to sideways locomotion, considered the attribute of brachyuran crabs) is found in podotreme crabs and in dorippids (preferentially, mixed with phases of lateral locomotion). It is a plesiomorphic behaviour. Field videos show dromiids with forward walking by P2, P3 and also chelipeds, and carrying behaviour by P4 and P5. Observations of *Hypoconcha* (Dromiidae Hypoconchinae) in aquaria show individuals moving like hermit crabs, i.e., forward, and walking with their P2, P3 and mainly the chelipeds (Wicksten 1986a: 319). The walk is slow in dromiids and fast in dorippids. Most homolids walk primarily forward (Vidal-Gadea *et al.* 2008), and videos in the natural environment from manned subsmersibles show their forward locomotion combined with carrying behaviour (Braga-Henriques *et al.* 2012).

Videos of dorippids reveal forward burying. Field videos clearly show dorippids with P4 and P5 carrying various organisms, running rapidly forward, moving the chelipeds forward like shovels to push back the sand and pulling back the long P2 and P3 to plant them in the substrate, with the body performing a wriggling movement. This burial does not require any specific morphological adaptations, apart from features related to respiration whilst buried in the sediment. Most dorippids live in sand, mud or muddy-sand bottoms, also sand and shells, sponge, occasionally in mangrove swamps, rarely in coral reefs and oyster beds (Holthuis & Manning 1990). The assertion by Guinot *et al.* (2013: 250) that they can be classified as 'back-burrowers' was inappropriate because they apparently bury themselves forward (and do not make burrows). Back-burying characterises raninoids, which enter first from the posterior end, and many heterotremes (called 'back-buriers') that bury and dig backward (see details in Guinot *et al.* 2013).

Neodorippe callida, which invariably carries a leaf with its strongly hooked P4 and P5 and is a "slow walker on the sea bottom and a slowler swimmer", buries itself in soft mud during the day and only emerges at night to feed; it swims upside down, just below the surface (Ng & Tan 1986; Ng 1987: 15; Tan & Ng 1992; Lim *et al.* 1994; Ng *et al.* 2008; Sahu 2012).

Burying may be an ancestral condition, evolving only in crabs living in habitats characterised by soft sediment. But such forward burying is not known in other Brachyura and seems to be unique to the Dorippidae.

Spermatozoal ultrastructure

It is widely accepted that sperm morphology traits, often extensively used, are reliable diagnostic traits in zoological taxonomy.

The sperm of the investigated *Neodorippe callida* (Jamieson 1991: fig. 7A, as *Neodorippe astuta*; Jamieson & Tudge 1990: figs 1A, 2, as *Neodorippe astuta*; 2000: 52, fig. 11B, as *Neodorippe astuta* (cf. *callida*); Jamieson *et al.* 1995; Tudge *et al.* 2014) have characteristically eubrachyuran features. Typical dorippid traits are as follow: very slight elongation of the acrosome beyond a spheroidal shape; perforatorium long, extending almost to the operculum, with convoluted tubules and basally two centrioles, its basal part being surrounded by a thickened ring; presence of an acrosome ray zone; absence of the central acrosome zone; and prominence of the operculum. As a result, dorippids occupy with majoids the more basal position in Eubrachyura. The projection (emergence) of the acrosome from the nucleus, which is complete in podotremes, is partial in dorippids and majoids, as well as in anomurans (Davie *et al.* 2015b: 947).

It would be very interesting to check if and to what extent the ultrastructure of the sperm varies, like other traits, within the family Dorippidae.

Palaeontological data

In this paper, morphology-based characters have been used extensively, which has the great advantage of integrating the many extinct taxa into the taxonomy to obtain a comprehensive system (Recent and fossil taxa), despite the absence in most cases of ventral surfaces and limbs, hence a source of error in our interpretations.

The taxonomic allocation of dorippoid fossil genera and species to the Recent subfamilies established in this paper is problematic because they are mostly devoid of cephalic appendages, sometimes of the frontal region, and very often of the entire ventral part and limbs. Preservation of the appendages allows us to know the nature of the P4 and P5 but generally not their small distal termination, which deprives us of essential information: is it subchelate as in

Dorippidae or non-chelate as in Ethusidae and Telamonocarcinidae Larghi, 2004? For the main differences between the extant Dorippidae, whose extant members are absent from the Americas, and the more widely distributed worldwide extant Ethusidae (see Table 1). As the distinction between the two families is difficult when it concerns their fossil representatives, fossil Ethusidae are included here in the palaeotonlogical part of this paper. Most of the characters in Table 1 cannot be used to distinguish the fossil species, which are mostly carapace-based entities, with only the dorsal surface of the carapace preserved in most cases. In the Recent Ethusidae, the accurate and still valid diagnoses provided by Castro (2005, 2020) show that the distinction between the two best known genera (*Ethusa*, *Ethusina*), containing a high number of species, is partly based on other criteria than carapace alone. However, data provided by the carapace of extant genera should be useful for the identification of fossil ethusids, as follows.

Ethusa
Carapace either with lateral margins almost parallel, only slightly diverging posteriorly; or with lateral margins clearly diverging posteriorly; exceptionally forming a noticeable widening of the carapace, resulting in a pear-shaped appearance. Dorsal surface of carapace flat, granular or coarsely granulated, bare but often tomentose; some distinct areas bounded by grooves. Four frontal teeth; dimensions, shapes and orientation of frontal teeth and outer orbital teeth varied, as did their interactions.

Ethusina
Dorsal surface of carapace typically granular, with setae or short tomentum; some regions distinct, limited by grooves. Outer orbital teeth in the form of short tubercle-like, conspicuous, acute, needle-like, or absent, straight or not. Four frontal teeth either in the form of two acute, triangular lateral and two sinuous lobe-like or slightly pointed median teeth, or in the form of four clearly defined acute or obtuse teeth. Eyestalks very small. Note that in *E. abyssicola* Smith, 1884, the abyssal 'sumo crab' and the only species of the genus occurring in the West Atlantic, the granulate surface of carapace is areolated, the cervical groove is well marked, the cardiac region is broadly open anteriorly, the outer orbital spines are pointed almost directly forward (Ocampo *et al.* 2014).

Parethusa
Dorsal surface of carapace smooth, without conspicuous setae or tomentum; regions not distinct, ill-defined. Lateral, frontal margins setose, otherwise smooth. Two or four frontal teeth; lateral tooth rounded, lobe-like, lower than medial tooth. Front produced in males, less produced in females.

Serpenthusa
Carapace subtriangular; regions ill-defined; setose only on lateral and frontal margins, otherwise smooth. Dorsal surface flat in males, convex in females.

In general, the Dorippidae are larger than the Ethusidae, whose carapace is much longer than wide, often narrow and with parallel edges, and usually only slightly posteriorly inflated. A main difference is the pleon, composed of six free somites plus telson in Dorippidae, as in the fossil Telamonocarcinidae, and of four free somites (somites 3-5 fused) plus telson in Ethusidae, as in the fossil Tepexicarcinidae Luque, 2015.

Another problem for the interpretation of the fossil material lies in the identification of carapaces with Recent genera. In the Dorippidae, even if the most reliable criteria are the G1 and the vulvae (Figs 31; 32), the precise and still valid diagnoses established by Holthuis & Manning (1990) allow several groups to be distinguished on carapace-based characters alone: one group (*Dorippe*, *Medorippe*, see Figs 3A, C; 5A, B) with an uneven dorsal surface subdivided by several grooves, bearing small or strong tubercles, and with the cardiac region showing a distinct V- or Y-shaped ridge; and a larger group (*Dorippoides*, *Heikeopsis*, *Neodorippe*, *Nobilum*, *Paradorippe*, *Philippidorippe*, *Phyllodorippe*, see Figs 3B, D-I, 5C, D) with only two deep main grooves, rounded branchial lobes and a cardiac region without ridge. Thus, for example, fossils attributed to *Dorippe* that do not show its typical carapace characters cannot belong to this genus.

Despite the lack of direct examination of the species, it is possible to present some remarks and hypotheses, to identify those that could be true dorippids, others ethusids, and finally others of extinct families, all in a hypothetical way.

According to Luque (2015: fig. 4), the oldest records of the Dorippidae occurred only belatedly, in the Eocene, as did those of the Ethusidae. In the crab tree of life of Luque *et al.* (2021: fig. 5), the Dorippidae is estimated to have appeared at the end of the Lower Cretaceous. In the stratigraphical distribution of dorippoid taxa by Van Bakel *et al.* (2020: fig. 10), the first record of *Ethusa* is from the Late Eocene, preceding that of the dorippid genera, which appeared in the Miocene. The Dorippoidea is currently thought to include three extinct families: the Telamonocarcinidae, so far represented in the fossil record since the Early Albian (Luque 2015: table 1; Schweitzer *et al.* 2021: 5) but whose recent inclusion of new taxa would delay its appearance to the Aptian (Van Bakel *et al.* 2020: 10, fig. 10); the Tepexicarcinidae from the Lower Cretaceous (Luque 2015: table 1), in the Upper Albian (Vega *et al.* 2022: 10); and the Goniochelidae Schweitzer & Feldmann, 2011 from the Early Eocene (Van Bakel *et al.* 2020: fig. 10; Schweitzer *et al.* 2021: fig. 4; Charbonnier & Garassino 2022: 193).

In Appendix 2 are listed in alphabetical order the fossil Dorippidae and Ethusidae. Next, we discuss two extinct dorippoid families, the Telamonocarcinidae Larghi, 2004 and the Tepexicarcinidae Luque, 2015, followed by fossil families or taxa that were at one time suspected of being dorippoids, namely the Goniochelidae Schweitzer & Feldmann, 2011, Lecythocaridae Schweitzer & Feldmann, 2009, and *Binkhorstia* Noetling, 1881.

Key to dorippid subfamilies based on morphological characters other than G1 and vulva

1. Surface of carapace more or less sculptured; cardiac region with a V- or Y-shaped median ridge. Long rim extending laterally along posterolateral margins and bordered medially by straight, narrow or even indistinct strip 2
— Surface of carapace weakly or not sculptured, without V- or Y-shaped median ridge. Long rim not extending laterally along posterolateral margins and bordered medially by distinct strip 3

2. Carapace longer than wide, much sculptured; dorsal surface rough, uneven and with strong tubercules. Pleon of male with distinct teeth on somites 2-4. Base of P3 with distinct callosity. .... Dorippinae n. stat.
— Carapace wider than long; dorsal surface only with some low elevations. Pleon of male without teeth. Base of P3 without callosity .... Medorippinae n. subfam.

3. Carapace weakly sculptured, with distinct epibranchial spine; dorsal surface only with granules and with raised tripartite ridge on swollen branchial region .... Phyllodorippinae n. subfam.
— Carapace with only two main grooves, without distinct epibranchial spine. 4

4. P3 with a calcified band forming a simple callosity at its base. Dorsal surface rather smooth and even. .... Dorippoidinae n. subfam.
— P3 without any callosity at its base. 5

5. Front consisting of two closely spaced triangular median teeth separated by a narrow emargination; opening of exhalant channels visible dorsally. Carapace inflated; dorsal surface naked and finely granular .... Philippidorippinae n. subfam.
— Front consisting of two triangular teeth separated by wide, shallow emargination. 6

6. Carapace longer than wide; dorsal surface smooth and bare (*Heikeopsis*, *Neodorippe*) or with some anterior tubercles (*Nobilum*). Openings of exhalant channels not at all visible in dorsal view (*Neodorippe*, *Nobilum*) or scarcely visible (*Heikeopsis* spp.). Erect axial spine present medially on sternite 8 in females. A process on dorsal sternite 8 overhanging pleonal somite 2 in females (pleonal retention) .... Heikeopsinae n. subfam.
— Carapace wider than long; dorsal surface either completely smooth or completely or partially granulated. Opening of exhalant channels clearly visible in dorsal view between rostral teeth. No erect axial spine medially on sternite 8. No process on dorsal sternite 2 in females .... Paradorippinae n. subfam.

Key to dorippid subfamilies based on G1 and vulva

1. G1 short, stout, abruptly constricted in midpart, then regularly bent; second part swollen, elaborate with distinct bulbs bearing several apical processes. Vulva situated on a more or less marked prominent portion of sternite 6 or may be recessed; opening large or very large, rounded or crescent-shaped, visible on surface and less largely exposed .... Paradorippinae n. subfam.
— G1 rather long, without swollen portion, not abruptly constricted. Vulva on prominences or on elevated portion of sternite 6; opening small, rounded or recessed as a slit 2

2. G1 variously curved. Vulva on inner part of sternal prominence or situated on raised flanks of sterno-pleonal cavity 3
— G1 straight. Vulva on elevated portion of sternite 6 or on clearly delimited, globular prominence, at end of setose raised sternal ridge 4

3. G1 strongly curved midpart, C-shaped, ending in lobes, consisting either of three blunt petaloid lobes (*Nobilum*) or several slender, unequal subdistal and distal processes (*Heikeopsis*, *Neodorippe*). Vulva at inner part of sternal prominence, either elongate, suboval and not sunken or as vertically oriented, recessed curved slit .... Heikeopsinae n. subfam.
— G1 regularly curved or S-shaped. Vulva situated on raised flanks of sterno-pleonal cavity 5

4. G1 straight, gradually tapering to single apex, with subdistal setae, and ending in tongue-shaped horny process. Vulva at summit of elevated portion of sternite 6; opening rather large, rounded, not recessed .... Dorippinae n. stat.
— G1 straight, with distal triangular setose tip directed sideways. Vulva at outer margin of salient sternal prominence; opening very small, recessed .... Medorippinae n. subfam.
— G1 straight, with a simple apical process, ending either in slender, long, spiral-shaped point (*D. facchino*) or in flattened, rectangular, horn-coloured projection, produced into narrow whip-like appendage (*D. nudipes*). Vulva on clearly delimited, globular prominence; opening relatively large, not recessed, near outer margin of prominence .... Dorippoidinae n. subfam.

5. G1 with basal lobe; regularly curved, with tip ending in two auricular lobes. Vulva situated on obliquely directed flanks of sterno-pleonal cavity; opening not recessed, quite large, elongated, crescent-shaped .... Philippidorippinae n. subfam.
— G1 without basal lobe; basally twisted, thin, S-shapedly curved; second half horn-coloured, with rather large, inverted subdistal lobe and recurved distal tip. Vulva situated on raised flanks of sterno-pleonal cavity; opening narrow, slit-shaped .... Phyllodorippinae n. subfam.

DISCUSSION

Rationale for seven dorippid subfamilies

The dorippid crabs are similar in general shape and size and show little difference in lifestyle, being restricted to the sea at largely comparable depths, and form a group with very few species and genera. Dorippidae is estimated to have appeared around the end of the Early Cretaceous (Luque *et al.* 2021: fig. 5) (see *Palaeontological data* and *Appendix 2*), whereas extinct families of Dorippoidea are known since the Aptian (Van Bakel *et al.* 2020: fig. 10). The above, which has highlighted the major and definitive characters of dorippids, gives an insight into their heterogeneous structural architecture, evidence of an extreme underlying diversity.

Conversely, a lineage such as the worldwide-distributed Hymenosomatoidea, which has successfully conquered a very wide range of environments (e.g. marine, brackish, freshwater, mangrove, terrestrial, lakes, caves) and extreme ecological niches as well as adopting a wide variety of body forms and lifestyles, constitutes a group of great species richness (Lucas 1980; Ng *et al.* 2008; Yeo *et al.* 2008; Guinot 2011). Recent discoveries provide evidence for a longtime Mesozoic hymenosomatoid lineage, through the record of two new genera and three new species in the late Barremian (Early Cretaceous) of northeast Brazil (Mendes *et al.* 2022). To what do we attribute these disparities, how to assess the time scale of diversification rates? (Henao Diaz *et al.* 2019)? The two clades Dorippoidea and Hymenosomatoidea, the oldest eubrachyurans to have appeared, were the earliest diverged lineages within the Heterotremata during the initial radiation of Eubrachyura, being paraphyletic with respect to the remaining heterotremes.

Morphological evidence

In this paper, we have examined the adult morphology of all recognised species of Dorippidae and reported several unique characters that clearly show that the family is not strictly related to other Eubrachyura, apart from the closely allied Ethusidae.The Dorippidae exhibits a number of different structural configurations that we believe reflect several separate, clearly isolated evolutionary lineages. Our proposal of seven taxa at the subfamily level is mainly supported by morphological evidence of seven distinct types of first gonopods (Fig. 31) and seven distinct types of vulvae (Fig. 32). In addition, the extremely dissimilar female reproductive systems, with various sperm storages organs and also various sites of fertilisation, provide a strong argument for the separation of at least six of the seven dorippid subfamilies (the Phyllodorippinae n. subfam. has not been studied by histologists): Dorippinae n. stat., Dorippoidinae n. subfam., Medorippinae n. subfam., Heikeopsinae n. subfam., Paradorippinae n. subfam., and Philippidorippinae n. subfam. (Figs 35; 37).

The configuration of the penial region studied in detail by Guinot *et al.* (2013: 98-105, figs 15-19; note that their fig. 15E erroneously depicts a misidentified *Medorippe lanata* instead of *Phyllodorippe armata*) shows a clear transformation series, with multistate characters varying from a coxal condition in Medorippinae n. subfam. to a variety of patterns of the coxo-sternal condition, which most likely correspond to our seven subfamilies. In general, it is accepted that male and female genitalia are conservative structures: they vary less than other characters, change slowly with evolution, and thus reveal relationships over time (Guinot 1979c). Regarding the 'lock-and-key hypothesis', atltough female genitalia have been considered more uniform than male structures (Eberhard 1985), an increasing number of studies show that male and female genital morphologies have co-evolved in several groups of animals, a fact particularly true for Arthropods (Peretti & Aisenberg 2015).

The dorippid two pairs of gonopods, penis and vulvae are conservative traits that are therefore of significant importance in classification. They are less affected by environmental changes than other external morphological characters since they only function during sperm transfer. This triple interaction is a synapomorphy of the Brachyura (Guinot *et al.* 2013: fig. 9). In Brachyura, changes in the morphology of the G1/G2/penis complex are presumed to have co-evolved with female reproductive structures. As the gonopods must reach and inseminate vulvae, co-adaptation is expected between male and female structures (see above, *G1*, *Vulva*). It is clear that, for example in *Paradorippe granulata* (Paradorippinae n. subfam.), the bulbous tip of G1 (Figs 25C-E; 31G) apparently fits tightly to the large, shallow and incompletely protected oval vulva (Figs 26B-D; 32G), with its terminal processes directly involved in sperm transfer by guiding the ejaculate and interacting with the twin bursae, as shown in the illustrations by Vehof *et al.* (2018b: 88, figs 1, 2). Thus, our new taxonomy based on numerous features, mainly on the first gonopods and the vulvae, seems well justified (see *Key to dorippid subfamilies based on G1 and vulva*).

Other morphological characters do not allow us to divide the Dorippidae entirely into seven subfamilies but only to cluster some of them together. For example, the proportions of the body, the sculpture of the dorsal surface, the shape of the front and lateral carapace margins only allow groupings. With regard to the rim of the carapace posterior margin and the posterior strip, only two subfamilies, the Dorippoidinae n. subfam. and Medorippinae n. subfam., are characterised by a long rim extending laterally along the posterolateral margins and by a straight, narrow or even indistinct strip; these same families also share a weak sexual dimorphism for this character. The branchiostegite is reduced but varies: reduced but present in dorippids with a swollen branchial region (e.g. Dorippoidinae n. subfam., Paradorippinae n. subfam., Philippidorippinae n. subfam.), and almost absent posteriorly (e.g. Dorippinae n. stat., Medorippinae n. subfam., Phyllodorippinae n. subfam.). The condition of the eystalk and antenna reveals two main dorippid groups: one group (Dorippinae n. status, Dorippoidinae n. subfam., Medorippinae n. subfam., Philippidorippinae n. subfam., Phyllodorippinae n. subfam.); and another group (Heikeopsinae n. subfam., Paradorippinae n. subfam.) (see above, *Cephalic appendages*). The openings of the exhalant channels are just or barely visible dorsally between the rostral teeth in Dorippoidinae n. subfam., clearly visible in Medorippinae n. subfam., Paradorippinae n. subfam., Philippidorippinae n. subfam., not visible in Dorippinae n. stat., Heikeopsinae n. subfam., and Phyllodorippinae n. subfam. The axial spine on the fused median portion of sternite 8 is present only in the females of Heikeopsinae n. subfam. (in all three genera) and Phyllodorippinae n. subfam. A callosity on P3 coxa characterises only two subfamilies, the Dorippinae n. stat. and Dorippoidinae n. subfam.

The modality of pleonal retention of females by a conspicuous process of sternite 8 that overhangs pleonal somite 2 is a subfamilial character of Dorippinae n. stat. (Figs 8C; 9C, 10B, D; 12A; 15E, F), Heikopsinae n. subfam. (Fig. 19B, F) (except in *Neodorippe* Fig. 20B), Philippidorippinae n. subfam. (Fig. 27B), Phyllodorippinae n. subfam. (Fig. 29B), but is absent in Dorippoidinae n. subfam. (Fig. 8A), Medorippinae n. subfam. and Paradorippinae n. subfam. (Fig. 24B).

The sites of fertilisation vary with a continuous spectrum, not always easy to identify: in any case, the site of fertilisation is external in the Paradorippinae n. subfam. or quasi external in the Dorippinae n. status. (whose existence is proved to exist at least in two species, *Dorippe quadridens* and *D. sinica*), whereas a definitive internal site of fertilisation characterises at least the Heikeopsinae n. subfam. (whose existence is proved in the species of the three genera, *Heikeopsis japonica*, *Neodorippe callida* and *Nobilum histrio*).

DNA Evidence (Fig. 38)

The first analysis, based on mitochondrial 16S rRNA sequences (Fan *et al.* 2004: 516, as Dorippinae) to study the phylogenetic relationships of four Chinese genera, suggested that *Dorippe* was basal and *Heikeopsis* closely related to *Neodorippe*. In a more robust phylogenetic framework, ten of the 13 dorippid genera (twelve species) were investigated by Sin *et al.* (2009) using three markers (mitochondrial 16S rRNA, 12S rRNA and COI).

In the study by Sin *et al.* (2009: 227, figs 1, 2), “sequence data of the 16S gene from 24 ingroup individuals revealed that each genus formed a distinct and highly supported clade (intrageneric species divergence 0-12.7% in 16S)”, with the COI and 12S gene trees concordant with the 16S tree. Two distinct major clades emerged: one with *Dorippe*, *Dorippoides* and *Medorippe* that clustered together (16S: BP values 96% in MP and 97% in ML analyses), the other with *Heikeopsis*, *Neodorippe* and *Paradorippe* (16S: BP values 88% in MP and 68% in ML analyses). The three *Dorippe* species tested formed a strongly supported clade, clearly divergent from *Dorippoide*s (average sequence divergences 17.5%, 18.4% and 18.3% in 16S, 12S and COI, respectively). The separation of *Medorippe* from *Dorippe* was also supported (average sequence divergences 15.5%, 18.5% and 14.9% in 16S, 12S and COI, respectively): it appeared to have a more ancestral origin and to be more basal than the sister group *Dorippe* + *Dorippoides*. *Philippidorippe philippinensis* clustered with the *Dorippe-Dorippoides-Medorippe* clade in the combined dataset, with weak to moderate support. *Paradorippe*, with two species *P. granulata* and *P. polita* analysed out of the four known species, formed a very distinct clade with the highest percentage of intrageneric divergence recorded (12.5% in 16S) and was more basal than the group *Heikeopsis-Neodorippe* (*Nobilum* was not sequenced), as in Fan *et al.* (2004). Although the tree of Sin *et al.* (2009) is not as complete as it should be because some taxa were not sequenced, we have great confidence in the topology of this phylogenetic framework.

For this paper, crabs were analysed with a new phylogenetic approach (see *Material and methods*). As the tissues samples from *Phyllodorippe armata* could not be successfully amplified and no genetic material could be extracted from *Nobilum histrio* as in Sin *et al.* (2009), our tree is not complete. Even though the general topology remains the same as that of Sin *et al.* (2009), our tree (Fig. 38) shows better support values overall. One notable change is the position of *Philippidorippe* that seems to be basal in our analysis (though only moderately supported), whereas its position was unresolved in Sin *et al.*’s 2009 trees (their figs 1, 2). Regardless, the subfamilies as defined by the morphological study can be assigned to six clades in the molecular phylogeny (Phyllodorippinae n. subfam. excluded).

Importantly, the analysis of the sequenced species reveals a robust framework, with each genus forming a distinct, highly supported clade of at least six genetically separate groups, and the sequenced generic taxa show relative correspondence with our proposed subfamily divisions based primarily on morphological features (including the female reproductive system) and, more fragmentarily, on larval and post-larval data. This correlation suggests that our subfamily divisions are justified. We have therefore been able to transpose here the sequence divergences found between genera or groups of genera into sequence divergences between our subfamily clades, as follows: two major clades are supported, one with Dorippinae n. stat., Dorippoidinae n. subfam. and Medorippinae n. subfam., the other with Heikeopsinae n. subfam. and Paradorippinae n. subfam.; Dorippinae n. stat. forms a strongly supported clade, well separated from the more basal Medorippinae; Paradorippinae n. subfam. forms a very distinct clade, more basal than the Heikeopsinae n. subfam. and with two groups, one with *P. granulata* and the other with *P. polita*; Philippidorippinae n. subfam. seems to be basal in the family.

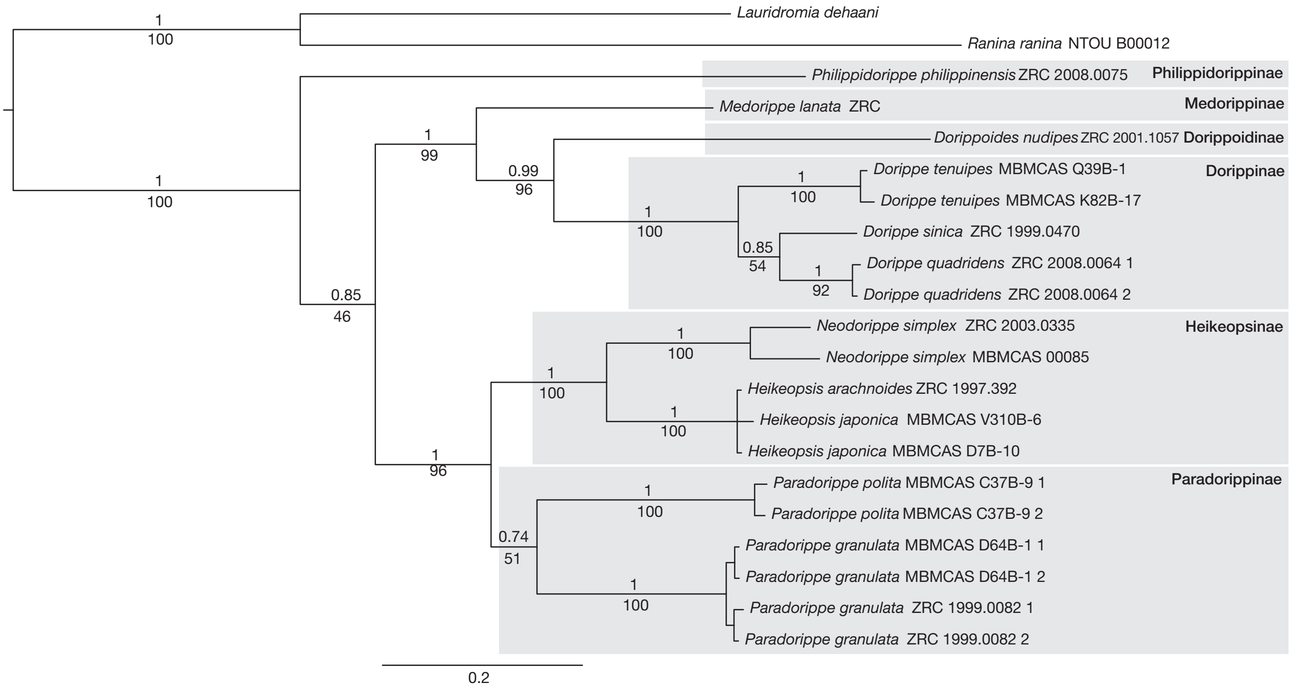

Fig. 38. — Phylogenetic tree of the concatenated dataset obtained by Bayesian Inference analysis. Numbers above branches indicate Bayesian posterior probabilities; numbers under branches indicate Maximum Likelihood bootstrap values (tree by Valentin de Mazancourt).

We briefly recall which morphological data support acceptance of these genetic data. The carapace silhouette (Fig. 3) supports the grouping Dorippinae n. stat. + Dorippoidinae n. subfam. + Medorippinae n. subfam. + possibly Phyllodorippinae n. subfam.; the separate group Heikeopsinae n. subfam.; and the separate group Paradorippinae n. subfam. Philippidorippinae n. subfam. remains ambiguous. The sister group Dorippinae n. stat. + Dorippoidinae n. subfam. is the only one to have distinct inner orbital teeth and callosities on P2 and P3. The condition of the eystalk and antenna reveals two main dorippid groups: one group with Dorippinae n. status + Dorippoidinae n. subfam. + Medorippinae n. subfam. + Philippidorippinae n. subfam. + Phyllodorippinae n. subfam.; another group with Heikeopsinae n. subfam. and Paradorippinae n. subfam. The morphology of the G1s (Fig. 31) and vulvae (Fig. 32) supports the separation of seven subfamilies, but with possible groupings as the group including Dorippinae n. stat. + Dorippoidinae n. subfam. + Medorippinae n. subfam. (+ possibly Phyllodorippinae n. subfam.); the group Heikeopsinae n. subfam.; and the separate group Paradorippinae n. subfam. Morphologically, Philippidorippinae n. subfam., with the only known species *P. philippinensis* unusual in Dorippidae by its occurrence in much deeper waters than the other dorippids, remains ambiguous. The distinctiveness of the clade Paradorippinae n. subfam. is supported by several synapomorphies: proportionally narrow thoracic sternum, with rectangular sternite 2 and weakly curved backwards suture 5/6 (Figs 25; 26); peculiar shape of G1 (Fig. 25C-E) and vulva (Fig. 26C, D); posterior rim and well-defined strip (Fig. 24A, B); exclusive carrying of bivalve molluscs, often intimately associated with sea anemones; peculiar female reproductive system and external fertilisation (Figs 35D; 36B).

With respect to the female reproductive system (Phyllodorippinae n. subfam. not studied), the genetic data support five/six distinct sperm storage chambers (Fig. 37): Dorippinae n. stat. and, rather close, Dorippoidinae n. subfam.; Medorippinae n. subfam.; Heikeopsinae n. subfam.; and apart from these, Paradorippinae n. subfam. and, perhaps rather closely, Philippidorippinae n. subfam.

Uniqueness of Dorippidae among Brachyura

Some features make the family Dorippidae unique among the Brachyura and separate it from other Eubrachyura, apart from the Heterotremata. Should a special rank, beyond the superfamily, be assigned to Dorippoidea?

Grooves on dorsal surface of carapace (Fig. 5B-D)

The original dorippid groove pattern, which is autapomorphic, requires the use of a special nomenclature, unknown in other Brachyura (except in Ethusidae). The epibranchial region delimited by the precervical and cervical grooves is narrow and obliquely oriented in living and fossil dorippids, an arrangement very rarely found in other Eubrachyura.

Strip along posterior margin of carapace (Figs 8A-C; 9C, D)

In Dorippidae (but not in the Ehusidae we examined), the straight posterior margin of the carapace, which forms a thick rim extending laterally to varying degrees, is lined posteriorly in both sexes by a conspicuous smooth strip separating the rim from the first pleonal somite. Since it should normally conform to the adjacent pleon, which is narrower in males than in females, the strip is in most cases sexually dimorphic. The strip varies in shape and size and from indistinct to quite distinct, sometimes as if inserted between the carapace and the first pleonal somite. This rim-plus-strip seems to be exclusive to Dorippidae. Only the Palicidae shows a long, keeled and detached strip running along the entire carapace posterior margin (see above, *Rim of carapace posterior margin and the posterior strip*), but of different shape, and perhaps not homologous.

Afferent branchial orifices (Milne Edwards openings) (Fig. 7C)
They appear as elongated, oval slits in the pterygostome and are separate from the chelipeds, an arrangement not found in any other eubrachyuran (autapomorphy).

Dorsal exposure of sternites 7 and 8 (Fig. 8C; 9C)

Additional pleonal-retention mechanism in females (Figs 8C; 9C; 33G)
The dorsally exposed thoracic sternite 8 bears a process overhanging pleonal somite 2 and acting as an additional pleonal-retention mechanism in the females of three genera, *Dorippe*, *Philippidorippe* and *Phyllodorippe.*

Dorsal exposure of lateral portions of pleurites 5-7 (Fig. 7A, B)
One particular arrangement, the dorsal exposure of the lateral portions of pleurites 5-7 with their latero-external ends inserted in a gutter ('setting gutter'), is unique to Dorippoidea and represents a synapomorphy of the superfamily. The arrangement in the Inachoididae, with the pleurites 5-8 widely exposed and the first pleonal somite 'integrated' into the carapace resulting in the formation of a continuous collar, is quite different, although proceeding from a similar process. In some majoids and other eubrachyurans, parts of some pleurites may be exposed but they occur only as small sclerites, without a setting gutter.

Axial skeleton
The dorippid axial skeleton is very poorly known. Based solely on dissection, which damages individuals, and on a difficult interpretation of its various parts, will this conservative structure be homogeneous in the subfamilies recognised here? A challenge. A particular configuration, with a sexually dimorphic arrangement, was described by Guinot *et al.* (2013), namely a median invagination with disjointed laminae at their base in males and without a true median plate in females. The absence of a median plate (see Fig. 7A) has been recently reported in both sexes (Hazerli *et al.* 2022: 44), who consider that, with respect to the axial skeleton, Dorippidae (exemplified by *Medorippe lanata*) is "positioned as sister to a clade comprising Heterotremata and Thoracotremata".

Penis and gonopods (Fig. 31)
The dorippid penis is very long and typically has several portions, including an exposed proximal penial bulb and a long penial tube that varies from vertical and angled to variously inclined. The bulb, which runs along a deep groove on the lateral side of the G1 basipodite, provides protection at the emergence of the penis; its distal end extends into a soft papilla inserted into a lateral foramen at the base of the G1 endopodite. G1 has a long protopodite consisting of an elongated coxopodite and a well-developed basipodite, which encircles most of the twisted endopodite. G2 also has a long protopodite (long coxopodite + basipodite) (Guinot *et al.* 2013). The long protopodites of both G1 and G2, which show a similar organisation in all dorippids, are related to the dorsal position of the first three pleonal somites. Such a disposition does not exist in any other eubrachyuran.

Coxo-sternal modalities of penis protection
Dorippidae does display a clear transformation series of the penial condition, from a nearly coxal condition in *Medorippe lanata* to a variously developed coxo-sternal condition in other species (Guinot *et al.* 2013: figs 15-19; Davie *et al.* 2015a: fig. 71-2.19H), corresponding to multistate characters of penis protection. In contrast, Ethusidae exclusively exhibits a single (probably with few variations, to be verified) coxo-sternal condition, with a single-part penis that is only obliquely inclined throughout (Guinot *et al.* 2013: figs 20-22). This unique arrangement, which is a synapomorphy of the Dorippidae, differs from the penis protection modalities encountered in other eubrachyurans, in which the penis usually runs along suture 7/8 and is protected within an invagination of sternite 8 that forms a gutter, as well as a varied juxtaposition of sternites 7 and 8 (Guinot *et al.* 2013: figs 8I-K, 24, 32A-E, 44B).

Female reproductive system (Figs 35; 37)
The female reproductive system of Eubrachyura was until now considered to follow the same common disposition, leading to internal fertilisation. A recently discovered new organisation (Hayer *et al.* 2016a; Vehof *et al.* 2017; 2018a, b; Vehof 2020), using modern analyses, presents a new challenge by revealing that the female reproductive system of Dorippidae is unique in the Eubrachyura in its wide diversity of systems of organisation and also deviates from the known types in the Brachyura. The dorippid disposition undoubtedly represents a new type of organisation unparalleled in the Brachyura. The five dorippid species studied show different fertilisation sites, with "a continuous spectrum from external to internal fertilisation" (Vehof 2020: 74).

Larval and post-larval features
Dorippid zoeae are so diverse that it is difficult to see a close relationship between them and the larvae of any other group of crabs, and the family is thought to have had an evolutionary history distinct from that of all brachyuran families (Rice 1980: fig. 22).

Sperm ultrastructure
In a cladistic analysis of sperm characters alone (Jamieson *et al.* 1995: fig. 1A), the majoids formed the plesiomorphic sister group to all other eubrachyurans, but in the combined analysis of morphological and sperm characters, it was *Neodorippe* that formed the plesiomorphic sister group to all other eubrachy-

urans studied (Jamieson *et al.* 1995: fig. 1B; see also Jamieson 1994: 390, 391; Jamieson & Tudge 2000). In comparison, the sperm characters of Hymenosomatidae, studied in two odiomarine species and *Elamena vesca* Ng &Richer de Forges, 1996, differed significantly in nine distinctive characters from those of all other brachyuran taxa investigated (Richer de Forges *et al.* 1997; Jamieson & Tudge 2000; Guinot 2011). A "majid-hymenosomatid" relationship was not supported by spermatozoal ultrastructure (Jamieson & Tudge 2000).

Carrying behaviour, burying and locomotion

Dorippoidea is unique among the Eubrachyura in that it has an elaborate carrying behaviour, combined with rapid and partial forward burying through the use of chelipeds: the body sinks into the sediment and the long P2 and P3 activate to penetrate the substrate. The Dorippidae and Ethusidae are the only carrier crabs within Eubrachyura whose carrying involves the last two pereiopods. In the Palicidae, carrying is performed exclusively by the P5. Carrying behaviour can be considered a relict behaviour. Forward locomotion (as opposed to sideways locomotion, the attribute of brachyuran crabs), often running - mixed preferentially with phases of lateral locomotion – using the chelipeds, P2 and P3, and forward burying in combination are not known in other Brachyura. A forward direction of locomotion direction, accompanied by a particular orientation of the legs, is a plesiomorphic feature found in many carrier podotremes (Homolodromiidae, Dromiidae, Homolidae) but without the rapid and partial burying forward as in the Dorippidae (Guinot *et al.* 2013: 252).

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REFERENCES

Abelló P. A., Valladares F. J. & Castellón A. 1988. — Analysis of the structure of decapod crustacean assemblages off the Catalan coast (North-West Mediterranean). *Marine Biology* 98: 39-49. https://doi.org/10.1007/BF00392657

Abelló P., Carbonell A. & Torres P. 2002. — Biogeography of epibenthic crustaceans on the shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications for the establishment of natural management areas. *Scientia Marina* 66: 183-198. https://doi.org/10.3989/scimar.2002.66s2183

Abrahamczik-Scanzoni H. 1942. — Beiträge zur Kenntniss der Muskulatur und des Innenskeletts der Krabben. *Zoologische Jahrbücher* 67 (3): 293-380.

Ahyong S. T. 2019. — The cymonomid crabs of New Zealand and Australia (Crustacea: Brachyura: Cyclodorripoida [sic]). *Records* *of the Australian Museum* 71 (2): 33-69. https://doi.org/10.3853/j.2201-4349.71.2019.1682

Ahyong S. T. & Ng P. K. L. 2008. — Deepwater crabs from seamounts and chemosynthetic habitats off eastern New Zealand (Crustacea: Decapoda: Brachyura). *Zootaxa* 1708: 1-72. https://doi.org/10.11646/zootaxa.1708.1.1

Ahyong S. T. & Ng P. K. L. 2009. — Aphanodactylidae, a new family of thoracotreme crabs (Crustacea: Brachyura) symbiotic with polychaete worms. *Zootaxa* 2289: 33-47. https://doi.org/10.11646/zootaxa.2289.1.3

Ahyong S. T. & Ng P. K. L. 2017. — East Asian Cymonomid Crabs (Crustacea: Brachyura). *Zoological Studies* 56: 1-20. https://doi.org/10.6620/ZS.2017.56-24

Ahyong S. T., Lai J. C. Y., Sharkey D., Colgan D. J. & Ng P. K. L. 2007. — Phylogenetics of the brachyuran crabs (Crustacea: Decapoda): the status of Podotremata based on small subunit nuclear ribosomal RNA. *Molecular Phylogenetics and Evolution* 45 (2): 576-586. https://doi.org/10.1016/j.ympev.2007.03.022

Aikawa H. 1937. — Further notes on brachyuran larvae. *Records of Oceanographic Works in Japan* 2 (1): 17-55.

Akash M., Tabassum A., Shafi S. M. & Biswas J. 2020. — Four new records of crabs (Brachyura, Dorippidae, Galenidae, Portunidae, Xanthidae) from the Bay of Bengal, Bangladesh. *Crustaceana* 93 (8): 867-879. https://doi.org/10.1163/15685403-bja10046

Alcock A. 1896. — The Brachyura Oxystoma: materials for a carcinological fauna of India, No. 2. *Journal of the Asiatic Society of Bengal* 65 (2): 134-296.

Alcock A. & Anderson A. R. 1894. — List of the shore and shallow-water Brachyura collected during the season 1893-1894. Natural History notes from H.M. Indian Marine Survey Steamer «Investigator», Commander C. F. Oldham, R.N., Commanding. Series n. No. 17. *Journal of the Asiatic Society of Bengal* 63 (Part 2: 4): 197-209.

Alcock A. & Anderson A. R. 1896. — *Illustrations of the Zoology of the Royal Indian Marine Surveying Steamer Investigator, under the command of Commander C.F. Oldham, R.N. Crustacea. Published under the Authority of Captain J. Hert, R.N., C.I.E., Director of the Royal Indian Marine.* Printed and sold by the Superintendent of Government Printing, Calcutta. Part IV: pls 16-27.

Al-Khafaji K., Al-Maliky T. H. Y. & Al-Maliky A. M. J. 2019. — First record of the crab, *Droippe* [sic] *quadridens* (Fabricius, 1793) (Brachyura: Dorippidae), from the Iraqi coastal waters of the NWArabian Gulf, with notes on the occurrence of seven species of crabs in the region. *Arthropods* 8 (4): 118-126.

Ando Y., Kawano S. & Ugi H. 2015. — Fossil stomatopods and decapods from the upper Pleistocene Ogushi Formation, Kyushu, Japan. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen* 276 (3): 303-313.

Ando Y., Ito T., Morik K., Kuma R. & Nishioka Y. 2022. — Ito's fossil decapod collections from the Holocene deposits in the Shimizu Port, Shizuoka City, Japan. *Bulletin of the Mizunami Fossil Museum* 49: 129-143.

André M. 1931. — Crustacés Décapodes provenant de l'Institut Océanographique de Nha-Trang (Annam). *Bulletin du Muséum national d'Histoire naturelle 2e série* 3 (7): 638-650.

André M. 1937. — Coquilles vides de Bivalves habitées par des Crustacés. *Journal de Conchyliologie* 81: 72-81.

André M. 1939. — Un crabe japonais à face humaine. *Sciences naturelles* 1: 169-170.

André M. 1958. — Les Crustacés dans les légendes anciennes et actuelles. *L'Ethnographie nlle sér.* 52: 107-131.

Anker A. & Paulay G. 2013. — A remarkable new crab-like hermit crab (Crustacea, Decapoda, Paguridae) from French Polynesia, with comments on carcinization in the Anomura. *Zootaxa* 3722: 283-300.

Antunes M., Zara F. J., López-Greco L. S. & Negreiros-Fransozo M. L. 2016. — Morphological analysis of the female reproductive system of *Stenorhynchus seticornis* (Brachyura: Inachoididae) and comparisons with other Majoidea. *Invertebrate Biology* 135 (2): 75-86. https://doi.org/10.1111/ivb.12118

Apel M. 2001. — *Taxonomie und Zoogeographie der Brachyura, Paguridea und Porcellanidae (Crustacea: Decapoda) des Persisch-Arabischen Golfes*. Doctoral thesis, Johann Wolfgang Goethe-Universität, Frankfurt am Main, 260 p.

Artal P. & Gilles A. 2007. — New Miocene crabs from Pignan (southeast France), *in* Garassino A., Feldmann R. M. & Teruzzi G. (eds), 3rd Symposium on Mesozoic and Cenozoic decapod crustaceans, Museo civico di Storia Naturale di Milano, 23-25 May, 2007. *Memorie della Società Italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* 35: 8-11.

Artal P., Ferratges F. A., Van Bakel B. W. M. & Zamora S. 2022. — A highly diverse dromioid crab assemblage (Decapoda, Brachyura) associated with pinnacle reefs in the lower Eocene of Spain. *Journal of Paleontology* 96 (3): 591-610. https://doi.org/10.1017/jpa.2021.114

Artüz M. L. 2007. — First record of *Medorippe lanata* (Linnaeus, 1767) in Sea of Marmara. *Zoonatantia*: 64-65.

Assugeni C. O. & Zara F. J. 2022. — Functional morphology of the seminal receptacle of *Mithrax*, *Mithraculus* and *Omalacantha* spider crabs (Brachyura: Mithracidae). *Tissue and Cell* 76: 101806. https://doi.org/10.1016/j.tice.2022.101806

Bachmayer F. & Rutsch R. F. 1962. — Brachyurenfunde (Crustacea) aus der miozänen Meeresmolasse der Schweiz. *Eclogae geologicae Helvetiae* 55 (2): 675-682.

Baldanza A., Bizzarri R., De Angeli A., Famiani F., Garassino A., Pasini G. & Pizzolato F. 2017. — A distinctive shallow marine crustacean fauna from the early Pleistocene of Poggi Gialli (Tuscany, central Italy): taxonomic inferences and palaeoenvironmental reconstruction. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 286 (1): 35-74. https://doi.org/10.1127/njgpa/2017/0685

Balss H. 1921. — Decapoda Anomura (Paguridea) und Brachyura (Dromiacea bis Brachygnatha I): Crustacea VI, *in* Michaelsen W. (ed.), *Beitrage zur Kenntnis der Meeresfauna Westafrikas* 3 (2). Hamburg: 38-67, figs 1-7.

Balss H. 1922. — Die Dromiaceen, 0xystomen und Parthenopiden. Ostasiatische Decapoden, III. *Archiv für Naturgeschichte* 88, Abteilung A, Heft 3: 104-140.

Balss H. 1940. — Decapoda. III. Morphologischer Teil, *in* Dr Bronn H. G. (ed.), *Klassen und Ordnungen des Tierreichs*. Fünfter Band, 1. Abteilung, 7. Buch, 1. Lieferung. Akademische Verlagsgesellschaft, Geest & Portig K.-G., Leipzig: 22-160.

Balss H. 1957. — Decapoda. VIII. Systematik, *in* Dr Bronn H. G. (ed.), *Klassen und Ordnungen des Tierreichs*. Fünfter Band, 1. Abteilung, 7. Buch, 12. Lieferung. Akademische Verlagsgesellschaft, Geest & Portig K.-G., Leipzig: 1505-1672. https://www.biodiversitylibrary.org/part/146103

Barnard K. H. 1950. — Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). *Annals of the South African Museum* 38: 1-837. https://biodiversitylibrary.org/page/40853502

Barnard K. H. 1955. — Additions to the fauna list of South African Crustacea and Pycnogonida. *Annals of the South African Museum* 43: 1-107.

Basso A., Babbucci M., Pauletto M., Riginella E., Patarnello T. & Negrisolo E. 2017. — The highly rearranged mitochondrial genomes of the crabs *Maja crispata* and *Maja squinado* (Majidae) and gene order evolution in Brachyura. *Scientific Reports* 7 (4096): 1-17. https://doi.org/10.1038/s41598-017-04168-9

Bauer R. T. 1986. — Phylogenetic trends in sperm transfer and storage complexity in decapod crustaceans. *Journal of Crustacean Biology* 6 (3): 313-325. https://doi.org/10.2307/1548173

Bauer R. T. 1994. — Usage of the terms thelycum and spermatheca in the reproductive morphology of the Decapoda, with special reference to the Penaeoidea. *Journal of Crustacean Biology* 14 (4): 715-721. https://doi.org/10.2307/1548864

Becker C. & Bauer R. T. 2020. — Multiple matings and sperm competition, *in* Thiell M. & Cothran R. D. (eds), *The Natural History of the Crustacea: Reproductive Biology*. Volume VI.

Oxford University Press: 332-363. https://doi.org/10.1093/oso/9780190688554.003.0012

Becker C. & Scholtz G. 2017. — Phylogenetic implications of sperm storage in Podotremata: histology and 3D-reconstructions of spermathecae and gonopores in female carrier crabs (Decapoda: Brachyura: Homoloidea). *Journal of Morphology* 278 (1): 89-105. https://doi.org/10.1002/jmor.20621

Becker C., Brandis D. & Storch V. 2011. — Morphology of the female reproductive system of European pea crabs (Crustacea, Decapoda, Brachyura, Pinnotheridae). *Journal of Morphology* 272: 12-26. https://doi.org/10.1002/jmor.10884

Bedini R., Canali M. G. & Bedini A. 2003. — Use of camouflaging materials in some brachyuran crabs of the Mediterranean infralittoral zone. *Cahiers de Biologie Marine* 44: 375-383.

Beleem I., Poriya P. & Gohil B. 2019. — An annotated checklist of marine brachyuran crabs of Gujarat waters, India. *Iranian Journal of Animal Biosystematics* 15 (1): 9-46.

Bell T. 1858. — *A Monograph of the Fossil Malacostracous Crustacea of Great Britain.* Part I. *Crustacea of the London Clay*. Monograph of the Palaeontographical Society, London 10 (for 1856), viii + 44 p. https://www.biodiversitylibrary.org/bibliography/11701

Bellwood O. 1996. — A phylogenetic study of the Calappidae H. Milne Edwards 1837 (Crustacea: Brachyura) with a reappraisal of the status of the family. *Zoological Journal of the Linnean Society* 118: 165-193. https://doi.org/10.1111/j.1096-3642.1996.tb00225.x

Bellwood O. 2002. —The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea: Brachyura). *Journal of Natural History* 36 (10): 1223-1238. https://doi.org/10.1080/00222930110048891

Beninger P. G., Elner R. W., Foyle T. P. & Odense P. H. 1988. — Functional anatomy of the male reproductive system and the female spermatheca in the snow crab *Chionoecetes opilio* (O. Fabricius) (Decapoda: Majidae) and a hypothesis for fertilization. *Journal of Crustacean Biology* 8 (3): 322-332. https://doi.org/10.2307/1548271

Bento M. & Paula J. 2018. — Keys and bibliography for the identification of larval stages of brachyuran crabs from the Western Indian Ocean. *Western Indian Ocean Journal of Marine Science* 17 (1): 13-51.

Beschin C. & De Angeli A. 2013. — *Cenomanocarcinus nammourensis* sp. nov. (Crustacea, Decapoda, Brachyura, Cenomanocarcinidae) del Cretaceo superiore (Cenomaniano) del Libano. *Lavori, Società Veneziana di Scienze Naturali* 38: 93-101.

Beschin C., Busulini A., Tessier G. & Zorzin R. 2019. — La fauna di crostacei dell'Eocene superiore di Parona di Verona (Italia nordorientale): nuovi ritrovamenti. *Bolletino del Museo di Storia Naturale di Venezia* 70: 71-142.

Biagi F., Sartor P., Ardizzone G. D., Belcari P., Belluscio A. & Serena F. 2002. — Analysis of demersal assemblages off the Tuscany and Latium coasts (north-western Mediterranean). *Scientia Marina* 66: 233-242.

Bhat M., Trivedi J. & Rivonker C. 2021. — *An annotated checklist of marine brachyuran crabs (Crustacea, Decapoda, Brachyura) from Goa, west coast of India with ten new records.* Proceedings of the "Marine Biology Research Symposium – MBRS 2021" Organized by Sathyabama Institute of Science and Technology, Chennai, in association with ICAR-National Bureau of Fish Genetic Resources, Lucknow. Taxonomy, Biodiversity and Conservation, TBC-111-0R: 26-44.

Bishop G. A. 1978. — Two new crabs, *Sodakus tatankayotankaensis* n. gen., n. sp. and *Raninella oaheensis* n. sp. (Crustacea, Decapoda), from the Upper Cretaceous Pierre Shale of South Dakota. *Journal of Paleontology* 52 (3): 608-617.

Boas J. E. V. 1880. — Studier over decapodernes slægtskabsforhold. *Kongelige Danske Videnskabernes Selskabs Skrifter, 6 Række, Naturvidenskabelig Mathematisk Afdeling* 1 (2): 23-210. https://www.biodiversitylibrary.org/part/161306

Borradaile L. A. 1903. — Marine Crustaceans. IV, Some Remarks on the Classification of the Crabs. V, The Crabs of the Catametope Families. VI, Oxystomata. VII, The Barnacles, *in* Gardiner J. S. (ed.), *The Fauna and Geography of the Maldive and Laccadive Archipelagoes, Being the Account of the Work Carried on and of the Collections Made by an Expedition During the Years 1899 and 1900.* 1 (4): 424-443, pl. 22. https://www.biodiversitylibrary.org/part/119088

Bouvier E.-L. 1896. — Sur l'origine homarienne des Crabes: étude comparative des Dromiacés vivants et fossiles. *Bulletin de la Socété philomatique de Paris sér. 8*, 8 (2) (1895-1896): 34-110.

Bouvier E.-L. 1897a. — Observations sur les crabes de la famille des Dorippidés. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences* (Paris) 125 (20): 784-787.

Bouvier E.-L. 1897b. — Sur la classification, les origines et la distribution des crabes de la famille des Dorippidés. *Bulletin de la Socété philomatique de Paris sér. 8*, 9 [1897]: 54-70. [sometimes erroneously dated 1898].

Bouvier E.-L. 1898. — Observations on the crabs of the family Dorippidae. *Annals and Magazine of Natural History ser. 7*, 1: 103-105. https://www.biodiversitylibrary.org/part/51567

Bouvier E.-L. 1899. — Sur une collection de Crustacés du Japon offerte au Muséum par M. Boucard. *Bulletin du Muséum d'Histoire naturelle* (Paris) 5: 173-176.

Bouvier E.-L. 1940. — Décapodes marcheurs, *in Faune de France*, 37. Paris, Lechevalier, 404 p. https://www.biodiversitylibrary.org/part/254827

Bracken H. D., Toon A., Felder D. L., Martin J. W., Finley M., Rasmussen J., Palero F. & Crandall K. A. 2009. — The decapod tree of life: compiling the data and moving toward a consensus of decapod evolution. *Arthropod Systematics & Phylogeny* 67: 99-116.

Braga-Henriques A., Carreiro-Silva M., Tempera F., Porteiro F. M., Jakobsen K., Jakobsen J., Albuquerque M. & Santos R. S. 2012. — Carrying behaviour in the deep-sea crab *Paromola cuvieri* (Northeast Atlantic). *Marine Biodiversity* 42 (1): 37-46. https://doi.org/10.1007/s12526-011-0090-3

Breton G. 2009. — Description of *Priscinachus elongatus* n. gen., n. sp., and Priscinachidae n. fam. for the earliest spider crab (Crustacea, Decapoda, Majoidea), from the French Cretaceous (Cenomanian). *Geodiversitas* 31: 509-523. https://doi.org/10.5252/g2009n3a2

Brocchi P. 1875. — Recherches sur les organes génitaux mâles des Crustacés Décapodes. *Annales de Sciences naturelles* (Zoologie) (6) 2: 1-131, pls 1-19.

Brockerhoff A. M. & McLay C. L. 2011. — Human-mediated Spread of Alien Crabs, *in* Galil B., Clark P. F. & Carlton J. T. (eds), *In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Invading Nature.* Springer Series in Invasion Ecology 6. Springer, Dordrecht, Heidelberg, London, New York: 27-106. https://doi.org/10.1007/978-94-007-0591-3_2

Burton M. 1969. — *Animal Partnerships*. Frederick Wame & Co., New York and London, 107 p.

Cano G. 1891. — Sviluppo postembrionale dei Dorippidei, Leucosiadi, Corystodei e Grapsidi. *Memorie di Matematica e di Fisica della Società Italiana delle Scienze ser. 3* 8 (4): 1-14.

Capart A. 1951a. — Liste des stations, *in Expédition océanographique Belge dans les eaux côtières africaines de l'Atlantique Sud (1948-1949).* Résultats Scientifiques, 1 (Annexe). Institut Royal des Sciences Naturelles de Belgique, Bruxelles: 1-65, 1 map, 1 pl. https://www.biodiversitylibrary.org/part/285922

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

Carter J. 1898. — A contribution to the palaeontology of the Decapod Crustacea of England. *Quarterly Journal of the Geological Society* London 54: 15-44. https://doi.org/10.1144/GSL.

JGS.1898.054.01-04.06

Casadío S., Feldmann R. M., Parras A. & Schweitzer C. E. 2005. — Miocene fossil Decapoda (Crustacea Brachyura) from Patagonia, Argentina, and their paleoecological setting. *Annals of Carnegie Museum* 74 (3): 151-188. https://doi.org/10.2992/0097-4463(2005)74[151:MFDCBF]2.0.CO;2

Castro P. 2000. — Crustacea Decapoda: A revision of the Indo-west Pacific species of palicid crabs (Brachyura Palicidae), in Crosnier A. (ed.), Résultats des Campagnes MUSORSTOM, vol. 21. Muséum national d'Histoire naturelle, Paris: 437-610. (*Mémoires du Muséum national d'Histoire naturelle* 184).

Castro P. 2005. — Crabs of the family Ethusinae Guinot, 1977 (Crustacea, Brachyura, Dorippoidea) of the Indo-West Pacific region. *Zoosystema* 27 (3): 499-600.

Castro P. 2010. — A new species and new records of palicoid crabs (Crustacea, Decapoda, Brachyura, Palicoidea, Palicidae, Crossotonotidae) from the Indo-West Pacific region. *Zoosystema* 32 (1): 73-86. https://doi.org/10.5252/z2010n1a3

Castro P. 2013. — Brachyuran crabs (Crustacea, Brachyura: Crossotonotidae, Ethusidae, Euryplacidae, Goneplacidae, Latreilliidae, Palicidae, Tetraliidae, Trapeziidae) of the MAINBAZA, MIRIKI, and ATIMO VATAE expeditions to the Mozambique Channel and Madagascar, *in* Ahyong S. T., Chan T.-Y., Corbari L. & Ng P. K. L. (eds), *Tropical Deep-Sea Benthos 27*. Muséum national d'Histoire naturelle, Paris (*Mémoires du Muséum national d'Histoire naturelle*; 204): 437-466.

Castro P. 2015. — Symbiotic Brachyura. (Chapter 71-10), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), Decapoda: Brachyura, *Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-1, Crustacea. Brill, Leiden and Boston: 543-581. https://doi.org/10.1163/9789004190832_012

Castro P. 2020. — Brachyuran crabs (Crustacea: Brachyura) of eleven families of Dorippoidea, Goneplacoidea, Homoloidea, Palicoidea, Pilumnoidea, and Trapezioidea from Papua New Guinea. in Corbari L., Ahyong S. T. & Chan T.-Y. (eds), *Deep-Sea Crustaceans from Papua New Guinea*. Tropical Deep-Sea Benthos 31. Muséum national d'Histoire naturelle, Paris: 141-205 (Mémoires du Muséum national d'Histoire naturelle; 213). https://doi.org/10.1163/9789004190832_012

Castro P. & Naruse T. 2014. — New species of *Latreillopsis* Henderson, 1888 (Brachyura: Homolidae) and *Neopalicus* Moosa & Serène, 1981 (Brachyura: Palicidae) from the Hawaiian Islands. *Zootaxa* 3764 (2): 169-180. https://doi.org/10.11646/zootaxa.3764.2.4

Çelik E. S., Ateş A. Ş. & Akbulut M. 2007. — A Survey on the Brachyura (Crustacea, Decapoda) in the Dardanelles. *Turkish Journal of Zoology* 31: 181-183.

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

Charbonnier S. & Garassino A. 2022. — Fossil Decapod Crustacea in the historical collections. (*Mémoires du Muséum national d'Histoire naturelle,* 216): 1-292.

Charbonnier S., Audo D., Garassino A. & Hyžný M. 2017. — Fossil Crustacea of Lebanon. (*Mémoires du Muséum national d'Histoire naturelle*; 210): 1-248.

Chen H. 1980. — Two new species of crabs from South China Sea. *Oceanologia et Limnologia Sinica* 11 (2): 154-160, pls 1-2 (In Chinese with English abstract).

Chen H. 1986a. — Decapod Crustacea: Dorippidae, *in* Crosnier A. (ed.), Résultats des Campagnes MUSORSTOM I et II. Philippines (1976, 1980), vol. 2. (*Mémoires du Muséum national d'Histoire naturelle Série A* – Zoologie; 133 (5) [1985]): 179-203, 2 pls.

Chen H. 1986b. — Studies on the Dorippidae (Crustacea, Brachyura) of Chinese waters. *Transactions of the Chinese Crustacean Society* 1: 118-139 (In Chinese with English abstract).

Chen H. 1988. — Dorippidae (Crustacea Decapoda Brachyura) collected in Madagascar waters. *Bulletin du Muséum national d'Histoire naturelle 4e série* 9A (3) [1987]: 677-693.

Chen H. 1993. — Crustacea Decapoda: Dorippidae of New Caledonia, Indonesia and the Philippines, *in* Crosnier A. (ed.), Résultats des Campagnes MUSORSTOM, vol. 10. (*Mémoires du Muséum national d'Histoire naturelle*; 156): 315-345.

Chen H. & Sun H. 2002. — Brachyura. Marine primitive crabs, *in Fauna Sinica, Invertebrata*, vol. 30. *Arthropoda, Crustacea*. Academia Sinica, Science Press, Beijing, China, xiii + 597 p. (In Chinese with English abstract). https://www.biodiversitylibrary.org/part/119053

Chen H. & Xu Z. 1991. — Study on the crabs of the Nansha Islands, China, *in Studies on the Marine Organisms of the Nansha Islands and Surrounding Seas* 3: 48-108 (In Chinese with English abstract).

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

Chertoprud E. S., Spiridonov V. A., Ponomarev S. A. & Mokievsky V. O. 2012. — Commercial crabs (Crustacea Decapoda Brachyura) from Nhatrang Bay (Vietnam), Chapter 6 *in* Britayev T. A. & Pavlov D. S. (eds), *Benthic fauna of the Bay of Nhatrang, Southern Vietnam*. Vol. 2. Moscow, KMK Scientific Press Ltd.: 289-338. https://doi.org/10.1016/j.gene.2018.06.088

Chopra B. N. 1935. — Further Notes on Crustacea Decapoda in the Indian Museum. III. On the Decapod Crustacea collected by the Bengal Pilot Service off the Mouth of the River Hughli. Dromiacea and Oxystomata. *Records of the Indian Museum* 35 (1): 25-52.

Chou W.-R., Lai S.-H. & Fang L.-S. 1999. — Benthic crustacean communities in waters of southwestern Taiwan and their relationships to environmental characteristics. *Acta Zoologica Taiwanica* 10: 25-35.

Chu K. H., Tsang L. M., Lai J. C. Y., Ahyong S. & Ng P. K. L. 2009a. — Molecular phylogeny of the true crabs (Crustacea: Decapoda: Brachyura) with an estimation of divergencetime for the major lineages. *Integrative and Comparative Biology* 49: E212. [Poster abstract.]

Chu K. H., Tsang L. M., Ma K. Y., Chan T.-Y. & Ng P. K. L 2009b. — Decapod phylogeny: what can protein-coding genes tell us?, *in* Martin J. W., Crandall K. A. & Felder D. L. (eds), *Decapod Crustacean Phylogenetics.* Crustacean Issues. Taylor & Francis, CRC Press, Boca Raton, Florida 18: 89-99.

Chu K. H. C., Schubart C. D., Shih H.-T. & Tsang L. M. 2015. — Genetic diversity and evolution of Brachyura (Chapter 71-13), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9, Part C, 2 vols, *Crustacea*. Brill, Leiden and Boston: 775-820. https://doi.org/10.1163/9789004190832_016

Ciércoles C., García-Ruíz C., Abelló P., Hidalgo M., Torres P., González M., Mateo-Ramírez A. & Rueda J. L. 2022. — Decapod crustacean assemblages on trawlable grounds in the northern Alboran Sea and Gulf of Vera. *Scientia Marina* 86 (3): e039. https://doi.org/10.3989/scimar.05265.039

Clark P. F. & Webber W. R. 1991. — A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura). *Journal of Natural History* 25: 1259-1279. https://doi.org/10.1080/00222939100770781

Clark P. F., Fujita Y., Ball A. D. &. Ng P. K. L. 2012. — The first zoeal stage morphology of *Crossotonotus spinipes* (De Man, 1888) and *Pseudopalicus serripes* (Alcock & Anderson, 1895), with implications for palicoid systematics (Crustacea: Brachyura: Palicoidea). *Zootaxa* 3367: 191-203. https://doi.org/10.11646/zootaxa.3367.1.18

COLAVITE J., LÓPEZ R., HERNÁNDEZ J., BOLAÑOS J. & SANTANA W. 2016. — First zoeal stage of *Macrocoeloma subparallelum* (Stimpson, 1860) (Decapoda: Brachyura: Majoidea) described from laboratory hatched material. *Nauplius* 24: e2016016. https://doi.org/10.1590/2358-2936e2016016

COLAVITE J., WINDSOR A. & SANTANA W. 2019. — Three new species and a new genus of majoid crabs from the eastern Pacific (Decapoda, Brachyura). *ZooKeys* 825: 1-24. https://doi.org/10.3897/zookeys.825.32271

COLLINS J. S. H. 2003. — A taxonomic review of British decapod Crustacea. *Bulletin of the Mizunami Fossil Museum* 29 [2002]: 81-92.

COLLINS J. & JAKOBSEN S. L. 2004. — New crabs (Crustacea, Decapoda) from the Eocene (Ypresian/Lutetian) Lillebælt Clay Formation of Jutland, Denmark. *Bulletin of the Mizunami Fossil Museum* 30 (for 2003): 63-96.

COLLINS J. S. H. & SMITH R. 1993. — Ypresian (Lower Eocene) crabs (Decapoda, Crustacea) from Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 63: 261-270.

COLLINS J. S. H., FRAAYE R. H. B. & JAGT J. W. M. 1995. — Late Cretaceous anomurans and brachyurans from the Maastrichtian type area. *Acta Palaeontologica Polonica* 40 (2): 165-210.

COLLINS J. S. H., KANIE Y. & KARASAWA H. 1993. — Late Cretaceous crabs from Japan. *Transactions and Proceedings of the Palaeontological Society of Japan (New Series)* 172: 292-310.

COLLINS J. S. H., LEE C. & NOAD J. 2003. — Miocene and Pleistocene crabs (Crustacea, Decapoda) from Sabah and Sarawak. [Systematic Palaeontology by Collins J. S. H.]. *Journal of Systematic Paleontology* 1 (3): 187-226. https://doi.org/10.1017/S1477201903001068

COLLINS J. S. H., MELLISH C. J. T., ROSS A. J., CRABB P. R. & DONOVAN S. K. 2020. — A guide to the fossil Decapoda (Crustacea: Axiidea, Anomura, Brachyura) of the British Isles. *Proceedings of the Geologists' Association* 131: 19e50.

CRANDALL K. A., PORTER M. L. & PÉREZ-LOSADA M. 2009. — Crabs, shrimps, and lobsters (Decapoda), *in* HEDGES B. S. & KUMAR S. (eds), *The Timetree of Life*. Oxford University Press: 293-297.

CRÔNIER C. & BOURSICOT P.-Y. 2009. — A new decapod crustacean faunule from the Middle Jurassic of north-west France. *Palaeontology* 52: 1275-1289.

CROSNIER A. 1964. — Fonds de pêche le long des côtes de la République fédérale du Cameroun. *Cahiers ORSTOM* (*série Océanographie)* N° Spécial: 1-133.

CROSNIER A. 1970. — Crustacés Décapodes brachyoures et macroures recueillis par 1' « Undaunted » au sud de l'Angola: description de *Scyllarus subarctus* sp. nov. *Bulletin du Muséum national d'Histoire naturelle* 2^e *série* 41 (5) [1969]: 1214-1227. https://www.biodiversitylibrary.org/page/55600202

CUMBERLIDGE N., JOHNSON E. C., LEEVER E. M., SOMA J. B., AHLES K. M., KAMANLI S. A. & CLARK P. F. 2021. — The significance of female dimorphic characters of primary freshwater crabs for the systematics of Eubrachyura (Crustacea: Decapoda: Brachyura). *Journal of Crustacean Biology* 41 (4): 1-27. https://doi.org/10.1093/jcbiol/ruab058

DAI A. & SONG Y. 1986. — Intertidal crabs from Beibu Gulf of Guangxi. *Transactions of the Chinese Crustacean Society* 1: 54-62 (In Chinese with English abstract).

DAI A. & YANG S. 1991. — *Crabs of the China Seas*. China Ocean Press, Beijing and Springer-Verlag, Berlin Heidelberg New York Tokyo, English edition. (Translation from Chinese original 1986): 1-682, figs 1-295, pls 1-74.

DAI A.-Y., YANG S.-L., SONG Y.-Z. & CHEN G.-X. 1986. — *Crabs of the China Seas*. China Ocean Press, Beijing, 11 + 642 p. (In Chinese).

DANA J. D. 1851. — On the markings of the carapax of crabs. *American Journal of science and arts 2e sér.* 11 (31): 95-99.

DANA J. D. 1852. — Crustacea. Part I. *United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U. S. N.* Volume 13. Sherman, Philadelphia: i-viii, 1-685. https://www.biodiversitylibrary.org/bibliography/57937

DANA J. D. 1853. — *On the classification and geographical distribution of Crustacea from the report on Crustacea of the United States exploring expedition, under Captain Charles Wilkes, U. S. N., during the years 1838-1842. A review of the classification of the Crustacea, with references to certain principles of classification*. C. Sherman, Philadelphia: 1395-1450.

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

DAVIE P. J. F., GUINOT D. & NG P. K. L. 2015a. — Anatomy and functional morphology of Brachyura (Chapter 71-2), *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-I. Brill, Leiden and Boston: 11-163. https://doi.org/10.1163/9789004190832_004

DAVIE P. J. F., GUINOT D. & NG P. K. L. 2015b. — Phylogeny of Brachyura (Chapter 71-16) *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-1. Brill, Leiden and Boston: 921-979. https://doi.org/10.1163/9789004190832_004

DAVIE P. J. F., GUINOT D. & NG P. K. L. 2015c. — Systematics and classification of Brachyura (Chapter 71-18), *in* CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9 Part C, 2 vols, *Crustacea*. Brill, Leiden and Boston: 1049-1130. https://doi.org/10.1163/9789004190832_021

DAVIE P. J. F., NG P. K. L., KAENPHET A. & AUNGTONYA C. 2002. — Annotated checklist of Brachyura (Crustacea: Decapoda) principally obtained during the BIOSHELF survey off western Thailand from 1996-1998. *Phuket Marine Biological Center Research Bulletin* Spec. Publ., 23: 313-339.

DAVIS K. E., DE GRAVE S., DELMER C., PAYNE A. R. D., MITCHELL S. & WILLS M. A. 2022. — Ecological transitions and the shape of the decapod tree of life. *Integrative and Comparative Biology* 62 (2): 332-344. https://doi.org/10.1093/icb/icac052

DAWYDOFF M. C. 1952. — Contribution à l'étude des invertébrés de la faune marine benthique de l'Indochine. *Bulletin Biologique de la France et de la Belgique* Supplement 37: 1-158.

DAWSON J. & GRIFFITHS C. L. 2012. — Revision of the crown crabs, genus *Hymenosoma* (Crustacea: Hymenosomatidae), of South Africa. *African Natural History* 8: 17-29.

DE ANGELI A. 2016. — Nuovi crostacei Cymonomidae (Decapoda: Brachyura) dell'Eocene dei Monti Berici (Vicenza, Italia settentrionale). *Studi Trentini di Scienze Naturali* 95: 25-32.

DE ANGELI A. & BESCHIN C. 2008. — Crostacei decapodi dell'Oligocene di Soghe e Valmarana (Monti Berici, Vicenza - Italia settentrionale). *Studi e Ricerche, Associazione Amici del Museo, Museo civico "G. Zannato", Montecchio Maggiore* (Vicenza) 15: 15-39.

DE ANGELI A. & CECCON L. 2014. — Nuovi crostacei brachiuri (Decapoda) dell'Eocene inferiore di Monte Magrè (Vicenza, Italia settentrionale). *Lavori, Società Veneziana di Scienze Naturali* 39: 77-92.

DE ANGELI A. & GARASSINO A. 2006. — Catalog and bibliography of the fossil Stomatopoda and Decapoda from Italy. *Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* 35: 1-95.

DE ANGELI A. & GARASSINO A. 2021. — Report of ethusid crabs (Brachyura, Ethusidae) from the late Eocene of San Feliciano hill (Monti Berici, Vicenza, NE Italy). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 301 (1): 17-23. https://doi.org/10.1127/njgpa/2021/0995

De Angeli A., Garassino A. & Pasini G. 2009. — New reports of anomurans and brachyurans from the Cenozoic of Tuscany (Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 150 (2): 163-196.

De Angeli A., Garassino A. & Pasini G. 2019. — Catalog and bibliography of fossil Stomatopoda and Decapoda from Italy (2007-2018). *Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 45: 1-86.

De Angeli A., Garassino A. & Ceccon L. 2010. — New report of the coral-associated decapods from the 'Formazione di Castelgomberto' (early Oligocene) (Vicenza, NE Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 151 (2): 145-177.

Defrance J. L. M. 1819. — *Dorippe*. (Foss.), *in Dictionnaire des Sciences naturelles* 13. Strasbourg et Paris: 444-445.

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

De Haan W. 1833-1849. — Crustacea, *in* Von Siebold P. F., *Fauna Japonica sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India batava Imperium tenent, suscepto, annis 1823-1830 collegit, notis, observationibus et adumbrationibus illustravit*. Lugduni Batavorum, Leiden, 1839, fasc. 4: 73-108, pls 25-32, G, H; 1841, fasc. 5: 109-164, pls 33-37, 39-42, 47; 1849, fasc. 7: 197-243, i-xxxi. https://biodiversitylibrary.org/page/53607674

De Matos-Pita S. S., Castillo S. & Ramil F. 2017. — Contribution to the knowledge of the deep brachyuran fauna (Crustacea: Decapoda) in waters off Mauritania (NW Africa). *Journal of the Marine Biological Association of the United Kingdom* 97 (6): 1273-1305. https://doi.org/10.1017/S002531541600062X

Desmarest A.-G. 1817. — Crustacés fossiles. *Nouveau Dictionnaire d'Histoire naturelle, Appliquée aux Arts, à l'Agriculture, à l'Économie rurale et domestique, à la Médecine, etc.* Déterville, Paris. 8: 495-519. https://www.biodiversitylibrary.org/bibliography/66799

Desmarest A.-G. 1822. — Les Crustacés proprement dits, *in* Brongniart A. & Desmarest A.-G. (eds), *Histoire naturelle des Crustacés Fossiles, sous les Rapports Zoologiques et Géologiques*. F.-G. Levrault, Paris: 67-154, pls 5-11.

Dessouassi C. E., Chikou A., Lederoun D., Adandedjan D., Gangbe L. & Laleye P. 2018. — Diversity, biology and exploitation of brackish water crabs in West Africa: A review. *International Journal of Biological and Chimical Sciences* 12 (5): 2355-2370. https://doi.org/10.4314/ijbcs.v12i5.34

Dev Roy M. K. 2008. — An annotated checklist of mangrove and coral reef inhabiting Brachyuran crabs of India. *Records of Zoological Survey of India* Occasional Paper, 289: 1-212.

Dev Roy M. K. & Bhadra S. 2011. — Brachyuran crabs (Crustacea: Decapoda: Brachyura), *in* Director, Zoological Survey of India, Kolkata (ed.), *Fauna of Tamil Nadu. State Fauna Series, 17. Part 2*. Zoological Survey of India, Kolkata: 109-269.

Dev Roy M. K. & Nandi N. C. 2001. — Crustacean biodiversity in mangrove ecosystems of Sundarbans and Bay Islands. *Bulletin of the National Institute of Ecology* 11: 9-23.

Dev Roy M. K. & Nandi N. C. 2007. — Brachyuran diversity in coastal ecosystems of Tamil Nadu. *Journal of Environment and Sociobiology* 4 (2): 169-192.

Dev Roy M. K. & Nandi N. C. 2008. — Checklist and distribution of Brachyuran crabs of West Bengal. *Journal of Environment and Sociobiology* 5 (2): 191-214.

Dev Roy M. K. & Rath S. 2017. — An inventory of crustacean fauna from Odisha Coast, India. *Journal of Environment and Sociobiology* 14 (1): 49-112.

Devi S. S. & Kumar A. B. 2017. — On two species of crabs (Decapoda, Brachyura): *Cycloes marisrubri* Galil & Clark, 1996 (Calappidae) and *Dorippoides nudipes* Manning & Holthuis, 1986 (Dorippidae) from India. *Crustaceana* 90 (5): 625-630. https://doi.org/10.1163/15685403-00003670

Diesel R. 1989. — Structure and function of the reproductive system of the symbiotic spider crab *Inachus phalangium* (Decapoda: Majidae): observations on sperm transfer, sperm storage, and spawning. *Journal of Crustacean Biology* 9 (2): 266-277. https://doi.org/10.2307/1548506

Diesel R. 1991. — Sperm competition and the evolution of mating behaviour in Brachyura, with special reference to spider crabs (Decapoda Majidae), *in* Bauer R. T. & Martin J. W. (eds), *Crustacean Sexual Biology*. Columbia University Press, New York: 145-163. https://doi.org/10.7312/baue90796-010

Do Van Nhuong, Tran Duc Hau, Nguyen Duc Hung & Tran Nam Hai 2021. — Community structure and ecological distribution of benthic animals in Tien Hai mangrove forest, Northern Vietnam. *Academia Journal of Biology* 43 (3): 95-112. https://doi.org/10.15625/2615-9023/14941

Döderlein L. 1883. — Faunistische Studien in Japan. Enoshima und die Sagami-Bai. *Archiv fur Naturgeschichte* 49 (1): 102-103, pl. 2.

Doflein F. 1904. — Brachyura, *in* Chun C., *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia", 1898-1899*. Vol. 6. Jena, xiv + 314 p., figs 1-68. Atlas, 58 pls. https://www.biodiversitylibrary.org/part/119053

Drach P. & Guinot D. 1982. — Connexions morphologiques et fonctionnelles d'un type nouveau dans le squelette des Brachyoures du genre *Paradasygius* [sic] Garth (carapace, pleurites, sternites, pléon). *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences Série 3, Sciences de la vie* 295: 715-720. https://gallica.bnf.fr/ark:/12148/bpt6k5673614d/f237.item

Drach P. & Guinot D. 1983. — Les Inachoididae Dana, famille de Majoidea caractérisée par des connexions morphologiques d'un type nouveau entre carapace, pleurites, sternites et pléon (Crustacea Decapoda). *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences Série 3, Sciences de la vie* 297: 37-42.

Drach P. & Jacques F. 1982. — Dispositifs tégumentaires dorsaux liés aux mouvements de l'abdomen chez les Crustacés Décapodes. *Bulletin de la Société zoologique de France* 107 (1): 127-135.

Dubois A. 2012. — The distinction between introduction of a new nomen and subsequent use of a previously introduced nomen in zoological nomenclature. *Bionomina* 5: 57-80. https://doi.org/10.11646/bionomina.5.1.2

Eberhard W. G. 1985. — *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, MA – Science, xii + 244 p.

Edgar R. C. 2004. — MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32 (5): 1792-1797. https://doi.org/10.1093/nar/gkh340

Edkins M. D., Teske P. R., Papadopoulos I. & Griffiths C. L. 2007. — Morphological and genetic analyses suggest that Southern African crown crabs, *Hymenosoma orbiculare*, represent five distinct species. *Crustaceana* 80 (6): 667-683. https://doi.org/10.1163/156854007781360694

El Lakhrach H., Hattour A., Jarboui O., Elhasni K. & Ramos-Espla A. A. 2012. — Spatial distribution and abundance of the megabenthic fauna community in Gabes gulf (Tunisia, eastern Mediterranean Sea). *Mediterranean Marine Science* 13 (1): 12-29. https://doi.org/10.12681/mms.19

Elner R. W. & Beninger P. G. 1992. — The reproductive biology of snow crab, *Chionoecetes opilio*: a synthesis of recent contributions. *American Zoologist* 32: 524-533. https://doi.org/10.1093/icb/32.3.524

Emmerson W. D. 2016. — *A Guide to, and Checklist for, the Decapoda of Namibia, South Africa and Mozambique*. Cambridge Scholars Publishing. Volume 2, x + 745 p.

Eisner T. 2003. — *For love of insects*. Harvard University Press, Cambridge, MA: 1-448. https://www.biodiversitylibrary.org/part/347752

ESTAMPADOR E. P. 1937. — A check list of the Philippine Crustacean Decapods. *The Philippine Journal of Science* 62 (4): 465-559.

ESTAMPADOR E. P. 1959. — Revised check list of Philippine Crustacean Decapods. *Natural and Applied Science Bulletin* (Quezon City, Philippines) 17 (1): 1-127.

EVANS N. 2018. — Molecular phylogenetics of swimming crabs (Portunoidea Rafinesque, 1815) supports a revised family-level classification and suggests a single derived origin of symbiotic taxa. *PeerJ* 6: e4260. https://doi.org/10.7717/peerj.4260

EWERS-SAUCEDO C., HAYER S. & BRANDIS D. 2015. — Functional morphology of the copulatory system of box crabs with long second gonopods (Calappidae, Eubrachyura, Decapoda, Crustacea). *Journal of Morphology* 276 (5): 517-525. https://doi.org/10.1002/jmor.20322

EWERS-SAUCEDO C., WARES J. P., HANEL R. & BRANDIS D. 2016. — Evolution of male copulatory organs in box crabs (Crustacea, Brachyura, Calappidae). *Journal of Crustacean Biology* 36 (6): 804-814. Https://doi.org/10.1163/1937240X-00002479 https://doi.org/10.1163/1937240X-00002479

FABRICIUS J. C. 1793. — *Entomologia Systematica Emendata et Aucta. Secundum Classes, Ordines, Genera, Species. Adjectis Synonimis, Locis, Observationibus, Descriptionibus.* Hafniae, vii + 519.

FABRICIUS J. C. 1798. — *Supplementum Entomologiae Systematicae.* Hafniae, 572 p. https://www.biodiversitylibrary.org/bibliography/123559

FAN Y., LI X., SONG L. & CAI Z. 2004. — Phylogenetic relationships of five species of Dorippinae (Crustacea, Decapoda) revealed by 16S rDNA sequence analysis. *Acta Oceanologica Sinica* 23 (3): 513-519.

FANELLI E., COLLOCA F. & ARDIZZONE G. 2007. — Decapod crustacean assemblages off the West coast of central Italy (western Mediterranean). *Scientia Marina* 71 (1): 19-28. https://doi.org/10.3989/scimar.2007.71n119

FARIAS N. E., SPIVAK E. D. & LUPPI T. A. 2017. — Functional morphology of the female reproductive system of a crab with highly extensible seminal receptacles and extreme sperm storage capacity. *Journal of Morphology* 278 (7): 919-935. https://doi.org/10.1002/jmor.20685

FAUTIN D. G., TAN R., YAP W. L. N., TAN S. H., CROWTHER A., GOODWILL R., SANPANICH K. & TAY Y. C. 2015. — Sea anemones (Cnidaria: Actiniaria) of Singapore: shallow-water species known also from the Indian subcontinent. *Raffles Bulletin of Zoology* Supplement 31: 44-59.

FAUVEL A. A. 1880. — Promenades d'un naturaliste dans l'archipel des Chusan et sur les côtes du Chekiang (Chine). (Suite). *Mémoires de la Societé des Sciences naturelles et mathémathiques*, Cherbourg, 23: 29-201, 2 pls.

FELDER D. L., MARTIN J. W. & GOY J. W. 1985. — Patterns in early postlarval development of decapods, *in* WENNER A. M. (ed), *Crustacean Issue 2, Larval Growth*. A. A. Balkema, Rotterdam.

FENIZIA G. 1937. — Sull'istinto di mascheramento dell'*Ethusa mascarone* Herbst. *Bulletin de l'Institut océanogaphique de Monaco* 732: 1-15.

FERRATGES F. A., ZAMORA S. & AURELL M. 2022. — Systematics and paleoecology of a new species of Varunidae H. Milne Edwards, 1853 (Decapoda: Brachyura) from the lower Eocene of Spain. *Journal of Crustacean Biology* 42 (2): 1-9. https://doi.org/10.1093/jcbiol/ruac013

FOREST J. & GUINOT D. 1966. — Campagne de la *Calypso* dans le Golfe de Guinée et aux îles Principe, São Tomé et Annobon (1956). 16. Crustacés Décapodes: Brachyoures, *in* Résultats scientifiques des campagnes de la «Calypso», fasc. 7. *Annales de l'Institut océanographique de Monaco* 44: 23-124.

FÖRSTER R. 1979. — Decapod crustaceans from the Middle Miocene (Badenian) deposits of Southern Poland. *Acta Geologica Polonica* 29: 89-106.

FÖRSTER R. 1985. — Evolutionary trends and ecology of Mesozoic decapod crustaceans. *Transactions of the Royal Society of Edinburgh* 76: 299-304. https://doi.org/10.1017/S0263593300010518

FRAAYE R. H. B. 1996. — Late Cretaceous swimming crabs: radiation, migration, competition, and extinction. *Acta Geologica Polonica* 46 (3/4): 269-278.

FRAAIJE R. H. B., MENKVELD-GFELLER U. E., VAN BAKEL B. W. M. & JAGT J. W. M. 2010. — Decapod crustaceans from the type area of the Helvetian Stage (lower Miocene) in the Bern area, Switzerland. *Bulletin of the Mizunami Fossil Museum* 36: 1-11.

FRANSEN C. H. J. M., HOLTHUIS L. B. & ADEMA J. P. H. M. 1997. — Type-Catalogue of the Decapod Crustacea in the collections of the Nationaal Natuurhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandlingen* 311: i-xvi, 1-344.

FRANȚESCU O. D. 2011. — Brachyuran decapods (including five new species and one new genus) from Jurassic (Oxfordian- Kimmeridgian) coral reef limestones from Dobrogea, Romania. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 259: 271-297. https://doi.org/10.1127/0077-7749/2010/0110

GALIL B. S. 2005. — *Dorippe quadridens* (Decapoda, Dorippidae) - first record of alien dorippid in the Mediterranean Sea. *Crustaceana* 78 (4): 497-498. https://doi.org/10.1163/1568540054473576

GALIL B. S. 2011. — The Alien Crustaceans in the Mediterranean Sea: An Historical Review, *in* GALIL B., CLARK P. F. & CARLTON J. T. (eds), *In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Invading Nature.* Springer Series in Invasion Ecology 6. Springer, Dordrecht, Heidelberg, London, New York: 377-401. https://doi.org/10.1007/978-94-007-0591-3_13

GALIL B. S. & SHLAGMAN A. 2010. — An annotated list of the decapod Crustacea of the Mediterranean coast of Israel — half a century later, *in* FRANSEN C. H. J. M., DE GRAVE S. & NG P. K. L. (eds), *Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume*. Crustaceana Monographs. Fransen C. H. J. M. & von Vaupel Klein J. C. (series eds), Vol. 14. Brill, Leiden: 269-281. https://doi.org/10.1163/9789047427759_018

GARASSINO A. & LARGHI C. 2000. — *The brachyurans of the Cenomanian (Upper Cretaceous) of Lebanon*. 1st Workshop on Mesozoic and Tertiary Decapod Crustaceans, Studi e Ricerche, Associazione Amici del Museo, Museo Civico "G. Zannato", October 6th-8th 2000, Montecchio Maggiore: 53-54.

GARASSINO A., DE ANGELI A., GALLO L. M. & PASINI G. 2004. — Brachyuran and anomuran fauna from the Cenozoic of Piedmont (NW Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 145 (2): 251-281.

GARASSINO A., DE ANGELI A. & PASINI G. 2007. — New decapod assemblage from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, southeastern Morocco. 3rd Symposium on Mesozoic and Cenozoic Decapod Crustaceans. Museo di Storia Naturale di Milano, May 23-25, 2007. *Memorie della Società italiana di Scienze Naturali e del Museo civico di Storia naturale di Milano* 35 (2): 45-47.

GARASSINO A., DE ANGELI A. & PASINI G. 2008. — New decapod assemblage from the Upper Cretaceous (Cenomanian-Turonian) of Gara Sbaa, southeastern Morocco. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 49 (1): 37-67.

GARASSINO A., PASINI G., DE ANGELI A., CHARBONNIER S., FAMIANI F., BALDANZA A. & BIZZARRI R. 2012. — The decapod community from the Early Pliocene (Zanclean) of "La Serra" quarry (San Miniato, Pisa, Toscana, central Italy): sedimentology, systematics, and palaeoenvironmental implications. *Annales de Paléontologie* 98: 1-61. https://doi.org/10.1016/j.annpal.2012.02.001

GARASSINO A., DE ANGELI A. & & PASINI G. 2014a. — A new porcellanid genus (Crustacea, Decapoda) to accommodate the Late Cretaceous *Paragalathea africana* Garassino, De Angeli & Pasini, 2008 from southeast Morocco, *in* FRAAIJE R. H. B., HYŽNÝ M., JAGT J. W. M., KROBICKI M. & VAN BAKEL B. W. M. (eds), Proceedings of the 5th Symposium on Mesozoic and Cenozoic

Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geologica* 147: 117-124.

Garassino A., Pasini G., De Angeli A. & Hyžný M. 2014b. — The decapod fauna (Axiidea, Anomura, Brachyura) from the Late Pleistocene of Trumbacà, Reggio Calabria (Calabria, southern Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 1 (2): 119-130.

Garcia Bento M. A., Miranda I., Mantelatto F. L. & Zara F. J. 2019a. — Comparative spermatozoal ultrastructure and molecular analysis in dromiid crabs and their phylogenetic implications for Dromiidae and Podotremata (Decapoda: Brachyura). *Arthropod Structure & Development* 47 (6): 627-642.

Garcia Bento M. A., López Greco L. S. & Zara F. J. 2019b. — Seminal fluid production and sperm packaging in dromiid crabs (Brachyura, Podotremata). *Zoology* 132: 17-30. https://doi.org/10.1016/j.zool.2018.09.001

Garcia Bento M. A., López Greco L. S., Mantelatto F. L. & Zara F. J. 2022. — From copula to fertilization: the reproduction of primitive crab *Hypoconcha parasitica* (Linnaeus, 1763) (Podotremata: Dromiidae). *Anatomical Record*: 1-15. https://doi.org/10.1002/ar.24920

García-Isarch E. & Muñoz I. 2015. — Biodiversity and biogeography of decapod crustaceans in the Canary Current Large Marine Ecosystem, *in* Valdés L. & Déniz-González I. (eds), *Oceanographic and biological features in the Canary Current Large Marine Ecosystem*. IOC Technical Series No. 115: 257-271. http://hdl.handle.net/10508/9566

Garstang W. 1897. — Contributions to marine bionomics. II. The function of antero-lateral denticulations of the carapace in sand-burrowing crabs. *Journal of the Marine Biological Association of the United Kingdom* 4: 396-401. https://doi.org/10.1017/S002531540000552X

Gemmellaro M. 1914. — Crostacei e pesci fossili del "Piano Siciliano" dei dintomi di Palermo. *Giornale della Società di scienze naturali ed economiche di Palermo* 30: 75-94.

Gilet M. 1952. — Métazoé de *Dorippe lanata* (Linné) et sa mégalope. *Vie et Milieu* 3 (4): 415-420.

Giusberti L., Fornasiero M. & Zorzin R. 2014. — The Pesciara-Monte Postale Fossil-Lagerstätte: 4. The "minor fauna" of the laminites, *in* Papazzoni C. A., Giusberti L., Carnevale G., Roghi G., Bassi D. & Zorzin R. (eds), *The Bolca Fossil-Lagerstätten: A window into the Eocene World. Rendiconti della Società Paleontologica Italiana* 4: 73-87.

Glaessner M. F. 1929. — *Crustacea Decapoda*, *in* Pompeckj J. F. (ed.), *Fossilium Catalogus, I. Animalia. Pars 41*. W. Junk, Berlin, 464 p. https://doi.org/10.26515/rzsi/v8/i3/1913/163155

Glaessner M. F. 1933. — Die Krabben der Juraformation. *Zentralblatt für Mineralogie, Geologie und Paläontologie* B (3): 178-191.

Glaessner M. F. 1960. — New Cretaceous and Tertiary crabs (Crustacea: Brachyura) from Australia and New Zealand. *Transactions of the Royal Society of South Australia* 104 (6): 171-192.

Glaessner M. F. 1969. — Decapoda, *in* Moore R. C. (ed.), *Treatise on Invertebrate Paleontology, Part R, Arthropoda* 4 (2). University of Kansas Press, Lawrence and Geological Society of America, Boulder, Colorado: R399-R533, R626-R628. https://doi.org/10.1016/b978-012370626-3.00169-1

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

González J. A. 2018. — Checklists of Crustacea Decapoda from the Canary and Cape Verde Islands, with an assessment of Macaronesian and Cape Verde biogeographic marine ecoregions. *Zootaxa* 4413 (3): 401-448. https://doi.org/10.11646/zootaxa.4413.3.1

González-Pisani X. & López Greco L. S. 2007. — *Estructura de la espermateca del cangrejo araña Leurocyclus tuberculosus (Majoidea)*. Proceedings of the XII Congreso Latinoamericano de Ciencias del Mar, Florianópolis, Brasil: 14-17. [Abstract]

González-Pisani X., Barón P. & López Greco L. S. 2007a. — *Macroscopic and histological characterization of the seminal receptacles in Libinia spinosa (Majoidea)*. Proceedings of the Mid-Year Meeting of the Crustacean Society, Coquimbo, Chile, October 2007, p. 73. [Abstract]

González-Pisani X., Barón P. & López Greco L. S. 2007b. —*Toward the understanding of being mature in the females of the spider crab Leurocyclus tuberculosus (Majoidea) from Golfo Nuevo, Argentina*. Proceedings of the Mid-Year Meeting of the Crustacean Society, Coquimbo, Chile, October 2007, p. 98. [Abstract]

González-Pisani X., Barón P. & López Greco L. S. 2011. — Functional anatomy of the female reproductive systems of two spider crabs (Decapoda, Majoidea). *Invertebrate Biology* 131 (1): 61-74. https://doi.org/10.1111/j.1744-7410.2011.00252.x

Gordon I. 1950. — Crustacea Dromiacea. Part I: Systematic account of the Dromiacea collected by the "John Murray" Expedition. Part II. The morphology of the spermatheca in certain Dromiacea. *The John Murray Expedition 1933-34, Scientific Reports* 9 (3): 201-253.

Gordon I. 1963. — On the relationship of Dromiacea, Tymolinae and Raninidae to the Brachyura, *in* Whittington H. B. & Rolf W. D. I. (eds), *Phylogeny and Evolution of Crustacea*. Special Publication, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.: 51-57.

Gordon I. 1966. — On the spermatheca in the Raninidae (Crustacea: Decapoda), *in* Barnes H. (ed.), *Some Contemporary Studies in Marine Science*. Allen and Unwin, London: 343-354.

Gosavi S., Purohit B., Mitra S., Patel K., Vachhrajani K. & Trivedi J. 2021. — *Annotated checklist of marine decapods (Crustacea: Decapoda) of Gujarat state with three new records*. Proceedings of the "Marine Biology Research Symposium – MBRS 2021" Organized by Sathyabama Institute of Science and Technology, Chennai, in association with ICAR-National Bureau of Fish Genetic Resources, Lucknow. Taxonomy, Biodiversity and Conservation, TBC–115-PO: 45-66.

Gravely F. H. 1941. — Shells and other animals remains found on the Madras beach. I. Groups other than snails, etc. (Mollusca Gastropoda). *Bulletin of the Madras Government Museum new series* (Natural History) 5 (1): 1-112.

Gripp K. 1964. — *Erdgeschichte von Schleswig-Holstein*. Neumünster, Wachholtz: 1-411, 57 pls, 3 maps.

Griffith E. & Pidgeon E. 1833. — *The Classes Annelida, Crustacea, and Arachnida, Arranged by the Baron Cuvier, with Supplementary Additions to Each Order*. London, viii + 450 p., 8 + 25 + 27 pls.

Guérin F. É. 1829-1837. — Crustacés, *in Iconographie du Règne animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables et souvent encore non figurées, de chaque genre d'animaux. Avec un texte descriptif mis au courant de la science. Ouvrage pouvant servir d'atlas à tous les traités de zoologie*. J. B. Baillère, Paris and London: 1-48, pls 1-35. (For dates of publication of Brachyura plates, see Holthuis & Manning 1990: 139; Low *et al.* 2013: table 1). https://doi.org/10.5962/bhl.title.10331

Guinot D. 1967. — Les espèces comestibles de Crabes dans l'océan Indien occidental et la mer Rouge. *In* Réunion de spécialistes C. S. A. sur les Crustacés, Zanzibar 1964. *Mémoires de l'Institut français d'Afrique Noire* (77): 355-390.

Guinot D. 1976. — Constitution de quelques groupes naturels chez les Crustacés Décapodes Brachyoures. I. La superfamille des Bellioidea et trois sous-familles de Xanthidae (Polydectinae Dana, Trichiinae de Haan, Actaeinae Alcock). (*Mémoires du Muséum national d'Histoire naturelle*, sér. A - Zoologie; 97): 1-308. https://www.biodiversitylibrary.org/part/282217

Guinot D. 1977. — Proposition pour une nouvelle classification des Crustacés Décapodes Brachyoures. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences* (*Paris*), *sér. D*, 285: 1049-1052. https://gallica.bnf.fr/ark:/12148/bpt6k5497404n/f355.item

Guinot D. 1978. — Principes d'une classification évolutive des

Crustacés Décapodes Brachyoures. *Bulletin biologique de la France et de la Belgique n.s.* 112 (3): 211-292.

Guinot D. 1979a. — Données nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyoures. (*Mémoires du Muséum national d'Histoire naturelle, Série A* – Zoologie; 112): 1-354, 27 pls.

Guinot D. 1979b. — Problème pratique [*sic* pour Problèmes pratiques] d'une classification cladistique des Crustacés Décapodes Brachyoures. Actes de la VIe Réunion des Carcinologistes de langue française, Nabeul, Tunisie, 4-9 septembre 1979. *Bulletin de l'Office national des Pêches de Tunisie* 3 (1): 33-46.

Guinot D. 1979c. — Examen des théories actuelles de la classification zoologique. *History and Philosophy of the Life Sciences* 1 (1): 119-138.

Guinot D. 1984. — Le genre *Leurocyclus* Rathbun, 1897 (Crustacea Decapoda Brachyura). *Bulletin du Muséum national d'Histoire naturelle 4e série*, 6, sect. A (2): 377-395.

Guinot D. 1995. — Crustacea Decapoda Brachyura: Révision des Homolodromiidae Alcock, 1900, *in* Crosnier A. (ed.), Résultats des Campagnes MUSORSTOM. Vol. 13. Muséum national d'Histoire naturelle, Paris: 155-282 (Mémoires du Muséum national d'Histoire naturelle; 163). https://biodiversitylibrary.org/page/58815048

Guinot D. 2008. — A re-evaluation of the Dynomenidae Ortmann, 1892 (Crustacea, Decapoda, Brachyura, Podotremata), with the recognition of four subfamilies. *Zootaxa* 1850: 1-26.

Guinot D. 2011. — The position of the Hymenosomatidae MacLeay, 1838, within the Brachyura (Crustacea, Decapoda). *Zootaxa* 2890: 40-52. https://doi.org/10.11646/zootaxa.2890.1.4

Guinot D. 2012. — Remarks on Inachoididae Dana, 1851, with the description of a new genus and the resurrection of Stenorhynchinae Dana, 1851, and recognition of the inachid subfamily Podochelinae Neumann, 1878 (Crustacea, Decapoda, Brachyura, Majoidea). *Zootaxa* 3416: 22-40.

Guinot D. 2019. — New hypotheses concerning the earliest brachyurans (Crustacea, Decapoda, Brachyura). *Geodiversitas* 41 (22): 747-796. https://doi.org/10.5252/geodiversitas2019v41a22. http://geodiversitas.com/41/22

Guinot D. & Bouchard J.-M. 1998. — Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). *Zoosystema* 20 (4): 613-694. http://www.biodiversitylibrary.org/page/56145935

Guinot D. & Quenette G. 2005. — The spermatheca in podotreme crabs (Crustacea, Decapoda, Brachyura, Podotremata) and its phylogenetic implications. *Zoosystema* 27 (2): 267-342.

Guinot D. & Richer de Forges B. 1995. — Crustacea, Decapoda, Brachyura : révision de la famille des Homolidae de Haan, 1841, *in* Crosnier A. (ed.), Résultats des Campagnes MUSORSTOM. Vol. 13. Muséum national d'Histoire naturelle, Paris: 283-517 (Mémoires du Muséum national d'Histoire naturelle; 163). https://biodiversitylibrary.org/page/58815176

Guinot D. & Richer de Forges B. 1997. — Affinités entre les Hymenosomatidae MacLeay, 1838 et les Inachoididae Dana, 1851 (Crustacea Decapoda Brachyura). *Zoosystema* 19 (2-3): 453-502.

Guinot D. & Ribeiro A. 1962. — Sur une collection de Crustacés Brachyoures des îles du Cap-Vert et de l'Angola. *Memórias Junta de Investigaçoes do Ultramar* (2) (40): 9-89.

Guinot D. & Tavares M. 2000. — *Conchoedromia alcocki* Chopra, 1934: megalopa of *Conchoecetes artificiosus* (Fabricius, 1798) (Decapoda, Brachyura, Dromiidae). *Journal of Crustacean Biology* 20, Special Number 2: 301-309. https://doi.org/10.1163/1937240X-90000032

Guinot D. & Tavares M. 2001. — Une nouvelle famille de Crabes du Crétacé, et la notion de Podotremata Guinot, 1977 (Crustacea, Decapoda, Brachyura). *Zoosystema* 23 (3): 507-546.

Guinot D. & Tavares M. 2003. — A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and description of new genera and species (Crustacea, Decapoda, Brachyura). *Zoosystema* 25 (1): 43-129.

Guinot D. & Van Bakel B. W. M. 2020a. — Extraordinary majoid crabs: the genus *Esopus* A. Milne-Edwards, 1875 in the new subfamily Esopinae subfam. nov., and erection of Paulitinae subfam. nov. (Crustacea, Decapoda, Brachyura, Majoidea, Inachoididae Dana, 1851). *Zootaxa* 4766 (1): 101-127. https://doi.org/10.11646/zootaxa.4766.1.5

Guinot D. & Van Bakel B. W. M. 2020b. — Diagnosis of the inachoidid subfamily Paradasygyiinae subfam. nov. (Crustacea, Decapoda, Brachyura, Majoidea). *Zootaxa* 4801 (1): 198-200.

Guinot D. & Wicksten M. K. 2015. — Camouflage: carrying behaviour, decoration behaviour, and other modalities of concealment in Brachyura (Chapter 71-11), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Decapoda: Brachyura. Treatise on Zoology - Anatomy, Taxonomy, Biology*, vol. 9, Part C, 2 vols, *Crustacea*. Brill, Leiden and Boston: 583-638. https://doi.org/10.1163/9789004190832_013

Guinot D., Doumenc D. & Chintiroglou C. C. 1995. — A review of the carrying behavior in brachyuran crabs, with additional information on the symbioses with sea anemones. *Raffles Bulletin of Zoology* 43 (2): 377-416.

Guinot D., Vega F. & Van Bakel B. W. M. 2008. — Cenomanocarcinidae n. fam., a new Cretaceous podotreme family (Crustacea, Decapoda, Brachyura, Raninoidia), with comments on related families. *Geodiversitas* 30 (4): 681-719.

Guinot D., De Angeli A. & Garassino A. 2010. — *Holthuisea* n. gen., a new genus from the Eocene of Italy (Decapoda, Brachyura, Hexapodidae), *in* Fransen C., De Grave S. & Ng P. (eds), *Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume. Crustaceana Monographs* 14: 283-304. https://doi.org/10.1163/9789047427759_019

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

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

Guinot D., Carbot-Chanona G. & Vega F. J. 2019. — Archaeochiapasidae n. fam., a new early Cenomanian brachyuran family from Chiapas, Mexico, new insights on Lecythocaridae Schweitzer & Feldmann, 2009, and phylogenetic implications (Crustacea, Decapoda, Brachyura, Eubrachyura). *Geodiversitas* 41 (7): 285-322. https://doi.org/10.5252/geodiversitas2019v41a7

Guinot D., Davie P. J. F., Tsang L. M. & Ng P. L. K. 2022. — Formal re-establishment of Macrocheiridae Dana, 1851 (Decapoda: Brachyura: Majoidea) for the giant spider crab *Macrocheira kaempferi* (Temminck, 1836) based on a morphological reappraisal of adult and genetic characters. *Journal of Crustacean Biology* 42 (2): 1-24. https://doi.org/10.1093/jcbiol/ruac022

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

Hartnoll R. G. 1969. — Mating in the Brachyura. *Crustaceana* 16 (2): 161-181. https://doi.org/10.1163/156854069X00420

Hartnoll R. G. 1974. — Variations in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). *Crustaceana* 27 (2): 131-136. https://doi.org/10.1163/156854074X00334

Hartnoll R. G. 1975. — Copulatory structures and function in the Dromiacea, and their bearing on the evolution of the Brachyura, *in* VIII European Marine Biology Symposium Sorrento (Naples) 1973. *Pubblicazioni della Stazione Zoologica di Napoli* 9 (supplement): 657-676.

Hartnoll R. G. 1979. — The phyletic implications of spermathecal structure in the Raninidae (Decapoda: Brachyura). *Journal of Zoology* 187: 75-83. https://doi.org/10.1111/j.1469-7998.1979.tb07714.x

Hartnoll R. G. 2001. — Growth In Crustacea – twenty years on. *Hydrobiologia* 449: 111-122. https://doi.org/10.1023/A:1017597104367

Hartnoll R. G. 2015. — Postlarval life histories of Brachyura. (Chapter 71-7), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Decapoda: Brachyura*. Treatise on Zoology - Anatomy, Taxonomy, Biology, vol. 9C-I. Brill, Leiden and Boston: 3745-416. https://doi.org/10.1163/9789004190832_009

Hasan H. 2008. — *Biodiversité spécifique des crustacés Decapoda et Stomatopoda de Syrie : systématique, taxonomie, écologie, origine biogéographique*. Unpublished doctoral thesis, Muséum national d'Histoire naturelle, Paris, 519 p.

Hayer S., Schubart C. D. & Brandis D. 2015. — Morphology and function of the female reproductive system of *Ebalia tumefacta* (Decapoda, Brachyura, Leucosiidae). *Journal of Morphology* 276: 517-525. https://doi.org/10.1002/jmor.20359

Hayer S., Köhnk S., Boretius S. & Brandis D. 2016a. — Ever more complex: a new type of organization of the reproductive organs in female *Dorippe sinica* Chen, 1980 (Decapoda: Brachyura: Dorippidae). *Zoology* 119 (5): 455-463. https://doi.org/10.11646/zootaxa.3665.1.1

Hayer S., Köhnk S., Boretius S. & Brandis D. 2016b. — A new type of brachyuran seminal receptacle in the masked crab *Ethusa mascarone* (Brachyura, Ethusidae). *Journal of Morphology* 277 (11): 1497-1508. https://doi.org/10.1002/jmor.20591

Hayer S., Köhnk S., Schubart C. D., Boretius S., Gorb S. N. & Brandis D. 2017. — Comparative study of the morphology of the female seminal receptacles of *Ilia nucleus* and *Persephona mediterranea* (Decapoda, Brachyura, Leucosiidae). *Arthropod Structure & Development* 46 (2): 274-286. https://doi.org/10.1016/j.asd.2016.12.006

Hayer S., Köhnk S., Kabus J., Boretius S., Gorb S. N., Kihara T. & Brandis D. 2018. — *Reproduction At Depth – the Reproductive Morphology of Hydrothermal Vent Crabs*. 9th International Crustacean Congress (ICC9), Washington D.C, USA, May 22-25, 2018. Abstract.

Hazerli D., Höpel C. G. & Richter S. 2022. — New insights into the evolution of portunoid swimming crabs (Portunoidea, Heterotremeta, Brachyura) and the brachyuran axial skeleton. *Frontiers in Zoology* 19 (24): 1-56. https://doi.org/10.1186/s12983-022-00467-8

Henao Diaz L. F., Harmon L. J., Sugawara M. T. C., Miller E. T. & Pennell M. W. 2019. — Macroevolutionary diversification rates show time dependency. *Proceedings of the National Academy of Sciences of the United States of America* 116: 7403-7408. https://doi.org/10.1073/pnas.1818058116

Henderson J. R. 1893. — A Contribution to Indian Carcinology. *Transactions of the Linnean Society of London* (2) 5: 325-458.

Hendrickx M. E. 1989. — Notes on the genus *Ethusa* Roux, 1828, and description of *Ethusa steyaerti* n.sp. (Crustacea Decapoda, Dorippidae) from the continental shelf of the Gulf of California, Mexico. *Bulletin du Muséum national d'Histoire naturelle 4e série* 11 (A) (2): 407-423.

Henriksen C. S. 2009. — Investigation of crustaceans from shelf areas in the Gulf of Guinea, with special emphasis on Brachyura. Master Thesis in marine biodiversity, University of Bergen, 162 p.

Herbst J. F. W. 1782-1804. — *Versuch einer Naturgeschichte der Krabben und Krebse.* Gottlieb August Lange, Berlin and Stralsund, 515 p., 62 pls [Volumes 1-3 [1 (1782-1790): 1-274; 2 (1791-1796): viii + 226; 3 (1799-1804): 1-66, 1-46, 1-54, 1-49]. https://doi. org/10.5962/bhl.title.64679

Herklots J. A. 1861. — Symbolae Carcinologicae. I. Catalogue des Crustacés qui ont servi de base au système carcinologique de M. W. de Haan, rédigé d'après la collection du Musée des Pays-Bas et les Crustacés de la faune du Japon. *Tijdschrift Entomologie* 4: 116-156. (Also issued separately under the title: *Symbolae Carcinologicae. Etude sur la classe des Crustacés*: 1-43).

Hessler R. 1982. —The structural morphology of walking mechanisms in Eumalacostracan Crustaceans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 296 (1081): 245-298.

Hill B. J. & Forbes A. T. 1979. — Biology of *Hymenosoma Orbiculare* Desm in Lake Sibaya. *South African Journal of Zoology* 14 (2): 75-79. https://doi.org/10.1080/02541858.1979.11447651

Holthuis L. B. 1962. — *Dromia* Weber, 1795 (Crustacea, Decapoda): Proposed Designation of a Type-Species under the Plenary Powers. Z.N. (S.) 1488. *Bulletin of Zoological Nomenclature* 19 (l): 51-57, pl. 3.

Holthuis L. B. & Manning R. B. 1985. — *Neodorippe* Serène and Romimohtarto, 1969 (Crustacea, Decapoda): Proposed Designation of a Type Species. *Bulletin of Zoological Nomenclature* 42 (3): 304-305. https://doi.org/10.5962/bhl.part.942

Holthuis L. B. & Manning R. B. 1990. — Crabs of the subfamily Dorippinae MacLeay, 1838, from the Indo-West Pacific Region (Crustacea: Decapoda: Dorippidae). *Researches on Crustacea* Special no. 3: i-iii, 1-151.

Holthuis L. B. & Sakai T. 1970. — *Ph. F. von Siebold and Fauna Japonica; A History of Early Japanese Zology*. Academic Press of Japan, Tokyo, i-xviii + 323 p., 38 pls, 1 map. https://www.biodiversitylibrary.org/bibliography/162655

Hong S. Y. 1976. — Zoeal stages of *Orithyia sinica* (Linnaeus) (Decapoda, Calappidae) reared in the laboratory. *Publications of the Institute of Marine Science, National Fisheries University* (Korea) 9: 17-23.

Horikoshi M., Fujita T., Takeda M., Okiyama M., Ohta S., Tsuchida E. & Yamamoto M. 1982. — Preliminary Compilation of the Results Obtained by the "Survey of Continental Shelf Bordering Japan" Carried out on Board the S/S Soyo-Maru during 1923-1930, *in* Horikoshi M. (ed.). *Report for a part of Grant-in-Aid for Co-operative Research (A), Ministry of Education, Science and Culture: «Studies on Off-Shore and Deep-Sea Faunas in the West Pacific and Indian Oceans»*. Ocean Research Institute. University of Tokyo, 252 p.

Hornell J. S. 1922. — Some commensals of Indian Alcyonarians and Crabs. *Journal of the Bombay Natural History Society* 28 (4): 926-936. https://www.biodiversitylibrary.org/part/154427

Hose C. 1929. — *The Field-Book of a Jungle-Wallah: being a Description of Shore, River and Forest Life in Sarawak*. London, H. F. & G. Witherby, viii + 216 p., 14 pls.

Hu C.-H. & Tao H.-J. 1996. — *Crustacean fossils of Taiwan*. Ta-Jen Printers, Taipei, Taiwan, Republic of China, 228 p. (In Chinese).

Huang L., Zhong S., Liu Y., Huang G. & Chen X. 2021. — The complete mitochondrial genome of *Matuta victor* (Decapoda: Matutidae) from Beibu Bay. *Mitochondrial DNA* Part B 6 (1): 241-242. https://doi.org/10.1080/23802359.2020.1861999

Huang Z.-G. (chief ed.) 1994. — Brachyura, *in Marine species and their distributions in China's Seas*. Department of Ocean Management and Monitoring State Oceanic Administration. China Ocean Press, Beijing: 576-600. https://www.biodiversitylibrary.org/part/119053

Huard P. & Guinot D. 1965. — Les crabes de Chine dans une série d'aquarelles de Dabry de Thiersant. *Bulletin de l'Ecole française d'Extrême-Orient* 52 (2): 551-557. https://doi.org/10.3406/befeo.1965.1620

Hultgren K. M., Guerao G., Marques F. P. L. & Palero F. P. 2009. — Assessing the Contribution of Molecular and Larval Morphological Characters in a Combined Phylogenetic Analysis of the Superfamily Majoidea, *in* Martin J. W., Crandall K. A. & Felder D. L. (eds), *Decapod Crustacean Phylogenetics. Crustacean Issues.* Taylor & Francis, CRC Press, Boca Raton, Florida 18: 437-455. https://doi.org/10.3406/befeo.1965.1620

Huxley J. S. 1952. — Evolution's Copycats. *Life Magazine* 32 (26) [June 1952]: 67-76.

HUXLEY T. H. 1877. — *A Manual of the Anatomy of Invertebrated Animals*. J. & A. Churchill, London, viii + 698 p., 158 figs. https://www.biodiversitylibrary.org/bibliography/4179

HYŽNÝ M. 2016. — Diversity and distribution patterns of the Oligocene and Miocene decapod crustaceans (Crustacea: Malacostraca) of the Western and Central Paratethys. *Geologica Carpathica* 67 (5): 471-494. https://doi.org/10.1515/geoca-2016-0030

HYŽNÝ M. & DULAI A. 2021. — *Badenian decapods of Hungary*. GeoLitera Publishing House, Institute of Geosciences, University of Szeged, Hungary, 296 p.

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) 1999. — *International Code of Zoological Nomenclature*. Fourth edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London, xxx + 306 p. https://www.biodiversitylibrary.org/bibliography/50608

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) 2012. — Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Bulletin of Zoological Nomenclature* 69 (3): 161-169. https://doi.org/10.21805/bzn.v69i3.a8.161

IHLE J. E. W. 1916. — Die Decapoda Brachyura der Siboga-Expedition. II. Oxystomata, Dorippidae. *Siboga Expeditie* 39b1, livr. 78: 97-158. https://www.biodiversitylibrary.org/bibliography/13009

IHLE J. E. W. 1918. — Die Decapoda Brachyura der Siboga-Expedition. III. Oxystomata: Calappidae, Leucosiidae, Raninidae. *Siboga Expeditie* 39b2: 159-322. https://www.biodiversitylibrary.org/bibliography/13009

INIESTO M., THOMAZO C., FARA E., THE PARIS BIOTA TEAM 2019. — Deciphering the exceptional preservation of the Early Triassic Paris Biota (Bear Lake County, Idaho, USA). *Geobios* 54: 81-93. https://doi.org/10.1016/j.geobios.2019.04.002

INGLE R. W. 1982. — Crustacea, *in* WALLS J. G. (ed.), *Encyclopedia of Marine lnvertebrates*. T. F. H. Publications, Neptune, New Jersey: 514-662. https://doi.org/10.1007/978-3-662-43978-4_739

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1964. — Opinion 688. *Dromia* Weber, 1795 (Crustacea, Decapoda): Designation of a Type-Species Under the Plenary Powers. *The Bulletin of Zoological Nomenclature* 44 (2): 16-19. https://www.biodiversitylibrary.org/part/28443

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1987a. Opinion 1437. — *Neodorippe* Serène & Romimohtarto, 1969 (Crustacea, Decapoda): *Dorippe callida* Fabricius, 1798 designated as type species. *The Bulletin of Zoological Nomenclature* 44 (2): 139-140.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1987b. — *Official Lists and Indexes of Names and Works in Zoology*. London, iii + 366 p. https://www.biodiversitylibrary.org/bibliography/2471

ITANI G. & FUJIHARA H. 2001. — Carrying behaviour in a dorippid crab *Heikea japonica* (Arthropoda, Decapoda) - utilization of the sea pen (Cnidaria, Pennatulacea*)*. *Nankiseibutu* 43: 47-49 (In Japanese, with English abstract).

IVES J. E. 1891. — Echinoderms and Arthropods from Japan. *Proceedings of the Academy of Natural Sciences of Philadelphia*: 210-223. https://www.biodiversitylibrary.org/part/84955

JAGT J. W. M., VAN BAKEL B. W. M., GUINOT D., FRAAIJE R. H. B. & ARTAL P. 2015. — Fossil Brachyura, *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-2. *The Crustacea*. Leiden/Boston, Brill: 847-920. https://doi.org/10.1163/9789004190832_018

JAMIESON B. G. M. 1991. — Ultrastructure and phylogeny of Crustacean spermatozoa. *Memoirs of the Queensland Museum* 31: 109-142. https://www.biodiversitylibrary.org/part/303626

JAMIESON B. G. M. 1994. — Phylogeny of the Brachyura with particular reference to the Podotremata: evidence from a review of spermatozoal ultrastructure (Crustacea, Decapoda). *Philosophical Transactions of the Royal Society*, sér. B 345: 373-393. https://doi.org/10.1098/rstb.1994.0116

JAMIESON B. G. M. & TUDGE C. C. 1990. — Dorippids are Heterotremata: evidence from ultrastructure of the spermatozoa of *Neodorippe astuta* (Dorippidae) and *Portunus pelagicus* (Portunidae) (Brachyura: Decapoda). *Marine Biology* 106: 347-354. https://doi.org/10.1007/BF01344311

JAMIESON B. G. M. & TUDGE C. C. 2000. — Crustacea-Decapoda, *in* ADIYODI K. G. & ADIYODI R. G. (series eds), JAMIESON B. G. M. (volume ed.), *Reproductive Biology of Invertebrates*. Volume 9, part C. John Wiley and Sons, Chichester: 1-95.

JAMIESON B. G. M., GUINOT D. & RICHER DE FORGES B. 1995. — Phylogeny of the Brachyura: evidence from spermatozoal ultrastructure (Crustacea, Decapoda), *in* JAMIESON B. G. M., AUSIO J. & JUSTINE J.-L. (eds), *Advances in Spermatozoal Phylogeny and Taxonomy*. (*Mémoires du Muséum national d'Histoire naturelle*; 166): 265-283.

JENSEN P. C., ORENSANZ J. M. & ARMSTRONG D. A. 1996. — Structure of the female reproductive tract in the dungeness crab (*Cancer magister*) and implications for the mating system. *Biological Bulletin* 190: 336-349. https://doi.org/10.2307/1543026

JENSEN P. C. & BENTZEN P. 2012. — A molecular dissection of the mating system of the Dungeness crab, *Metacarcinus magister* (Brachyura: Cancridae). *Journal of Crustacean Biology* 32 (3): 443-456. https://doi.org/10.1163/193724012X626458

JEYABASKARAN R., AJMAL KHAN S. & RAMAIYAN V. 2000. — Brachyuran crabs of Gulf of Mannar, *in Biodiversity project on Gulf of Mannar biosphere reserve*. Annamalai Universtiy, Centre of Advanced Study in Marine Biology: 1-99, pls 1-78.

JI Y.-K., WANG A., LU X.-L., SONG D.-H., JINY.-H., LU J.-J., & SUN H.-Y. 2014. — Mitochondrial genomes of two brachyuran crabs (Crustacea: Decapoda) and phylogenetic analysis. *Journal of Crustacean Biology* 34 (4): 494-503. https://doi.org/10.1163/1937240X-00002252

JENSEN P. C. & BENTZEN P. 2012. — A molecular dissection of the mating system of the dungeness crab, *Metacarcinus magister* (Brachyura: Cancridae). *Journal of Crustacean Biology* 32: 443-456. https://doi.org/10.1163/193724012X626458

JIVOF P., HINES A. H. & QUACKENBUSH L. S. 2007. — Reproduction biologyand embryonic development, *in* KENNEDY V. S. & CRONIN L. E. (EDS), *The Blue Crab* Callinectes sapidus. Maryland Sea Grant College, Maryland: 255-298.

JOHNSON P. T. 1980. — The reproductive system, *in Histology of the Blue Crab*, Callinectes sapidus. *A Model for the Decapoda*, Chapter 15. Praeger Publishers, New York: 327-367. https://www.biodiversitylibrary.org/part/38171

KALK M. 1995. — *The Natural History of Inhaca Island, Mozambique*. Witwatersrand University Press, Johannesburg, 395 p.

KANEKO S. 1958. — Crustacean Remains from the Holocene Deposits in Osaka City (Pt. 1), *in Jubilee Publication in the Commemoration of Professor H. Fujimoto Sixtieth Birthday*: 331-339, pl. 15 (In Japanese).

KARASAWA H. 1993. — Cenozoic Decapod Crustacea from Southwest Japan. *Bulletin of the Mizunami Fossil Museum* 20 (1): 1-92.

KARASAWA H. 1999. — The Cenozoic crustacean fauna of southwest Japan, *in* SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Crustaceans and the Biodiversity Crisis*. Proceedings of the Fourth International Crustacean Congress. Brill, Leiden: 29-44.

KARASAWA H. 2000. — *Medorippe tanabei*, a new species of Miocene dorippid crab (Crustacea: Decapoda: Brachyura) from the Katsuta Group, West Honshu, Japan. *Proceedings of the Biological Society of Washington* 113 (3): 810-814.

KARASAWA H. 2020. — A first recognition of the orithyiid crab (Decapoda: Brachyura) from the Miocene Mizunami Group, Japan. *Bulletin of the Mizunami Fossil Museum* 4: 97-103.

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

Karasawa H. & Nobuhara T. 2008. — Decapoda and Isopoda (Crustacea) from the Pliocene Shimajiri Group in the Miyakojima island, Ryukyus, Japan. *Bulletin of the Mizunami Fossil Museum* 34: 23-30.

Karasawa H., Nakagawa T. & Kaede T. 2011a. — Axiidea and Brachyura (Decapoda) from the Miocene Shimo Formation, Uchiura Group, Fukui Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum* 37: 31-36.

Karasawa H., Schweitzer C. E. & Feldmann R. M. 2011b. — Phylogenetic analysis and revised classification of podotrematous Brachyura (Decapoda) including extinct and extant families. *Journal of Crustacean Biology* 31: 523-565. https://doi.org/10.1651/10-3423.1

Karasawa H., Kobayashi N., Goda T., Ohira N. & Ando Y. 2014. — A diversity of crabs (Decapoda) from the middle Pleistocene Atsumi Group, Japan. *Bulletin of the Mizunami Fossil Museum* 40: 55-73.

Karasawa H., Kobayashi N., Goda T., Ohira N. & Ando Y. 2021. — An illustrated catalogue of Decapoda from the Middle Pleistocene Atsumi Group, Japan. *Bulletin of the Mizunami Fossil Museum* 47: 137-159.

Kato H. & Karasawa H. 1998. — Pleistocene fossil decapod Crustacea from the Boso Peninsula, Japan. *Natural History Research* Special Issue 5: 1-31.

Kato H. & Kitamura K. 2020. — Pleistocene decapod crustaceans from the Sahama Mud Member, Hamamatsu Formation, Shizuoka Prefecture, central Japan. *Bulletin of the Mizunami Fossil Museum* 46: 45-56.

Keiler J., Wirkner C. S. & Richter S. 2017. — One hundred years of carcinization – the evolution of the crab-like habitus in Anomura (Arthropoda: Crustacea). *Biological Journal of the Linnean Society* 20: 1-23.

Kemp S. 1917. — Notes on Crustacea Decapoda in the Indian Museum. X. Hymenosomatidae. *Records of the Indian Museum* 13 (5): 243-279. https://doi.org/10.5962/bhl.part.5861

Kienbaum K. 2019. — *Evolutionary transformations of the reproductive system in Eubrachyura (Crustacea: Decapoda).* Thesis, Doctor rerum naturalium, Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin.

Kienbaum K., Scholtz G. & Becker C. 2017. — The morphology of the male and female reproductive system in two species of spider crabs (Decapoda: Brachyura: Majoidea) and the issue of the *velum* in majoid reproduction. *Arthropod systematics and phylogeny* 75 (2): 245-260.

Kienbaum K., Scholtz G. & Becker C. 2018a. — The morphology of the reproductive system in the crab *Percnon gibbesi* (Decapoda: Brachyura: Grapsoidea) reveals a new combination of characters in Thoracotremata. *Journal of Morphology* 279 (7): 883-894. https://doi.org/10.1002/jmor.20818

Kienbaum K., Vehof J., Becker C. & Scholtz G. 2018b. — The reproductive system of *Limnopilos naiyanetri* indicates a thoracotreme affiliation of Hymenosomatidae (Decapoda, Eubrachyura). *Arthropod Structure & Development* 47: 513-520.

Kim M.-H., Kim H.-S., Park W. & Choi J.-W. 2014. — Description of the megalopal stage of *Orithyia sinica* (Decapoda: Brachyura: Orithyiidae) reared in the laboratory. *Journal of Fisheries and Marine Sciences Education* 26 (2): 437-443. https://doi.org/10.13000/JFMSE.2014.26.2.437

Kim H. S. 1970. — A checklist of the Anomura and Brachyura (Crustacea, Decapoda) of Korea. *Seoul National University Journal (Biology and Agriculture Series, B)* 21: l-34.

Kim H. S. 1973. — Anomura – Brachyura, *in Illustrated Encyclopedia of Fauna & Flora of Korea* vol. 14. Ministry of Education, Seoul, 694 p., 112 pls. [In Korean]

Kim J.-I., Do T. D., Karagozlu M. Z. & Kim C.-B. 2019. — Analysis of complete mitochondrial genome of *Matuta planipes* (Decapoda, Brachyura Matutidae) from South Korea. *Mitochondrial DNA* B 4 (1): 906-907. https://doi.org/10.1080/23802359.2019.1579070

Klaus S., Goh G. H., Malkowsky Y., Becker C. & Plath M. 2014. — Seminal receptacle of the pill box crab *Limnopilos naiyanetri* Chuang and Ng, 1991 (Brachyura: Hymenosomatidae). *Journal of Crustacean Biology* 34 (3): 407-411. https://doi.org/10.1163/1937240X-00002245

Klompmaker A. A. 2013. — Extreme diversity of decapod crustaceans from the mid-Cretaceous (late Albian) of Spain: implications for Cretaceous decapod paleoecology. *Cretaceous Research* 41: 150-185. https://doi.org/10.1016/j.cretres.2012.12.003

Klompmaker A. A., Hyžný M., Portell R. W., Jauvion C., Charbonnier S., Fussell S. S., Klier A. T., Tejera R. & Jakobsen S. L. 2019. — Muscles and muscle scars in fossil malacostracan crustaceans. *Earth-Science Reviews* 194: 306-326. https://doi.org/10.1016/

Klompmaker A. A., Starzyk N., Fraaije R. H. B. & Schweigert G. 2020. — Systematics and convergent evolution of multiple reef-associated Jurassic and Cretaceous crabs (Decapoda, Brachyura). *Palaeontologia Electronica* 23 (2): a32. https://doi.org/10.26879/104

Klompmaker A. A., Karasawa H., Portell R. W., Fraaije R. H. B. & Ando Y. 2013. — An overview of predation evidence found on fossil decapod crustaceans with new examples of drill holes attributed to gastropods and octopods. *Palaios* 28: 599-613. https://doi.org/10.2110/palo.2013.p13-026r

Koh S. & Lee S. H. 2013. — Invertebrate Fauna of Korea, vol. 21 no. 30, *in Crabs and Zoeas III Arthropoda: Malacostraca: Decapoda: Brachyura: Cancridae, Cheiragonidae, Dorippidae*, *Euryplacidae, Goneplacidae, Hymenosomatidae, Portunidae*. National Institute of Biological Resources, Ministry of Environment, 77 p.

Kobayashi N., Goda T., Ohira N. & Karasawa H. 2008. — New records of crabs and barnacles (Crustacea: Decapoda and Cirripedia) from the middle Pleistocene Atsumi Group of Aichi Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum* 34: 111-115.

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

Kobjakova Z. I. 1955. — Order Decapoda, *in* Pavlovskii E. N. (ed.), *Atlas of the Invertebrates of the Far Eastern Seas of the USSR*. Akademia nauk SSSR, Moscow: 146-157 (In Russian). https://www.biodiversitylibrary.org/part/34467

Kobjakova Z. I. 1966. — Order Decapoda, *in* Pavlovskii E. N. (ed.), *Atlas of the Invertebrates of the Far Eastern Seas of the USSR*. Akademia nauk SSSR: 200-215 (In Russian). https://doi.org/10.1163/ej.9789004164413.i-562.27

Kocataş A. & Katağan T. 2007. — The Decapod Crustacean fauna of the Turkish Seas. *Zoology in the Middle East* 29 (1): 63-74. https://doi.org/10.1080/09397140.2003.10637971

Köhnk S., Baudewig J., Brandis D. & Boretius S. 2017a. — What's in this crab? MRI providing high-resolution three-dimensional insights into recent finds and historical collections of Brachyura. *Zoology* 121: 1-9. https://doi.org/10.1016/j.zool.2016.11.004

Köhnk S., Gorb S. N., Boretius S. & Brandis D. 2018. — Not only for males: the pleon-holding mechanism in female calappids (Crustacea Decapoda Brachyura). *Invertebrate Biology* 137 (2): 93-104. https://doi.org/10.1111/ivb.12208

Köhnk S., Kleinteich T., Brandis D. & Gorb S. N. 2017b. — Biomechanics of pleon attachment in the European shore crab *Carcinus maenas* (Linnaeus, 1758) (Brachyura: Portunoidea: Carcinidae). *Journal of Crustacean Biology* 37 (2): 142-150. https://doi.org/10.1093/jcbiol/rux010

Kollmann M. 1937. — Coaptations et formes correspondantes chez les Crustacés décapodes. *Annales de la Faculté des Sciences de Marseille* 10: 117-220.

Komai T. & Fujita Y. 2018. — A new genus and new species assigned to Macrophthalmidae (Decapoda: Brachyura: Thoracotremata) from the Ryukyu Islands, Japan. *Zootaxa* 4531 (1): 109-116. https://doi.org/10.11646/zootaxa.4531.1.5

Kottelat M. 2001. — Nomenclatural status of names of tetraodontiform fishes based on Bibron's unpublished work. *Zoosystema* 23 (3): 605-618.

Krishnamoorthy P. 2007. — Brachyura, *in* Director, Zoological Survey of India, Kolkata (ed.), *Fauna of Chennai Coast*. Marine Ecosystem Series 1: 83-109. https://www.biodiversitylibrary.org/part/119053

Krobicki M. & Zatoń M. 2008. — Middle and Late Jurassic roots of brachyuran crabs: palaeoenvironmental distribution during their early evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 263: 30-43. https://doi.org/10.1016/j.palaeo.2008.01.025

Krzemińska E., Starzyk N., Fraaije R. H. B. & Schweigert G. 2019. — *Augenrest morphology in* Bucculentum *Wehner (Decapoda: Brachyura)*. 7th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, 17-21 June, 2019, Ljubljana (Slovenia): Volume of Abstracts: 25, 26.

Krzemińska E., Starzyk N., Fraaije R. H. B., Schweigert G. & Lukeneder A. 2021. — Jurassic brachyurans of the genus *Bucculentum*. *Zootaxa* 5032 (3): 395-410. https://doi.org/10.11646/zootaxa.5032.3.5

Kumar S., Stecher G. & Tamura K. 2016. — MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution* 3 (7): 1870-1874. https://doi.org/10.1093/molbev/msw05

Kurata H. 1964. — Larvae of decapod Crustacea of Hokkaido. 8. Dorippidae (Brachyura). *Bulletin of the Hokkaido Regional Fisheries Research Laboratory* 29: 71-74.

Lamarck J. B. P. A. de Monet de 1801. — *Système [sic] des Animaux sans vertèbres, ou Tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution d'après les considérations de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire naturelle, parmi leurs dépouilles conservées; précédé du discours d'ouverture du cours de zoologie donné dans le Muséum national d'Histoire naturelle l'an VIII de la République*. Déterville, Paris.

Lanchester W. F. 1900. — On a collection of Crustaceans made at Singapore and Malacca. Part I. Crustacea Brachyura. *Proceedings of the Zoological Society of London* 1900: 719-770. https://www.biodiversitylibrary.org/part/49623

Lanchester W. F. 1902. — On the Crustacea collected during the "Skeat" Expedition to the Malay Penainsula, together with a note on the genus *Actaeopsis*, Part 1. Brachyura, Stomatopoda, and Macrura. *Proceedings of the Zoological Society of London* (2) (1901): 534-574, pls 33, 34.

Lanfear R., Calcott B., Ho S. Y. W. & Guindon S. 2012. — PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29 (6): 1695-1701. https://doi.org/10.1093/molbev/mss020

Larghi C. 2004. — Brachyuran decapod Crustacea from the Upper Cretaceous of Lebanon. *Journal of Paleontology* 78 (3): 528-541. https://doi.org/10.1666/0022-3360(2004)078<0528:BDCFTU>2.0.CO;2

Latreille P. A. 1810. — *Considérations générales sur l'Ordre naturel des Animaux composant les Classes des Crustacés, des Arachnides et des Insectes; avec un Tableau Méthodique de leurs Genres, disposés en Familles*. F. Schoell, Paris, 144 p. https://doi.org/10.5962/bhl.title.39620

Latreille P. A. 1818. — *Crustacés, Arachnides et Insectes. Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature*. Volume 24. Paris: 1-38, pls 133-397.

Lautenschlager A., Brandis D. & Storch V. 2010. — Morphology and function of the reproductive system of representatives of the genus *Uca*. *Journal of Morphology* 271: 1281-1299. https://doi.org/10.1002/jmor.10869

Lee S.-K., Lee C., Noh J., Song S. J. & Khim J. S. 2021. — First comprehensive ecological checklist of Brachyura in Korea: 1879-2020. *Marine Pollution Bulletin* 171: 112742. https://doi.org/10.1016/j.marpolbul.2021.112742

Le Loeuff P. & Intès A. 1999. — Macrobenthic communities on the continental shelf of Côte-d'Ivoire. Seasonal and diel cycles in relation to hydroclimate. *Oceanologica Acta* 22 (5): 529-550. https://doi.org/10.1016/S0399-1784(00)87685-9

Le Loeuff P., Konan J., Zabi G. S. & Von Cosel R. 2000. — *L'écosystème benthique au large de Grand-Bassam (Côte-d'Ivoire). Situations comparées en saisons froides 1969 et 1998 (résultats de la campagne BENCHACI, 15-17 août 1998)*. Document Scientifique et Technique du Centre IRD de Bretagne, 85, 45 p.

Levin S. 1976. — Decapoda, *in* Golikov A. N. *et al.* (eds), *Animals and Plants of Peter the Great Bay*. Akademia nauk SSSR, Leningrad: 49-56 (In Russian). https://doi.org/10.1016/b978-012370626-3.00169-1

Lim S. S. L., Ng P. K. L., Tan L. W. H. & Chin W. Y. 1994. — *Rhythm of the Sea. The Life and Times of Labrador Beach*. Nanyang Technological University, School of Science, Singapore, 160 p.

Lin F., Tan H., Fazhan H., Xie Z., Guan M., Shi X. & Ma H. 2018. — The complete mitochondrial genome and phylogenetic analysis of *Matuta planipes* (Decapoda: Brachyura: Matutidae). *Mitochondrial* DNA *B Resources* 3: 157-158. https://doi.org/10.1080/23802359.2018.1437802

Linnaeus C. 1758. — *Systema Naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. Tomus I. Laurentii Salvii, Holmiæ, [iv] + 824 p. https://doi.org/10.5962/bhl.title.542

Linnaeus C. 1763. — *Centuria Insectorum, quam, praeside D. D. Car. von Linné, proposuit Boas Johansson, Calmariensis, in* C. Linnaeus, *Amoenitates Academicae; seu dissertationes variae physicae, medicae, botanicae, antehac seorsim editae, nunc collectae et auctae*. Volume 6. Holmiae: 384-415.

Linnaeus C. 1764. — *Museum S:ae R:ae M:tis Ludovicae Ulricae Reginae Suecorum, Gothorum, Vandalorumque &c. &c. &c. In quo Animalia rariora, exotica, imprimis Insecta & Conchilia*. Holmiæ: 1-720.

Linnaeus C. 1767. — *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Edition 12, volume 1, part 2. Holmiæ: 533-1327. https://www.biodiversitylibrary.org/bibliography/156772

Liu P., Duan Y., Mao Z., Li J., Gao B. & Li J. 2013. — Sequence comparison and phylogenetic analysis of mtDNA 16S rRNA and COI gene sequences in *Orithyia sinica*. *Journal of Fisheries of China* 37: 1441-1451. https://doi.org/10.3724/SP.J.1231.2013.38763

López Greco L. S. 2013. — Functional anatomy of the reproductive system (Chapter 15), *in* Watling L. & Thiel M. (eds), Vol. I. *The Functional Morphology & Diversity of the Crustaceans*: 413-450.

López Greco L. S., López G. C. & Rodríguez E. M. 1999. — Morphology of spermathecae in the estuarine crab *Chasmagnathus granulata* Dana, 1851 (Grapsidae, Sesarminae). *Journal of Zoology* 249: 490-493. https://doi.org/10.1111/j.1469-7998.1999.tb01222.x

López-Greco L. S., Fransozo V., Negreiros-Fransozo M. L. & Carvalho dos Santos D. 2009. — Comparative morphology of the seminal receptacles of *Ocypode quadrata* (Fabricius, 1787) (Brachyura, Ocypodoidea). *Zootaxa* 2106: 41-50. https://doi.org/10.11646/zootaxa.2106.1.3

Lőrenthey E. 1911. — Újabb adatok Budapest kőrnyéke harmadidőszaki űledékeinek geolőgiájához. *Mathematikai ès termeszettudományi Ertesitő* 29: 515-535.

Lőrenthey E. 1913. — Neuere Beiträge zür Stratigraphie der Tertiârbildungen in der Umgebung von Budapest. *Mathematische und Naturwissenschaftliche Berichte aus Ungarn* 27: 282-294.

Lőrenthey E. & Beurlen K. 1929. — Die fossilen Decapoden der Länder der Ungarischen Krone. *Geologica Hungarica* 3: 1-421 (Palaeontologica).

Low M. E., Ng P. K. L. & Evenhuis N. L. 2013. — Names and publication dates of the Brachyura in F. É. Guérin (Guérin-Méneville) (Crustacea: Decapoda). *Zootaxa* 3736 (2): 101-127. https://doi.org/10.11646/zootaxa.3736.2.1

Lucas J. S. 1980. — Spider crabs of the family Hymenosomatidae (Crustacea: Brachyura) with particular reference to Australian species: systematics and biology. *Records of the Australian Museum* 33 (4): 148-247. https://doi.org/10.3853/j.0067-1975.33.1980.199

Luque J. 2015. — The oldest higher true crabs (Crustacea: Decapoda: Brachyura): insights from the Early Cretaceous of the Americas. *Palaeontology* 58 (2): 251-263. https://doi.org/10.1111/pala.12135

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

Luque J., Feldmann R. M., Vernygora O., Schweitzer C. E., Cameron C. B., Kerr K. A., Vega F. J., Duque A., Strange M., Palmer A. R. & Jaramillo C. 2019. — Exceptional preservation of mid-Cretaceous marine arthropods and the evolution of novel forms and mode of life via heterochrony. *Science Advances* 5: eaav3875. https://doi.org/10.1126/sciadv.aav3875

Luque J., Xing L., Briggs D. E. G., Clark E. G., Duque A., Hui J., Mai H. & McKellar R. C. 2021. — Crab in amber reveals an early colonization of nonmarine environments during the Cretaceous. *Science Advances* 7: eabj5689. https://doi.org/10.1126/sciadv.abj5689

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

Macnae W. & Kalk M. (eds) 1958. — *A Natural History of lnhaca Island, Moçambique.* Johannesburg, v + 163 p., pls 1-11.

Macnae W. & Kalk M. (eds) 1969. — *A Natural History of Inhaca Island, Moçambique.* Johannesburg, v + 163 p., pls 1-11.

Manning R. B. 1993. — Two new dorippid crabs from Australia (Crustacea: Decapoda: Dorippidae). *Records from the Australian Museum* 45: 1-4. https://doi.org/10.3853/j.0067-1975.45.1993.124

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

Manning R. B. & Holthuis L. B. 1986. — Preliminary descriptions of four new species of dorippid crabs from the Indo-west Pacific region (Crustacea: Decapoda: Brachyura). *Proceedings of the biological Society of Washington* 99 (2): 363-365.

Mantelatto F. L., Robles R., Schubart C. D. & Felder D. L. 2009. — Molecular phylogeny of the genus *Cronius* Stimpson, 1860, with reassignment of *C. tumidulus* and several American species of *Portunus* to the genus *Achelous* De Haan, 1833 (Brachyura: Portunidae), *in* Martin J. W., Crandall K. A. & Felder D. L. (Eds), *Decapod Crustacean Phylogenetics. Crustacean Issues.* Taylor & Francis, CRC Press, Boca Raton, Florida 18: 567-579.

Marramà G., Bannikov A. F., Tyler J. C., Zorzin R. & Carnevale G. 2016. — Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 454: 228-245. https://doi.org/10.1016/j.palaeo.2016.04.021

Marangon S. & De Angeli A. 2007. — New decapod assemblage from the lower Oligocene (Rupelian) of Ligure Piemontese Basin (NO Italy). 3rd Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Museo di Storia Naturale di Milano, May 23-25, 2007. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 35 (2): 73-75.

Marques F. P. L. & Pohle G. 1998. — The use of structural reduction in phylogenetic reconstruction of decapods and a phylogenetic hypothesis for 15 genera of Majidae: testing previous larval hypotheses and assumptions. *Invertebrate Reproduction and Development* 33: 241-262. https://doi.org/10.1080/07924259.1998.9652636

Marques F. P. L. & Pohle G. 2003. — Searching for larval support for majoid families (Crustacea: Brachyura) with particular reference to Inachoididae Dana, 1851. *Invertebrate Reproduction and Development* 43: 71-82. https://doi.org/10.1080/07924259.2003.9652523

Martin J. W. 1993. — The Samurai Crab. *Terra* 31 (4): 30-34.

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

Martin J. W. & Truesdale F. M. 1989. — Zoeal development of *Ethusa microphthalma* Smith, 1881 (Brachyura: Dorippidae) reared in the laboratory, with a comparison of other dorippid zoeae. *Journal of Natural History* (London) 23: 205-217. https://doi.org/10.1080/00222938900770111

Matos-Pita S. S. de, Castillo S. & Ramil F. 2016. — Contribution to the knowledge of the deep brachyuran fauna (Crustacea: Decapoda) in waters off Mauritania (NW Africa). *Journal of the Marine Biological Association of the United Kingdom* 97 (6): 1273-1305. https://doi.org/10.1017/S002531541600062X

Maurin C. 1968. — Les crustacés capturés par la "Thalassa" au large des côtes nord-ouest africaines. *Revue Roumaine de Biologie, Série de Zoologie* 13 (6): 479-493.

Mayr E. 1988. — Toward a New Philosophy of Biology: Observations of an Evolutionist, Cambridge, Harvard University Press.

McEnnulty F. R., Gowlett-Holmes K. L., Williasms A., Althaus F., Fromont J., Poore G. C. B., O'Hara T. D., Marsh L., Kott P., Slack-Smith S., Alderslade P. & Kitahara M. V. 2011. — The deepwater megabenthic invertebrates on the western continental margin of Australia (100-1100 m depths): composition, distribution and novelty. *Records of the Western Australian Museum* Supplement 80: 1-191. https://doi.org/10.18195/issn.0313-122x.80.2011.001-191

McLay C. L. 1993. — Crustacea Decapoda: The sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera, *in* Crosnier A. (ed.), *Résultats des Campagnes MUSORSTOM, Volume 10.* Muséum national d'Histoire naturelle, Paris: 111-251 (*Mémoires du Muséum national d'Histoire naturelle*; 156).

McLay C. L. 1999. — Crustacea Decapoda: Revision of the Family Dynomenidae, *in* Crosnier A. (ed.), *Résultats des Campagnes MUSORSTOM, Volume 20.* Muséum national d'Histoire naturelle, Paris: 427-569 (Mémoires du Muséum national d'Histoire naturelle; 180).

McLay C. L. 2015. — Moulting and Growth in Brachyura (Chapter 71-5), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Decapoda: Brachyura.* Treatise on Zoology - Anatomy, Taxonomy, Biology, vol. 9C-I. Brill, Leiden and Boston: 245-316. https://doi.org/10.1163/9789004190832_007

McLay C. L. 2020. — Rediscovery of the sponge crab *Cryptodromia fallax* (Latreille in Milbert, 1812) (Decapoda: Brachyura: Dromiidae) at Mauritius, with the description of a new genus and the confirmation of an unusual seaweed-carrying camouflage mode. *Journal of Crustacean Biology* 40 (1): 82-88. https://doi.org/10.1093/jcbiol/ruz085

McLay C. L. & Becker C. 2015. — Reproduction in Brachyura (Chapter 71-4), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Decapoda: Brachyura.* Treatise on Zoology - Anatomy, Taxonomy, Biology, vol. 9C-I. Brill, Leiden and Boston: 185-243. https://doi.org/10.1163/9789004190832_006

McLay C. L. & López Greco L. S. 2011. — A hypothesis about the origin of sperm storage in the Eubrachyura, the effects of crab diversity: how did a race to be the first become a race to be last? *Zoologischer Anzeiger* 250: 378-406. https://doi.org/10.1016/j.jcz.2011.06.002

McLay C. L. & Naruse T. 2019. — Revision of the shell-carrying crab genus *Conchoecetes* Stimpson, 1858 (Crustacea: Brachyura: Dromiidae). *Zootaxa* 4706 (1): 1-47. https://doi.org/10.11646/zootaxa.4706.1.1

McNeill F. A. 1923. — Crustacean camoufleurs. *Australian Museum Magazine* 1 (8): 243-246.

Melrose M. J. 1975. — The marine fauna of New Zealand: Family Hymenosomatidae (Crustacea, Decapoda, Brachyura). *Memoirs of the New Zealand Oceanographic Institute* 34: 1-123.

Mendes I. D., Santana W. & De Souza-Carvalho I. S. 2022. — Fossil hymenosomatid crabs (Crustacea: Decapoda) from the lower Cretaceous of NE Brazil. *Cretaceous Research* 134: 105174. https://doi.org/10.1016/j.cretres.2022.105174

Miers E. J. 1881. — On a collection of Crustacea made by Baron Hermann Maltzam [*sic*] at Goree Island, Senegambia. *Annals and Magazine of Natural History series 5*, 8: 204-220, 259-281, 364-377, pls 13-16.

Miers E. J. 1884. — Crustacea, *in Report on the Zoological Collections Made in the Indo-Pacific Ocean during the Voyage of H. M. S. 'Alert' 1881-2*. British Museum (Natural History) London: 178-322, pls 18-34. https://www.biodiversitylibrary.org/bibliography/57937

Miers E. J. 1886. — Report on the Brachyura collected by H. M. S. Challenger during the Years 1873-76. *Report on the scientific results of the voyage of H. M. S. Challenger* 17 (49): i-xlix, 1-362, pls 1-2. https://biodiversitylibrary.org/page/49400162

Miller M. A., Pfeiffer W. & Schwartz T. 2010. — Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*: 1-8. https://doi.org/10.1109/GCE.2010.5676129

Milne-Edwards A. & Bouvier E.-L. 1900. — Crustacés Décapodes. Première partie. Brachyures et Anomoures, *in Expéditions scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882, 1883*. Masson, Paris, 396 p., 32 pls. https://www.biodiversitylibrary.org/bibliography/181156

Milne-Edwards A. & Bouvier E.-L. 1902. — Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78), in the Caribbean Sea (1878-79), and along the Atlantic coast of the United States (1880), by the U. S. Coast Survey Steamer "Blake". XXXIX. Les Dromiacés et Oxystomes. *Memoirs of the Museum of Comparative Zoology at Harvard College* 27 (1): 1-127.

Milne Edwards H. 1834, 1837, 1840. — *Histoire Naturelle des Crustacés comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux*. Librairie Encyclopédique de Roret, Paris. Vol. 1 (1834), xxxv + 468 p.; vol. 2 (1837), 1-531 p.; Atlas (1834-1840), 42 pls. https://doi.org/10.5962/bhl.title.16170

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

Miyake S. 1983. — Brachyura (Crabs). *Japanese Crustacean Decapods and Stomatopods in Color*, 2. Hoikusha, Osaka: i-viii, 1-277, pls 1-64 (In Japanese).

Minemizu R. 2000. — *Marine decapod and stomatopod Crustaceans mainly from Japan*. Bun-Ichi Sogo Shuppan, Tokyo: 1-344 (In Japanese).

Modena M., Mori M. & Vacchi M. 2001. — Note su alcuni crostacei malacostraci raccolti in aree adiacenti alla M/C Haven (Mar Ligure). *Biologia Marina Mediterranea* 8: 675-679.

Monod T. 1933a. — Brachyura maroccana. 2e partie: Dromiidea, Oxystomata, Oxyrhyncha, Brachychyncha (excl. Pinnoteridae). *Bulletin de la Société des Sciences naturelles du Maroc* 12 (7, 8) [1932]: 199-220.

Monod T. 1933b. — Sur quelques Crustacés de l'Afrique Occidentale. (Liste des Décapodes mauritaniens et des Xanthidés ouest-africains). *Bulletin du Comité d'Etudes historiques et scientifques de l'Afrique Occidentale française* 15 (2, 3) [1932]: 456-548 [p. 1-93 in reprint].

Monod T. 1937. — Crustacés, *in* Mission A. Gruvel dans le Canal de Suez. I. *Mémoires présentés à l'Institut d'Égypte* 34: 1-19. https://www.biodiversitylibrary.org/bibliography/181156

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

Mori M. 1986. — Observations on the biology of *Medorippe lanata* (Linnaeus) (Crustacea: Decapoda: Dorippidae) in the Gulf of Genoa (Mediterranean Sea). *Oebalia* 13: 77-87.

Morita S. 1977. — Decapoda, *in* Baba Y. (ed.), *The Fossils Excavated in Aichi Prefecture, Japan (The First Series). The Alluvial Fauna Discovered in the Artificial Land of Reclaimed Sand Around the Nagoya Port.* Tokai Fossil Society, Nagoya.

Morris S. F. & Collins J. S. H. 1991. — Neogene crabs from Brunei, Sabah and Sarawak. *Bulletin of the British Museum (Natural History), Geology Series* 47 (1): 1-33. https://www.biodiversitylibrary.org/part/49676

Morton B. & Morton J. 1983. — *The Sea Shore Ecology of Hong Kong*. Hong Kong University Press, xiv + 350 p. https://doi.org/10.1017/S0025315400059816

Müller P. 1978. — Decapoda (Crustacea) fauna a budapesti miocénből (5) [Faune de Décapodes (Crustacea) dans le Miocène de Budapest (5)]. *Földtani Közlöny* (Budapest) 108 (3): 272-312. (in Hungarian, with French summary)

Müller P. 1984a. — Decapod Crustacea of the Badenian. *Geologica Hungarica (ser. Paleontologica),* fasciculus 42, Budapest, 317 p.

Müller P. 1984b. — Messinian and older decapods from the Mediterranean with description of two new species. *Annales géologiques des pays helléniques* 32: 25-34.

Müller P. 1996. — Miocene Decapod Crustacea from southern Poland. *Prace paleozoologiczne Muzeum Ziemi* 43: 3-14.

Müller P. M. 2006. — New decapods from the Miocene of Hungary - with remarks about their environment. *Földtani Közlöny* 136 (1): 37-49.

Müller P. M. & Collins J. S. H. 1991. — Late Eocene coral associated decapods (Crustacea) from Hungary. *Contributions to Tertiary and Quaternary Geology* 28 (2-3): 47-92.

Müller P. M., Krobicki M. & Wehner G. 2000. — Jurassic and Cretaceous primitive crabs of the family Prosopidae (Decapoda: Brachyura) – Their taxonomy, ecology and biogeography. *Annales Societatis Geologorum Poloniae* 70: 49-79.

Muñoz I., García-Isarch E., Sobrino I., Burgos C., Funny R. & González-Porto M. 2012. — Distribution, abundance and assemblages of decapod crustaceans in waters off Guinea-Bissau (north-west Africa). *Journal of the Marine Biological Association of the United Kingdom* 92: 475-494. https://doi.org/10.1017/S0025315411001895

Muraoka K. 1982. — *"Kani (Crabs), Junior's Picture Book" number 2*. Osaka, 90 p. (In Japanese).

Naderloo R. 2017. — *Atlas of Crabs of the Persian Gulf*. Springer, Switzerland, xi + 444 p. https://doi.org/10.1007/978-3-319-49374-9

Naderloo R., Ebrahimnezhad S. & Sari A. 2015. — Annotated checklist of the decapod crustaceans of the Gulf of Oman, northwestern Indian Ocean. *Zootaxa* 4028 (3): 397-412. https://doi.org/10.11646/zootaxa.4028.3.5

Naruse T. & Guinot D. 2023. — A new species of the genus *Hymenosoma* Desmarest, 1823 (Crustacea, Decapoda, Brachyura, Hymenosomatidae) from Madagascar, *in* Corbari L., Richer De Forges B. & Macpherson E. (eds). *Tropical Deep-Sea Benthos 33, Deep-Sea Crustaceans from South-West Indian Ocean*. Muséum national d'Histoire naturelle, Paris (Mémoires du Muséum national d'Histoire naturelle, 217): 203-214.

Naruse T. & Ng P. K. L. 2007. — On the taxonomy of the genus *Hymenicoides* Kemp, 1917 (Crustacea: Decapoda: Brachyura: Hymenosomatidae), with resurrection of *Limnopilos* Chuang & Ng, 1991, and descriptions of two new species. *Zootaxa* 1621: 17-31. https://doi.org/10.11646/zootaxa.1621.1.2

Naruse T., Castro P. & Ng P. K. L. 2009. — A new genus and new species of Ethusidae (Decapoda, Brachyura) from Vanuatu, Western Pacific. Special Issue on the Occasion of the 80th Birthday of A. J. (Sandy) Bruce — 50 Years of Shrimping in the Indo-West Pacific. *Crustaceana* 82 (7): 931-938. https://doi.org/10.1163/156854009X427450

Naruse T., Yeo D. C. J. & Osawa M. 2014. — Notes on a collection of stomatopod and decapod crustaceans from Cambodia. *Cambodian Journal of Natural History* 1: 24-36.

Neuville H. 1938. — Quelques remarques sur le crabe dit “à face humaine” ou “des Samouraïs” (*Dorippe japonica* von Siebold) et son rôle dans le folklore de l’Extrême-Orient. *Bulletin du Muséum national d’Histoire naturelle 2e série* 10: 48-56.

Ng N. K. 2006. — *The systematics of the crabs of the family Varunindae* [*sic*] *(Brachyura, Decapoda)*. Unpublished thesis, National University of Singapore, 914 p.

Ng P. K. L. 1987. — The master camoufleurs: the upside down world of the leaf porter crab. *Nature Malaysiana* 12 (2): 14-15.

Ng P. K. L. 1998. — Crabs, *in* Carpenter K. E. & Niem V. H. (eds), *The Living Marine Resources of the Western Central Pacific. Cephalopods, Crustaceans, Holothurians and Sharks, FAO Species Identification Guide for Fishery Proposes*. FAO, Rome, Vol. 2: 1045-1155. https://doi.org/10.1007/978-3-319-49374-9_21

Ng P. K. L. & Castro P. 2013. — On the genus *Scalopidia* Stimpson, 1858 (Crustacea: Brachyura: Goneplacoidea: Scalopidiidae), with the description of one new genus and three new species. *Zootaxa* 3731 (1): 58-76. https://doi.org/10.11646/zootaxa.3731.1.2

Ng P. K. L. & Castro P. 2016. — Revision of the family Chasmocarcinidae Serène, 1964 (Crustacea, Brachyura, Goneplacoidea). *Zootaxa* 4209 (1): 1-182. https://doi.org/10.11646/zootaxa.4209.1.1

Ng P. K. L. & Chuang C. T. N. 1996. — The Hymenosomatidae (Crustacea: Decapoda: Brachyura) of Southeast Asia, with notes on other species. *Raffles Bulletin of Zoology* Supplement 3: 1-82.

Ng P. K. L. & Davie P. J. F. 2002. — A checklist of the brachyuran crabs of Phuket and western Thailand. *Phuket Marine Biological Center Special Publication* 23 (2): 369-384.

Ng P. K. L. & Huang J.-F. 1997. — Unrecorded crabs (Crustacea: Decapoda: Brachyura) from Taiwan and Tungsha Islands, with description of a new genus and species of Xanthidae. *Zoological Studies* 36: 261-276.

Ng P. K. L. & Rahayu D. R. 2002. — A new species of leaf porter crab of the genus *Neodorippe* Serène et Romimohtarto, 1969 (Crustacea, Decapoda, Brachyura, Dorippidae) from Irian Jaya, Indonesia. *Proceedings of the Biological Society of Washington* 115 (4): 754-759.

Ng P. K. L. & Rahayu D. R. 2014. — Revision of the family Acidopsidae Števčić, 2005, and the systematic position of *Typhlocarcinodes* Alcock, 1900, *Caecopilumnus* Borradaile, 1902, and *Raoulia* Ng, 1987, with descriptions of two new genera and five new species (Crustacea: Brachyura: Goneplacoidea). *Zootaxa* 3773: 1-63. https://doi.org/10.11646/zootaxa.3773.1.1

Ng P. K. L. & Tan L. W. H. 1986. — The leaf-carrying behaviour of *Neodorippe (Neodorippe) callida* (Fabricius, 1798), with a note on carrying behaviour of dorippid crabs (Crustacea, Decapoda, Brachyura). *Journal of the Singapore National Academy of Science* 15: 45-47.

Ng P. K. L., Guinot D. & Davie P. J. F. 2008a. — Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology*, S]upplement 17: 1-286. [updates at http://rmbr.nus.edu.sg/research/cotw/supplement17php]

Ng P. K. L., Keng W. L & Lim K. K. P. 2008b. — *Private Lives: An Exposé of Singapore’s Mangroves*. The Raffles Museum of Biodiversity Research, Singapore, 249 p.

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

Ng P. K. L., Shih H.-T., Ho P.-H. & Wang C.-H. 2017. — An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *Journal of the Taiwan Museum* 70 (3, 4): 1-185.

Nguyen T. S. & Ng P. K. L. 2010. — On a new genus in the family Portunidae (Crustacea: Decapoda: Brachyura) and the identity of *Portunus* (*Cycloachelous*) *yoronensis* Sakai, 1974. *Zootaxa* 2677: 38-48. https://doi.org/10.11646/zootaxa.2677.1.4

Nishimura S. & Suzuki K. 1971. — *Common Seashore Animals of Japan in Color.* Osaka: 1-195, pls 1-84.

Nobili G. 1903. — Crostacei di Singapore. *Bolettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 18 (455): 1-39, 1 pl.

Nyborg T., Garassino A., Vega F. J. & Kovalchuck G. 2019a. — Fossil decapod crustaceans from the Early Cretaceous (Albian) of Oregon, USA. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 293 (2): 27-138.

Nyborg T., McLachan S. M. S., Garassino A., Vega F. J., Phillippe S. C. & Ch ampagne D. E. 2019b. — New and revised species of *Archaeopus* Rathbun, 1908 (Decapoda: Brachyura: Retroplumidae) from the eastern Pacific. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 292 (1): 25-56. https://doi.org/10.1127/njgpa/2019/0807

Ocampo E. H., Farías N. E. & Luppi T. A. 2014. — New record of the deep-sea crab *Ethusina abyssicola* from the Mar del Plata Canyon, Argentina. *New Zealand Journal of Zoology*: 1-4. https://doi.org/10.1080/03014223.2014.927773

Oh S. J. & Hankin D. G. 2004. — The sperm plug is a reliable indicator of mating success in female Dungeness crabs, *Cancer magister*. *Journal of Crustacean Biology* 24: 314-326. https://doi.org/10.1651/C-2389

Orensanz J. M., Parma A. M., Armstrong D. A., Armstrong J. & Wardrup P. 1995. — The breeding ecology of *Cancer gracilis* (Crustacea: Decapoda: Cancridae) and the mating systems of cancrid crabs. *Journal of Zoology* 235: 411-437. https://doi.org/10.1111/j.1469-7998.1995.tb01760.x

Ortega G., Fernàndez M., Ferratges F. A., Kwekel A., Laguna A., Maza L. M. & Méndez J. M. 2013. — *Bacapluma aragonensis* (Crustacea, Decapoda), nuevo género del Eoceno inferior de Huesca (Aragón, España). *Paleotipos aragoneses –Instituto Geológico y Minero de España*: 1-13.

Ortmann A. 1892. — Die Decapoden-Krebse des Strassburger Museums V. Theil. Die Abtheilungen Hippidea, Dromiidea und Oxystomata. *Zoologische Jahresbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere* 6: 532-588, pl. 26.

Ortmann A. 1901. — Decapoda, *in* Gerstaecker A. & Ortmann A. E., *Bronns Klassen und Ordnungen des Tierreichs*. Bd. 5. Abtheilung. 2 (Crustacea). 2. Heft (Malacostraca). C.F. Winter’sche Verlagshandlung, Leipzig: 544-1319. https://www.biodiversitylibrary.org/part/146103

Osman M. M., Madkour F. F., Sallam W. S. & Zakaria S. M. 2015. — Seasonal occurrence and distribition of brachyuran crabs caught along the Suez Canal, Egypt. *Egyptian Journal of Aquatic Biology and Fishries* 80: 21-28.

Osman M., Sallam W., Madkour F. & Wicksten M. 2021. — Morphology and distribution of carapace setae in the porter crab *Dorippe quadridens* (Fabricius, 1793) (Decapoda: Brachyura: Dorippidae) inhabiting the Suez Canal, Egypt. *Cahiers de Biologie Marine* 62: 109-119.

Ossó À. 2016. — *Eogeryon elegius* n. gen. and n. sp. (Decapoda: Eubrachyura: Portunoidea), one of the oldest modern crabs from late Cenomanian of the Iberian Peninsula. *Boletín de la Sociedad Geológica Mexicana* 68 (2): 231-246. https://doi.org/10.18268/BSGM2016v68n2a5

Pálfy J., Dulai A., Gasparik M., Ozsvárt P., Pazonyi P. & Szives O. 2008. — *Catalogue of Invertebrate and Vertebrate Paleontological Type Specimens of the Hungarian Natural History Museum*. Hungarian Natural History Museum, Budapest, 209 p.

Pardo L. M., Riveros M., Fuentes J. P. & López-Greco L. L. 2013. — Functional morphology of the seminal receptacle in the crab *Metacarcinus edwardsii*. *Invertebrate Biology* 132: 386-393. https://doi.org/10.1111/ivb.12038

Pardo L. M., Ceroni C., Riveros M. P., Ernst B. & Pino J. 2017. — Morphology of seminal receptacle of the harvested golden crab *Chaceon chilensis* and its implication in the fertilization process. *Invertebrate Biology* 136 (2): 199-206.

Porter M. L., Perez-Losada M. & Crandall K. A. 2005. — Model-based multi-locus estimation of decapod phylogeny and divergence times. *Molecular Phylogenetics and Evolution* 37: 355-369. https://doi.org/10.1016/j.ympev.2005.06.021

Parisi B. 1914. — Oxystomata. I Decapodi giapponesi del Museo di Milano, I. *Atti della Società Italiana di Scienze Naturali* 53: 280-312 [p. 5-35 on separate]. https://www.biodiversitylibrary.org/bibliography/12872

Pasini G. & Garassino A. 2011. — Predation on brachyuran (Crustacea, Decapoda), an unique direct evidence from the Late Cretaceous (Cenomanian) of Hadjoula (Lebanon). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 152 (2): 233-239.

Pasini G. & Garassino A. 2016. — *Ethusa* sp. (Decapoda, Brachyura, Ethusidae) from the Pliocene of Valduggia (Vercelli, Piedmont, NW Italy). *Atti della Società Italiana di Scienze Naturali* 3 (1): 53-54.

Pasini G., Garassino A. & Sami M. 2019a. — Decapod assemblage from the late Miocene (early-middle Messinian) of the Romagna Apennines nearby Brisighella, Emilia-Romagna (N Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano* 6 (1): 27-32.

Pasini G., Garassino A., Bizzarri R., Baldanza A. & Famiani F. 2022. — The decapod fauna from Belvedere di Selvamaggio (Tuscany, Italy): sedimentological context and palaeoenvironmental inferences. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 303 (2): 143-168. https://doi.org/10.1127/njgpa/2022/1041

Pasini G., Garassino A., De Angeli A., HyŽný M., Giusberti L. & Zorzin R. 2019b. — Eocene decapod faunas from the Konservat-Lagerstätten laminites of "Pesciara" (Bolca, Verona) and Monte Postale (Altissimo, Vicenza) in northeast Italy: a review and update. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 293 (3): 233-270. https://doi.org/10.1127/njgpa/2019/0840

Patrulius D. 1959. — Contributions à la systématique des décapodes néojurassiques. *Revue de Géologie et Géographie* 3 (2): 249-257.

Patrulius D. 1966. — Les Décapodes du Tithonique inférieur de Woźniki (Carpathes Polonaises Occidentales). *Annales de la Société géologique de Pologne* 36 (4): 495-517, pls 30, 31.

Patton W. K. 1967. — *Commensal Crustacea*. Proceedings of the Symposium on Crustacea held at Ernakulam from January 12 to 15, 1965. Marine Biological Association of India, 3: 1228-1243.

Paula J. 1987a. — Seasonal distribution of Crustacea Decapoda larvae in S. Torpes bay, South-western Portugal. *Investigación Pesquera* 51, suppl. 1: 267-275.

Paula J. 1987b. — Planktonic stages of brachyuran crabs from the south western iberian coast crustacea decapoda brachyura. *Journal of Natural History* 21 (3): 717-756. https://doi.org/10.1080/00222938700770411

Paula J. 1991. — The zoeal stages of the crab *Medorippe lanata* (Linnaeus, 1767) (Brachyura, Dorippidae) reared in the laboratory, and the larval characters of the Dorippidae. *Journal of Natural History* (London) 25: 75-89. https://doi.org/10.1080/00222939100770071

Paula J. 1996. — A key and bibliography for the identification of zoeal stages of brachyuran crabs (Crustacea, Decapoda, Brachyura) from the Atlantic coast of Europe. *Journal of Plankton Research* 18 (l): 17-27.

Pearson J. 1908. — *Cancer. Liverpool Marine Biology Committee Memoirs* 16: 1-209. https://www.biodiversitylibrary.org/part/43644

Pechüel-Loesche E. 1882. — Ein Reisewerk in drei Abtheilungen, *in* Güssfeldt P., Falkenstein J. & Pechüel-Loesche E. (eds), *Die Loango Expedition ausgesandt von der Deutschen Gesellschaft zur Erforschung Aequatorial-Africas, 1873-1876*, 3 (1): Leipzig: 1-304. https://www.biodiversitylibrary.org/bibliography/58601

Peretti A. V. & Aisenberg A. (eds) 2015. — *Cryptic Female Choice in Arthropods: Patterns, Mechanisms and Prospects*. Springer, Cham, Heidelberg, New York, Dordrecht: 255-284. https://www.biodiversitylibrary.org/bibliography/58601

Pérez-De La Fuente R., Peñalver E., Delclòs X. & Engel M. S. 2012a. — Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera). *ZooKeys* 204: 1-40.

Pérez-De La Fuente R., Delclòs X., Peñalver E., Speranza M., Wierzchosc J., Ascaso C. & Engel M. S. 2012b. — Early evolution and ecology of camouflage in insects. *Proceedings of the National Academy of Sciences of the United States of America* (A) 109: 21414-21419. https://doi.org/10.1073/pnas.1213775110

Pesta O. 1918. — *Die Deacapodenfauna der Adria. Versuch einer Monographie*. Leipzig und Wien, ix + 600 p., 150 figs, 1 map.

Pichod-Viale D. 1966. — L'exuviation céphalique au cours de la mue des Crustacés Décapodes. *Vie et Milieu sér. A,* Biologie Marine 17 (3A): 1235-1271.

Pillai K. K. & Nair N. B. 1970. — Observations on the reproductive cycles of some crabs from the South-West coast of India. *Journal of the Marine Biological Association of India* 10 (2): 384-386.

Pillai K. K & Nair N. B. 1976. — Observations on the breeding biology of some crabs from the Southwest coast of India. *Journal of the Marine Biological Association of India* 15 (2) [1973]: 754-770.

Pipitone C. & Arculeo M. 2003. — The marine Crustacea Decapoda of Sicily (central Mediterranean Sea): a checklist with remarks on their distribution. *Italian Journal of Zoology* 70 (1): 69-78. https://doi.org/10.1080/11250000309356498

Plancus J. 1760. — *De conchis minus notis liber. Cui accessit specimen aestus reciproci maris superi ad littus portumque Arimini.* Roma. Edition 2, 136 p., 19 pls [First edition, 1739, 88 p., 5 pls, with same title, but published in Venice]. https://www.biodiversitylibrary.org/bibliography/15328

Pohle G. W. 1991. — Larval development of Canadian Atlantic oregoniid crabs (Brachyura: Majidae), with emphasis on *Hyas coarctatus alutaceus* Brandt, 1851, and a comparison with Atlantic and Pacific conspecifics. *Canadian Journal of Zoology* 69: 2717-2737. https://doi.org/10.1139/z91-384

Pohle G. & Marques M. 2000. — Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae. *Proceedings of the Biological Society of Washington* 113: 739-760.

Polkowsky S. 2014. — *Krebse und Krabben aus norddeutschen Geschieben – Lobsters and crabs from erratics in northern Germany*. Tassados 2, Norderstedt, Books on Demand, 444 p., 12 pls.

Poore G. C. B. 2004. — *Marine Decapod Crustacea of Southern Australia. A Guide to Identification with Chapter on Stomatopoda by Shane Ahyong*. CSIRO Publishing, Melbourne, 574 p.

Poore G. C. B. 2016. — The names of the higher taxa of Crustacea Decapoda. *Journal of Crustacean Biology* 36 (2): 248-255.

Porter M. L., Pérez-Losada M. & Crandall K. A. 2005. — Model-based multi-locus estimation of decapod phylogeny and divergence times. *Molecular Phylogenetics and Evolution 37*: 355-369. https://doi.org/10.1016/j.ympev.2005.06.021

Quayle W. J. & Collins J. S. H. 1981. — New eocene crabs from the Hampshire Basin. *Palaeontology* 24 (4): 733-758. https://www.biodiversitylibrary.org/part/173589

Quintana R. 1987. — Later zoeal and early postlarval stages of three dorippid species from Japan (Brachyura: Dorippidae: Dorippinae). *Publications of the Seto Marine Biological Laboratory* 32 (4-6): 233-274.

Rajan R., Paramasivam K., Shrinivaasu S., Venkatraman C., Venkataraman K., Padmanaban P., Surendar C., Kumar R. & Vanishree J. 2017. — Fauna (Epibenthic and Epifauna) associated with Sea Grass Ecosystemsin Palk Bay and Gulf of Mannar. Fauna (Epibenthic and Epifauna) associated with Sea Grass Ecosystems in Palk Bay and Gulf of Mannar. *Records of the Zoological Survey of India*, Occ. Paper No. 387: 1-96.

Rambaut A., Suchard M. A., Xie D. & Drummond A. J. 2014. — *Tracer v1.6.* http://beast.bio.ed.ac.uk/Tracer

Rathbun M. J. 1910. — Brachyura. The Danish Expedition to Siam 1899-1900, V. *Det Kongelige Danske Videnskabernes Selskabs Skrifter 7. Raekke*, Naturvidenskabelig og Mathematisk Afdeling, 5 (4): 301-367. https://www.biodiversitylibrary.org/part/119053

Rathbun M. J. 1918. — The grapsoid crabs of America. *Bulletin of the United States National Museum* 97: 14-61, pls 11-61. https://doi.org/10.5962/bhl.title.1051

Rathbun M. J. 1924. — Brachyura Albuneidae and Porcellanidae. Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. 37. *Arkiv för Zoologi* 16 (23): 1-33.

Rathbun M. J. 1925. — The spider crabs of America. *Bulletin of the United States National Museum* 129: i-xx, 1-613, 47 figs, 283 pls. https://biodiversitylibrary.org/page/7846075

Rathbun M. J. 1930. — The cancroid crabs of America. *Bulletin of the United States National Museum* 152: i-xvi, 1-609, 85 figs, 230 pls.

Rathbun M. J. 1931. — New and rare Chinese crabs. *Lingnan Science Journal* 8 (1929): 75-104, pls 5-15.

Rathbun M. J. 1937. — The oxystomatous and allied crabs of America. *Bulletin of the United States National Museum*: i-vi, 1-278, 47 figs, 86 pls. https://www.biodiversitylibrary.org/part/70815

Ravichandran S. & Kannupandi T. 2007. — *Biodiversity of crabs in Pichavaram mangrove environment.* Zoological Survey of India, National Symposium on Conservation and Valuation of Marine Biodiversity: 331-340.

Razak I. H. A., Shamsuddin M. A., Ramasamy A. B. M. A., Samuthirapandian R. & Martin M. B. 2022. — Decapoda Crustaceans at the South China Sea Repository and Reference Centre in Terengganu, Peninsular Malaysia, in Chuan O. M. *et al.* (eds) *Geography of the Physical Environment. Bidong IslandNatural History and Resources.* Springer: 62-73. https://doi.org/10.1007/978-3-030-91924-5_6

Renaud B. 1977. — Les régions et les limites de la carapace d'un Crustacé Décapode *Carcinus maenas* (L.) [Brachyrhyncha Portunidae] ; leurs rapports avec les systèmes fonctionnels principaux. *Bulletin du Muséum national d'Histoire naturelle 3e série* 454, Zoologie 317: 769-794.

Rice A. L. 1964. — The metamorphosis of a species of *Homola* (Crustacea, Decapoda, Dromiacea). *Bulletin of marine science of the Gulf and Caribbean* 14: 221-238.

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

Rice A. L. 1981. — Crab zoeae and brachyuran classification: a re-appraisal. *Bulletin of the British Museum of Natural History* 40 (5): 287-296. https://biodiversitylibrary.org/page/2357372

Rice A. L. 1983. — Zoeal evidence for brachyuran phylogeny, *in* Schram F. R. (ed.), *Crustacean Phylogeny. Crustacean Issues.* Vol. 1. CRC Press: 313-329.

Rice A. L. 1988. — The megalopa stage in majid crabs, with a review of spider crabs relationships based on larval characters, *in* Fincham A. A. & Rainbow P. S. (eds), *Aspects of Decapod Crustacean Biology.* Proceedings of a Symposium, Zoological Society of London. Clarendon Press, Oxford: 27-46.

Richer de Forges B., Jamieson B. G. M., Guinot D. & Tudge C. C. 1997. — Ultrastructure of the spermatozoa of Hymenosomatidae (Crustacea: Brachyura) and the relationships of the family. *Marine Biology* 130: 233-242. https://doi.org/10.1007/s002270050243

Rodgers P. J., Reaka M. L. & Hines A. H. 2011. — A comparative analysis of sperm storage and mating strategies in five species of brachyuran crabs. *Marine Biology* 158: 1733-1742. https://doi.org/10.1007/s00227-011-1687-6

Ronquist F. & Huelsenbeck J. P. 2003. — MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572-1574. https://doi.org/10.1093/bioinformatics/btg180

Rossetti I., Sartor P., Francesconi B., Mori M. & Belcari P. 2006. — Biological aspects of *Medorippe lanata* (Linnaeus, 1767) (Brachyura: Dorippidae) from the eastern Ligurian Sea (western Mediterranean). *Hydrobiologia* 557: 21-29. https://doi.org/10.1007/s10750-005-1304-0

Rumphius G. E. 1705. — *D'Amboinsche Rariteitkamer, behelzende eene beschryvinge van allerhande zoo weeke als harde schaalvisschen, te weeten raare krabben, kreeften, en diergelyke zeedieren, als mede allerhande hoorntjes en schulpen, die men in d'Amboinsche Zee vindt: daar beneven zommige mineraalen, gesteenten, en soorten van aarde, die in d'Amboinsche, en zommige omleggende Eilanden gevonden worden.* 1st édition. François Halma, Amsterdam, 28 unnumbered pages + 340 p. + 43 unnumbered pages, 60 pls.

Ryan E. P. 1968. — Structure and function of the reproductive system of the crab *Portunus sanguinolentus* (Herbst) (Brachyura: Portunidae). 2. The female system, *in* Proceedings of the Symposium on Crustacea, Ernakulam, 1965. Mandapam Camp. *Marine Biological Association of India* 2 [1967]: 522-544, pls 1-3.

Sagan C. 1980. — *Cosmos.* Ballantine Books, New York, 324 p. [1985 edition paperback]. https://www.biodiversitylibrary.org/bibliography/6191

Sahu B. 2012. — The Leaf Porter crab from mangrove area of Andaman. *Seshaiyana* 20 (2): 6.

Saint Laurent M. de 1980. — Sur la classification et la phylogénie des Crustacés Décapodes Brachyoures. I. Podotremata Guinot, 1977. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences*, série D, 290: 1265-1268.

Saint Laurent M. de 1989. — La nouvelle superfamille des Retroplumoidea Gill, 1894 (Decapoda, Brachyura): systématique, affinités et évolution, *in* Forest J. (ed.), *Résultats des Campagnes MUSORSTOM, vol. 5.* Mémoires du Muséum national d'Histoire naturelle, sér. A, Zoologie, vol. 144: 103-179.

Sainte-Marie G. & Sainte-Marie B. 1998. — Morphology of the spermatheca, oviduct, intermediate chamber, and vagina of the adult snow crab (*Chionoecetes opilio*). *Canadian Journal of Zoology* 76 (8): 1589-1604. https://doi.org/10.1139/z98-106

Sakai K. & Nakano T. 1983. — List of Decapod Crustacea in Laboratory of Crustacea, Shikoku Women's University, Tokushima, I. *Bulletin of Shikoku Women's* 3 (l): 73-94.

Sakai T. ca 1930. — [Life of Crabs and Shrimps]. Pages 1-98, plates 1-10 (In Japanese).

Sakai T. 1936. — *Crabs of Japan. 66 Plates in Life Colours with Descriptions.* Tokyo. 239 p. [bibliography and index, 27 p.], frontispiece, pls 1-66 (Dated 1935, published 1936).

Sakai T. 1937. — Studies on the Crabs of Japan. II. Oxystomata. *Science Reports of the Tokyo Bunrika Daigaku* 3, Supplement n°2: 67-192.

Sakai T. 1940. — Bio-geographic review on the distribution of Crabs in Japanese waters. *Records of Oceanographic Works in Japan* 11 (l): 27-63.

Sakai T. 1956. — *Crabs.* Edtion 1. Shisei-Shoin, Tokyo: 1-60 [List of Latin names], 1-224 p. [Japanese text], 1-4 [Introduction], 69 figs, 6 pls (two coloured). https://www.biodiversitylibrary.org/bibliography/163328

Sakai T. 1976. — *Crabs of Japan and the Adjacent Seas.* 3 vols, xxix + 773 p. [English vol.]; 16 p., 251 pls [Plates vol.]; 461 p.

[Japanese vol.]. Kodansha Ltd, Tokyo, Japan.

Sakai T. 1980. — *Crabs. Their morphology and myth*. Second edition. Tokyo: 1-299, 8 pls. https://www.biodiversitylibrary.org/bibliography/163328

Sakai T. 1985. — Heike-gani, its prosperity and fossils. *Aquabiology* Tokyo 7 (5): 330-336. (In Japanese: 330-333; in English: 334-336).

Sakai T., Tomiyama T., Hibiya T. & Takeda M. 1983. — *Fisheries in Japan, Crab.* Tokyo, 179 p.

Sal Moyano M. P., Gavio M. A. & Cuartas E. I. 2010. — Morphology and function of the reproductive tract of the spider crab *Libinia spinosa* (Crustacea, Brachyura, Majoidea): pattern of sperm storage. *Helgoland Marine Research* 63 (3): 213-221. https://doi.org/10.1007/s10152-009-0180-9

Sal Moyano M., Gavio M. & Cuartas E. I. 2011. — Copulatory system of the spider crab *Libinia spinosa* (Crustacea: Brachyura: Majoidea). *Journal of the Marine Biological Association of the United Kingdom* 91 (8): 1617-1625. https://doi.org./10.1017/S0025315411000257

Sal Moyano M. P., Luppi T., Medesani D. A., McLay C. L. & Rodríguez E. M. 2017. — Hard-shell mating in *Neohelice granulata*: the role of ecdysone in female receptivity and mate attraction. *Journal of Comparative Physiology A* 203 (3): 233-243. https://doi.org/10.1007/s00359-017-1159-7

Sankarankutty C. 1966. — On Decapoda Brachyura from the Gulf of Mannar and Palk Bay. *Proceedings of the Symposium on Crustacea Held at Ernakulam from January 12 to 15, 1965,* 1. Marine Biological Association of India: 347-362, pls 1-2.

Sant'Anna B. S., Pinheiro M. A. A., Mataqueiro M. & Zara F. J 2007. — Spermathecae of the mangrove crab *Ucides cordatus*: a histological and histochemical view. *Journal of the Marine Biological Association of the United Kingdom* 87: 903-911. https://doi.org/10.1017/S0025315407056676

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

Schmidt M., Hazerli D. & Richter S. 2020. — Kinematics and morphology: a comparison of 3D-patterns in the fifth pereiopod of swimming and non-swimming crab species (Malacostraca, Decapoda, Brachyura). *Journal of Morphology* 281: 1547-1566. https://doi.org/10.1002/jmor.21268

Schmitt W. L. 1921. — The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the United States Bureau of Fisheries Steamer "Albatross" in connection with the Biological Survey of San Francisco Bay during the years 1912-1913. *University of California Publications in Zoology* 23: 1-469.

Schmitt W. L. 1931. — Crustaceans, *in* Bassler R. S., Resser C. E., Schmitt W. L. & Bartsch P. (eds), Shelled Invertebrates of the Past and Present, with Chapters on Geological History. Part II. *Smithsonian Scientific Series* 10: 85-248, pls 32-71.

Schmitt W. L. 1968. — *Crustaceans*. Ann Arbor, the University of Michigan Press, 199 p. https://www.biodiversitylibrary.org/bibliography/2687

Scholtz G. 2014. — Evolution of crabs – history and deconstruction of a prime example of convergence. *Contribution to Zoology* 83: 87-105. https://doi.org/10.1163/18759866-08302001

Scholtz G. & McLay C. L. 2009. — Is the Brachyura Podotremata a monophyletic group?, *in* Martin J. W., Crandall K. A. & Felder D. L. (eds), *Decapod Crustacean Phylogenetics.* Crustacean Issues. Taylor & Francis, CRC Press, Boca Raton, Florida, 18: 417-435. https://doi.org/10.1201/9781420092592-c21

Schweigert G. 2018. — An additional representative of Lecythocaridae (Decapoda: Brachyura: Dromiacea) from the Upper Jurassic of southern Germany. *Journal of Crustacean Biology* 39 (1): 36e39. https://doi.org/10.1093/jcbiol/ruy092

Schweigert G. & Robins C. M. 2016. — Earliest representatives of Lecythocaridae (Crustacea: Brachyura) from the Upper Jurassic of southern Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 280 (3): 325-330. https://doi.org/10.1127/njgpa/2016/0583

Schweitzer C. E. 2001. — Paleobiogeography of Cretaceous and Tertiary Decapod Crustaceans of the North Pacific Ocean. *Journal of Paleontology* 75 (4): 808-826.

Schweitzer C. E. & Feldmann R. M. 2000. — New species of calappid crabs from western North America and reconsideration of the Calappidae sensu lato. *Journal of Paleontology* 74 (2): 230-246. https://doi.org/10.1666/0022-3360(2000)074<0230:NSOCCF>2.0.CO;2

Schweitzer C. E. & Feldmann R. M. 2009. — Revision of the Prosopinae *sensu* Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including four new families, four new genera, and five new species. *Annalen des Naturhistorischen Museums in Wien series A* 110: 55-121.

Schweitzer C. E. & Feldmann R. M. 2011a. — New fossil Brachyura (Decapoda: Homoloidea, Dorippoidea, Carpilioidea) from the United Kingdom. *Bulletin of the Mizunami Fossil Museum* 37: 1-11.

Schweitzer C. E. & Feldmann R. M. 2011b. — Revision of some fossil podotrematous Brachyura (Homolodromiidae; Longodromitidae; Torynommidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 260: 237-256. https:// doi.org/10.1127/0077-7749/2011/0138.

Schweitzer C. E. & Feldmann R. M. 2018. — *Treatise Online, Number 106. Part R, Revised, Volume 1, Chapter 8T17: Systematic Descriptions: Superfamily Retroplumoidea Gill, 1864.* Paleontological Institute, Lawrence, Kansas, USA: 1-6.

Schweitzer C. E., Feldmann R. M. & Karasawa H. 2007. — Revision of the Carcineretidae Beurlen, 1930 (Decapoda: Brachyura: Portunoidea) and remarks on the Portunidae Rafinesque, 1815. *Annals of Carnegie Museum* 76: 15-37. https://doi.org/10.2992/0097-4463(2007)76[15:ROTCBD]2.0.CO;2.

Schweitzer C. E., Feldmann R. M. & Karasawa H. 2021. — *Treatise Online, Number 159. Part R, Revised, Volume 1, Chapter 8T17: Systematic Descriptions: Superfamily Dorippoidea*. Paleontological Institute, Lawrence, Kansas, USA: 1-8.

Schweitzer C. E., Lacovara K. J., Smith J. B., Lamanna M. C., Lyon M. A. & Attia Y. 2003. — Mangrove-dwelling crabs (Decapoda: Brachyura: Necrocarcinidae) associated with dinosaurs from the Upper Cretaceous (Cenomanian) of Egypt. *Journal of Paleontology* 77 (6): 888-894. https://doi.org/10.1666/0022-3360(2003)077<0888:MCDBNA>2.0.CO;2

Schweitzer C. E., Feldmann R. M., Garassino A., Karasawa H. & Schweigert G. 2010. — A classification of the fossil decapod crustaceans, *in* Systematic list of fossil decapod crustacean species. *Crustaceana Monographs* 10: 8-146. https://doi.org/10.1163/ej.9789004178915.i-222.7

Schweitzer C. E., Lazăr I., Feldmann R. M., Stoica M. & Franțescu O. D. 2017. — Decapoda (Anomura; Brachyura) from the Late Jurassic of Dobrogea, Romania. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 286 (2): 207-228. https://doi.org/10.1127/njgpa/2017/0696

Secretan S. 1964. — Les Crustacés Décapodes du Jurassique supérieur et du Crétacé de Madagascar. Muséum national d'Histoire naturelle, Paris: 1-226, figs 1-114, pls 1-20, tables 1-2 (*Mémoires du Muséum national d'Histoire naturelle Série C*; 14).

Secretan S. 1966. — Transformations squelettiques liées à la céphalisation chez les Crustacés Décapodes. *Comptes Rendus des Séances hebdomadaires de l'Académie des Sciences* (Paris) *Série D* 262: 1062-1065.

Secretan S. 1972. — *L'évolution segmentaire squelettique des Crustacés supérieurs*. 24th International Geological Congress, Canada, Montréal, 1972. *Palaeontology* sect. 7: 612-620.

Secretan S. 1975. — Les Crustacés du Monte Bolca. - Studi e

Ricerche sui Giacimento Terziari di Bolca II. *Miscellanea Paleontologica, Museo Civico di Storia Naturale, Verona* 2: 315-388, pls 1-37.

Serène R. 1937. — Inventaire des invertébrés marins de l'Indochine (1re Liste). *Notes de l'Institut Océanographique de l'Indochine* 30: 1-84.

Serène R. 1982. — Trois nouvelles espèces de Brachyoures (Crustacea, Decapoda) provenant de la Baie de Nhatrang (Vietnam). *Bulletin du Muséum national d'Histoire naturelle 4e série* 3 (Section A, number 4) (for 1981): 1127-1138.

Serène R. & Romimohtarto K. 1969. — Observations on the species of *Dorippe* from the Indo-Malayan Region. *Marine Research in Indonesia* (*Penelitian Laut di Indonesia*) 9: 1-35.

Serène R. & Vadon C. 1981. — Crustacés Décapodes: Brachyoures. Liste préliminaire, description de formes nouvelles et remarques taxonomiques, *in* Forest J. (ed.), Résultats des Campagnes MUSORSTOM I - Philippines (18-28 Mars 1976), Muséum national d'Histoire naturelle, Paris, 1: 117-140. (*Mémoires du Muséum national d'Histoire naturelle;* Série A, Zoologie: 91).

Shelford R. W. C. 1916. — *A Naturalist in Borneo*. London, xxviii + 331 p., 32 pls. [A facsimile reprint edition was published in 1985 by Oxford University Press]. https://www.biodiversitylibrary.org/bibliography/32180

Shen C.-C. 2006. — *Behaviour associated with shell competition in the urchin crab,* Dorippe quadridens. Master Thesis. Institute of Marine Biology, National Sun Yat-Sen University, Kaohsiung, Taiwan, 43 p. (In Chinese with English abstract).

Shen C.-J. 1931. — The Crabs of Hong Kong. Part I. *HongKong Naturalist* 2 (2): 92-110.

Shen C. J. 1932. — The Brachyuran Crustacea of North China. *Zoologia Sinica* Peiping (A) 9 (1): i-x, 1-320.

Shen C. J. 1937a. — On some account of the crabs of North China. *Bulletin of the Fan Memorial Institute of Biology* (Zoology) Peiping 7 (5): 167-185.

Shen C. J. 1937b. —Second addition to the fauna of Brachyuran Crustacea of North China, with a check list of the species recorded in this particular region. *Contributions from the Institute of Zoology, National Academy of Peiping* 3 (6): 277-313.

Shen C. J. 1940a. — The Brachyuran Fauna of Hong Kong. *Journal of the Hong Kong Fisheries Research Station* 1 (2): 211-242.

Shen C. J. 1940b. — On the collection of Crabs of South China. *Bulletin of the Fan Memorial Institute of Biology* (Zoology) Peiping 10 (2): 69-104.

Shi G., Cui Z., Hui M., Liu Y., Chan T. Y. & Song C. 2015. — The complete mitochondrial genomes of *Umalia orientalis* and *Lyreidus brevifrons*: the phylogenetic position of the family Raninidae within brachyuran crabs. *Marine Genomics* 21: 53-61. https://doi.org/10.1016/j.margen.2015.02.002

Shi G., Cui Z., Hui M., Liu Y., Chan T. Y. & Song C. 2016. — Unusual sequence features and gene rearrangements of primitive crabs revealed by three complete mitochondrial genomes of Dromiacea. *Comparative Biochemistry and Physiology* D 20: 65-73.

Shih H.-T., Ng P. K. L., Davie P. J. F., Schubart C. D., Türkay M., Naderloo R., Jones D. & Liu M.-Y. 2016a. — Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera. *Raffles Bulletin of Zoology* 64: 139-175.

Shih H.-T., Lee J.-H., Ho P.-H., Liu H.-C., Wang C.-H., Suzuki H. & Teng S.-J. 2016b. —Species diversity of fiddler crabs, genus *Uca* Leach, 1814 (Crustacea: Ocypodidae), from Taiwan and adjacent islands, with notes on the Japanese species. *Zootaxa* 4083 (1): 57-82. https://doi.org/10.11646/zootaxa.4083.1.3

Siebold G. T. de [Ph. F. von] 1824. — *De Historiae naturalis in Japonia statu, nee non de augmento emolumentisque in decursu perscrutationum exspectandis Dissertatio, cui accedunt Spicilegia Faunae Japonicae.* Batavia: 1-16. [Facsimile reprint edition published in Tokyo on 5 June 1937, with an *Introduction to Siebold's De Historiae naturalis in Japonia statu* by T. Esaki: 3 p.]

Siebold G. T. de [Ph. F. von] 1826. — *De Historiae naturalis in Japonia statu nec non de augmento emolumentisque in decursu perscrutationum exspectandis Dissertatio, cui accedunt Spicilegia Faunae Japonicae*: 1-20. Wirceburgi (= Würzburg, Germany). [Facsimile reprint edition published in Tokyo in 1937 together with reprint of previous item.]

Siebold G. T. de [Ph. F. von] 1850. — Commentatio physico-historica de Crustaceis Japonicis *in* Ph. F. von Siebold, *Fauna Japonica (Crustacea)*: vii-xvii.

Sin Y. W., Lai J. C. Y., Ng P. K. L. & Chu K. H. 2009. — Phylogeny of Dorippoidea (Crustacea: Decapoda: Brachyura) inferred from three mitochondrial genes. *Invertebrate Systematics* 23 (3): 223-230. https://doi.org/10.1071/IS09020

Sourie R. 1954. — Étude écologique sommaire des fonds sableux en Baie de Dakar. *Annales de l'Ecole Supérieure des Sciences* 1: 141-155.

Souza L. P. de & Silva J. R. F. 2009. — Morphology of the female reproductive system of the red-clawed mangrove tree crab (*Goniopsis cruentata* Latreille, 1803). *Scientia Marina* 73: 527-539. https://doi.org/10.3989/scimar.2009.73n3527

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

Souza L. P. de, Ogawa C. Y., Silva J. R. F. & Camargo-Mathias M. I. 2017. — Comparative morphology of the female genital ducts of seven eubrachyuran crabs (Saint-Laurent, 1980). *Acta Zoologica* (Stockholm) 98 (2): 125-135. https://doi.org/10.1111/azo.12154

Spalding J. F. 1942. — The nature and formation of the spermatophore and sperm plug in *Carcinus maenas*. *Quarterly Journal of microscopical Science* 83: 399-422.

Spiridonov V. A. 2020. — An update of phylogenetic reconstructions, classification and morphological characters of extant Portunoidea Rafinesque, 1815 (Decapoda, Brachyura, Heterotremata), with a discussion of their relevance to fossil material. *Geologija* 63 (1): 133-166. https://doi.org/10.5474/geologija.2020.014

Spiridonov V. A. & Türkay M. 2007. — Deep sea crabs of the subfamily Ethusinae Guinot, 1977 from the north-western Indian Ocean (Crustacea: Decapoda: Brachyura: Dorippidae). *Fauna of Arabia* 23: 125-150.

Springthorpe R. & Lowry J. 1994. — Catalogue of crustacean type specimens in the Australian Museum: Malacostraca. *Technical Reports of the Australian Museum* (11): 1-134.

Starzyk N. 2013. — Jurassic crabs: new characters of carapace diagnostic to known tanidromitid species. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 269 (2): 173-187. https://doi.org/10.1127/0077-7749/2013/0343

Starzyk N., Krzemińska E. & Krzemiński W. 2011. — Intraspecific variation in the Jurassic crab *Bucculentum bucculentum* (Decapoda: Homolodromioidea: Bucculentidae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 260 (2): 203-210. https://doi.org/10.1127/0077-7749/2011/0169

Starzyk N. 2020. — The oldest species of the genus *Laeviprosopon* (Decapoda: Brachyura: Prosopidae) from the Oxfordian of Poland. *Acta zoologica cracoviensia* 63 (1): 9-13. https://doi.org/10.3409/azc.63.02

Starzyk N., Van Bakel B., Klompmaker A. A., Schweigert G. & Fraaije R. H. B 2023. — A new approach to the systematics of *Laeviprosopon* (Brachyura: Homolidae), with remarks on the molting process of early brachyurans. *Palaeontologia Electronica* 26 (1): a10. https://doi.org/10.26879/1204

Stephensen K. 1946. — The Brachyura of the Iranian Gulf with an appendix: the male pleopods of the Brachyura, *in* Jessen K. &

Spärck R. (eds), *Danish Scientific Investigations in Iran*, part 4 [1945]. Copenhagen, Munksgaard: 1-237.

Stamatakis A. 2014. — RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30 (9): 1312-1313. http://doi.org/10.1093/bioinformatics/btu033

Starzyk N., Van Bakel B., Klompmaker A. A., Schweigert G. & Fraaije R. H. B. 2023. — A new approach to the systematics of Laeviprosopon (Brachyura: Homolidae), with remarks on the molting process of early brachyurans. *Palaeontologia Electronica* 26 (1): a10. https://doi.org/10.26879/1204

Sternberg R. von 1996. — Carcinization as an underlying synapomorphy for the decapod crustacean taxon Meiura. *Evolutionary Theory* 11: 153-162.

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

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

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

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

Stimpson W. 1855. — Descriptions of some of the new marine Invertebrata from the Chinese and Japanese Seas. *Proceedings of the Academy of Natural Sciences of Philadelphia* 7: 375-384. https://www.biodiversitylibrary.org/bibliography/51444

Studer T. 1892. — Ueber zwei fossile dekapode Krebse aus den Molasse ablagerungen des Belpberges. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 19: 1-11.

Sun S., Jiang W., Yuan Z. & Sha Z. 2022. — Mitogenomes provide insights into the evolution of Thoracotremata (Brachyura: Eubrachyura). *Frontiers in Marine Science* 9 | Article 848203: 1-12.

Takeda M. 1975. — Brachyura, *in* Utinomi H. (ed.), *Aquatic Invertebrates.* Gakken Chukosei Zukan 9: 120-149 (figs with Latin names, and indications of characters with arrows), 188-331 (descriptions of the species figured in order of the Japanese names according to the Japanese alphabet) (In Japanese. Second printing in 1976). https://www.biodiversitylibrary.org/part/119053

Takeda M. 1982a. — Biogeographical notes on the crabs obtained by dredging off the Southeast Coast of the Izu Peninsula, Central Japan. *Bulletin of the Biogeographical Society of Japan* 37 (1-6): 15-21.

Takeda M. 1982b. — *Keys to the Japanese and Foreign Crustaceans Fully Illustrated in Colors*. First Edition. Tokyo: i-vi, 1-58 [keys], 1-285.

Takeda M. 1983. — Brachyura, *in* Utinomi H. (ed.), *The Aquatic Lower Animals of Japan.* Gakken Illustrated Nature Encyclopedia. Gakken Co Ltd, Tokyo: 1-342 (120-149: illustrations with Latin names, and indications of characters by arrows; 188-331: descriptions) (In Japanese). (Second edition of Takeda, 1975, without change. Second printing in 1985). https://www.biodiversitylibrary.org/part/119053

Takeda M. & Tachikawa H. 2015. — Crabs of the families Palicidae and Crossotonotidae (Crustacea, Decapoda, Brachyura, Palicoidea) from the Ogasawara Islands, Japan, with the description of a new species. *Zootaxa* 3918 (1): 141-150. https://doi.org/10.11646/zootaxa.3918.1.7

Takeda M. & Manuel-Santos M. R. 2006. — Crabs from Balicasag Island, Bohol, the Philippines: Dromiidae, Dynomenidae, Homolidae, Raninidae, Dorippidae, and Calappidae. *Memoirs of the National Science Museum* (Tokyo) 44: 83-104.

Takeda M. & Miyake. S. 1970. — Gymnopleura, Dromiacea and Oxystomata. Crabs from the East China Sea, IV. *Journal of the Faculty of Agriculture, Kyushu University* 16 (3): 193-235. https://doi.org/10.5109/22804

Takeda M., Komai T., Komatsu H. & Ikeda H. 2006. — [Crab fauna of the Sagami Sea, Pacific coast of central Japan, in *Study on environmental changes in the Sagami Sea and adjacent coastal area with time serial comparison of fauna and flora.* II. Marine organisms (animals [Arthropods-Chordates]). *Memoirs of the National Science Museum* (Tokyo) (41): 183-215. (in Japanese with English abstract, not seen).

Takeda M., Furuta S., Miyanaga T., Tamura A. & Wada T. 2011. — Crabs from the southwestern Sea of Japan along Tottori Prefecture and its vicinity, Japan. *Bulletin of the Tottori Prefectural Museum* 48: 29-94.] (in Japanese with English abstract, not seen).

Takeda M., Komatsu H., Shikatani N., Maenosono T. & Naruse T. 2019. — Annotated list of subtidal crabs in the Shikatani Collection made at Nakagusuku Bay, Okinawa Island, the Ryukyu Islands, Japan. *Fauna Ryukyuana* 50: 1-69, 20 pls (In Japanese, with English abstract and figure captions).

Tan S. H. & Ng P. K. L. 1988. — *A guide to Seashore Life*. First edition. Singapore, Singapore Science Centre, 160 p.

Tan S. H. & Ng P. K. L. 2007a. — Description of new genera from the subfamily Parthenopinae (Crustacea: Decapoda: Brachyura: Parthenopidae). *Raffles Bulletin of Zoology* Supplement 16: 95-119.

Tan S. H. & Ng P. K. L. 2007b. — Review of the subfamily Daldorfiinae Ng *&* Rodríguez*,* 1986 (*C*rustacea: Decapoda: Brachyura: Parthenopidae). *Raffles Bulletin of Zoology* Supplement 16: 121-167.

Tan L. W. H. & Ng P. K. L. 1992. — *A Guide to Seashore Life*, second edition. Singapore Science Centre, Singapore, 160 p.

Tavares. M. 1993. — Crustacea Decapoda: Les Cyclodorippidae et Cymonomidae de l'Indo-Ouest-Pacifique à l'exclusion du genre *Cymonomus*, *in* Crosnier A. (ed.), Résultats des campagnes MUSORSTOM, 10. Muséum national d'Histoire naturelle, Paris: 253-313. (*Mémoires du Muséum national d'Histoire naturelle*; 156).

Tavares. M. 2003. — A new theoretical approach for the study of monophyly of the Brachyura (Crustacea: Decapoda) and its impact on the Anomura. *Memoirs of Museum Victoria* 60 (1): 145-149. https://doi.org/10.24199/j.mmv.2003.60.17

Tavares M. & Franco G. M. O. 2004. — Why the spermathecal openings are so displaced forward in the Podotremata (Decapoda: Brachyura)? Ontogenetic changes and phylogenetic implications. *Nauplius* 12 (2): 127-134.

Tavares. M. & Secretan S. 1993. — La notion de thelycum et de spermathèque chcz les Crustacés Décapodes. *Comptes Rendus des Séances de l'Académie des Sciences* (Paris) *Série 3*, 316: 133-138.

Terada M. 1981. — Zoeal development of three species of crabs in the subfamily Dorippinae. *Zoological Magazine* (Tokyo) 90: 21-32. https://doi.org/10.1016/j.ympev.2009.05.03

Teske P. R., McLay C. L., Sandoval-Castillo J., Papadopoulos I., Newman B. K., Griffiths C. L., McQuaid C. D., Barker N. P., Borgonie G. & Beheregaray L. B. 2009. — Tri-locus sequence data reject a "Gondwanan origin hypothesis" for the African/ South Pacific crab genus *Hymenosoma. Molecular Phylogenetics and Evolution* 53: 23-33. https://doi.org/10.1016/j.ympev.2009.05.031

Thoma B. T. 2007. — Notes on crabs of the families Goneplacidae and Dorippidae (Decapoda Brachyura) from the Dampier Archipelago, Western Australia. Records of the Western Australian Museum Supplement 73 (1): 299-302. Https://doi.org/10.18195/issn.0313-122x.73.2007.299-302

Trivedi J. N., Trivedi D. J., Vachrajani K. D. & Ng P. K. L. 2018. — An annotated checklist of the marine brachyuran crabs (Crustacea: Decapoda: Brachyura) of India. *Zootaxa* 4502 (1): 1-83. https://doi.org/10.11646/zootaxa.4502.1.1

Tsang L. M., Schubart C. D., Ahyong S. T., Lai J., Au E., Ng P. K. L., Chan T. Y. & Chu K. H. 2014. — Evolutionary history of the true crabs (Crustacea, Decapoda, Brachyura), including the origin of the freshwater crabs. *Molecular Phylogenetics and Evolu-*

tion 31 (5): 1173-1187. https://doi.org/10.1093/molbev/msu068

Tsang C. T. T., Schubart C. D., Chu K. H., Ng P. K. L. & Tsang M. L. 2022. — Molecular phylogeny of Thoracotremata crabs (Decapoda, Brachyura): toward adopting monophyletic superfamilies, invasion history into terrestrial habitats and multiple origins of symbiosis. *Molecular Phylogenetics and Evolution* 177: 107596. https://doi.org/10.1016/j.ympev.2022.107596

Tudge C. C., Asakura A. & Ahyong S. T. 2012. — Infraorder Anomura MacLeay, 1838, *in* Schram F. R. & Von Vaupel Klein J. C. (eds), *Treatise on Zoology. Anatomy, taxonomy, biology.* The Crustacea, 9, part B: 221-333. Brill, Leiden. https://doi.org/10.1163/9789047430179_005

Tudge C. C., Scheltinga D. M., Jamieson B. G. M., Guinot D. & Richer De Forges B. 2014. — Comparative ultrastructure of the spermatozoa of the Majoidea (Crustacea, Decapoda, Brachyura) with new data on six species in five genera. *Acta Zoologica* 95: 1-20. https://doi.org/10.1111/azo.12005

Türkay M. 1976. — Decapoda Reptantia von der portugiesischen und marokkanischen Küste. Auswertung der Fahrten 8, 9c (1967), 19 (1970), 23 (1971) und 36 (1975) von F.S. «Meteor». *«Meteor» Forschungsergebnisse, Reihe D Biologie* 23: 23-44, figs 1-35.

Uchida T. 1960. — *Carcinactis ichikawai* n. gen., n. sp., an Actiniarian commensal with the crab *Dorippe granulata*. *Japanese Journal of Zoology* 12 (4): 595-601.

Udekem d'Acoz C. d' 1994. — Contribution à la connaissance des Crustacés Décapodes Helléniques 1: Brachyura. Bios (Macedonia, Greece). *Scientific Annals of the school of biology* 1 (2) [1993]: 9-47.

Udekem d'Acoz C. d' 1999. — *Inventaire et Distribution des Crustacés Décapodes de l'Atlantique Nord-Oriental, de la Méditerranée et des Eaux Continentales Adjacentes au nord de 25°N.* Collection "Patrimoines Naturels" (Muséum national d'Histoire naturelle/S. P.N.), Paris, vol. 40, x + 383 p.

Umemoto M. & H. Karasawa H. 1998. — Decapod crustaceans from the Holocene Nanyo Formation of Aichi Prefecture, Japan. Kasekinotomo 45: 10-19.

Ungaro N., Marano C. A., Ceriola L. & Martino M. 2005. — Distribution of demersal crustaceans in the southern Adriatic Sea. *Acta Adriatica* 46: 27-40.

Urita T. 1942. — Decapod Crustaceans from Saghalien, Japan. *Bulletin of the Biogeographical Society of Japan* 12 (1): 1-78.

Van Bakel B. W. M., Jagt J. W. M., Fraaije R. H. B. & Coole Y. 2003. — New data on the crab *Binkhorstia ubaghsii* (Late Maastrichtian; NE Belgium, SE Netherlands), *in* Jagt J. W. M., Van Bakel B. W. M. & Fraaije R. H. B. (eds), Second Symposium on Mesozoic and Cenozoic decapod crustaceans. Boxtel/Maastricht, The Netherlands, September 3-6, 2003. *Contributions to Zoology* 72: 85-89. https://doi.org/10.1163/18759866-0720203003

Van Bakel B. W. M., Fraaije R. H. B. & Jagt J. W. M. 2006. — Synopsis of Cenozoic decapod crustaceans from Belgium. *Revista Mexicana de Ciencias Geológicas* 23 (3): 370-374.

Van Bakel B. W. M., Guinot D., Artal P., Fraaije R. H. B. & Jagt J. W. M. 2012a. — A revision of the Palaeocorystoidea and the phylogeny of raninoidian crabs (Crustacea, Decapoda, Brachyura, Podotremata). *Zootaxa* 3215: 1-216. https://doi.org/10.11646/zootaxa.3215.1.1

Van Bakel B. W. M., Guinot D., Jagt J. W. M. & Fraaije R. H. B. 2012b. — *Mithracites takedai*, a new homoloid crab (Decapoda, Brachyura) from the lower Cretaceous (Aptian) of Colombia, *in* Komatsu H., Okuno J. & Fukuoka K. (eds), *Studies on Eumalacostraca: a homage to Masatsune Takeda. Crustaceana Monographs* 17: 81-90. https://doi.org/10.1163/9789004202894_007

Van Bakel B. W. M., Mychko E. V., Spiridonov A., Jagt J. W. M. & Fraaije R. H. B. 2020. — New Cretaceous crabs (Crustacea, Brachyura) from Moscow Oblast and Dagestan (Russia): patterns in phylogeny and morphospace of the oldest eubrachyurans (Dorippoidea). *Cretaceous Research* (2021) 119: 104675. https://www.sciencedirect.com/science/article/pii/S0195667120303621?via%3Dihub - aep-article-footnote-id12

Van den Brink A. M. 2006. — *The reproductive ecology and biology of the pill-box crab*: Halicarcinus cookii *Filhol, 1885 (Brachyura: Hymenosomatidae)*. Unpublished master thesis, Canterbury University, Christchurch, New Zealand.

Van den Brink A. M. & McLay C. L. 2009. — Use of the sterile male technique to investigate sperm competition in a pill box crab, *Halicarcinus cookii* Filhol, 1885 (Brachyura: Hymenosomatidae). *Journal of Crustacean Biology* 29 (1): 62-69. https://doi.org/10.1651/08-2989.1

Van Straelen V. 1921. — Catalogue des Crustacés décapodes des terrains tertiaires de la Belgique. *Annales de la Société royale de Zoologie et de Malacologie de Belgique* 51 (1920): 111-131.

Van Straelen V. 1925. — Contribution à l'étude des Crustacés Décapodes de la période Jurassique. *Mémoires de l'Académie royale de Belgique, Classe des Sciences Series 2*, 7: 1-462, pls 1-10.

Van Straelen V. 1938. — Crustacés décapodes Cénozoiques des Indes Orientales Néerlandaises. *Leidsche Geologische Mededeelingen* 10: 90-103.

Varadharajan D. & Soundarapandian P. 2014. — Crab biodiversity from Arukkattuthurai to Pasipattinam, southeast coast of India. *Indian Journal of Geo-Marine Sciences* 43 (4): 676-698.

Veiga Ferreira O. da 1965. — Nova contribuição para o conhecimento dos Malacostráceos do Miocénio Marinho de Portugal. *Communicaçoes dos Serviços Geologicos de Portugal* 48: 5-17, plates 1-2.

Vega F. J., González-León O. & Moreno-Bedmara J. A. 2019. — Early Cretaceous (late Barremian) Crustacea from Puebla, Mexico. *Journal of South American Earth Sciences* 96: 10233. https://doi.org/10.1016/j.jsames.2019.102330

Vega F. J., Bruce N. L., Serrano L., Bishop G. A. & Perrilliat M. D. C. 2005. — A review of the Lower Cretaceous (Tlayúa Formation: Albian) Crustacea from Tepexi de Rodríguez, Puebla, Central Mexico. *Bulletin of the Mizunami Fossil Museum* 32: 25-30. https://doi.org/10.1016/j.jsames.2019.102330

Vega F. J., Nyborg T.., Kovalchuk G., Etayo F., Luque J., Rojas-Briceño A., Patarroyo P., Porras-Múzquiz H., Armstrong A., Bermúdez H. & Garibay L. 2010. — On some Panamerican Cretaceous crabs (Decapoda: Raninoida). *Boletin de la Sociedad Geológica Mexicana* 62 (2): 263-279. https://doi.org/10.18268/BSGM2010v62n2a6

Vega F. J., Alvarado-Ortega J., Luque J., Porras-Múzquiz H., Carbot-Chanona G., González-Rodríguez K. A., Cevallos-Ferriz S. R. S. & Ifrim C. 2022. — Cretaceous Crustacea from plattenkalk deposits of Mexico. *Journal of South American Earth Sciences* 116: 103839. https://doi.org/10.1016/j.jsames.2019.102330

Vehof J. 2020. — *Evolution of sperm storage organs in the early diverging lineage of eubrachyuran Dorippidae (Brachyura, Decapoda).* Unpublished Doctoral thesis, Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin, 109 p.

Vehof J., Van der Meij S. E. T., Türkay M. & Becker C. 2016. — Female reproductive morphology of coral-inhabiting gall crabs (Crustacea: Decapoda: Brachyura: Cryptochiridae). *Acta Zoologica* (Stockholm) 97: 117-126. https://doi.org/10.1111/azo.12111

Vehof J., Scholtz G. & Becker C. 2017. — Morphology of the female reproductive system of three dorippid crabs (Crustacea: Decapoda: Brachyura: Dorippidae) and the role of accessory cuticle structures associated with seminal receptacles. *Invertebrate Biology* 136 (3): 271-289. https://doi.org/10.1111/ivb.12181

Vehof J., Scholtz G. & Becker C. 2018a. — *Marching to a Different Drummer – the Female Reproductive System of Dorippid Crabs.* 9th International Crustacean congress, Washington D. C., May 22-25, 2018. Abstract Book: 68.

Vehof J., Scholtz G. & Becker C. 2018b. — *Paradorippe granulata* – a crab with external fertilization and a novel type of sperm storage organ challenges prevalent ideas on the evolution of reproduction in Eubrachyura (Crustacea: Brachyura: Dorippidae). *Athropod Structure & Development* 47 (1): 82-90. https://doi.org/10.1016/j.asd.2017.12.002

Vences M., Guayasamin J. M., Miralles A. & De La Riva I. 2013. — To name or not to name: criteria to promote economy of change in Linnaean classification schemes. *Zootaxa* 3636 (2): 201-244. https://zoobank.org/10.11646/zootaxa.3636.2.1

Venkataraman K., Jeyabaskaran R., Raghuram K. P & Alfred J. R. B. 2004. — Bibliography and checklist of corals and coral reef associated organisms of India. *Records of the Zoological Survey of India*, Occ. Paper 226: 1-468.

Vernet-Cornubert G. 1957. — Existence de caractères sexuels périodiques chez certains Décapodes Reptantia: *Dromia vulgaris* (Fabricius), *Pilumnus hirtellus* (Linné). *Bulletin de l'Institut océanographique de Monaco* 54: 1-14.

Verrill A. E. 1869a. — Actiniaria, with Supplement and Geographical Lists. Synopses of the Polyps and Corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Captain John Rodgers, U. S. N., from 1853 to 1856, Collected by Dr. William Stimpson, Naturalist to the Expedition, Part IV. *Proceedings of the Essex Institute* 6: 51-104, pls 1-2.

Verrill A. E. 1869b. — On the parasitic habits of Crustacea. *American Naturalist* 3: 239-250. https://doi.org/10.1086/270420

Verrill A. E. 1928. — Havaiian shallow water Anthozoa. *Bernice P. Bishop Museum Bulletin* 49: 1-30.

Via Boada L. 1988. — Els decàpodes, *in Història Natural dels Països Catalans, Enciclopèdia Catalana*. S. A., Barcelona, 15: 343-352.

Vidal-Gadea A. G., Rinehart M. D. & Belanger J. H. 2008. — Skeletal adaptations for forwards and sideways walking in three species of decapod crustaceans. *Arthropod Structure & Development* 37: 95-108. https://doi.org/10.1016/j.asd.2007.06.002

Vidhya V., Jawahar P. & Karuppasamy K. 2017. — Annotated check list of the brachyuran crabs (Crustacea: Decapoda) from Gulf of Mannar region, south east coast of India. *Journal of Entomology and Zoology Studies* 5 (6): 2331-2336.

Vinogradov L. G. 1950. — Keys to the Lobsters, Shrimps and Crabs of the Far East. *Journal of the Institute for Scientific Research of the Pacific Ocean, Fishery Economics and Oceanography* 33: 179-358 (In Russian).

Vosmaer A. 1763. — Mémoire sur un nouveau genre de Crabes de Mer (*Notogastropus*), qui a des pattes sur le dos & sous le ventre. *Mémoires de mathématique et de physique, tirez des régistres de l'Académie Royale des Sciences* (Paris) 4: 635-645, pl. 18.

Vosmaer A. 1765. — Verhandeling over een nieuw geslacht van zee-krabben, welk zo wel Pooten op de Rug als onder aan den Bulk heeft, Noto-Gastropus genaamd. *Uitgezogte Verhandelingen uit de Nieuwste Werken van de Societeiten der Weetenschappen in Europe en van andere Geleerde Mannen.* Amsterdam 10: 119-135, pl. 64.

Voss G. L. 1966. — Narrative of the Cruises: The R/V Pillsbury Deep-Sea Biological Expedition to the Gulf of Guinea, 1964-65, 1. *Studies in Tropical Oceanography* (Miami) 4 (1): 1-60.

Wang C. S. 1927. — The crab in China. *China Journal* 7: 148-151.

Wang L.-P. 2005. — *World of Intertidal Organisms of Kinmen*. Kinmen National Park, Kinmen, 179 p. (In Chinese).

Wang L.-P. 2009. — *Intertidal Organisms of Kinmen (revised edition).* Kinmen National Park, Kinmen, 240 p. (In Chinese).

Wang T.-W., Chan T.-Y., Huang C.-W. & Chan B. K. K. 2013. — Thirty years of changes in the decapod community from the deep-water fishing grounds off Kueishan Island, Taiwan. *Crustaceana* 86: 1382-1409. https://doi.org/10.1163/15685403-00003218

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

Wang T.-W., Kuo P.-H., Lin C.-W., Huang C.-W., Chan T.-Y. & Chan B. K. K. 2017. — Assessing the biodiversity of deep-sea large crustaceans through fishing ports. *Journal of Crustacean Biology* 37: 490-495. https://doi.org/10.1093/jcbiol/rux044

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

Weber F. 1795. — *Nomenclator entomologicus secundum Entomologiam Systematicam ill. Fabricii adjectis speciebus recens detectis et varietatibus.* Kiel and Hamburg, viii + 171 p. https://www.biodiversitylibrary.org/bibliography/12297

White A. 1847. — *List of species in the collection of the British Museum*. British Museum, London, viii + 143 p.

Wicksten M. K. 1986a. — Shell-carrying in *Hypoconcha sabulosa* (Herbst, 1799) (Decapoda, Brachyura). *Crustaceana* 50 (3): 319-320. https://doi.org/10.1163/156854086X00340

Wicksten M. K. 1986b. — Carrying behavior in brachyuran Crabs. *Journal of Crustacean Biology* 6 (3): 364-369. https://doi.org/10.1163/193724086X00217

Williamson D. I. 1965. — Some larval stages of three Australian crabs belonging to the families Homolidae and Raninidae, and observations on the affinities of these families (Crustacea: Decapoda). *Australian Journal of Marine and Freshwater Research* 16: 369-398. https://doi.org/10.1071/MF9650369

Windsor A. M. & Felder D. L. 2014. — Molecular phylogenetics and taxonomic reanalysis of the family Mithracidae Macleay (Decapoda: Brachyura: Majoidea). *Invertebrate Systematics* 28 (2): 145-173. https://doi.org/10.1071/IS13011

Wisespongpand P., Jaingam W., Thamrongnawasawat T. & Khaodon K. 2014. — *Life history of porter crab (*Dorippe quadridens *Fabricius, 1793) and the carrying behavior*. Proceedings of 52nd Kasetsart University Annual Conference: Fisheries, Agricultural Extension and Home Economics, Bangkok (Thailand) 4-7 Feb 2014. Abstract: 242-249. [in Thai, with an abstract in English].

Wolfe J. M., Breinholt J. W., Crandall K. A., Lemmon A. R., Lemmon E. M., Timm L. E., Siddall M. E. & Bracken-Grissom H. D. 2019. — A phylogenomic framework, evolutionary timeline and genomic resources for comparative studies of decapod crustaceans. *Proceedings of the Royal Society B* 286: 20190079. https://doi.org/10.1098/rspb.2019.0079

Wolfe J. M., Luque J. & Bracken-Grissom H. D. 2021. — How to become a crab: phenotypic constraints on a recurring body plan. *BioEssays*: e2100020. https://doi.org/10.1002/bies.202100020

Wolfe J. M., Ballou L., Luque J., Watson-Zink V. M., Ahyong S. T., Barido-Sottani J., Tin-Yam Chan T., Chu K. H., Crandall K. A., Daniels S. R., Felder D. L., Harrison Mancke H., Martin J. W., Ng P. K. L., Ortega-Hernández J., Palacios Theil E., Pentcheff N. D., Robles R., Thoma B. P., Tsang. L. M., Wetzer R., Windsor A. M. & Bracken-Grissom H. D. 2022 (pers. comm.). — Convergent adaptation of true crabs (Decapoda: Brachyura) to a gradient of terrestrial environments. https://doi.org/10.1101/2022.12.09.519815

Wong K. J. H., Tao L. S. R. & Leung K. M. Y. 2021. — Subtidal crabs of Hong Kong: Brachyura (Crustacea: Decapoda) from benthic trawl surveys conducted by the University of Hong Kong, 2012 to 2018. *Regional Studies in Marine Science* 48: 102013. https://doi.org/https://doi.org/10.1016/j.rsma.2021.102013

Wong K. J. H., Tsao Y.-F., Qiu J.-W. & Chan B. K. K. 2023. — Diversity of coral-associated pit crabs (Crustacea: Decapoda: Cryptochiridae) from Hong Kong, with description of two new species of *Lithoscaptus* A. Milne-Edwards, 1862. *Frontiers in Marine Science* 9: 1003321. https://doi.org/10.3389/fmars.2022.1003321

Woods J. T. 1953. — Brachyura from the Cretaceous of Central Queensland. *Memoirs of the Queensland Museum* 13 (1): 50-57. https://www.biodiversitylibrary.org/part/303451

Wright C. W. 1997. — New information on Cretaceous crabs. *Bulletin of the Natural History Museum London* (Geology) 53: 135-138. https://www.biodiversitylibrary.org/part/314058

Wright C. W. & Collins J. S. H. 1972. — British Cretaceous crabs. *Monograph of the Palaeontographical Society of London* 126 (533): 1-113, pls 1-22. https://doi.org/10.1080/25761900.2022.12131720

Xin Z.-Z., LIU-Y., Zhang D.-Z., Chai X.-Y., Wang Z.-F., Zhang H.-B., Zhou C.-L., Tang B.-P. & Liu Q.-N. 2017a. — Complete mitochondrial genome of *Clistocoeloma sinensis* (Brachyura: Grapsoidea): gene rearrangements and higher-level phylogeny of the Brachyura. *Scientific Reports* 7 (1): 4128. https://doi.org/10.1038/s41598-017-04489-9

Xin Z.-Z., LIU-Y., Zhang D.-Z., Wang Z.-F., Zhang H.-B., Tang B.-P., Zhou C.-L., Chai X.-Y. & Liu Q.-N. 2017b. — Mitochondrial genome of *Helice tientsinensis* (Brachyura: Grapsoidea: Varunidae): gene rearrangements and higher-level phylogeny of the Brachyura. *Gene* 627: 307-314. https://doi.org/10.1016/j.gene.2017.06.036

Xing Y., Ma X., Wei Y., Pan D., Liu W. & Sun H. 2016. — The complete mitochondrial genome of the semiterrestrial crab, *Chiromantes neglectum* (Eubrachyura: Grapsoidea: Sesarmidae). *Mitochondrial DNA* Part B, 1 (1): 461-463. https://doi.org/10.1080/23802359.2016.1186509

Xuan F.-J., Guan W.-B., Dai J. & Zhu J.-F. 2009. — Structure and content of spermathecae of *Portunus trituberculatus* from East China Sea. *Chinese Journal of Zoology* 44: 1-11.

Yamada K. & Watanabe K. 2012. — Partial sequence of cytochrome *c* oxidase subunit I gene from *Paradorippe granulata* (Crustacea: Decapoda). *Report of Systematic Zoology Lab Practicum*, July, 2012.

Yamaguchi T. 1993. — A list of species described in the Crustacea Volume of Fauna Japonica as belonging to the Japanese Fauna, *in* Yamaguchi T. (ed.), *Ph. von Siebold and Natural History of Japan*. Crustacea. Carcinological Society of Japan.

Yamaguchi T. & Baba K. 1993. — Crustacean Specimens collected in Japan by Ph. F. Von Siebold and H. Bürger and Held by the Nationaal Natuurhistorisch Museum in Leiden and Other Museums, *in* Yamaguchi T. (ed.), *Ph. F. von Siebold and Natural History of Japan: Crustacea*. The Carcniological Society of Japan. Shimoda Printing, Kumamoto: 145-570.

Yamaguchi T. & HolthuiS L. B. 2001. — *Kai-ka Rui Siya-sin*, a collection of pictures of crabs and shrimps, donated by Kurimoto Suiken to Ph. F. von Siebold. *Calanus*. (*Bulletin of the Aitsu Marine Biological Station*) Special Number 3: 1-156.

Yamaguchi T., Harada K., Takeda M. & Kikuchi T. 1987. — Crab fauna of the Amakusa Islands. *Calanus* 10: 1-71.

Yamaguchi T., Takeda M. & Tokudome K. 1976. — A list of crabs collected in the vicinity of the Aitsu Marine Biological Station and a preliminary report on the cheliped asymmetry of the crabs. *Calanus* 5: 31-46.

Yang C. M. 1979. — *A List of the Brachyura in the Zoological Reference Collection of the Department of Zoology, University of Singapore*. Department of Zology, University of Singapore, Guide number 14: viii + 60 p. [Mimeographed].

Yang S. 1986. — The diagnostic value of gastric mill's construction as taxonomic character on the classification of crabs (Brachyura: Crustacea). *Acta Zootaxonomica Sinica* 11 (2): 151-159 (In Chinese).

Yao F., Shi B., Wang X., Pan D., Bai M., Yan J., Cumberlidge N. & Sun H. 2020. — Rapid divergent coevolution of *Sinopotamon* freshwater crab genitalia facilitates a burst of species diversification. *Integrative Zoology* 15: 174-186. https://doi.org/10.1111/1749-4877.12424

Yasser A. & Naser M. 2019. — A new record of *Dorippe quadridens* (Fabricius, 1793) (Decapoda, Brachyura, Dorippidae) from the north western Persian-Arabian Gulf, Iraq. *Journal of Biological Studies* 2 (1): 1-3.

Yeo D. C. J., Ng P. K. L., Cumberlidge N., MagalhÃes C., Daniels S. R & Campos M. R. 2008. — Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater. *Hydrobiologia* 595: 275-286. https://doi.org/10.1007/s10750-007-9023-3

Yokoya Y. 1933. — On the distribution of Decapod Crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. Sôyô-Maru, during the years 1923-1930. *Journal of the College of Agriculture, Tokyo Imperial University* 12 (1): 1-226.

Yuhui X., Lijun Z., Yue H., Xiaoqi W., Chen Z., Huilun Z., Ruoran W., Da P., Hongying S. 2017. — Complete mitochondrial genomes from two species of Chinese freshwater crabs of the genus *Sinopotamon* recovered using next-generation sequencing reveal a novel gene order (Brachyura, Potamidae). *ZooKeys* 705: 41e60. https://doi.org/10.3897/zookeys.705.11852

Zairion Z., Hakim A. A., Mashar A., Fahrudin A., Adrianto L., Widigdo B. & Wardiatno Y. 2018. — *Diversity and distribution of Dorippid Crabs (Brachyura: Dorippidae) in East Coast of Lampung, Indonesia.* IOP Conf. Series: Earth and Environmental Science 149: 012056.

Zakirah M. T., Nurul-Zalizahana Z., Yahya N., Nasir A. S. A. & Bachok Z. 2022. — Community Study of Brachyuran Crab at Setiu Lagoon, Terengganu, Malaysia. *Borneo Journal of Resource Science and Technology* 12 (2): 11-23. https://doi.org/10.33736/bjrst.4518.2022

Zamponi M. O. 2002. —The association between medusa *Lychnorhiza lucerna* (Scyphomedusae, Rhizostomeae) and decapod *Libinia spinosa* (Brachyura, Majidae) recorded for the first time in neritic waters of Argentina. *Russian Journal of Marine Biology* 28 (4): 267-269. https://doi.org/10.1023/A:1020229328660

Zara F. J., Pereira G. R. R. & Sant'anna B. S. 2014. — Morphological changes in the seminal receptacle during ovarian development in the speckled swimming crab *Arenaeus cribrarius. Biological Bulletin* 227 (1): 19-32. https://doi.org/10.1086/BBLv227n1p19

Zarenkov N. A. 1971. — On the Species Composition and Ecology of the Decapod Crustacea of the Red Sea, *in* Vodiartitsky V. A. (ed.), *Benthos shel'fa Krasnogo moria [Benthos of the Shelf of the Red Sea]*. Akademia nauk USSR, Kiev: 155-203 (In Russian).

Zarenkov N. A. 1972. — New data on Indo-Pacific crabs (Families Goneplacidae, Pinnotheridae, Parthenopidae, Dorippidae) and the question of seasonality in reproduction of decapods in the Gulf of Tonkin. *Multi-aspect investigations of the Ocean Nature (Kompleksnye Issledovania Prirody Okeana*) 3: 229-253 (In Russian).

Zariquiey Alvarez R. 1968. — *Crustáceos Decápodos Ibéricos*. Investigación Pesquera (Barcelona) 32, xv + 510 p., 164 figs.

Zenetos A., Cinar M. E., Pancucci-Papadopoulou M. A., Harmelin J. G., Furnari G., Andaloro F., Bellou N., Streftaris N. & Zibrowius H. 2005. — Annotated list of marine alien species in the Mediterranean with records of the worst invasive species. *Mediterranean Marine Science* 6/2: 63-118.

Zoological Survey of India, The Director 2018. — *Animal Discoveries 2017. New Species and New Records*. Government of India, Ministry of Environment, Forest and Climate Change, Zoological Survey of India, Calcutta, 102 p.

Zhong S., Zhao Y. & Zhang Q. 2018. — The first complete mitochondrial genome of Dorippoidea from *Orithyia sinica* (Decapoda: Orithyiidae). *Mitochondrial DNA* Part B, 3 (2): 554-555. https://doi.org/10.1080/23802359.2018.1467237

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APPENDICES

Appendix 1. — The dorippids in legend and myth.

The 'human face' of dorippids (Fig. 3) has long attracted the curiosity of humans. Scientific names (such as *facchino* = *porter*, *carrier*, given to *Dorippoides facchino* by the inhabitants of Rimini on the Italian coast) appeal to the resemblance of these crabs to a human face. Vernacular names often originate in the folklore of Asian countries, where the expressive features of the carapace are likened to deceased persons whose souls have passed through the crabs. The dorippids named 'ghost', 'demon-faced crab' have been a source of popular beliefs evoked in tales and legends and have inspired artists. *Heikeopsis japonica*, the iconic crab native to Japan is known as the 'samurai crab' or 'Heike-gani' according to the famous legend that the human-faced carapaces, with a characteristic pattern resembling the angry face of a samurai (Figs 2; 39), house the souls of the proud and fierce samurai of the Japanese feudal family Heike, who died in the battle of Dan-no-ura, immortalised in the Heike Monogatari (*Tale of the Heike*, a 13th-century historical epic and one of the great classics of Japanese literature) (Wang 1927; André 1937, 1939, 1958; Neuville 1938; Huard & Guinot 1965; Sakai 1985; Holthuis & Manning 1990: frontispiece; Martin 1993).

The year is 1185 AD, a spring morning, probably the 24th of April; the location is a tiny bay called Dan-no-ura, in the Japanese Inland Sea between Shikoku and Honshu. Two powerful fleets, on one side the Heike clan (or Taira clan), the imperial rulers of Japan with a thousand ships, and on the other the Genji clan (or Minamoto) with three thousand ships, fight to the death for control of the throne. And at stake is the control of the whole of Japan. The battle of Dan-no-ura was preceded by a huge struggle between these two clans, which had fought each other at the end of the 12th century during the Genpei War (1180-1185).

The ruling Taira clan (Heike) is led by its child-Emperor Antoku and his grandmother. The Heike, who had been ruling for many decades, are routed after half a day of fighting and must face defeat. During the battle, a member of the royal household (presumably his grandmother) takes the seven-year-old Emperor Antoku and dives with him into the water of the Shimonoseki Straits (also known as Kanmon Straits), drowning the child emperor to prevent him from falling into Minamoto's hands. His mother follows him in her grief. During the fierce battle, hundreds of Samurai warriors lose their lives, and their bodies slip through the waves to the bottom of the sea. Those not killed in battle commit suicide by drowning, with most of the Heike clan members and generals tying themselves to the ship anchor to sink to the bottom of the sea (Figs 2; 39). The Heike, with their wives and children, perished. Another version says that the loyal Heike were thrown into the sea by the conquerors. Only a few wives and consorts were allowed to live as spoils of war by Gengi, the victor of the battle. Minamoto Yoritomo became the first Shogun, the military ruler of Japan, and established the first shogunate (military dictatorship). This was a cultural and political turning point in Japanese history. Dan-no-ura marks the beginning of seven centuries in which Japan is ruled by warriors and shoguns instead of emperors and aristocrats. Referred to by historians as the period of Medieval and Feudal Japan, the shogunate lasted until 1868. According to other narratives, Emperor Antoku survived in small hamlets of Tokushima, Shikoku.

According to Japanese folklore, the Heike-gani crabs, which have haunted the coasts for hundreds of years and roam the depths of the oceans around Japan in search of the lost legacies of their empire, are the reincarnations of the samurai killed at Dan-no-ura, with the souls of the dead Heike warriors having been transferred to the crabs and their faces etched forever on the backs of the crabs. Actually, some survivors of the Heike lineage do survive, and they commemorate the battle of Dan-no-ura in Japanese villages along the coast every April. It is also told that on dark nights, thousands of ghostly lights hover on the beach or fly over the waves, forming pale lights that the fishermen call Oni-bi or demon fires. *Biwa hōshi*, known as 'lute priests', mostly blind and adopting the robes common to Buddhist monks, are famous for narrating tales at night and playing the *Heike-biwa* to accompany their recitations about legends, wars, histories, and mythologies, with a musical style referred to as *heikyoku*, which literally means '*heike* music'.

The scientific name of the crab called Heike-gani or Heike-crab, sometimes samurai crab, was originally *Dorippe japonica* von Siebold, 1824. Von Siebold (1850: xiii) used the spelling 'Heike-Kani', explaining in a footnote: "Heike est nomen imperatoris antiquii", and many later authors confirm that this is the best-known Japanese name for the species. It later became *Heikea japonica*, and is now *Heikeopsis japonica* (von Siebold, 1824). Its carapace does indeed have a pattern resembling a human face (Fig. 1), but this is simply the result of the sculpture of the dorsal surface and the arrangement of the grooves, which are in fact the points of attachment of the underlying muscles, although with variations in detail between species (Fig. 3). It should also be pointed out that all species of the family Dorippidae, whether or not they live in Japan, share this design, amounting to about 27 species worldwide. In addition, many species of various families of primitive crabs also have a human face delineated on the carapace. Schmitt (1931: 222, pl. 64; 1968: 143, fig. 63) comments that in some places in the East, namely in China, *Dorippe* sp. is considered to be sacred, the face on the crab being the reflection of a dead relative whose soul resides in the crab. It is also said that even today, fishermen who catch crabs with human faces on their carapaces throw them back into the water in memory of the Heike samurai warriors, who are somehow still alive. J. S. Huxley (1952), impressed by the carapace of *Heikeopsis japonica*, of which he published a colour photograph in *Life Magazine* alongside a picture of a warrior, and Carl Sagan (1980; and in the popular science television series *Cosmos: a Personal Voyage*) have speculated that the resemblance of the crabs to samurai is due to artificial selection: the Japanese fishermen throw these crabs back into the sea, thus favouring samurai-like patterns and prosperity. The idea that human superstition conspires to reproduce a species of crabs with realistic samurai face is denied by all. To consider some kind of artificial selection here has been deemed 'a fault' (Sakai 1985: 336), 'ludicrous' (Holthuis & Manning 1990: 80), and 'not true' (Martin 1993: 32). Instead, dorippid crabs are rejected because they are too small or have an unappetising taste. And in fact, they are not mentioned as edible crabs (Guinot 1967; Holthuis & Sakai 1970: 116; Sakai 1985: 335; Holthuis & Manning 1990: 80; Ng 1998), being at least sold in limited numbers on the wholesale market at landing sites in Vietnam (Chertoprud *et al.* 2012).

Dorippid crabs have greatly inspired Japanese art, especially in popular ceramics, for example in sake cups (Neuville 1938: figs 2, 4, 5). Various decorative objects of this kind and specimens of Heike-gani are traded as curiosities and souvenirs. At the Akama Shrine for Emperor Antoku in Yamaguchi Prefecture, beautiful Heike clay bells with gilded human faces are sold.

The 12th century Tale of Gengi inspired the renowned Japanese artist Utagawa Kuniyoshi (1798-1861), one of Japan's last great masters of woodblock printings and a painter of historical scenes, such as ancient warriors and scenes of legend, literature and religion. One among his several magnificent paintings and printings shows the sea battle of Dan-no-ura (1185) between the two clans, the 'Ghost of Taira Tomomori' and the anchor with which he drowned, and Heike-gani crabs with the faces of fallen soldiers in the sea. Some crabs have all the characteristics of dorippids: the human face on the carapace, the last two legs reduced and carried dorsally, and even the first pleonal somites visible dorsally (Figs 2A, B; 39). We pay tribute to Kuniyoshi who depicted the Heike-gani in a very precise way, not forgetting the long and slender P2 and P3 typical of the true *Heikeopsis japonica*. A painting, the original of which I have long admired in the office of my esteemed colleague Lipke B. Holthuis in Leiden and which is the frontispiece of the book by Holthuis & Manning (1990), represents the same desperate battleship between the two clans: but this time the crabs, with their transversely elongated carapace and paddle-shaped legs, are well recognisable portunids (other crabs with quadrangular carapace belong to another family), depicted near the spirits of dead samurais represented as pale ghostly figures that haunt the seas. When Martin (1993: 30) writes "None of these crabs looks at all like a Dorippidae, the family of the samurai crab", he is referring to that painting showing swimming crabs and, apparently, he has not seen the one with the dorippids reproduced here (Figs 2; 39).

It seems likely, according to Sakai (1980, 1985), that the man-crab legend perhaps predated the date of the battle of Dan-no-mura and was simply adapted to those events later, rather than being newly created at that time. The Wakan-sansai-zue, the second encyclopaedia published in Japan (1716), contains illustrations of *Dorippe japonica* called either 'Takebun-gani' in honour of Takebun, who came to Japan at the time of the Mongol invasions (in 1274 and 1281) and drowned, or Shimamura-gani in honour of Danjo Shimamura who drowned to death in the fourth year of the Kyoroku era (1528-1532) and was painted by Kuniyoshi "riding the waves on the backs of large crab", which is a portunid and not a dorippid.

Emperor Antoku is worshipped as Mizu-no-kami ('god of water'). In a small seaside park near the Kanmonkyo Bridge in the Japanese city of Shimonoseki, two bronze statues, flanked by replica cannons and ships, depict two Samurai warriors engaged in mortal combat: this monument commemorates the historic battle that took place in this area over nine centuries ago.

Heikeopsis japonica (and/or aff. *japonica*) has captured the imagination in other Asian countries. In China, it bears the vernacular names Kuan Kung Hsieh (= General Kuan Kung's crab), from the Han era, or Kuei Lien Hsieh (= Ghost or Demon faced crab) (Shen 1931: 102; Neuville 1938: 53, 54) or Jen mien Hsieh that means 'crab with a human face' (Fauvel 1880: 79). Martin (1992) recounted how, in several countries, dorippids play an important role in local folklore, sometimes being considered sacred, with the face representing that of a deceased relative, as in the myth of samurai reincarnated as crabs.

Dorippe sinica Chen, 1980 has the vernacular name Kimen gani (= Devil-faced crab) in Japan (De Haan 1841: 121, as 'Kimem gani, i.e., Demonis facie Cancer', see Holthuis & Manning 1990: 36). Ingle (1982: 650) noted that in parts of the Orient *Dorippe sinica* is regarded as sacred because the "face is thought to be that of a deceased relative whose soul has passed in the crab". Two dorippids, with Chinese names, are mentioned in a series of watercolours that Dabry de Thiersant (1826-1898), a travelling naturalist who studied fish farming in China and Chinese medicine in particular, produced in Canton. These beautiful watercolours are now kept at the Muséum national d'Histoire naturelle, Paris (Ms. 276) under the title 'Crustacés de Chine', with notably *Heikeopsis japonica* as *Dorippe japonica* (Huard & Guinot 1965: pl. 79a). In European literature, the vernacular name for *Dorippe frascone* (Herbst, 1785) is 'Fratzengesicht' in German, which means 'gargoyle face'.

Fig. 39. — *The ghost of Taira Tomomori along with the anchor he drowned with, and heikegani with faces of fallen soldiers*, colour print by Utagawa Kuniyoshi illustrating the legend of the iconic 'samurai crab' known in Japan as 'heike-gani', a dorippid whose current scientific name is *Heikeopsis japonica* (von Siebold, 1824). It depicts the naval battle of Dan-no-ura in the Japanese Inland Sea in 1185 between the two clans Heike and Gengi. Members of the Heike clan and generals tie themselves to the anchor of the ship to sink to the bottom of the sea and to rejoin the drowned. The souls of deceased Heike warriors were passed on to the crabs, and their faces were etched forever on the carapaces of the crabs. In Japan, Heike-gani crabs are considered to be the reincarnations of the samurai who died at Dan-no-ura.

Appendix 2. — Fossil taxa assigned to the Dorippoidea and doubtful dorippoids.

Below are listed in alphabetical order the fossil taxa assigned to the Dorippidae and Ethusidae in the literature, each species under its original name or the last name given. Next are examined two extinct dorippoid families, Telamonocarcinidae and Tepexicarcinidae. Finally are discussed fossil families or taxa being presumed to be doubtful Dorippoidea, namely Goniochelidae, Lecythocaridae and *Binkhorstia* Noetling, 1881.

FOSSILS ASSIGNED TO DORIPPIDAE H. MILNE EDWARDS, 1837

Archaeocypoda veronensis Secretan, 1975

Archaeocypoda veronensis Secretan, 1975: 363, figs 21, 22, pl. 23, fig. 2, pls 24, 25.

REMARKS

The status of this species from the Early Eocene of Bolca Fossil-Lagerstätten, Italy (Secretan 1975: 363-369, figs 21, 22, pl. 23, fig. 2, pls 24, 25) (see De Angeli & Garassino 2006: 79), has been fully revised with numerous figures by Pasini *et al.* (2019b: 253, fig. 12). Casadío *et al.* (2005: 175) stated that it was not an ocypodid and suggested that it might be a member of the Dorippidae. Subsequently Schweitzer *et al.* (2010: 79) and Schweitzer *et al.* (2021: 1, fig. 1.2) included it in the Dorippidae, while Pasini *et al.* (2019b: 255) preferred to consider it as a 'doubtful dorippid'. Figures of the holotype and paratypes (Giusberti *et al.* 2014: fig. 6d; Pasini *et al.* 2019b: fig. 12; Schweitzer *et al.* 2021: fig. 1.2) show crabs with an unreduced P4 and a poorly or not at all reduced P5, which excludes *Archaeocypoda veronensis* from being a dorippid. The hypothesis that at least part of this material could be an ethusid (only P5 reduced) is to be considered. See literature in Sasaki (2019: 7771).

Bartethusa hepatica Quayle & Collins, 1981

Bartethusa hepatica Quayle & Collins, 1981: 738, pl. 104, fig. 4. — De Grave *et al.* 2009: 31. — Schweitzer *et al.* 2010: 79. — Sasaki 2019: 7771. — Collins *et al.* 2020: 42, fig. 8A. — Van Bakel *et al.* 2020: fig. 10.24 — Schweitzer *et al.* 2021: 3, fig. 1.3.

REMARKS

This species, from the Middle Eocene (Bartonian) of the Isle of Wight, considered a dorippid and not an ethusid by their authors (despite its genus name), does indeed have the appearance of a representative of the Dorippidae. The short, wide carapace is subquadrate, with several recognisable regions on the dorsal surface, including a large hepatic region, and prominent grooves, the anterior called 'hepatic' corresponding to the precervical groove (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae*). The slightly concave posterior border is 'bounded by a thin ridge' (Quayle & Collins 1981: 739). The front is divided into four equidistant triangular teeth of wich the innermost, separated by a deep V-shaped emargination, are the largest. The subquadrate carapace, the deeply grooved and weakly ornamented surface are more like that of Dorippoidinae n. subfam. and other genera with a similar facies (Fig. 3).

Dorippe astuta Van Straelen, 1938

Dorippe astuta Van Straelen, 1938: 91. — Guinot *et al.* 2013: 187.

Dorippoides facchino – Van Bakel *et al.* 2020: fig. 10.36.

REMARKS

The remains of a species from the Pliocene of Indonesia (Java) were recorded but not figured by Van Straelen (1938) as *Dorippe astuta* Fabricius, 1798, a species placed in the synonymy of *Dorippoides facchino* by Holthuis & Manning (1990) (Fig. 16A, B).

Dorippe*? *carpathica Förster, 1979

Dorippe? *carpathica* Förster, 1979: 91, fig. 3, pl. 2, fig. 3. — Holthuis & Manning 1990: 7

?*Dorippe carpathica* – Müller 1984a: 66, 100.

Neodorippe? *carpathica* – Müller 1996: 9. — Schweitzer *et al.* 2010: 79. — Sasaki 2019: 7796.

"*Dorippe*" *carpathica* – Müller 2006: 42.

Medorippe carpathica – Karasawa 2000: 811.

Neodorippe carpathica – Hyžný 2016: table 1. — Van Bakel *et al.* 2020: fig. 10.25.

REMARKS

This species, known from the Miocene of the Carpathians by an internal mould with a diagenetically deformed and laterally compressed carapace, has been considered to bear some resemblance to extant *Cymonomus* A. Milne-Edwards, 1880 and even *Tymolus* Stimpson, 1858 or to homoloids (Müller 1984a: 66, 100, respectively). It may also be noted that transversely aligned ridges cross the branchial regions in Eocene Cymonomidae (De Angeli 2016). Currently, *D. carpathica* is regarded as a dorippid, tentatively assigned to either *Dorippe* (Förster 1979) or *Neodorippe* (Müller 1996; Schweitzer *et al.* 2010; Hyžný 2016) or *Medorippe* (Karaswa 2000); it has also been assumed to be an ethusid (Müller 2006). The posterior margin is 'bilobated' (Förster 1979: 92, fig. 3, pl. 2, fig. 3) and concave. In Förster's sketch and photograph (1979: 92, fig. 3, pl. 2, fig. 3), the carapace dorsal surface bears three parallel lines on each branchial region, the posterior line corresponding to an oblique 'prominent ridge'. The deep groove that reaches the orbital border is much stronger than that of extant dorippids. It is difficult to assign this species to an existing genus, at least not to *Dorippe*, *Medorippe* or

Neodorippe. ?*Dorippe carpathica* is somewhat reminiscent of *Ethusa popognensis* De Angeli, Garassino & Pasini, 2009, which bears two granulated ridges on each branchial region (see below).

Dorippe fankhauseri Studer, 1892

Dorippe Fankhauseri Studer, 1892: 6, pl. 1, figs 1-4.

D. Frankhauseri [sic] – Glaessner 1929: 137.

Dorippe fankhauseri – Bachmayer & Rutsch 1962: 677, pl. 2, fig. 1. — Holthuis & Manning 1990: 7. — Müller 2006: 42. — Fraaije *et al.* 2010: 2, 5. — Schweitzer *et al.* 2010: 79. — Hyžný 2016: table 1. — Sasaki 2019: 7773. — Van Bakel *et al.* 2020: fig. 10.28.

REMARKS
The species, with a partially preserved carapace, is originating from the Miocene of Switzerland. Considering several inaccuracies in Studer's illustrations, Bachmayer & Rutsch (1962: pl. 2, fig. 1) reproduced the holotype, which has a well-delineated 'human face'. The sculptured and apparently rounded carapace shows the two main grooves typical of Dorippidae, e.g. the deep precervical and cervical grooves, and a rather straight, prominent posterior rim. The carapace dorsal surface exhibits an ornamented and coarsely granular cardiac region and a tripartite ridge on the branchial region. It is a true dorippid, but not a species of *Dorippe* and Dorippinae n. status (Fig. 3A) and could more likely belong to Phyllodorippinae n. subfam. (Fig. 3I) despite the absence of a lateral spine on the margins of the carapace.

Dorippe judicis Gripp, 1964

Dorippe judicis Gripp, 1964: 105, 106, pl. 17, fig. 7a, b. — Sasaki 2019: 7774.

REMARKS
Dorippe judicis, from the Lower Miocene of northern Germany, represented by a carapace and a partially dorsally exposed pleon, is a poorly known species as most palaeontologists have not treated it (e.g. not listed by Schweitzer *et al.* 2010, 2021), with the exception of Polkowsky (2014: 125). The wider than long and short carapace, without lateral spine, the wide front, the two deep main grooves, easily identifiable with the precervical and cervical grooves of Recent Dorippidae (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae*), leading to a strongly subdivided dorsal surface with a prominent, three-ridged cardiac region, the absence of tubercles or granules, and the first dorsally exposed pleonal somites are typical dorippid characters (Fig. 40A). We would not agree with Müller (2006: 42) followed by Jagt *et al.* (2015) that it could be an ethusid. It cannot be a species of *Dorippe* or a representative of Dorippinae n. stat. (Fig. 3A). Gripp (1964: 106, *as Dorippe lanata*) compared it with the extant *Medorippe lanata* (Fig. 3C) and with the Miocene *Dorippe fankhauseri* (see above). The genus needs to be clarified.

Dorippe lanata Gemmellaro, 1914

REMARK
See below under *Medorippe lanata.*

Dorippe margaretha
(Lőrenthey *in* Lőrenthey & Beurlen, 1929)

REMARK
See below under *Medorippe margaretha.*

Dorippe ornatissima Müller, 2006

Dorippe ornatissima Müller, 2006: 41, pl. 1, fig. 1. — Schweitzer *et al.* 2010: 79. — Hyžný 2016: table 1. — Sasaki 2019: 7775. — Van Bakel *et al.* 2020: fig. 10.29. — Hyžný & Dulai 2021: 167, fig. 62.6.

REMARKS
Dorippe ornatissima, from the Middle Miocene (Upper Badenian) marine layers of the Budapest area (Hungary), characterised by a wide carapace, slightly elongated anteriorly, with a rimmed posterior margin, a heavily ornamented dorsal surface, without deep grooves, with the branchial and cardiac regions covered with a set of tubercles of various sizes, could belong to those dorippids with a sculptured and ornamented carapace like the members of the Dorippinae n. stat.. The photograph of the holotype by Hyžný & Dulai (1921: 167, fig. 62.6a) might convince us that it could be a Dorippinae n. stat., with a prominent posterior margin and a distinct strip, but the much rounder carapace makes us somewhat doubtful of this attribution.

Dorippe rissoana Desmarest, 1817

Dorippe Rissoana A.-G. Desmarest, 1817: 509; 1822: 119, pl. 10, figs 1-3. — H. Milne Edwards 1837: 158.

Dorippe quadridens – Holthuis & Manning 1990: 18, 34-35. — Schweitzer *et al.* 2021: 1.

REMARKS
A.-G. Desmarest (1817; 1822) introduced and depicted a new fossil species of unknown origin as *Dorippe rissoana*. Defrance (1819) provided a slightly modified version of the Desmarest's original (1817) description. According to Desmarest himself (1822: 121), it was a dubious fossil since, although brown and shiny like most East Indian fossil crabs, it was much lighter in colour, more friable and less strongly embedded in clay than the true fossils. Desmarest pointed out that this species was similar to the *Dorippe nodosa* A.-G. Desmarest (*nomen nudum*) collected by Péron (= *D. quadridens*) and could not be distinguished from it. Glaessner (1929: 137), who considered Desmarest's specimen a subfossil, treated *D. rissoana* as a synonym of *D. quadridens* (Fabricius, 1793) (Fig. 10A, B), an action followed by Holthuis & Manning (1990: 18, 34-35). This species belongs to the Dorippinae n. stat..

Dorippe sinica Chen, 1980

Dorippe (*Dorippe*) *sinica* Chen, 1980: 154, fig. 1, pl. 1.

Dorippe sinica – Karasawa *et al.* 2021: 139, 146, pl. 2, fig. 20. — Ando *et al.* 2022: 132, pl. 2, fig. A.

REMARKS

Two carapace fragments allocated to the Recent species *Dorippe sinica* are shown in the *Illustrated catalogue of Decapoda from the Middle Pleistocene Atsumi Group, Japan* by Karasawa *et al.* (2021). The strongly tuberculated carapace, although it appears longer and too narrow anteriorly, is reminiscent of the extant *Dorippe sinica* (Fig. 10C, D), very common in Japan. *Dorippe sinica* was recently found in Holocene deposits in the Shimizu Port, Shizuoka City, Japan (Ando *et al.* 2022: 132, pl. 2, fig. A). The species belongs to the Dorippinae n. stat..

Heikeopsis japonica (von Siebold, 1824)

Dorippe Japonica von Siebold, 1824: 14.

Dorippe japonica – De Haan 1841: 12. — Kaneko 1958: 331, 332, 336, pl. 15, fig. 10.

Neodorippe (*Neodorippe*) *japonica* – Morita 1977: 16, pl. 2, figs 1-4.

Heikea japonica – Umemoto & Karasawa 1998: 11, fig. 7. — Sasaki 2019: 7788.

REMARKS

Well-sculpted carapaces similar to that of the extant and iconic *Heikeopsis japonica* (Figs 1; 19A-D) have been recorded from the Holocene of the Umeda Formation, Osaka City (Kaneko 1958), of the 'Reclaimed Sand' around the Nagoya Port, Aichi Prefecture (Morita 1977) or Nanyo Formation, Aichi Prefecture (Umemoto & Karasawa 1998). It is a pity that none of the pereiopods 2 or 3 of these crabs have been preserved to check if they are long and thin as in the typical *H. japonica* in the living fauna.

Heikeopsis tuberculata (Morris & Collins, 1991)

Dorippe (*Dorippe*) *frascone tuberculata* Morris & Collins, 1991: 5, fig. 1a, b.

Dorippe frascone tuberculata – Karasawa 2000: table 1.

Heikea tuberculata – Collins *et al.* 2003: 200, pl. 1, fig. 5.

Heikeopsis tuberculata – Schweitzer *et al.* 2010: 79. — Guinot *et al.* 2013: 187; 2019: 300. — Sasaki 2019: 7790. — Van Bakel *et al.* 2020: fig. 10.27. — Schweitzer *et al.* 2021: 2, fig. 1.5a, b.

REMARKS

Heikeopsis tuberculata, from the Lower Miocene Miri Formation of Sarawak, established without knowledge of the contemporary work of Holthuis & Manning (1990), is one of the few fossil dorippids with a well-preserved ventral part (Morris & Collins 1991: 5, fig. 1a, 1b). Based on examination of the type series (holotype and two paratypes) and better preserved specimens, the new description and figures of Collins *et al.* (2003: 200, pl. 1, fig. 5a-d, as *Heikea japonica*) confirm all the characteristic features of the family Dorippidae, e.g. the clearly recognisable Milne Edwards openings and the curvature of the sternal suture 5/6 including the press-button for pleonal locking. This crab is undeniably a dorippid, with the two typical main carapace grooves: a 'hepatic furrow' that corresponds to the precervical groove; and a 'wide, fairly deep, and broadly V-shaped' cervical groove (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae*). The well-marked posterior rim, described as 'a broad ridge [that] bounds the deeply sinuous, not concave posterior margin', is similar to that of the extant *Heikeopsis*. The thoracic sternum, depicted upside down by Morris & Collins (1991) but correctly oriented by Collins *et al.* (2003) (see Guinot *et al.* 2013: 187), was shown by Schweitzer *et al.* (2021: 2, fig. 1.5b). The shape of the carapace, the sculpted and ornamented dorsal surface and the ridged thoracic sternum are not reminiscent of *Heikeopsis japonica* (Figs 1; 19A-D), just as the posterolateral tubercle that becomes a sharp spine in some large adults casts doubt on this generic identification. Furthermore, as the present distribution of *H. japonica* most probably includes only Japan and the nearby region, it may be preferable to assign it to another genus and species. The holotype of *Heikeopsis tuberculata* represented by Schweitzer *et al.* (2021: 2, fig. 1.5a, b), with the correct registration number (NHMUK In. 61853), has a sculptured carapace and ridged thoracic sternum that do not conform to the material assigned to *H. japonica* by Morris & Collins (1991) and Collins *et al.* (2003), and thus clearly correspond to another genus, most likely in Dorippinae n. subfam. (if the anterior part of the carapace is proven to be narrowed).

Heikeopsis sp.

Heikeopsis sp. – Kato & Kitamura 2020: 47, fig. 5.4.

REMARKS

A fragmentary external mould of carapace was obtained from the Middle Pleistocene Sahama Mud Member of the Hamamatsu Formation, Shizuoka Prefecture, central Japan. The moderately convex, smooth dorsal regions, without nodes or tubercles, the deep main grooves could be characters of *Heikeopsis* but were considered insufficient for more accurate identification.

Medorippe ampla

Garassino, De Angeli, Gallo & Pasini, 2004

Medorippe ampla Garassino, De Angeli, Gallo & Pasini, 2004: 260, figs 5, 6a, b. — De Angeli & Garassino 2006: 40. — De Angeli *et al.* 2009: 174, fig. 6; 2019: 47, 51. — Schweitzer *et al.* 2010: 79. — Jagt *et al.* 2015: 882. — Pasini *et al.* 2019a: 29, fig. 2B. — Van Bakel *et al.* 2020: fig. 10.33. — Schweitzer *et al.* 2021: 3.

Medorippe cf. *M. ampla* – Garassino *et al.* 2012: 27. — Sasaki 2019: 7791.

Remarks

Medorippe ampla, described for two specimens from the Messinian (Late Miocene) of Piedmont, northern Italy (Garassino *et al.* 2004), was subsequently reported from the Messinian of Livorno in Tuscany (central Italy) (De Angeli *et al.* 2009: 174), and from the Early-Middle Messinian (Late Miocene) of the Romagna Apennines, Emilia-Romagna (Pasini *et al.* 2019a). The first record from the Early Pliocene of Italy is recent (Garassino *et al.* 2012: 27). The species, remarkably represented by a sketch in Garassino *et al.* (2004: fig. 5) and a photograph in De Angeli *et al.* (2009: 175, fig. 6), shows the characteristics of the Recent *Medorippe lanata* (Figs 3C; 22A, B), e.g. an enlarged carapace with a lateral spine, a narrow front with two short teeth, two branchial lobes and a Y-shaped cardiac ornament, but differs in having a wider carapace, with a shorter anterolateral margin and granular ridges on the supraorbital, hepatic and branchial regions. The sharp lateral spine could also be reminiscent of *Phyllodorippe armata* (Figs 3I; 29A, B), an extant species from West Africa, but without a Y-shaped ridge on the cardiac region and with a tripartite ridge on the branchial region. Failing to belong with certainty to the genus *Medorippe*, this species could be assigned to the Medorippinae n. subfam.

Medorippe lanata (Linnaeus, 1767)

Cancer lanatus Linnaeus, 1767: 1044.

?*Dorippe lanata* – Gemmellaro 1914: 78, pl. 1, fig. 2 (nec *Cancer lanatus* Linnaeus, 1767); see Garassino *et al.* 2004: 262 (as *Medorippe lanata*).

Dorippe lanata – Glaessner 1929: 137.

Medorippe lanata – Holthuis & Manning 1990: 7. — Schweitzer *et al.* 2010: 79. — Garassino *et al.* 2014b: 124, fig. 2C. — De Angeli *et al.* 2019: 58. — Sasaki 2019: 7792. — Van Bakel *et al.* 2020: fig. 10.35. — Schweitzer *et al.* 2021: 3.

Remarks

Gemmellaro (1914, as *Dorippe lanata*) was the first to report some specimens from the Late Pleistocene of Sicily. The second fossil report in the Mediterranean area is from Garassino *et al.* (2014b: fig. 2C) for a well-preserved male specimen (carapace and ventral surface) from the Late Pleistocene of Calabria (southern Italy): all its features seem to indicate a *Medorippe lanata* (Figs 3C; 22A, B), with its lateral spine, the two main carapace grooves, the rather straight posterior margin of the carapace. The cardiac region is ornamented, but the Y-shaped ridge characteristic of the extant species is not clearly distinct. Anyway, the species belongs to the Medorippinae n. subfam.

Medorippe margaretha
(Lőrenthey *in* Lőrenthey & Beurlen, 1929)

Dorippe margaretha Lőrenthey *in* Lőrenthey & Beurlen, 1929: 135, pl. 6, fig. 1a-c. — Lőrenthey 1911: 528 (*nomen nudum*); 1913: 326 (*nomen nudum*). — Glaessner 1929: 137; 1969: R492, fig. 304.8. — Müller 1978: 279, 287, pl. 13, fig. 4; 1984a: 66, pl. 34, figs 1-5. — Holthuis & Manning 1990: 7.

Medorippe Margaretha – Karasawa 2000: 811, 812, table 1.

Dorippe (*Medorippe*) *margaretha* – Müller 2006: 42.

Dorippe margaretha – Schweitzer *et al.* 2010: 79. — Hyžný 2016: table 1. — Sasaki 2019: 7774. — Hyžný & Dulai 2021: fig. 62.1-5.

Medorippe margaretha – Guinot *et al.* 2013: 187. — Jagt *et al.* 2015: 882. — Van Bakel *et al.* 2020: fig. 10.34.

Dorippe sp. aff. *margaretha* – Polkowsky 2014: 123, pl. 125, figs 1-4.

Remarks

By its outline, its anterolateral spine in the figre of Lőrenthey & Beurlen (1929: pl. 6, fig. 1a), its two closely spaced triangular frontal teeth, the carapace of this species, from the Miocene of Hungary, Portugal, Germany (Upper Miocene) and Hungary (Middle Miocene), indeed resembles that of extant species *Medorippe lanata*. In Polkowsky's (2014: pl. 125, figs 1-4) four good figures of several Schleswig-Holstein specimens, the cardiac region does not show the characteristic Y-shaped ridge of the extant *Medorippe lanata* (Fig. 22A, B), and the strong tripatite branchial ridge is more reminiscent of *Phyllodorippe armata* (Fig. 29A, B); but the shape of the carapace, the strong lobulation, the spaced frontal teeth, the absence of a lateral spine (possibly lost) are not typical of this genus. But most importantly, the valuable figures of the holotype and other specimens provided by Hyžný & Dulai (2021: fig. 62.1-5) show the characteristic Y-shaped ridge on the cardiac region, a small spine on the carapace lateral margin, all of which are characters in favour of belonging to *Medorippe*, if not, at least, to the subfamily Medorippinae n.subfam. It should be noted that a second species of *Medorippe*, under the name of *M. crosnieri* (Fig. 23A, B, D), with a similar facies, including the cardiac region, probably exists, but with a still questionable status (see *Remarks about* Medorippe crosnieri *Chen, 1988*).

Medorippe tanabei Karasawa, 2000

Medorippe tanabei Karasawa, 2000: 811, fig. 2. — Schweitzer *et al.* 2010: 79; 2021: 3. — Jagt *et al.* 2015: 882. — Van Bakel *et al.* 2020: fig. 10.31.

Remarks

According to Guinot *et al.* (2013: 18), the generic status of *Medorippe tanabei*, known only by a carapace from the Miocene of Japan, is not certain, but its attribution to the Medorippinae n. subfam. is plausible.

Nobilum wenchii Hu & Tao, 1996

Nobilum wenchii Hu & Tao, 1996: 65, pl. 11, fig. 9. — Karasawa 2000: table 1. — Müller 2006: 42. — Schweitzer *et al.* 2010: 80. — Guinot *et al.* 2013: 187. — Sasaki 2019: 7797. — Van Bakel *et al.* 2020: fig. 10.26.

REMARKS

The carapace of *Nobilum wenchii*, from the Miocene of Taiwan, is longer and narrower than that of the extant *N. histrio* (Figs 3F; 21A) and this shape more resembles a *Neodorippe*, except that in the latter the carapace is smooth (Figs 3E; 20A, B). In addition, the posterior border of the carapace is described as "similar to a lip, protruded medially and inwardly", which is not the case in *Neodorippe* where the rim is faint and the strip very narrow. It is however possible that the species belongs to the Heikeopsinae n. subfam.

Paradorippe sp. cf. ***granulata*** and ***Paradorippe granulata*** (De Haan, 1841)

Dorippe granulata De Haan, 1841: 122, pl. 3, fig. 2.

Paradorippe granulata – Morita 1977: 16, pl. 2, figs 5-8. — Kaneko 1958: 331, 332, 336, pl. 15, fig. 10. — Holthuis & Manning 1990: 125. — Kato & Karasawa 1998: 9, pls 3.10, 11, 13, 14. — Umemoto & Karasawa 1998: 11, fig. 8. — Kobayashi *et al.* 2008: 112, pl. 1, fig. 5. — Schweitzer *et al.* 2010: 80. — Klompmaker *et al.* 2013: 607, fig. 3J, K, tables 1, 3. — Karasawa *et al.* 2014: 61, fig. 7.3-7.6; 2021: 139, 146, pl. 2, figs 21-24 — Ando *et al.* 2015: 306, pl. 2.10; 2022: 232. — Sasaki 2019: 7803. — Van Bakel *et al.* 2020: fig. 10.37. — Schweitzer *et al.* 2021: 3, fig. 2.4a, b.

REMARKS

Chelae or only dactyli and fixed fingers of *Paradorippe granulata* have been recorded from the Middle Pleistocene of the Atsumi Group (Kobayashi *et al.* 2008; Karasawa *et al.* 2014, 2021), from the Middle Pleistocene Ogushi Formation, Japan (Klompmaker *et al.* 2013) and from the Late Pleistocene Ogushi Formation, Kyushu, Japan (Ando *et al.* 2015). Van Bakel *et al.* (2020: fig. 10.27) also reported it from the Pleistocene. Carapaces have been recorded from the Holocene Deposits in Osaka City, Honshu Island (Kaneko 1958: pl. 15, fig. 10) and Holocene deposits in the Shimizu Port, Shizuoka City, Japan (Ando *et al.* 2022: 132, pl. 2, figs B, C); carapaces with ventral parts have been well preserved in the Reclaimed Sand around the Nagoya Port, Honshu Island (Morita 1977: pl. 2, figs 5-8) and in the Nanyo Formation, Aichi Prefecture (Umemoto & Karasawa 1998: 11, fig. 8). All of these could well correspond to *P. granulata* (Fig. 25A, B), with a typical granulated carapace. Drill holes attributed to traces of predation by octopodes were found on the propodus by Klompmaker *et al.* (2013: fig. 3J-K). It is not surprising to find many Japanese fossil remains of the extant species *P. granulata* that is very common in Japan and has a wide distribution. The single fingers and the complete chela as for example in Kobayashi *et al.* (2008: pl. 1, fig. 5) and in Karasawa *et al.* (2014: fig. 7.3, 7.4; 2021: pl. 2, figs 21, 22) might not completely match the shape of the extant *P. granulata* whose fingers form a distinct curve with the palm, but this is probably due to the angle of the photographs. The carapace fragments in Karasawa *et al.* (2014: figs 7.5, 7.6; 2021: figs 23, 24) have a front with a median emargination that appears to be much more pronounced than in extant *P. granulata* but the granulation of the dorsal surface corresponds to that of this species (Fig. 25A, B). With regards to fragments of *Paradorippe* sp. cf. *granulata* found in the Pleistocene of the Boso Peninsula, Japan, the granular major chela of a male with an inflated palm and a short inclined fixed finger as well as the minor chela represented by Kato & Karasawa (1998: pl. 3, figs 10-11, 13-14, respectively) could be assigned to *P. granulata*; this is also consistent with the sexual dimorphism encountered in the extant species as illustrated in our figures of the male (Figs 24A; 25A) and female (Fig. 24B). The species belongs to the Paradorippinae n. subfam.

Paradorippe sp.

Paradorippe sp. – Karasawa & Nobuhara 2008: 25, fig. 2.12, 13. — Schweitzer *et al.* 2010: 80.

REMARKS

A *Paradorippe* without specific identification has been recorded from the Pliocene of the Ryukyus, Japan. The specimens consist of a broken granular carapace, a well preserved male thoracic sternum and a male pleon (not shown). The thoracic sternum displays the curved suture 4/5 including the press-button: its finely granular surface with an oblique suture 4/5 instead of horizontal as in *P. granulata* (Fig. 26B-D) does not allow a definite assignment to this species, and we agree with Karasawa & Nobuhara (2008) that a specific identification awaits the discovery of a better preserved carapace.

Titanodorippe eocenica Blow & Manning, 1996

Titanodorippe eocenica Blow & Manning, 1996: 6, pl. 2, fig. 2. — Müller 2006: 42. — Schweitzer *et al.* 2010: 80; 2021: 3, fig. 2.7a, b. — Sasaki 2019: 7772.

REMARKS

The subfamilial identity of this Middle Eocene species from the Carolinas, USA, known only from a single large and granular cheliped propodus, cannot be determined. Note that dorippids are not present in the living fauna of the New World.

Dorippid 'Genus and species indeterminate' in Karasawa, Nakagawa & Kaede (2011)

We agree with the authors (Karasawa *et al.* 2011a: 32, fig. 2.7) that this species, from the Miocene of Fukui Prefecture, Japan, can be referred to a dorippid, but that more complete material will be needed for a generic identification. In any case, the subdivided carapace is not that of *Paradorippe*, hence not a member of the Paradorippinae n. subfam., and would rather be that of a Dorippinae n. stat. (Figs 3A; 10).

Dorippidae sp.

Dorippidae sp. – Artal & Gilles 2007: 8, fig. 3C.

Medorippe sensu Artal & Gilles 2007 – Van Bakel *et al.* 2020: fig. 10.30.

REMARKS
The crab found in the Miocene of Pignan (southeastern France), attributed to the Dorippidae by Artal & Gilles (2007: 8, fig. 3C), with a possible assignment to *Medorippe*, indicated as '*Medorippe* sp. *sensu* Artal & Gilles 2007' by Van Bakel *et al.* (2020: fig. 10.30), is not a dorippid. The narrow carapace with parallel lateral margins, the simple and spatulate rostrum and the sinuous entire orbital margin are like those of a retroplumid. Generally, the carapace of Retroplumidae is wide, rectangular and has several transverse ridges, therefore this unnamed species with a subquadrate carapace and an apparently lobulated and granulated dorsal surface would represent a rare form in this family. *Bacapluma aragonensis* Ortega, Fernández, Ferratges, Kwekel, Laguna, Maza & Méndez, 2013, from the Eocene of Huesca (Aragon, Spain) (not cited in Schweitzer & Feldmann (2018), could be the closest form. A comparison with the many species of *Archaeopus* Rathbun, 1908, where there is a wide range of carapace morphology, from quadrate to subquadrate and in which transveres ridges are replaced by swellings or linear tubercles over defined regions (Nyborg *et al.* 2019b), would be useful.

FOSSILS ASSIGNED TO ETHUSIDAE GUINOT, 1977

Ethusa berica De Angeli & Beschin, 2008

Ethusa berica De Angeli & Beschin, 2008: 22, fig. 5, pl. 2, figs 1, 2. — Schweitzer *et al.* 2010: 80; 2021: 3. — De Angeli *et al.* 2010: 154, fig. 7; 2019: 23. — Beschin *et al.* 2019: 96, fig. 57. — Sasaki 2019: 7812. — Van Bakel *et al.* 2020: fig. 10.16. — De Angeli & Garassino 2021: 21.

REMARKS
Ethusa berica, a true ethusid from the Lower Oligocene of Vicentina (De Angeli & Beschin 2008; De Angeli *et al.* 2010) and the Upper Eocene of Parona di Verona, Italy (Beschin *et al.* 2019), has a fairly long carapace, a smooth dorsal surface, with well-defined grooves, and four frontal spines, the inner ones protruding and close together, only separated by a V-shaped sinus, as revealed in the figure of a more complete and more recent specimen (De Angeli *et al.* 2010: fig. 7). The posterior rim is marked, wide; the presence of a strip should be checked.

Ethusa cf. *E. berica*

Ethusa cf. *E. berica* – De Angeli & Garassino 2021: 20, fig. 4A, B.

REMARKS
This specimen, from the Late Eocene (Priabonian) of San Feliciano hill, Vicenza (NE Italy), differs from *Ethusa berica* in its smaller size, the dorsal regions more strongly marked by deep grooves, and the presence of developed cardiac tubercles. As in *Ethusa berica,* there is a wide, slightly concave and marked posterior rim, perhaps bordered by a strip.

Ethusa chibai Karasawa, 1993

Ethusa chibai Karasawa, 1993: 44, fig. 4, pl. 8, fig. 12; 1999: fig. 6. — Karasawa & Kato 2001: Database. — Schweitzer *et al.* 2010: 80; 2021: 3. — Sasaki 2019: 7812. — Van Bakel *et al.* 2020: fig. 10.21.

REMARKS
In this crab from the Lower Pliocene of southwestern Japan, the "inflated branchial region", the two epibranchial lobes "divided into two by a shallow, oblique groove", which are not very visible in the figure, are somewhat reminiscent of the ridged branchial region of *Ethusa popognensis* (see below). According to De Angeli *et al.* (2009: 176), *E. chibai* can be distinguished from *E. popognensis* by "a carapace longer, dorsal surface smoother, and shallow branchiocardiac groove".

Ethusa evae Müller & Collins, 1991

Ethusa evae Müller & Collins, 1991: 66, fig. 3h, pl. 4, figs 1, 2. — Pálfy *et al.* 2008: Catalogue. — De Angeli *et al.* 2010: 176. — Schweitzer *et al.* 2010: 80; 2021: 3. — Baldanza *et al.* 2017: 52. — Beschin *et al.* 2019: table 1. — Sasaki 2019: 7814. — Van Bakel *et al.* 2020: fig. 10.15.

REMARKS
Ethusa evae, from the Upper Eocene (Priabonian), Hungary, has a subsquare carapace, well-developed outer orbital spines and fairly wide orbits. These characters are not typical of either *Ethusa* or an ethusid and we agree with Müller & Collins (1991: 67) that the outline of *E. evae* is somewhat reminiscent of *Binkhorstia ubaghsi* (Van Binkhorst, 1857) from the Late Cretaceous (Maastrichtian). The identification of this species, in any case not a dorippoid, should be carefully reconsidered.

Ethusa aff. *mascarone sensu* Müller 1984

Cancer mascarone Herbst, 1785: 191, pl. 11, fig. 69.

REMARKS
Müller (1984b: 26) and Via Boada (1988) reported specimens from the Miocene (Messinian) of Santa Pola (Alicante, Spain) that are regarded as a probable new subspecies of *E. mascarone* by De Angeli *et al.* (2009: 176), with no subsequent record or discussion (De Angeli & Garassino 2021: 19), see Van Bakel *et al.* 2020: fig. 10.19. The type species of *Ethusa*, *E. mascarone* (Herbst, 1785), is shown by Schweitzer *et al.* (2021: 3, fig. 3) from a Holocene specimen from Portugal.

Ethusa cf. *E. mascarone*

Cancer mascarone Herbst, 1785: 191, pl. 11, fig. 69.

Ethusa cf. *E. mascarone* – Baldanza *et al.* 2017: 52, fig. 9E. — Van Bakel *et al.* 2020: fig. 10.23. — Pasini *et al.* 2022: 146, fig. 3F.

REMARKS

This crab, from the Early Pleistocene of Poggi Gialli (Tuscany), with an oval, pear-shaped carapace and indistinct regions, has been tentatively ascribed to the Mediterranean *Ethusa mascarone*, the type species of *Ethusa.* An incomplete carapace from the Lower Pleistocene of Tuscany (Italy) is similarly ascribed by Pasini *et al.* (2022: 149, fig. 3F).

Ethusa octospinosa Müller, 2006

Ethusa octospinosa Müller, 2006: 42, pl. 1, figs 2, 3. — Schweitzer *et al.* 2010: 80; 2021: 3. — Van Bakel *et al.* 2020: fig. 10.18. — Hyžný & Dulai 2021: 165, fig. 61.1-2.

REMARKS

This species from the Miocene (Upper Badenian) of Hungary has well-developed frontal and outer orbital teeth as well as shallow grooves on carapace dorsal surface that are in favour of a true ethusid. It shares carapace proportions and ornamentation with the extant *Ethusa mascarone*, but *E. octospinosa* has a more protruding front (Hyžný & Dulai 2021: 165, figs 61.1-2 and 61.1-3a, b, respectively).

Ethusa orgianensis De Angeli & Garassino, 2021

Ethusa orgianensis De Angeli & Garassino, 2021: fig. 3.

REMARKS

Ethusa orgianensis, based on two carapaces from the late Eocene of Monti Berici, Vicenza, San Feliciano hill (NE Italy), is an ethusid, having – as well discussed by the authors – a carapace much longer than wide, a straight and rimmed posterior margin, a dorsal surface without deep grooves but with very distinct regions, four almost subequal frontal teeth and developed outer orbital teeth that are thin, acute and directed outwards. The well-marked regions and posterior rim are typical of fossil ethusids.

Ethusa popognensis De Angeli, Garassino & Pasini, 2009

Ethusa popognensis De Angeli, Garassino & Pasini, 2009: 175, fig. 7A, B. — Schweitzer *et al.* 2010: 80; 2021: 3. — Jagt *et al.* 2015: 882. — De Angeli 2019: 51. — Sasaki 2019: 7829. — Van Bakel *et al.* 2020: fig. 10.20.

REMARKS

This species from the Upper Miocene (Messinian) of Livorno, Italy, is charaterised by the characters as follows: carapace longitudinally oval and posteriorly wider; dorsal surface sculptured, regions distinct, finely tuberculate in the median part of the gastric, cardiac, hepatic and branchial areas; front produced, with two pairs of triangular teeth separated by a V-shaped depression; anterolateral margins elongated and divergent; posterior margin concave and with a clearly thickened rim. *Ethusa popognensis* is distinguished mainly by well-developed branchial regions crossed transversely by two granulated ridges, a character shared with '*Dorippe*? *carpathica*' (see above) and some other fossil *Ethusa*.

Ethusa sp.

Dorippidae sp. – Artal & Gilles 2007: 8, fig. 2F. — Van Bakel *et al.* 2020: fig. 10.17.

REMARKS

The crab found by Artal & Gilles (2007: 8, fig. 2F) in the Miocene of Pignan (southeastern France) and without a specific assignment, is known only from a photograph of the carapace. Its posterior border, concave in the middle, seems strongly rimmed, a feature not typical of extant ethusids but which seems more common in fossil representatives, unless the fossils considered to be ethusids turn out to be dorippids. The shape of the carapace suggests that it is an Ethusidae.

Ethusa sp.

Ethusa sp. – Marangon & De Angeli 2007: 73.

REMARKS

Marangon & De Angeli (2007: 73) recorded an undescribed species of *Ethusa* from the Lower Oligocene (Rupelian) of the Ligure Piemontese Basin, NW Italy, with the preservation of part of the pleon, a P4 and/or P5, and a smooth carapace with deep grooves (see also De Angeli & Beschin 2008). It will soon be described (De Angeli, pers. comm.). This would be the oldest known ethusid.

Ethusa sp.

Ethusa sp. – Pasini & Garassino 2016: 54, fig. 2. — Van Bakel *et al.* 2020: fig. 10.22.

REMARKS

This species, from the Pliocene of Valduggia (Vercelli, Piedmont) has been described as having "a pear-shaped carapace, wider posteriorly; dorsal regions well defined by marked grooves, and developed branchial regions crossed transversely by two branchial grooves forming two ridges" (Pasini & Garassino 2016: 54). It shares some dorippid characters, e.g. the deep precervical and cardiac grooves; the marked rim along the concave posterior margin of the carapace. The two branchial ridges, which are not clearly visible in the photograph, are reminiscent of those present in *Ethusa popognensis.*

Fossils assigned to Telamonocarcinidae Larghi, 2004

Dorippoidea has been represented in the fossil record since the Early Aptian by the family Telamonocarcinidae, with *Telamonocarcinus* Larghi, 2004 as type genus. Initially considered a subfamily of Dorippidae (Larghi 2004; Schweitzer & Feldmann 2011a), it was elevated to family status by Guinot *et al.* (2013: 188, 268, 306), an action subsequently followed by all authors (Luque 2015; Jagt *et al.* 2015; Charbonnier *et al.* 2017; Van Bakel *et al.* 2020; Schweitzer *et al.* 2021: 5; Luque *et al.* 2021: fig. 5; Vega *et al.* 2022). The presence of an oxystomatous disposition is not supported by any figure, as the anterior part of the ventral surface is hardly preserved or too blurred in the fossils concerned, and is only presumed from the arrangement of the other structures.

Telamonocarcinus gambalatus Larghi, 2004, the type species of the genus, was established on the basis of abundant and well-preserved material from the Cenomanian of Lebanon, allowing the use of ventral morphology and appendages (Larghi 2004: 539, figs 5, 6, 7.2-7.8; see also Pasini & Garassino 2011: 237), then redescribed with numerous figures by Charbonnier *et al.* (2017: 207, figs 451-463). Reconstructions of the holotype (Larghi 2004: fig. 5; Charbonnier *et al.* 2017: fig. 457; Van Bakel *et al.* 2020: fig. 6B) and photographs of the holotype and paratypes (Luque 2015: fig. 2B; Charbonnier *et al.* 2017: figs 453-456; Van Bakel *et al.* 2020: fig. 6A; Schweitzer *et al.* 2021: fig. 2.5) depict a narrow crab, with a deeply grooved and ornamented dorsal surface, with obliquely oriented epibranchial region, deep orbits, long eyestalks, overdeveloped outer orbital teeth and (where known), non-chelate P4 and P5 dactyli. Charbonnier *et al.* (2017: 207), who examined the holotype and about 50 specimens from Lebanon, confirmed the main characters of *T. gambalatus*, as follows: carapace pyriform, heavily sculptured; dorsal surface with overall granular ornamentation; long, sharp outer orbital teeth directed outwardly; orbits broad and arcuate; eyes well developed; and P4 and P5 reduced, subdorsal/dorsal, with dactyli that are non-subchelate (as in ethusids). Charbonnier *et al.* (2017: 209) referred to the dactyli as 'falciform', which is not visible in photographs and not in Larghi's 2004 reconstruction, reproduced by Charbonnier *et al.* (2017: fig. 457). The outline of the reconstructed *T. gambalatus* is reminiscent of extant ethusids but also of these dorippids with an elongated and anteriorly narrowed body, such as the extant species of the genus *Dorippe* (Figs 10; 12A; 14A, B; 15A, C, E, F). The ventral surface of a topotypic specimen illustrated by Guinot *et al.* (2019: fig. 15) shows a wide thoracic sternum and a posteriorly positioned male pleon, with six free somites plus the telson, and the tip of the telson just reaching suture 5/6. The non-subchelate ending, if preserved, is the most important difference from the Dorippidae (see Table 1).

Garassino *et al.* (2007: 45; see also Garassino *et al.* 2014a: table 1) discovered several specimens from the Cenomanian-Turonian of southern Morocco that they named *Telamonocarcinus* cf. *gambalatus* (previously 'indeterminate crab' of Garassino & Larghi 2000: fig. 2), with preservation of the carapaces, the first pleonal somites, and P2 and P3. Garassino *et al.* (2008: 61) suggested that this Moroccan crab might be the same as the poorly preserved "genus and species indeterminate" from the Upper Cretaceous (Cenomanian) of Egypt referred to Necrocarcinidae Förster, 1968 by Schweitzer *et al.* (2003: 890, figs 1, 2). Luque (2015: 257), on the other hand, attributed the Egyptian taxon to Tepexicarcinidae until better material became available for study. Charbonnier *et al.* (2017: 207) considered that *T.* cf. *gambalatus* of Morocco was not different from *T. gambalatus* from Lebanon, without addressing the case of the enigmatic crab of Schweitzer *et al.* (2003).

Telamonocarcinus antiquus Luque, 2015 (Luque 2015: fig. 2A; Luque *et al.* 2017: fig. 8D; Van Bakel *et al.* 2020: figs 6G, 10.7), from the Upper Aptian-Lower Albian of Santander, Colombia, known only by its wide carapace, with a concave, rimmed dorippid-like posterior margin and the presence of a distinct precervical groove, represented the oldest eubrachyuran known at that time according to Luque *et al.* (2017: 2) and Van Bakel *et al.* (2020: fig. 10.7). This species does not conform to Larghi's 2004 reconstruction of the holotype of *T. gambalatus*, and, as only its dorsal carapace is known, it cannot be assumed that P4 and P5 are not subchelate, one of the main features that distinguishes the Telamonocarcinidae from the Dorippidae and shared with Ethusidae. There is a clear precervical groove and a narrow epibrachial region obliquely oriented like in extant dorippids (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae*, see fig. 5B-D). It could well be a dorippid.

In contrast, *Telamonocarcinus* sp. of Luque (2015: fig. 2C, D, table 1; see Van Bakel *et al.* 2020: fig. 10.7), from the Cenomanian of Japan, Mikasa City, with its narrow carapace, developed outer orbital teeth and dorsal sculpture, is consistent with Larghi's 2004 (fig. 5) reconstruction of the holotype of *T. gambalatus.* It would be important to ensure in well-preserved specimens that P4 and P5 are not chelated, a feature shared by telamonocarcinids and ethusids.

A second genus assigned to the Telamonocarcinidae is *Eodorippe* Glaessner, 1980 (p. 185, 186, 187), initially considered a podotreme included in the Torynommatidae by Glaessner (1980) (for the spelling Torynommatidae instead of Torynommidae, see the Code 1999, Art. 29; Collins 2003: 85; Guinot *et al.* 2013: 175), hence his hypothesis of "a Late Cretaceous origination of the heterotrematous Dorippidae from Tymoloidea" (i.e., Cyclodorippoidea Ortmann, 1892). Glaessner (1980: 186), who noted the "striking resemblance between the carapaces of *Eodorippe* and the genus *Dorippe*", also referred to "some resemblances between *Eodorippe* and *Palicus* Philippi, 1838", concurring with our view that Palicoidea and Dorippoidea share similarities or analogies (Guinot *et al.* 2013: 212). The type species, *Eodorippe spedeni* Glaessner, 1980 (Glaessner 1980: 183, figs 13, 13A) from the Upper Cretaceous (Campanian-Maastrichtian) of New Zealand, has a well-preserved, typically dorippid carapace, with the deeply emarginated posterior margin that characterises older forms. The 'rostrum long and narrow, spatulate, pointing forward' shown in the sketch of Glaessner (1980: fig. 13A) does correspond to the anterior region of the carapace and probably not – as in our earlier misinterpretation (see Guinot *et al.* 2013: 188, 189) – to the anterior projection of the endostomal gutter into the median incision of the front visible dorsally to a variable extent in Recent dorippids. The anterior groove on the carapace dorsal surface, delimiting a narrow, obliqley oriented epibranchial region, is convex and can be termed 'precervical' as in extant dorippids (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae*, Fig. 5B-D), and is a strong evidence for a dorippid origin. The ventral characters and pereiopods are missing. The new figure and redescription of the holotype (with a 'long rostrum') by Luque (2015: 256, fig. 2E) and Schweitzer *et al.* (2021: 6, fig. 1.4) support the hypothesis of a close relationship of *E. spedeni* with the Dorippidae. It is even questionable which main differences prevent it from belonging to the Dorippidae. The carapace of the holotype of *E. spedeni* and that of the holotype of *Telamonocarcinus antiquus* (Lower Cretaceous, Upper Aptian-Lower Albian of Colombia), placed side by side by Van Bakel *et al.* (2020: figs 6F and 6G, respectively), clearly show the proximity of the two species.

In adding a second species to *Eodorippe*, *E. binodosa* Collins, Kane & Karasawa, 1993, from the Cenomanian of Japan, Collins *et al.* (1993: 303, fig. 2.6) took the same view, also emphasising the similarity to the Dorippidae. *Eodorippe binodosa*, initially considered a podotreme in Cyclodorippoidea by Collins *et al.* (1993: 303) and assigned to the Telamonocarcinidae by Larghi (2004: 535), Guinot *et al.* (2013: 188, as *Telamonocarcinus binodosus*), Luque (2015: 256, fig. 2F), and Van Bakel *et al.* (2020: fig. 10.10), is indeed another thing. In our opinion, *E. binodosa* differs from *Eodorippe spedeni* by its subrectangular carapace (versus almost as wide as long in *E. spedeni*), its short rostrum (versus long in *E. spedeni*), and its dorsal surface with only shallow grooves (versus with conspicuous transverse grooves and ridges in *E. spedeni*). According to Luque (2015) *Telamonocarcinus* and *Eodorippe*, which occurred in both the Old and New Worlds, did not survive the K/Pg extinction.

Eodorippe connori Nyborg, Garassino, Vega & Kovalchuck, 2019 (Nyborg *et al.* 2019a: 134, fig. 5), from the Albian of Oregon, USA, which probably corresponds to the unpublished reported occurrence of *Eodorippe* from the Cretaceous of Oregon by Schweitzer (2001: 812), is the earliest record of the genus *Eodorippe*. It is a large species (17 × 16 mm) with long, quadrangular P2 and P3 meri preserved. The narrow, forward-projecting front is not a typical feature of extant dorippids. The preservation of a rather large falciform detached piece in their fig. 5C, which is not mentioned by Nyborg *et al.* (2019b) nor by Van Bakel *et al.* (2020), could have been the only preserved element of a lost P4 or P5 of this species, i.e. a thick propodus and a developed dactylus. But the shape does not conform to the non-chelate P4 and P5 dactyli of *Telamonocarcinus gambalatus*, the type genus and species of Telamonocarcinidae, and this fragment is not part of *E. connori*. It belongs to another crab, most likely a palaeocorystid, such as *Joeranina* Van Bakel, Guinot & Artal, Fraaije & Jagt, 2012 or *Eucorystes* Bell, 1863 (see Van Bakel *et al.* 2012a) (Van Bakel, personal communication). We will see below that Van Bakel *et al.* (2020: fig. 10.4) assigned *E. connori* to the new genus *Personadorippe* Van Bakel, Mychko, Spiridonov, Jagt & Fraaije, 2021. The removal of *E. connori* from *Eodorippe* restores its monophyletic status to the Telamonocarcinidae.

Nyborg *et al.* (2019a: 134) compared *E. connori* to *Withersella crepitans* Wright & Collins, 1972, from the Lower Aptian (Lower Greensand) of the Isle of Wight, UK, the type species of *Withersella* Wright & Collins, 1972 (see also Wright 1997: 138, figs 12, 16), attributed to the Carcineretidae Beurlen, 1930 by Collins *et al.* 1995; Fraaje 1996; Wright 1997; Collins 2003), an assignment disputed by Glaessner (1980: 180). The genus was subsequently considered podotreme and assigned to the family Torynommatidae by Van Bakel *et al.* (2003), Schweitzer *et al.* (2007: 19), Schweitzer *et al.* (2010: 79), Schweitzer & Feldmann (2011b: 249, fig. 7), Karasawa *et al.* (2011b: 548), Klompmaker (2013: 173), and Collins *et al.* (2020: 40).

In addition, Van Bakel *et al.* (2020: 14) established a new telamonocarcinid genus, *Personadorippe* (type species *P. kalashnikovi* Van Bakel, Mychko, Spiridonov, Jagt & Fraaije, 2021; other species included: *P. levashiensis* Van Bakel, Mychko, Spiridonov, Jagt & Fraaije, 2020). Van Bakel *et al.* (2020: 15, 19, figs 9, 10.4) removed *Eodorippe connori*, the oldest record of *Eodorippe*, from the Telamonocarcinidae to include it in *Personadorippe*, the sister taxon to *Eodorippe*. In fact, *Personadorippe connori* (Nyborg, Garassino, Vega & Kovalchuck, 2019) shares some characters with *P. kalashnikovi*, established from a single carapace from the Upper Cretaceous, Lower Cenomanian, Moscow Oblast (Van Bakel *et al.* 2020: 15, figs 3A-D, 6D, 7A, 10.4, table 1; see also Schweitzer *et al.* 2021: fig. 5): similar carapace shape and ornamentation, subdivision of dorsal surface into regions, posterior margin with deeply concave and strongly developed rim.

Personadorippe levashiensis, from the Lower Cretaceous, middle Aptian strata, northern Caucasus (Van Bakel *et al.* 2020: 17, figs 3E, F, 5, 7B, 10.3, table 1), shows a slightly different groove pattern and carapace areolation (including a narrow, obliquely oriented epibranchial region), as well as a peculiar arrangement of granules. The posterior margin was described as "concave, inverted V-shaped, divided into two curved portions, with acute rim": we wonder whether these 'two curved portions', clearly discernible in the photographs of Van Bakel *et al.* (2020: figs 3E, 7B), might not correspond to a developed strip in two parts as in the Recent *Dorippe facchino* (Fig. 8A), but it is more likely that they belong to the pleon. The preserved right chela of *P. levashiensis* (Van Bakel *et al.* 2020: fig 5), which consists of a compact propodus and long fingers, can be compared to the chelipeds of *Telamonocarcinus gambalatus* (Larghi 2004; Charbonnier *et al.* 2017). In Recent dorippids, heterochely with a robust major cheliped usually only appears in males that have reached a large size, depending on the species: in large males, the palm of the major cheliped becomes swollen, much higher than long, sometimes even with a bulbous ventrodistal protuberance, and the relatively short fingers form a slight angle with the palm axis. Chelae with a narrow palm and very long fingers like that of *P. levashiensis* are never found in dorippids.

Van Bakel *et al.* (2020: 11, 13, 18, figs 6E, 10.2) recently transferred *Withersella* to the Eubrachyura and included it in the family Telamonocarcinidae. *Withersella crepitans* has a square and flattened carapace with a long mesogastric anterior process, an axially sulcate rostrum, long outer orbital teeth, a rimmed posterior margin, some of these characters reminiscent of the features shared by telamonocarcinids and ethusids. Another former podotreme genus assigned to the Glaessneropsoidea Patrulius, 1959, in Longodromitidae (Klompmaker 2013; Schweitzer & Feldmann 2011b), *Navarrara betsieae* Klompmaker, 2013, from the Upper Albian, Eguino Formation of Koskobilo, northern Spain (Klompmaker 2013: 155, fig. 4, table 4), has recently been assigned to the Eubrachyura and included in the Dorippoidea within the Telamonocarcinidae by Van Bakel *et al.* (2020: 13, 15, figs 6C, 10.6). The carapace has a distinct outline, a quite different areolation of the dorsal surface and does not show the same groove pattern as other telamonocarcinids. In our opinion, the two monotypic genera *Withersella* and *Navarrara* Klompmaker, 2013 must still be able to justify their inclusion in the Dorippoidea. *Withersella crepitans* and *Personadorippe levashiensis*, supposed to represent the oldest dorippoids, may well be among the oldest eubrachyurans currently known, with the possible exception of the Hymenosomatidae recently discovered from the Barremian of Brazil by Mendes *et al.* (2022). It should be noted that Mendes *et al.* (2022: fig. 7) agreed with the inclusion of *Withersella, Navarrara* and *Personadorippe* into the Dorippoidea.

It is quite possible to recognise in *Telamonocarcinus gambalatus, T. antiquus*, *Eodorippe spedeni* and, to a lesser degree, in *Personadorippe* the dorippid groove pattern as we have interpreted it in the extant dorippids (see *Interpretation of grooves on the carapace dorsal surface in Dorippidae* and Fig. 5B-D), i.e., a short, more or less convex precervical groove and a long cervical groove on a well areolated dorsal carapace, with a narrow, oblique epibranchial region, a mesogastric region extending almost to the front and a well-defined metagastric (plus urogastric) region. Although these grooves are less perceptible in some species, such as *Eodorippe binodosa*, there is no doubt that they belong to the same group, the Dorippoidea.

Once again, it must be recognised how misleading the carapace is. For example, a crab, such as *Dioratiopus salebrosus* Woods 1953 (p. 53, fig. 2, pl. 2, figs 4, 5) from the Upper Albian of Central Queensland, with several well-preserved parts, assigned to the Cymonomidae by Wright & Collins (1972: 33), synonymised with *Glaessnerella* Wright & Collins, 1975 (*Glaessneria* Wright & Collins, 1972) by Glaessner (1980) and now in the podotreme family Longodromitidae (Karasawa *et al.* 2011b: 536; Schweitzer *et al.* 2017: 216), has a carapace that somewhat resembles that of certain telamonocarcinids. But the gonopore on the coxa of P3 (Woods 1953: 54) precludes any relationship. Van Bakel *et al.* (2012b) considered that some species of *Glaessnerella* might turn out to be members of the Homoloidea, and Van Bakel *et al.* (2020: 19, fig. 9) left the question open pending a revision, whereas Starzyk *et al.* (2023) recently demonstrated that the genus *Laeviprosopon* Glaessner, 1933 does indeed belong to the Homolidae.

Telamonocarcinids share an additional feature, seemingly not yet reported, namely the presence of at least four strong and well-aligned tubercles behind the frontal region. Five, including the weaker latero-external one, in *Telamonocarcinus gambalatus* (see Larghi 2004: figs 5, 6.4; Luque 2015: fig. 2B; Charbonnier *et al.* 2017: figs 451-463; Van Bakel *et al.* 2020: fig. 6A, B), in *T. antiquus* (see Luque 2015: fig. 2A; Van Bakel *et al.* 2020: fig. 6G) and in *Eodorippe spedeni*, where there is even a row of eight subfrontal tubercules (see Luque 2015: fig. 2E; Van Bakel *et al.* 2020: fig. 6F). Both *P. kalashnikovi* and *P. connori* have four tubercles behind the front. Interestingly, there are four subfrontal tubercles in the dorippid *Medorippe margaretha.*

If the above-mentioned taxa prove to be true Dorippoidea, the family Telamonocarcinidae would be older than the Albian Componocancridae Feldmann, Schweitzer & Green, 2008. According to Van Bakel *et al.* (2020: fig. 10), Telamonocarcinidae, with its records from the Aptian, would represent the earliest confirmed crown- and stem-group Eubrachyura known to date.

The Dorippidae was recovered basal in the brachyuran phylogenetic tree of life by Luque *et al.* (2021: fig. 5). However, the discovery in the Late Barremian of Central Mexico of *Cretamaja klompmakeri* Vega, González-León & Moreno-Bedma, 2019 (Vega *et al.* 2019: figs 29-3), if it proves to be a majoid, would call this precedence into question. Indeed, the genus *Cretamaja* Klompmaker, 2013 (type-species *C. granulata* Klompmaker, 2013 from the Late Albian of northern Spain, Koskobilo quarry) is considered to be a majoid by some authors (e.g. Vega *et al.* 2019), which would assign the Majoidae an earlier record than the Dorippoidea. But first, we disagree with the placement of *Cretamaja* in the Priscinachidae Breton, 2009 (Breton 2009), their differences being 'evident' as noted by Klompmaker (2013: 169), and, on the other hand, we doubt the majoid status of *Cretamaja,* whose carapace is morphologically closer to that of some Longodromitidae, a paraphyletic family that is podotreme in whole or in part (thus included, in whole or in part, in the Dynomeniformia Guinot, Tavares & Castro, 2013) and that has been restricted and rediagnosed by Van Bakel *et al.* (2020: 3).

FOSSILS ASSIGNED TO TEPEXICARCINIDAE LUQUE, 2015

The genus *Tepexicarcinus* Feldmann, Vega, Applegate & Bishop, 1998 (type species: *T. tlayuaensis* Feldmann, Vega, Applegate & Bishop, 1998, from the Upper Albian of Mexico), previously included within the Telamonocarcininae/ Telamonocarcinidae (Larghi 2004; Vega *et al.* 2005: 28, fig. 4, pl. 2, figs 2-12; Guinot *et al.* 2013) (although currently unrecognised, see Schweitzer *et al.* 2021: 6), was considered distinct from the Dorippidae, Ethusidae and Telamonocarcinidae by Luque (2015: 258, 260, fig. 4; 2017: 22). The latter established for it the new family Tepexicarcinidae as part of an uncertain superfamily, the Tepexicarcinoidea Luque, 2015 (see also

Ossó 2016). The family was questioned by Van Bakel *et al.* (2020: fig. 10.1).

Luque's hypothesis that Tepexicarcinidae may represent a separate evolutionary lineage from the early eubrachyurans or stem-eubrachyuran crabs has been replaced by the inclusion of the Tepexicarcinidae in the Dorippoidea by Vega *et al.* (2022: 10). Guinot *et al.* (2019: 300, fig. 3G, H), who illustrated a poorly preserved undeterminate possible tepexicarcinid from the Cenomanian Sierra Madre Formation of the El Chango quarry, with the frontal margin bearing sharp outer orbital spines, a triangular pleon with four free somites (two fused), plus telson, strong chelae, and long and slender P2 and P3 ending in sharp, unciform dactyli, did not comment. But, based on the same specimen and on new more complete specimens of *Tepexicarcinus tlayuaensis* from Tepexi, Upper Albian, Vega *et al.* (2022: 10, 25, figs 6I-L, 8, table 1) provided an emended diagnosis with new morphological details (pleon, thoracic sternum, pereiopods), which allowed for a more complete understanding of the morphology of *Tepexicarcinus*: notably, a nearly subquadrate carapace, the P5 more reduced than the P4, both being probably subdorsal. According to Vega *et al.* (2022, figs 14D; 19H, as Tepexicarcinidae?), these important new features support the inclusion of Tepexicarcinidae in the Dorippoidea, as also endorsed by Mendes *et al.* (2022: fig. 7).

Fossils assigned to Goniochelidae Schweitzer & Feldmann, 2011

The genus *Goniochele* Bell, 1858, with G. *angulata* Bell, 1858 (p. 25, 26, pl. 4, figs 8, 9) as the type species, from the Eocene London Clay, Isle of Sheppey, Kent, was introduced with a question mark into the anomalan Apterura H. Milne Edwards, 1837 (see Guinot *et al.* 2013: 299). It was included in Dromiacea (Carter 1898: 23, pl. 1, fig. 6), attributed to the Necrocarcinidae (Collins 2003: 85; Collins & Jakobsen 2004: pl. 3, figs 2a, 4a; Karasawa *et al.* 2011b: table 1; Schweitzer & Feldmann 2000: 241) or to the Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 (at that time within the Dorippoidea) by De Grave *et al.* (2009: 31, fig. 2G) and Schweitzer *et al.* (2010: 82), with both Necrocarcinidae and Orithopsidae families actually being podotremes (see Van Bakel *et al.* 2012a). The dorippoid affinities of *Goniochele* suggested by Glaessner (1969), Guinot *et al.* (2008: 709) and Vega *et al.* (2010: 275), primarily based on the dorsal position of the coxae of P4 and P5 in *G. angulata* (Bell 1858: pl. 4, fig. 5), were further developed by Schweitzer & Feldmann (2011a: 5, fig. 4) who established a separate family within Dorippoidea, the Goniochelidae Schweitzer & Feldmann, 2011, a status that is widely accepted (Luque 2015: 255, fig. 4; Jagt *et al.* 2015; Luque *et al.* 2017; Collins *et al.* 2020; Van Bakel *et al.* 2020: fig. 10.12; Schweitzer *et al.* 2021: 3, fig. 4; Charbonnier & Garassino 2022: 190, figs 540-546, table 8).

Goniochele angulata has been documented from its carapace, chelae, ventral surface, all well preserved (Bell 1858: 27, pl. 4, figs 3-7), male and female pleons (Bell 1858: 27, pl. 4, figs 8, 9; Carter 1898: 23, pl. 1, fig. 6; Collins & Jakobsen 2004: pl. 3, fig. 4a). A second species, *G. madseni* Collins & Jakobsen, 2004, from the Eocene (Ypresian/Lutetian) of Jutland, Denmark, has been documented by the carapace, the ventral surface of a female, the cheliped, the mxp3 (Collins & Jakobsen 2004: pl. 3, figs 1-3). There is perhaps a third species of *Goniochele*, from Belgium: *Goniochele* cf. *angulata sensu* Van Straelen 1921, Van Bakel *et al.* 2006 and Van Bakel *et al.* 2020 (B. van Bakel, pers. comm.).

Goniochele armata Rathbun, 1918, described from the Miocene (not Oligocene) Culebra Formation from the Panama Canal and only based on the dactylus of the left cheliped, was maintained in the genus but with uncertainty by Luque *et al.* (2017: 33, 37, fig. 11E).

The apparent absence of vulvae on sternite 6 of the two thoracic sterna represented in females of *G. madseni* and *G. angulata* (Collins & Jakobsen 2004: pl. 3, figs 2a, 4a, respectively) was considered confusing by Guinot *et al.* (2013: 201), who were mistaken in not recognising these structures. Furthermore, photographs of a topotypic female from Eocene London Clay, Isle of Sheppey (Fig. 40F) reveal large vulvae, as already noted by Schweitzer & Feldmann (2011a: 5, fig. 4.2) who wrote that the vulvae of *G. angulata* are "enormous, much larger than those seen in Dorippidae or Ethusidae".

The traits of the Goniochelidae, i.e., the hexagonal body shape, the prominent lateral spines of the carapace (Fig. 40B), the grooves on the dorsal surface and its areolation (Fig. 40B, C), the very narrow male pleon, the thoracic sternum with suture 5/6 lacking a strong curvature (Fig. 40D, E), and chela with sharp spines, not shared by any known dorippoid, are they compatible to be a family of Dorippoidea? And is the first condition, the oxystomatous disposition, for being a member of Dorippoidea, part of the former group Oxystomata ('sharp-mouthed') that contained these brachyurans with an extended forward buccal frame, present? The partial mxp3 (exopodite) of *G. madseni* figured by Collins & Jakobsen (2004: pl. 3, fig. 2B) seems rather long and may suggest respiratory modifications of the mouthparts, but this is not certain. In fact, we have no strong evidence for an oxystomatous arrangement in the Goniochelidae (though well preserved), any more than in the Telamonocarcinidae and Tepexicarcinidae, the latter most likely belonging to the Dorippoidea, in contrast to the Goniochelidae that share few dorippoid characters apart from the reduced P4 and P5.

The triangle formed by sternites 1-3 is different from the arrangement found in most dorippids where there is a short, pentagonal shield, with parallel margins and a rectangular sternite 2 in many subfamilies as Dorippoidinae n. subfam. (Figs 17A-C; 18), Paradorippinae n. subfam. (Figs 26A-D), Heikeopsinae n. subfam. (Figs 19C, D; 20C, D; 21B, C) and Phyllodorippinae n. subfam. (Figs 29C, D; 30A-C). In Medorippinae n. subfam. (Figs 4; 22B, C, F), the pentagonal shape is also present, with a small portion of sternite 1 visible and a rather long sternite 2

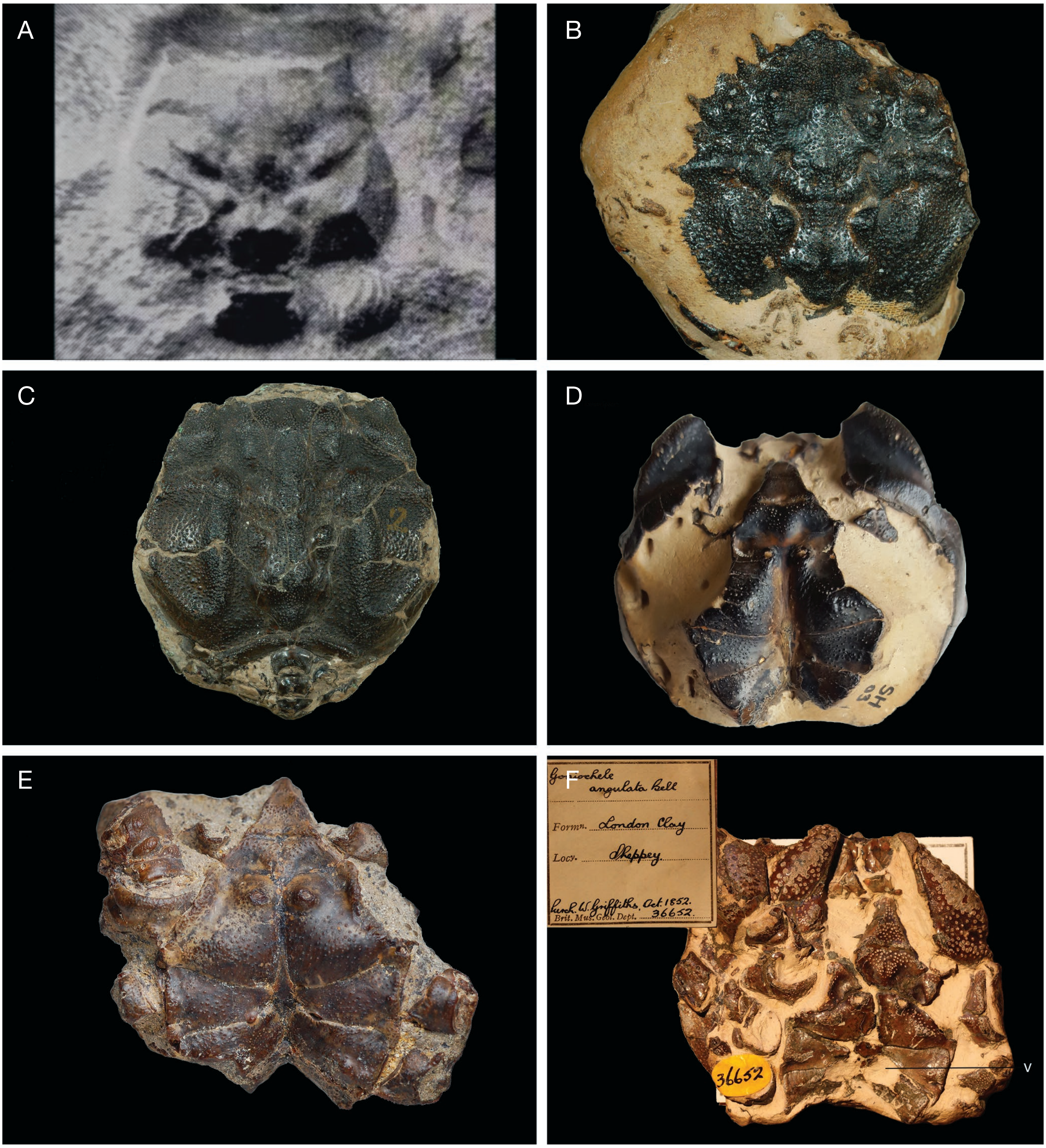

Fig. 40. — Fossil crabs: **A**, the poorly known true dorippid, *Dorippe judicis* Gripp, 1964 (pl. 17, fig. 7a), Lower Miocene of northern Germany, generic status to be reappraised: carapace and pleon partially dorsally exposed (photocopy from Gripp 1964: pl. 17, fig. 7a); **B**-**F**, *Goniochele angulata* Bell, 1858; **B**-**D**, **F**, Eocene London Clay, Ypresian, Isle of Sheppey, Kent; **E**, Ypresian, Forest, Brussels, Belgium: **B**, carapace with preserved lateral spines, except long epibranchial spine, broken, concealed with matrix (Griffiths' collection); **C**, carapace of paralectotype (lateral spines lost) with well-preserved protruding concave rim of posterior margin and narrow male pleon, with first three somites dorsally exposed (Wetherell's collection, NHM PL OR 59085); **D**, **E**, two views of male thoracic sternum, with triangular first sternites and press-buttons on suture 5/6 (**D**, Jeff Saward collection); **E**, original from Collins & Smith 1993: pl. 2, fig. 3, as *Silvacarcinus laurae* Collins & Smith, 1993; **F**, ventral view of a female, with narrow elongated sternites 1-4 and wider last sternites (Griffiths' collection, NHM 36652). Abbreviation: **v**, enormous vulvae. All, courtesy of Barry van Bakel.

with oblique margins. In Dorippinae n. stat. (Figs 11; 12B-E; 13; 14B, C, F, I; 15B), the shield is proportionally longer, narrower and with oblique margins. The only distinct case is that of the Philippidorippinae n. subfam. (Figs 27C, D; 28), in which the shield tends to become somewhat triangular.

The remarkable study of *G. angulata* by Bell (1858: 26, pl. 4, figs 3-9) reports that the concave posterior margin of the carapace is rimmed ("somewhat waved, and forms a raised border"), several pleonal somites are positioned dorsally in both sexes, and P4 and P5 are carried dorsally ("small size and dorsal direction of the posterior pair of feet" see Bell 1858: 27, also evident from the disposition of the coxae). These features eventually supported the attribution of *Goniochele* to the Dorippoidea (Jagt *et al.* 2015: 882; Luque 2015: 255, fig. 4; Luque *et al.* 2017; Guinot *et al.* 2019: 302; Van Bakel *et al.* 2020: fig. 10; Charbonnier & Garassino 2022: 190, figs 540-546, table 8). Did *Goniochele* crabs perform carrying behaviour? Only more precise knowledge of Goniochelidae, especially of the endostomial region, the mouthparts, the sternum/pterygostome junction and the Milne Edwards openings, will definitively allow its higher rank assignment.

Fossils assigned to Lecythocaridae Schweitzer & Feldmann, 2009

The Lecythocaridae, from the Upper Jurasssic of Europe, known only from a few tiny and poorly sclerotised carapaces, is a carapace-based taxon, like all Jurassic brachyuran crabs. The genus *Lecythocaris* von Meyer, 1860, though considered a 'precursor' of the Majoidea (Patrulius 1959: 253), was assigned to the Prosopidae von Meyer, 1860 (Patrulius 1966: 508, pl. 30, fig. 9) and the Homolodromioidea (Van Straelen 1925: 163; Müller *et al.* 2000: figs 1, 7, 17J). In establishing the family Lecythocaridae, Schweitzer & Feldmann (2009: 62, 94, tables 1, 6) included it in the Glaessneropsoidea within the Dromiacea De Haan, 1833. The Lecythocaridae comprises two genera: *Lecythocaris*, with three species: the type species: *L. paradoxa* (von Meyer, 1858) (see Krobicki & Zatoń 2008: fig. 1; Schweigert & Robins 2016: fig. 2C), *L. obesa* Schweitzer & Feldmann, 2009 (p. 99, figs 1.7, 6.6-6.8), *L. stoicai* Franțescu, 2011 (Franțescu 2011: 20, fig. 14); and *Prolecythocaris* Schweigert & Robins, 2016, with two species: the type species *P. hauckei* Schweigert & Robins, 2016 (Schweigert & Robins 2016: 327, fig. 2A, B), with an epibranchial lateral spine and a concave posterior rim; and *P. rieberi* Schweigert, 2018 (Schweigert 2018: 37, fig. 2). For all these authors, Lecythocaridae is a podotreme family (see also Karasawa *et al.* 2011b: tables 1; 2). Conversely, Guinot *et al.* (2019: 296, 308, fig. 13) and Guinot (2019: 768, 769, 782, fig. 10, table 1) argue for a eubrachyuran affiliation, probably with the more basal majoids as oregoniids, whereas Van Bakel *et al.* (2020: 13) suggest that Lecythocaridae could be "a possibly basal dorippoid family".

To date, no Jurassic brachyuran crab has been deemed to be non-podotreme. If our hypothesis that the Upper Jurassic Lecythocaridae could be a eubrachyuran family proves to be correct, the Eubrachyura (the 'true crabs') would date from the Jurassic, contrary to the current view that the first heterotremes did not appear until the Cretaceous. This would be strong evidence that the evolutionary history of brachyurans began much earlier than is generally believed. To establish the true status of the Lecythocaridae, it is first necessary to ensure that the family is truly monophyletic. In fact, the lecythocarid carapaces are more or less sculptured and differ, among other features, in their carapace grooves and epibranchial condensation. The strongly rimmed posterior margin is completed by a flange, a character absent in the Dorippidae. The carapace of the telamonocarcinid *Personadorippe kalashnikovi* (see Van Bakel *et al.* 2020: figs 6D, 7A) somewhat resembles that of a lecythocarid. If the Lecythocaridae, in whole or in part, is found to be a member of the dorippoid lineage, it would be ancestral to the Telamonocarcinidae.

All considered, a new reassessment, especially based on better preserved structures and rigorous interpretation, of fossil Dorippidae, Ethusidae, Telamonocarcinidae, Tepexicarcinidae, Goniochelidae and Lecythocaridae is highly desirable.

Fossils assigned to *Binkhorstia* Noetling, 1881

Binkhorstia Noetling, 1881, from the Upper Cretaceous, Maastrichtian, of the Netherlands and Belgium (type species: *Dromilites ubaghsii* Van Binkhorst, 1857; also with *B. euglypha* Collins, Fraaye & Jagt, 1995; see Collins *et al.* 1995; Fraaje 1996; Van Bakel *et al.* 2003; Schweitzer & Feldmann 2011b; Jagt *et al.* 2015), referred to various families or subfamilies, either podotreme or supposedly eubrachyuran, has been sometimes assigned to the Dorippidae (Glaessner 1969: R492; Quayle & Collins 1981: 738). P5 being the only reduced pereiopod, the first pleonal somites not exposed dorsally, the flat thoracic sternum and the carapace groove pattern are all characters that prevent *Binkhorstia* from belonging to the Dorippidae. It would be advisable to check whether some characters evoking certain Retroplumidae are actually accurate.

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