



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

Posodobitev filogenetske rekonstrukcije, klasifikacije in morfoloških znakov recentnih rakovic Portunoidea Rafinesque, 1815 (Decapoda, Brachyura, Heterotremata) z razpravo o njihovi pomembnosti za fosilni material

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Abstract

The classification of extant Portunoidea has recently been significantly rearranged on the basis of morphological revision and molecular phylogenetic reconstructions. There is an urgent need to reach compatibility of fossil portunoid taxa with this new classification. Furthermore, several genera with a variety of both Recent and fossil representatives, e.g., the genus *Portunus* (*sensu lato*), have been split into other genera, but referring fossil species to these is still problematic. In order to facilitate the development of an integrated system that includes both extant and extinct portunoid taxa, a review of recent results regarding the phylogeny of portunoid crabs, an update of their extant taxa classification and a reappraisal of important morphological characters that can be used for assessment of both fossil and contemporary species are presented. A new subfamily, Parathranitiinae, is established within the Carcinidae and within the Portunidae, another new subfamily, Achelouinae, is introduced. Integration of palaeontological data and the evolutionary classification of extant Portunoidea is a challenging task that requires further development of comparative morphological, ecological and molecular genetic studies of modern species.

Izvleček

Razvrstitev recentnih portunoidnih rakovic je bila v zadnjem času bistveno preurejena na podlagi revizije morfologije in molekularnih filogenetskih rekonstrukcij. Potrebno je zagotoviti združljivost fosilnih portunoidnih taksonov z novo klasifikacijo. Več rodov z živečimi in fosilnimi predstavniki, na primer rod *Portunus* (*sensu lato*), je bilo razdeljenih na druge rodove, zato je uvrščanje fosilnih vrst vanje problematično. Da bi zagotovili razvoj integriranega sistema, ki vključuje obstoječe in izumrle portunoidne taksoni, je potreben pregled novih spoznanj o filogeniji portunoidnih rakov, posodobitev njihove obstoječe klasifikacije in ponovna ocena pomembnih morfoloških znakov, ki jih je mogoče uporabiti za določanje fosilnih in recentnih vrst. V okviru družine Carcinidae je ustanovljena nova poddružina Parathranitiinae, znotraj Portunidae pa nova poddružina, Achelouinae. Vključevanje paleontološkega materiala in evolucijske klasifikacije recentnih portunoidnih rakovic je zahtevna naloga, ki zahteva nadaljnji razvoj primerjalno morfoloških, ekoloških in molekularno genetskih raziskav obstoječih vrst.

Introduction

Portunoid crabs (superfamily Portunoidea) comprise over 420 extant and more than 200 extinct species (De Grave et al., 2009), making it one of the most diverse and species-rich groups of Brachyura. Their characteristic features include a specific construction of pereopods 5, preadapted for burrowing and constituting part of the swimming apparatus (Garstang, 1897a, b; Schäfer, 1954; Hartnoll, 1971; Steudel, 1998; Spiridonov et al., 2014). Another important feature of portunoids is the peculiar morphology of the chelae, which is essential in maintaining the habit of active generalist predators and scavengers (Schäfer, 1954; Spiridonov et al., 2014). Portunoid crabs have a worldwide distribution (with the exception of subarctic waters of the North Pacific, Arctic and Antarctic), live in a variety of biotopes, although predominately on soft bottoms, from the intertidal and upper subtidal (Fig. 1) to deep waters of the continental slope and underwater rises (e.g., Geryonidae; see Manning & Holthuis, 1989; but also some representatives of generally shallow-water groups; see Spiridonov & Türkay, 2001). Particular groups have symbiotic relationships with a variety of animal and plant taxa (Evans, 2018). Being abundant predators, portunoid crabs play a significant role of ecosystems, hold a leading position among human-mediated invaders (Brockerhoff & McLay, 2011) and include several highly important commercial species (Figs. 1G, H). Classification of Recent portunoids had been stable for about half a century, owing to the dominating taxonomic concept of Stephenson (1972). This state was largely reflected in the ‘Systema Brachyurorum’ by Ng et al. (2008), although it accommodated several revisions of particular species and genera and descriptions of new taxa introduced during the 1990s and early 2000s. Right after this ground-laying publication the taxonomy and classification of the Portunoidea entered a major

revision. The impetus for this was given by palaeontologists (Karasawa et al., 2008), who suggested the first phylogenetic reconstruction of the Portunoidea based on morphological cladistics and attempted to construct a new classification for both extant and extinct portunoid taxa. Subsequent molecular phylogenetic reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018) have significantly changed the very concept of what are portunoids, challenged both the traditional (Stephenson, 1972; Ng et al., 2008) and Karasawa et al. (2008) views on major groups and evolutionary lineages, stimulated new comparative morphological analysis of extant groups and revised the classification of the Portunoidea (see a scheme that reflects recent changes in Evans, 2018, fig. 5).

In the present paper, I shall review recent developments in phylogenetic reconstruction, taxonomy, variability and classification of morphological structures and characters in order to facilitate the integration of palaeontological and neontological data in a coherent system of the Portunoidea. It is not really my intention here to classify extinct taxa but rather to comment on some of them to stimulate further taxonomic revision by palaeontologists or jointly by palaeontologists and neontologists. Therefore, palaeontological data are here presented only as examples without any ambitions to provide their comprehensive coverage.

The purpose of the present contribution is to review recent studies on extant Portunoidea and facilitate their integration with palaeontological data, in order to: 1) synthesise relevant molecular phylogenetic reconstructions and fossil records of extant genera; 2) update the classification of modern portunoid crabs; 3) make a comparative description of the taxonomic value of morphological characters that can be applied to both extant and fossil material.

Fig. 1. Examples of portunoid crabs showing characteristic habit and commercial importance. A: *Carcinus maenas* (Linnaeus, 1761), medium size (to about 80 mm carapace width, CW), common inhabitant of intertidal-low subtidal habitats, north-east Atlantic; a global invader; rocky intertidal, North Sea, German Bight, Wilhelmshaven. B. *Carcinus aestuarii* Nardo, 1869, medium-sized species, a common inhabitant of Mediterranean Sea, low subtidal, in semi-burrowed condition, Black Sea. C. *Liocarcinus vernalis* (Risso, 1816), medium-sized species, a common inhabitant of low subtidal sandy habitats in the Mediterranean Sea, swimming over sand bottom, Black Sea. D. same specimen as C, burrowed in sand. E. *Thalamita crenata* Rüppell, 1830, medium-sized species, a common inhabitant of intertidal habitats in Indo-Pacific; after burrowing in sediments, mangrove, Dam Bay, Tre Island, Vietnam, South China Sea. F. *Xiphonectes* sp., small (to about 50 mm CW) species, in coral rubble; Mot Island, Vietnam, South China Sea. G. *Portunus trituberculatus* Miers, 1879, a large (about 300 mm CW) commercially important species in East Asia; fish market in Busan, Korea. H. *Scylla paramamosain* Estampador, 1949, a large, commercially important and cultured species in southeast Asia, fish market in NhaTrang, Vietnam. Photograph credits: V. Spiridonov (A, E, G, H); S. Anosov (B, C, D) and T. Antokhina (F).

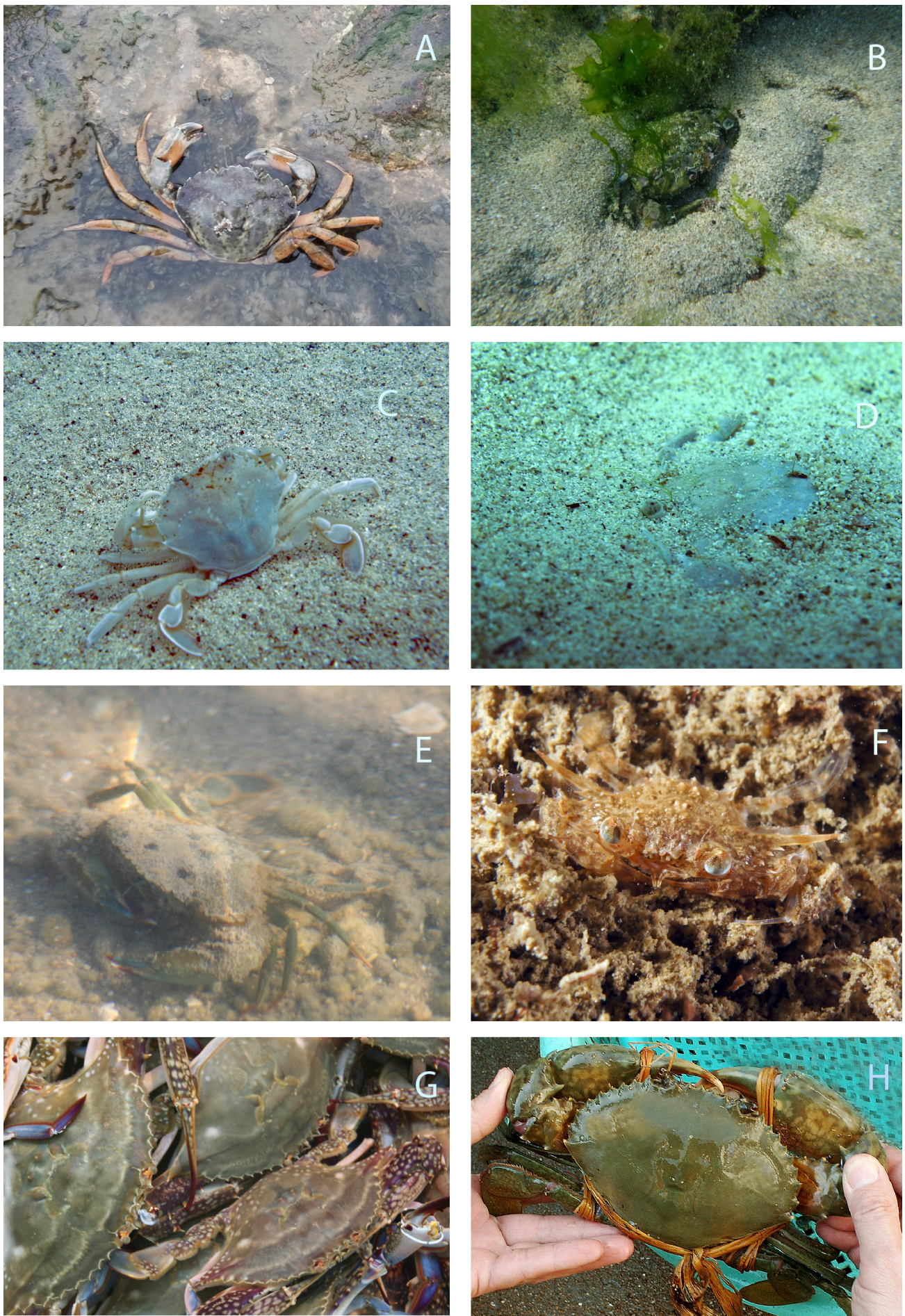


Fig. 1.

Material and methods

The present study is based on my 20+ years' work with collections of portunoid crabs at the Natural History Museum London, UK (NHMUK), the Naturhistorisches Museum Wien, Vienna, Austria (NHMW), the Senckenberg Museum, Frankfurt am Main, Germany (SMF), the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia (ZIN-RAS), the Zoological Museum of Moscow University, Moscow, Russia (ZMMU), the Zoologisches Museum, Museum für Naturkunde, Berlin, Germany (ZMB), where specimens illustrated are deposited, as well as other European, American and Australian collections.

Morphological terms generally follow usage in Stephenson & Hudson (1957), Apel & Spiridonov (1998), Ng et al. (2008) and Evans (2018). In the carapace description the epithets “quasi-hexagonal”, “quasi-trapezoidal” etc. are preferred over “subhexagonal”, “subtrapezoidal” etc.

The simplified scheme of the phylogenetic relationships of extant portunoid genera (Fig. 2) is based on results obtained by recent molecular phylogenetic reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018). The branching of the tree follows particular patterns agreed between different reconstructions; where there is no agreement between particular studies, the relationships are shown as an unresolved polytomy.

The updated classification of Recent Portunoidea is based on the principles of evolutionary systematics (Simpson, 1961), which requires compatibility with phylogenetic reconstructions but implies a thorough morphological analysis for definition of the boundaries of taxa.

In linking particular extant portunoid genera to their palaeontological records I generally follow Müller (1984) and Karasawa et al. (2008) with additions of recent fossil records, for instance, of *Geryon* Krøyer, 1838 (Feldmann et al., 2010), *Bathynectes* Stimpson, 1871 (Ossó & Stalennuy, 2011) and *Liocarcinus* Stimpson, 1871 (De Angeli et al., 2019). Since most pre-Pleistocene records of *Callinectes* Stimpson, 1860 are based on incomplete and poorly preserved material, the known range of *Callinectes* was corrected according to well-preserved specimens reported by Collins et al. (2014). As fossil crabs identified as *Portunus* (*sensu lato*) may indeed refer to several genera, I have specifically checked the original figure of one of the oldest representatives, namely *Portunus kochi* Bittner, 1893 (see Bittner, 1893, pl. 1, fig. 1). For further explanations, reference is made to the caption of Figure 2.

A review of the phylogeny of the Portunoidea based on published molecular genetic reconstructions and palaeontological history of extant taxa

The genera *Geryon* (living in the northeast Atlantic), *Chaceon* Manning & Holthuis, 1989 (inhabiting continental slopes and underwater rises worldwide), *Raymanninus* Ng, 2000 (occurring in the deep water of the Caribbean) form a distinct clade in all molecular phylogenetic reconstructions, which shows sister relationships to the deep-water Indo-Pacific *Benthochascon* Alcock & Anderson, 1899 or the *Benthochascon* + *Ovalipes* clade. Species of *Ovalipes* occur mostly in the Southern Hemisphere but are also known from the northeast Pacific and northwest Atlantic. This clade is interpreted as the basal portunoid lineage that possesses a number of plesiomorphic character states and shows a close affinity to one of the most ancient potential portunoid taxa, the genus *Eogeryon* Ossó, 2016 from the upper Cenomanian (Ossó, 2016). The clade comprises the family Geryonidae (*sensu* Evans, 2018) and shows sister relationships to other studied portunoids (Fig. 2).

The latter in turn are well separated into two major clades which are resolved in all reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018), although with varying internal topologies. Following the most comprehensive study by Evans (2018), one of this major lineages includes the Indo-Pacific taxa *Parathranites* Miers, 1886 and *Coelocarcinus* Edmondson, 1930 as basal groups. All published phylogenetic trees define the related clades *Carcinus* Leach, 1814 + *Portumnus* Leach, 1814 and *Pirimela* Leach, 1816 or *Pirimela* + *Sirpus* Gordon, 1953. All these taxa are originally confined to the North Atlantic. Their possible sister clade includes morphologically diverse genera such as *Thia* Leach, 1816, *Bathynectes*, *Macropipus* Prestandrea, 1833, *Necora* Holthuis, 1987 and *Liocarcinus*, also living mostly in the Atlantic. The topology of relationships between these groups differ in the reviewed studies, so in Figure 2 no resolved branching is shown. *Polybius* Leach, 1820 is nested within *Liocarcinus* in all reconstructions (see also Plagge et al., 2016) and is not shown in the present scheme (Fig. 2). All the genera mentioned were combined in the newly defined family Carcinidae (*sensu* Evans, 2018). Most fossil records of thus defined carcinids are no older than Miocene, and only records of *Liocarcinus* spp. date back to the Eocene (De Angeli et al., 2019; Á. Ossó, pers. comm., January 2020).

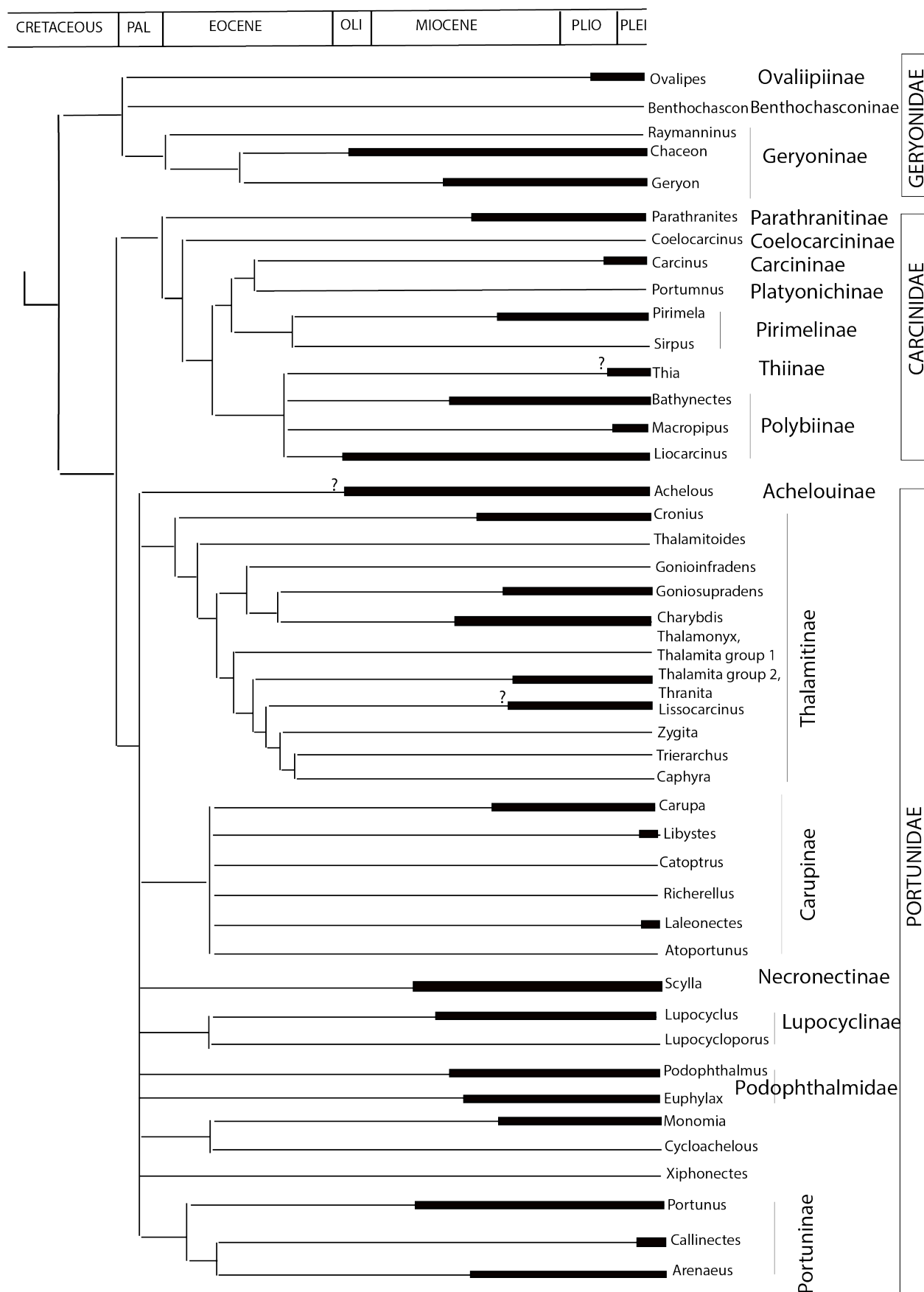


Fig. 2. Schematic phylogenetic tree of extant portunoid genera based on molecular phylogenetic reconstructions by Schubart & Reuschel (2010), Spiridonov et al. (2014), Evans (2018) and Mantelatto et al. (2018). Black bands indicate the temporal extension of particular genera from the first palaeontological record onwards. The tree does not have an unbiased temporal scale; the positions of nodes only indicate that the divergence between families occurred not later than the Cretaceous, the divergence between major genera not later than the Eocene, Oligocene or Miocene. Abbreviations of geological epochs: PAL – Paleocene; PLEI – Pleistocene; PLIO – Pliocene; OLI – Oligocene.

Another large group which shows sister relationships to the Carcinidae are the Portunidae (*sensu* Schubart & Reuschel, 2009; Spiridonov et al., 2014). The topology of clades within the Portunidae is not stable through reviewed reconstructions, although the clade of taxa referred to the Thalamitinae (*sensu* Apel & Spiridonov, 1998), plus symbiotic taxa formerly referred to the Caphyrinae Paulson, 1875 is always revealed (Fig. 2). The Atlantic-eastern Pacific genus *Cronius* Stimpson, 1860 was shown to be basal to this clade, the other species of which have a mostly Indo-Pacific distribution (Evans, 2018). All molecular phylogenetic studies indicate that the American and eastern Atlantic species earlier considered to belong to the subgenus *Achelous* De Haan, 1833 of the genus *Portunus* Weber, 1795 (Ng et al., 2008) constitute a distinct clade, which in some reconstructions show sister relationships to the Thalamitinae (Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018).

Species of *Portunus* (*sensu stricto*) (occurring in the Indo-Pacific and Atlantic) are revealed as having close phylogenetic relationships with the Atlantic genera *Arenaeus* Dana, 1851 and *Callinectes*. Several Indo-Pacific genera, most of them earlier included in the Carupinae (*sensu* Apel & Spiridonov, 1998), such as *Atoportunus* Ng & Takeda, 2003, *Carupa* Dana, 1851, *Catoptrus* A. Milne-Edwards, 1870, *Laleonectes* Manning & Chace, 1990, *Libystes* A. Milne-Edwards, 1867 and *Richerellus* Crosnier, 2003) are also phylogenetically related, although their tree cannot be perfectly resolved to date (Fig. 2). Other genera do not show a stable pattern of relationships in particular reconstructions (except for *Monomia* Gistel, 1848 and *Cycloachelous* Ward, 1942), and therefore the general phylogeny of the Portunidae may now be schematically presented as a polytomy ("bush" rather than a tree).

One of the oldest known portunids, "*Portunus*" *kochi* (Bittner, 1883) from the Upper Eocene, can be referred to *Achelous* according to the morphology of the frontorbital and anterolateral margins and carapace ornamentation (see Bittner, 1893: pl. 1, fig. 1). This suggests a significant geological age of the Achelouinae. Such genera as *Scylla* De Haan, 1833 are known to have occurred since at least the Miocene, while *Necronectes* A. Milne-Edwards, 1881, which is morphologically very similar to *Scylla*, is at least of Oligocene age (Karasawa et al., 2008; Ossó & Gagnaison, 2019). Therefore, the divergence of major portunid lineages most probably took place no later than Middle Eocene or even in pre-Eocene times (Fig. 2)

Updated classification of recent Portunoidea

Family Geryonidae Colosi, 1923

Diagnosis: Spiridonov et al. (2014).

Type genus: *Geryon* Krøyer, 1837.

Subfamily Benthochasconinae Spiridonov, Neretina & Schepetov, 2014

Diagnosis: Spiridonov et al. (2014).

Genus: *Benthochascon* Alcock & Anderson, 1899

Subfamily Geryoninae Colosi, 1923

Diagnosis: Spiridonov et al. (2014).

Genera: *Chaceon* Manning & Holthuis, 1989; *Geryon* Krøyer, 1837 (type genus); *Raymanninus* Ng, 2001 and *Zariquieyon* Manning & Holthuis, 1989.

Subfamily Ovalipiinae Spiridonov, Neretina & Schepetov, 2014

Diagnosis: Spiridonov et al. (2014).

Genera: *Ovalipes* Rathbun, 1898 (type genus).

Remarks: Originally, this taxon was established at the family level, although possible sister relationships to the Geryonidae were assumed (Spiridonov et al., 2014). On the basis of his molecular phylogenetic reconstruction, Evans (2018) argued for even closer relationships of *Ovalipes* with geryonids and suggested to consider this group as a subfamily of the Geryonidae. I accept his concept here. Although *Ovalipes* spp. are characterised by a number of apomorphies in relation to other geryonids, they share with them apparently plesiomorphic conditions of non-fused pleomeres of the male pleon and long gonopods 2, and an apparently apomorphic tendency for reduction of one of the orbital fissures (see below).

The grammatically correct form for the family/subfamily name is Ovalipiinae, not Ovalipinae as suggested by Spiridonov et al. (2014). It is corrected here.

Genera incertae sedis: *Echinolatus* Davie & Crosnier, 2006 and *Nectocarcinus* A. Milne-Edwards, 1861.

Remarks: These genera share with the Geryonidae such plesiomorphic conditions as non-fused pleomeres of the male pleon and long gonopods 2, a tendency for reduction of one orbital fissure,

as well as an even number of frontal lobes and four anterolateral teeth, characters not commonly found in the Carcinidae. On the other hand, species assigned to these genera have some characters that are unique to portunoid crabs, such as a double inner carpal spine and additional anterolateral teeth in *Echinolatus* spp. These genera have not yet been included in molecular phylogenetic reconstructions. I tentatively assign them to the Geryonidae, although they may deserve separate status.

Family Carcinidae MacLeay, 1838

Diagnosis: Evans (2018).

Type genus: *Carcinus* Leach, 1814.

Subfamily Carcininae MacLeay, 1838

Diagnosis: Spiridonov et al. (2014).

Genera: *Carcinus* Leach, 1814 (type genus).

Subfamily Coelocarcininae Števcíć, 1991

Diagnosis: Evans (2018).

Genera: *Coelocarcinus* Edmondson, 1930 (type genus).

Subfamily Parathranitiinae Spiridonov subfam. nov.

Zoobank: urn:lsid:zoobank.org:act:74EF-9937-1342-4BF6-8847-5F220ED11882

Diagnosis (new): Carapace distinctly quasi-hexagonal, regions well defined, with well-defined ridged and granular ornamentation. Frontal margin subdivided into 4 teeth. Infra-orbital margin consisting of several lobes. Posterior most of five anterolateral teeth distinctly longer than others. Posterolateral corners of carapace angular or spiniform. Cheliped with spines on anterior and posterior faces of merus, carpus with outer spines, propodus with upper spines, dactyli of last pereopods lanceolate.

Genera: *Parathranites* Miers, 1886 (type genus).

Remarks: *Parathranites* spp. (see Crosnier, 2002) differ from all Carcinidae in having well-defined regions of the carapace, spiniform posterolateral corners of the carapace, and from most of the carcinids by upper spines on the chela palm (propodus) and four frontal teeth/lobes. Molecular phylogenetic reconstruction (e.g., Evans, 2018; see Fig. 2 here) indicates the basal position of the genus in relation to other groups of

the family. To emphasise this peculiar position, I find it reasonable to define a new subfamily, Parathranitiinae, within the Carcinidae.

Subfamily Platyonichinae Dana, 1851 (= Portumninae Ortmann, 1899; see Davie et al., 2015 for a discussion of the synonymy).

Diagnosis: Spiridonov et al. (2014; as Portumninae).

Genera: *Portumnus* Leach, 1815 (type genus) and *Xaiva* MacLeay, 1838.

Subfamily Pirimelinae Alcock, 1899

Diagnosis: Spiridonov et al. (2014; as family Pirimelidae).

Genera: *Pirimela* Leach, 1816 (type genus) and *Sirpus* Gordon, 1953.

Subfamily Polybiinae Ortmann, 1893

Diagnosis: Spiridonov et al. (2014: 422, as family Polybiidae).

Genera: *Bathynectes* Stimpson, 1871; *Coenophthalmus* A. Milne-Edwards, 1873; *Liocarcinus* Stimpson, 1871; *Macropipus* Prestandrea, 1833; *Necora* Holthuis, 1987 and *Polybius* Leach, 1820 (type genus).

Subfamily Nautilocorystinae Ortmann, 1893

Diagnosis: Spiridonov et al. (2014).

Genera: *Nautilocorystes* H. Milne Edwards, 1837 (type genus).

Subfamily Thiinae Dana, 1852

Diagnosis: Spiridonov et al. (2014; as Thiidae)

Genera: *Thia* Leach, 1816 (type genus).

Remarks: *Nautilocorystes* was referred to the Thiidae by Ng et al. (2008) on the basis of important morphological similarities. In spite of an appearance that is highly unusual for portunoid crabs, *Nautilocorystes* has several characters, such as a cheliped morphology typical of portunids (Spiridonov et al., 2014). *Thia* has repeatedly been shown to nest within the polybiine clade (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018), although its significant morphological peculiarity calls for a separate status. Therefore, a subfamily rank for the Thiinae was accepted by Evans (2018) and it is here too. The relationships of *Nautilocorystes* to the Carcinidae in the current concept remain un-

clear, as no molecular phylogenetic study of this taxon has been conducted to date. Here, I tentatively place Nautilocorystinae as a separate subfamily of the carcinids.

Family Portunidae Rafinesque, 1815

Diagnosis: Spiridonov et al. (2014).

Type species: *Portunus* Weber, 1795.

Subfamily Achelouinae subfam. nov.

Zoobank: urn:lsid:zoobank.org:act:B094745A-E-EB2-408A-B91F-E30DE868449A

Diagnosis (new): Carapace more than 1.5 times wider than long, quasi-hexagonal; regions well expressed; with distinct granular ridges and groups of granules both in anterior and posterior parts. Nine sharp anterolateral teeth: teeth 1 to 8 subequal, last tooth distinctly longer than others. Front narrower than posterior border, consisting of 4 or 6 lobes; outer lateral lobes may be fused with inner supraorbital lobes. Chelipeds with several teeth on anterior margin and a single posterior tooth; carpus with a single outer spine; inner spine well expressed and may be very long, reaching to chela fingers; propodus strongly costate, with a single spine; heterochely moderate; larger chela with flattened molariform tooth. Dactyli of pereopods 2–4 strong, knife-shaped. Merus of pereopod 5 much broader than meri of pereopods 2–4, posterior spine may be present although obsolete; propodus without spinules on posterior margin, dactylus paddle-like. Male pleon triangular, unclear sutures may be present at fused pleomere 3–5. Gonopod 1 of generalised shape, curved, thinning apically, with microscopic spinules. Female genital opening large, occupying about one third of sternite.

Remarks: Numerous Atlantic and eastern Pacific species referred to *Achelous*, *Lupella* Rathbun, 1897 or *Portunus* (except for *Portunus sayi* (Gibbes, 1850) form a distinct monophyletic clade which does not show clear relationships to other groups (Spiridonov et al., 2014; Mantelatto et al., 2018) and are characterised by distinct morphological characters. It justifies placing them in a separate subfamily, Achelouinae.

Genera: *Achelous* De Haan, 1833 (type genus) and *Lupella* Rathbun, 1897.

Subfamily Carupinae Paulson, 1875

Diagnosis (extended from Apel & Spiridonov, 1998): Carapace much wider than long, up

to about twice, transversely oval, elliptical or indistinctly quasi-hexagonal, relatively convex; regions poorly expressed; usually with only epibranchial ridge or smooth; sometimes with diffuse granules. Supraorbital fissures may be reduced, infraorbital margin variously modified. Front much narrower than posterior border, four-, or two-lobed, or nearly entire; anterolateral border convex, toothed or entire. Posterolateral reentrant poorly developed, or not at all. Secondary sulci of sternum may be absent. Basal antennal segment narrow, long, lying obliquely, not lobulate, antennal peduncle entering orbital hiatus. Chelipeds of various construction, spines on cheliped segments usually reduced in number or absent. Some representatives are secondarily homiochelic and homiodontic, with long and thin chelae. Pereopods 2–4 usually long and thin, non-costate. Merus of pereopod 5 long and thin, not broader or not much broader than meri of pereopods 2–4, without posterior spinule; dactylus styliiform, lanceolate, or knife-shaped. Male pleon triangular. Gonopod 1 usually with relatively robust subterminal spines. Female genital openings large, without cuticular emargination and caps.

Genera: *Atoportunus* Ng & Takeda, 2003; *Carupa* Dana, 1851 (type genus); *Catoptrus* A. Milne-Edwards, 1870; *Kume* Naruse & Ng, 2012; *Laleonectes* Manning & Chace, 1990; *Libystes* A. Milne-Edwards, 1867; *Pele* Ng, 2011 and *Richerellus* Crosnier, 2003.

Remarks: The name of the author of the subfamily is often spelled “Paulson” following the English translation of the original monograph in the Russian language (Paulson, 1875). I prefer, however, “Paulson” because Otto Paulson used this spelling in his German-language publications (i.e. Paulson, 1862).

Subfamily Lupocyclinae Paulson, 1875

Diagnosis (new): Cephalothorax quasi-hexagonal or quasi-circular in outline, dorsally convex. Carapace with granular ridges and/or patches. Front narrower than posterior border, consisting of 4 lobes or teeth, markedly produced beyond inner supraorbital lobes. Orbit circular. Anterolateral margin with 5–9 teeth. Posterolateral margin with rounded corners. Expansion of basal antennal segment not produced into orbit being directed nearly anteriorly; flagellum standing in orbital hiatus. Chelipeds long, homiochelic or slightly heterochelic; merus with 4–7 spines on anterior margin and 2 spines on

posterior margin; carpus with a single spine on outer face; manus with two subdistal spines on dorsal face. Chelae very long and thin, distinctly thinner than cheliped meri. Heterodonty not expressed or poorly expressed. Distal parts of chelae fingers curved in sagittal plane. Pereopods 2–4 long, thin, dactyli narrow, ensiform, Merus of P 5 broader and shorter than meri of pereopods 2–4, with a small posterodistal spine; dactylus lanceolate or paddle-like. Male pleon triangular. Gonopod 1 of generalised shape, relatively straight or curved, with sharpened distal part, without large subterminal spines. Female genital openings large, occupying half or more of length of mesial part of sternite, without cuticular emargination and caps.

Genera: *Lupocycloporus* Alcock, 1899 and *Lupocylus* Adams & White, 1848 (type genus).

Subfamily Necronectinae Glaessner, 1928

Diagnosis (modified after Karasawa et al., 2008): Carapace of intermediate outline between quasi-hexagonal and oval, dorsally convex, smooth with recognisable gastric and epibranchial finely granular ridges. Front narrower than posterior border, usually consisting of 4 lobes or teeth, not produced beyond inner supraorbital lobes. Orbit semi-oval. Anterolateral margin with 9 (or 8 in some fossil taxa) teeth. Posterolateral margin with rounded corners. Basal antennal segment with latero-distal spine; flagellum standing in orbital hiatus. Cheliped merus with 3 spines on anterior margin and 2 distal spinules on posterior margin; carpus with 1–3 spinules (often reduced) on outer face; manus nearly smooth, with 1 or 2 subdistal spinules on dorsal face. Heterochely and heterodonty well expressed; chela inflated; molariform teeth present on both chelae. Distal parts of chelae fingers not curved in sagittal plane. Dactyli of pereopods 2–4 relatively broad and strong, ensiform. Merus of pereopod 5 much shorter than meri of pereopods 2–4, without a posterior spine; propodus without posterior spinules; dactylus paddle-like. Male pleon triangular. Gonopod 1 sinuous or slightly curved, without large subterminal spines. Female genital openings without cuticular emargination and caps.

Genera: *Scylla* De Haan, 1833 and *Sanquerus* Manning, 1989.

Type genus: *Necronectes* A. Milne-Edwards, 1881 (extinct).

Subfamily Podophthalminae Stimpson, 1860

Diagnosis: Apel & Spiridonov (1998: 169).

Genera: *Euphyllax* Stimpson, 1860 and *Podophthalmus* Lamarck, 1801 (type genus).

Subfamily Portuninae Rafinesque, 1815

Diagnosis (new): Cephalothorax quasi-hexagonal in outline, dorsally flattened. Carapace granular, usually with granular ridges and/or patches. Frontal margin of carapace divided into even number of lobes or teeth (usually 4), usually not distinctly produced beyond inner supraorbital lobes. Orbit elliptoidal. Anterolateral margin divided into 9 teeth, usually without indication of reduction of particular teeth. Posterolateral reentrant well developed; posterolateral margin usually with rounded corners. Expansion of basal antennal segment produced into orbit but not filling orbital hiatus completely, flagellum standing in orbital hiatus. Cheliped merus with 3–4 spines on anterior margin and 1–2 spines on posterior margin; on dorsal face along posterior margin there may be a suture and a granular line terminated at one of posterior spines. Carpus with a single spine or without spines but carina on outer face. Manus with one or two subdistal spines on dorsal face. Heterochely usually expressed. Heterodonty usually expressed by a molariform tooth developed to various degrees at base of larger chela dactylus; in some cases symmetrical chelae present. Distal parts of chelae fingers not curved in sagittal plane. Dactyli of pereopods 2–4 robust, ensiform or narrowly lanceolate. Merus of P 5 much shorter and broader than meri of pereopods 2–4, without a posterior spine, propodus without spinules on posterior margin, dactylus paddle-like. G 1 of simple shape or modified (very thin), without large subterminal spines. Female genital openings relatively compact, occupying less than half of length of mesial part of sternite, often with emarginations and caps.

Genera: *Arenaeus* Dana, 1851; *Callinectes* Stimpson, 1860 and *Portunus* Weber, 1795 (type genus).

Genera tentatively included here: *Cavoportunus* Nguyen & Ng, 2010; *Cycloachelous* Ward, 1942 and *Monomia* Gistel, 1848.

Remarks: Portuninae had been the largest subfamily of Portunidae when the lumping concept of Stephenson (1972) became dominant. With the subsequent revalidation and redefinition of the Lupocyclinae, Thalamitinae and Necronectinae, this subfamily has been considered in an in-

creasingly restricted sense (e.g., Apel & Spiridonov, 1998; Karasawa et al., 2008; Ng et al., 2008). To date, even this restricted concept is no longer supported by molecular phylogenetic reconstructions and comparative morphology (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018; Mantelatto et al., 2018). In particular, the genus *Portunus* (*sensu lato*) of Stephenson's (1972) classification is now considered to consist of several not closely related and morphologically different genera. The American-eastern Atlantic genus *Achelous* is here taken to represent a separate subfamily. *Xiphonectes* A. Milne-Edwards, 1873, which has been considered as a subgenus of *Portunus* (Ng et al., 2008), appears to be polyphyletic as well and is, for the time being, listed as a genus *incertae sedis* within the Portunidae. I tentatively include here in the Portuninae three additional genera previously combined in *Portunus*. This makes possible to formulate a consistent morphological diagnosis, until more detailed ongoing molecular genetics and comparative morphological studies provide sufficient data for a more appropriate classification of *Cavoportunus*, *Cycloachelous* and *Monomia*.

Subfamily Thalamitinae Paulson, 1875

Diagnosis: Evans (2018: 40).

Genera: *Caphyra* Guérin, 1832; *Charybdis* De Haan, 1833; *Cronius* Stimpson, 1860; *Gonioinfradens* Leene, 1938; *Goniosupradens* Leene, 1938; *Lissocarcinus* Adams & White, 1848; *Thalamita* Latreille, 1829 (type genus); *Thalamitoides* A. Milne-Edwards, 1869; *Thalamonyx* A. Milne-Edwards, 1873; *Thranita* Evans, 2018; *Trierarchus* Evans, 2018 and *Zygita* Evans, 2018.

Remarks: Thalamitinae was recognised as a morphologically distinct subfamily of Portunidae by Paulson (1875), but the taxon was subsequently largely ignored until revalidation and redefinition by Apel & Spiridonov (1998). Spiridonov et al. (2014) provided molecular phylogenetic support for the monophyly of the most speciose thalamitine genera, *Charybdis* and *Thalamita*. Recently, Evans (2018) has presented evidence of the basal position of *Cronius* (formerly assigned to the Portuninae) in the thalamitine phylogenetic tree and has demonstrated the phylogenetic relationships of Thalamitinae (*sensu stricto*) and *Caphyra* and *Lissocarcinus* (formerly considered to belong to the subfamily Caphyrinae Paulson, 1875, by Ng et al., 2008). The latter two genera, along with some groups formerly referred to *Thalamita* (*Trierarchus*, *Zygita*), form a symbiotic

clade within the Thalamitinae in the new concept (Evans, 2018).

Genus *incertae sedis*: *Carupella* Lenz & Strunk, 1914

Remarks: Two syntypes of *Carupella natalensis* Lenz & Schtrunk, 1914 that I have examined (ZMB 19917) are juvenile, just settled crabs, most likely belonging to the Portuninae (although assignment to the Lupocyclinae in its present concept cannot be completely ruled out). They may in fact belong to yet another known species for which precise identification is currently difficult due to a lack of knowledge on age-related variation in portunids. Thus, the genus *Carupella* may be synonymous with another, established genus. The holotype of *Carupella banlaensis* Tien, 1969 (ZIN-RAS 1/58265) is certainly a juvenile specimen of *Portunus* sp. The type of the third species of the genus, *Carupella epibranchialis* Zarenkov, 1970, has not been traced in the ZMMU collections where it would presumably have been deposited. It is thus appropriate to consider *Carupella* as a genus *incertae sedis* within the Portunidae until new comparative research will clarify its status.

Genus *incertae sedis*: *Xiphonectes* A. Milne-Edwards, 1873

Remarks: See above under the subfamily Portuninae.

Family Brusiniidae Števéčić, 1991

Genus: *Brusinia* Števéčić, 1991.

Remarks: *Brusinia* spp. are very peculiar morphologically (Spiridonov et al., 2014) and are not nested within the Portunoidea in updated phylogenetic trees based on the 16S RNA gene (Evans, 2018). The family is tentatively considered as a portunoid group until more comprehensive data become available.

Morphological characters of Portunoidea applicable to fossil material

Carapace morphology

Most portunoid crabs have a quasi-hexagonal carapace shape, with the maximum width usually exceeding the maximum length (Fig. 3). This general carapace outline portunoids share with a number of other heterotremate crabs such as the superfamilies Cancroidea, Goneplacoidea and Pilumnoidea (Guinot, 1979; Ng et al., 2008; Davie et al., 2015).

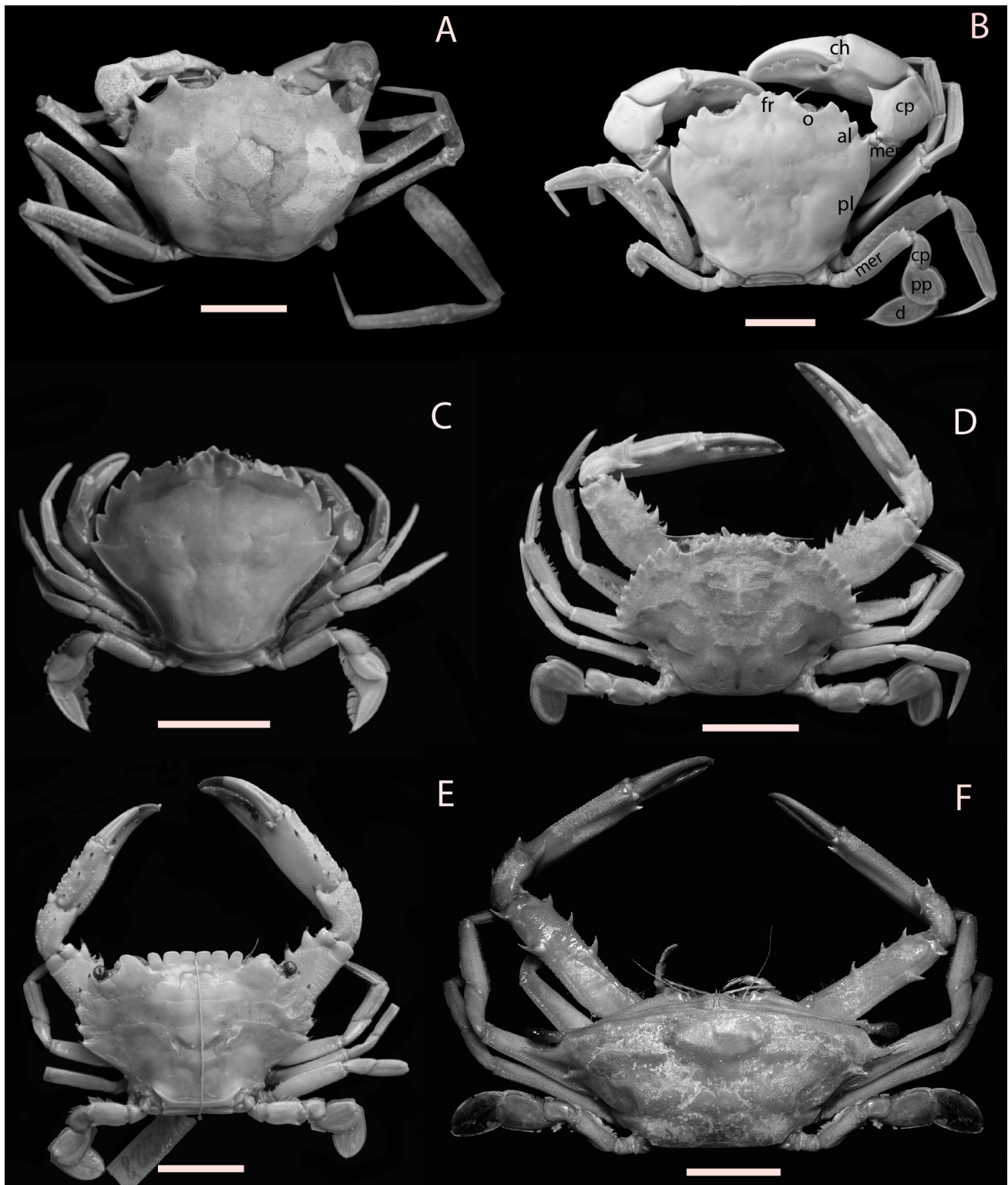


Fig. 3. Examples of portunoid crabs with a typical quasi-hexagonal (A–E) and a derived quasi-trapezoidal carapace (F). A. *Geryon trispinosus* Krøyer, 1838, North Sea, ZMMU Ma 2921; B. *Benthochascon hemmingi* Alcock & Anderson, 1899, South China Sea, ZIN-RAS 88509; C. *Xaiva biguttata* (Risso, 1816), North Sea, SMF 3969; D. *Achelous spinimanus* Latreille, 1819, Jamaica, SMF 31987; E. *Thalamita spinimana* Dana, 1852, Indo-Pacific, SMF 3881; F. *Podophthalmus vigil* Fabricius, 1798, Vietnam, collections of the Department of Hydrobiology of Moscow University. Abbreviations: f – frontal margin; o – orbit; al – anterolateral margin; pl – posterolateral margin; mer – merus; cp – carpus; pp – propodus; d – dactylus; ch – chela. Scale bar equals 5 mm.

In some portunoid taxa the cephalothorax is comparatively lengthened, so that the length becomes equal to or greater than the maximum width. The carapace morphology in such taxa shows a transition to a pear-shaped (*Portumnus*, *Brusinia*) or a nail-shaped (*Thia*, *Nautilocorystes*) outline (Fig. 4). The carapaces of *Brusinia* and *Nautilocorystes* are also distinctly longer than broad, which is an exception in the Portunoidea. The former genus may not even belong to the portunoid crabs phylogenetically (Evans, 2018), while the phylogenetic relationships of the latter are not yet reconstructed using molecular markers. However, all these taxa with a carapace shape that is unusual for portunoids have typical characters of burrower ecomorphs (Schäfer, 1954), while some of them (e.g., *Portumnus* and *Thia*; Figs. 4B, E) are definitely known to spend most of time burrowed in sandy sediments (Spiridonov et al., 2014).

In various subfamilies and genera of Recent portunoids one can also see transitions from quasi-hexagonal to other carapace shapes. Species of *Ovalipes* are flattened and approach an ovoid shape owing to arching of lateral carapace margins (Fig. 4A). Several actively swimming Podophthalminae, e.g., *Euphyllax dovii* Stimpson, 1860, are also flat and ovoid. Arching of lateral carapace margin is more expressed in the Lupocyclusinae which have a quasi-circular carapace and the Carupinae with broad quasi-oval carapaces (Fig. 5H). In the latter subfamily (genera *Atoportunus*, *Carupa* and *Catoptrus*) this type of carapace morphology is associated with living in reef cracks and caves (Spiridonov et al., 2014). In the non-reef-dwelling and likely non-swimming genus *Libystes* (Carupinae), e.g., *L. edwardsi* Alcock, 1900, the carapace is quasi-hexagonal with a convex anterolateral margin bearing notable teeth, while these teeth are strongly reduced and the general outline approaches the oval one in *Libystes* aff. *nitidus* (Apel & Spiridonov, 1998: figs 5a, 6a), reaching a perfect oval condition in *Libystes nitidus* A. Milne-Edwards, 1867 (Fig. 5H). Another group with ovoid or quasi-circular carapaces includes symbiotic *Caphyra* and *Trierarchus rotundifrons* (A. Milne-Edwards, 1869), associated with green algae (Crosnier, 1975; Evans, 2018). A very unusual quasi-circular carapace shape with protruding frontal and posterior regions is known for the Coelocarcininae which inhabit coarse coral sand and rubble (Ng, 2002).

A trapezoidal carapace is characteristic of several portunids with extended frontorbital margin, which approaches the maximum breadth

between posterior anterolateral teeth or becomes the widest part of the carapace. This is seen in *Podophthalmus vigil* (Fabricius, 1798) and some Thalamitinae. In the first case the extension is achieved owing to enlargement of the orbits, being associated with long eyestalks, and is commonly recorded among various and not closely related brachyuran taxa (e.g., Ocypodidae, Macropodophthalmidae, some Goneplacidae). The second case is associated with the extension of the basal antennal segment and the frontal margin and seems to be practically unique among crabs.

The posterior part of carapace may be markedly longer than the anterior one (Geryonidae and most Carcinidae), or be nearly equal to it (a quasi-symmetrical shape in relation to the maximum width axis carapace), and even shorter, which is characteristic of active swimmers in the Portunidae (see Schäfer, 1954: fig. 41). It is worth noting that the Parathranitiinae, a taxon apparently separate from most other extant carcinids, also has such quasi-symmetrical carapaces (see Crosnier, 2002). It is furthermore characteristic of *Echinolatus* (see Davie & Crosnier, 2006), a genus *incertae sedis*, which I here tentatively place in the Geryonidae.

Fossil portunoids, or taxa resembling portunoids, are mostly characterised by quasi-hexagonal or ovoid carapaces which are mostly asymmetrical in relation to the maximum width axis (e.g., Karasawa et al., 2008; Ossó, 2016). In some cases, for instance in the Lithophylacidae Van Straelen, 1936 from the Cenomanian (lower Upper Cretaceous) quasi-trapezoidal carapaces have been reported (Guinot & Breton, 2006). In the Cretaceous family Carcineretidae Beurlen, 1930 an intermediate condition between the quasi-quadrate and quasi-trapezoidal outline of the carapace is characteristic of the type genus *Carcineretes* Withers, 1922 (Withers, 1922, pl. 16; Vega et al., 2001, fig. 1; Schweitzer et al., 2007). Another Cretaceous taxon with a near-quadrate carapace is *Binkhorstia ubaghsii* (Van Binkhorst, 1857) currently included in the family Longosorbiidae Karasawa, Schweitzer & Feldmann, 2008 (see Schweitzer et al., 2007, figs. 2 A-C). The Late Cretaceous *Ophthalmoplax* Rathbun, 1935, earlier considered within the Carcineretidae and currently within the Macropipidae (*sensu* Karasawa, Schweitzer & Feldmann, 2008) also has a subquadrate carapace (Schweitzer et al., 2007; Vega et al., 2013). In general, the carapace outline and symmetry/asymmetry patterns are characters of considerable taxonomic value at the genus or family level.

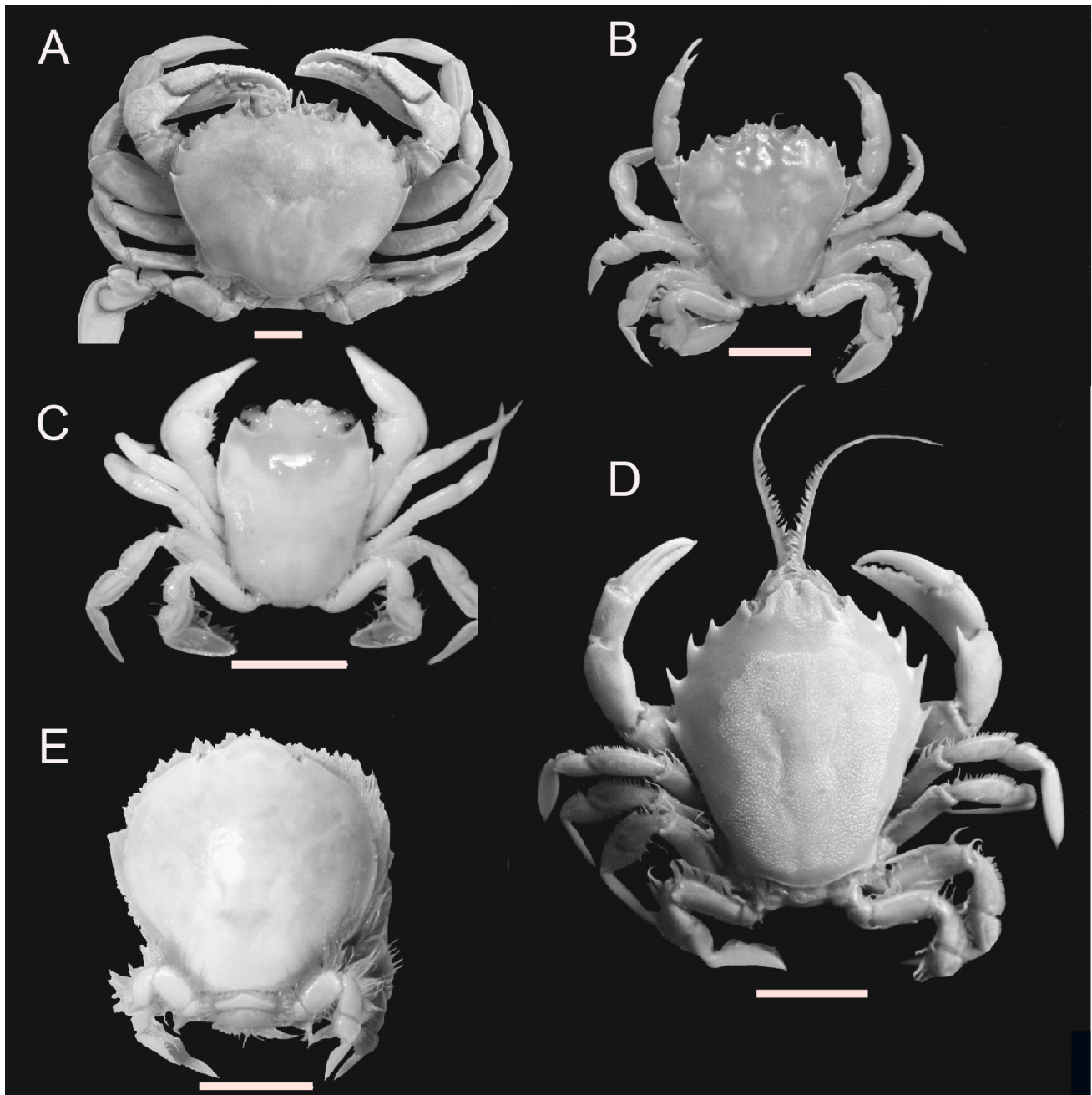


Fig. 4. Examples of portunoid crabs with modified carapace. A. *Ovalipes punctatus* De Haan, 1833, Japan, SMF, no catalogue number; B. *Portumnus latipes* Leach, 1814, Black Sea, ZIN-RAS 25087; C. *Brusinia brucei* Števcíć, 1991, southern Australia, Museum of Victoria MV J 61074; D. *Nautilocorystes ocellatus* H. Milne Edwards, 1837, NHMW, from the collection of the frigate “Novara” Expedition, # 83; E. *Thia scutellata* Fabricius, 1793, North Sea, SMF 38490. Scale bar equals 5 mm.

Carapace regions

The carapace of Decapoda is subdivided into regions which correspond to location of particular internal organs of the cephalothorax (Glaesner, 1960). These regions may be separated by furrows expressed with various degrees of distinctness, or practically smoothed (Figs. 1, 3, 4, 5E, H). Amongst the Portunoidea, relatively distinct carapace regions are usually found in many groups with quasi-hexagonal carapace outlines (Figs. 3B, D, 5E). The species with another cara-

pace outline, particularly ovoid or rounded, usually have smooth carapace regions (Fig. 4). The smooth carapace regions are typical of burrowing (*Portumnus* spp.; Fig. 4 B) or actively swimming species (e.g., *Charybdis smithii* MacLeay, 1838); in the latter case, this is in contrast to related species (see Türkay & Spiridonov, 2006, pl. 1).

Most fossil portunoids appear to have few differences from Recent representatives of the superfamily in the expression of carapace regions. Representatives of Cretaceous families referred to the Portunoidea are illustrated as having more

strongly separated carapace regions compared to those in extant families: Carcineretidae (see Vega et al., 2001, fig. 1), Lithophylacidae Van Straelen, 1936 (see Guinot & Breton, 2006), Longusorbiidae (see Schweitzer et al., 2007, figs 2A-C). Most records of *Ophthalmoplax brasiliiana* (Maury, 1930) also show quite distinct carapace regions, more expressively separated than in the majority of extant portunoid taxa (Vega et al., 2013, fig. 5). The distinctness of carapace regions may be considered as a character of varying taxonomic value although it tends characterise taxa at the genus level or higher.

Carapace ridges and cuticular structures

The dorsal carapace surface in portunoid crabs may be practically smooth as in *Brusinia*, *Benthochascon*, *Portumnus*, *Nautilocorystes* and *Thia*, evenly covered with granules (as in some *Ovalipes* and *Chaceon*) or carry complex sculpture, such as granular ridges, groups of granules, terraces and tubercles. Smooth carapaces are characteristic, first of all, of those species which spend a significant length of time burrowed in sandy sediments (see Garstang, 1897a, b; Schäfer, 1954), and also of those spending much time swimming in the water column, such as *Polybius henslowi* Leach, 1820 or *Charybdis smithii* (see Türkay & Spiridonov, 2006). The absence of sculpture on the carapace decreases friction and is most likely a derived condition. Most portunoid crabs possess epibranchial granular ridges that continue from last anterolateral tooth to the middle longitudinal axis of the body. In geryonids and carcinids these ridges consist of relatively sparse granules and are often interrupted and indistinct (Figs. 3A, B), similarly to many other heterotrenate crabs which have only epibranchial ridges. This is most probably a plesiomorphic condition for the Portunoidea. Among the Carcinidae, some species of *Liocarcinus* (e.g., *Liocarcinus corrugatus*; see Plagge et al., 2016) and *Necora* (see Holthuis, 1987) have additional granular ridges and even terraces. *Parathranites* (Fig. 5E) is characterised by a heavily sculptured carapace (see Crosnier, 2002), while in the Portunidae, particularly in the Thalamitinae and such genera as *Monomia* and *Xiphonectes* that sculpture is most diverse and spectacular (see e.g., Fig. 1F). The location of granular ridges and patches create specific patterns useful for distinguishing species and their groups in speciose genera such as *Achelous*, *Charybdis*, *Cycloachelous*, *Monomia*, *Thalamita* and related taxa, and *Xiphonectes*.

Fossil taxa also show a variety of dorsal carapace structures. Several Cretaceous genera have strong transverse ridges, even described as keels: across most of carapace regions as in *Ophthalmoplax* (see Vega et al., 2013, figs. 4-1) and Icriocarcinidae Števčić, 2005 (Phillips et al., 2014), or across the protogastric region as in *Carcinertes* (Schweitzer et al., 2007). Icriocarcinidae and Longusorbiidae are characterised by a row of massive tubercles along the posterolateral margin, particularly well developed in *Binkhorsitia* Noetling, 1881 (see Schweitzer & Feldmann, 2011, fig. 8.1). Significant differences in carapace ornamentation of fossil taxa, judging from the variation observed in extant portunoids, support their distinctness and a relatively high taxonomic rank (i.e. family).

Frontorbital margin

The front *per se* is usually subdivided into several lobes or teeth, the number of which is either even (2–6), or odd (1–3). The functionality of the frontal lobes and space between them may be related to the sensory functions of antennules, their protection and cleaning, although this is largely unstudied. In the Geryonidae, the subfamily Geryoninae is characterised by a pair of separated median teeth and the lateral teeth are completely fused with inner orbital lobes (Fig. 3A). This fusion can be inferred from the presence of inner orbital lobes in with distinct two parts in some species of *Chaceon* and *Zariquieyon* (Manning & Holthuis, 1989, figs. 12, 14, 18). In the Benthochasconinae the median lobes are fused and the lateral frontal lobes can be recognised as distinct from the much smaller outer lateral lobes (Fig. 3B). In most species of *Ovalipes*, the frontal margin has two teeth (Fig. 6A). In *O. molleri* (Ward, 1933) these teeth are fused at the base so that they can be considered as a single, bifid tooth. Low projections of the frontal margin, possible rudiments or vestiges of lateral frontal lobes, are located laterally (Fig. 6B). In *O. iridescens* Miers, 1886, the species most closely similar to *O. molleri*, only a single median tooth is present and lateral concavities can be recognised in the largest specimens (Fig. 6C). In *O. ocellatus* (Herbst, 1799) nothing besides a sharp median frontal tooth can be seen (Fig. 6D). *Nectocarcinus* (Fig. 5B) and *Echinolatus* (see Davie & Crosnier, 2006) have a 4-lobed front that provides additional support to their placement in the Geryonidae.

With few exceptions, Brusiniidae and Carcinidae mostly have a 3-lobed front. The 4-lobed frontal region of *Bathynectes* (Fig. 5D) and *Par-*

athranites (Fig. 5E) largely resembles the condition in the Benthochasconinae. *Nautilocorystes*, a taxon with a burrowing habit, is characterised by a narrow bilobed front with lateral frontal lobes fused with the inner supraorbital ones (Fig. 4D). However, the relationships of the above-mentioned three genera to the Carcinidae remain to be clarified. A unique, for Recent carcinids, case of a broad bilobed front is represented by *Coenophthalmus* whose position within the Carcinidae also remains unclear. There are several cases of transformation of a 3-lobed to an entire front, even within a single genus, e.g., in *Liocarcinus navigator* (Herbst, 1794) with indication of fusion of the original three lobes. Other examples of a practically entire front include *Coelocarcinus* (see Ng, 2002) and *Thia* (Fig. 4E).

The Portunidae show a variety of frontal shapes, although most have an even number of teeth/lobes. In some genera the number of lobes varies: 4 to 6 in *Achelous*, and 2 to 6 in *Thalamita* (*sensu lato*). In these, not closely related, taxa, some species with transitional states are also reported, for instance *Thalamita bevisi* (Stebbing, 1921) (= *T. dakini* Montgomery, 1931; see Apel & Spiridonov, 1998, fig. 53a, c, d). An entire frontal margin in some species of *Libystes* has been apparently evolutionarily derived from an indistinctly bilobed front, characteristic of other species of the genus, less deviating from the general portunoid appearance, like in *Libystes edwardsi* (see Apel & Spiridonov, 1998, fig. 5a). There are relatively few portunid taxa with 3-lobed fronts; most of these belong to the genus *Xiphonectes*, which is most probably heterogeneous (Spiridonov et al., 2014). In several *Xiphonectes* with a 4-lobed front the lateral lobes are broad and produced forwards, while the median ones are small and often partly fused. This may be a condition from which a 3-lobed front, characteristic of some species of the genus, such as *X. tenuipes* (De Haan, 1833), could evolve. Another example refers to some symbiotic species of *Lissocarcinus* in which the frontal margin is transitional between triangular entire and indistinctly 3-lobed ones, while other species of the genus have an indistinctly bilobed front (see Evans, 2018, fig. 3C, D). In the Podophthalminae the T-shaped frontal region is strongly reduced due to the enormous development of the orbits. Thus, the frontal margin shows a possibility for transformation, where both fusion and separation of the lobes seem possible in phylogeny, although the core groups of the main portunoid taxa are characterised by relatively constant patterns of frontal lobes.

Most fossil portunoid taxa were reported to have an even number of frontal teeth or lobes, or a flattened frontal margin with protuberances, usually even in number (Müller, 1984; Schweitzer & Feldmann, 2000; Karasawa et al., 2008). A 3-lobed front was particularly reported for species assigned to *Liocarcinus* and for such taxa as “*Xaiva*” *bachmayeri* Müller, 1984, *Mioxaiva psammophila* Müller, 1984 and “*Lissocarcinus*” *szoeraenyiae* (Müller, 1974) from the Miocene (Müller, 1984). An example of a possible portunoid, although not referable to any Recent family, is a species with an odd number of frontal teeth, *Psammocarcinus hericarti* Desmarest, 1822 from the Eocene, in which the prolonged front “has three spiniform teeth: the middle one is the largest; the lateral ones merge with the inner orbital angle” (A. Milne-Edwards, 1860, 279; translation by Karasawa et al., 2008). A unique frontal margin in the form of a deflected rostrum is characteristic of the Carcineretidae (Schweitzer et al., 2007). *Ophthalmoplax* spp. also possess a peculiar front: relatively narrow, deflected and bifid (Vega et al., 2013; Internet 1). Another frontal region that is unusual for portunoids is interpreted for *Longusorbis* Richards, 1975 (Upper Cretaceous–Eocene) as located “between interior-most orbital notches, axially produced into long, blunt-tipped rostrum, rostrum axially sulcate, strongly down-turned distally so that distal part is nearly perpendicular to dorsal carapace” (Karasawa et al., 2008, 95). The morphology of the frontal margin, its subdivision into teeth or lobes and inferred patterns of their transformation thus provide a set of characters highly applicable at the generic and suprageneric levels of taxonomic hierarchy.

Orbit

The orbit is a complex morphological structure, consisting of several lobes, separated by notches or fissures. The margins of the lobes may be rounded or polygonal. The number of lobes is a relatively stable character, although there are some exceptions. The supraorbital margin of one of the basal portunoid genera, *Chaceon*, consists of inner, median and outer supraorbital lobes separated by narrow fissures (Fig. 5A). The infraorbital part includes a tooth-like inner lobe, following which the inner orbital margin continues, smoothly forming an outer lobe (= 1st anterolateral tooth) (Fig. 5C). Such construction is similar to the one observed in most other portunoids although they usually have one more fissure or notch laterally of the outer lobe; moreover, in some taxa an outer infraorbital lobe,

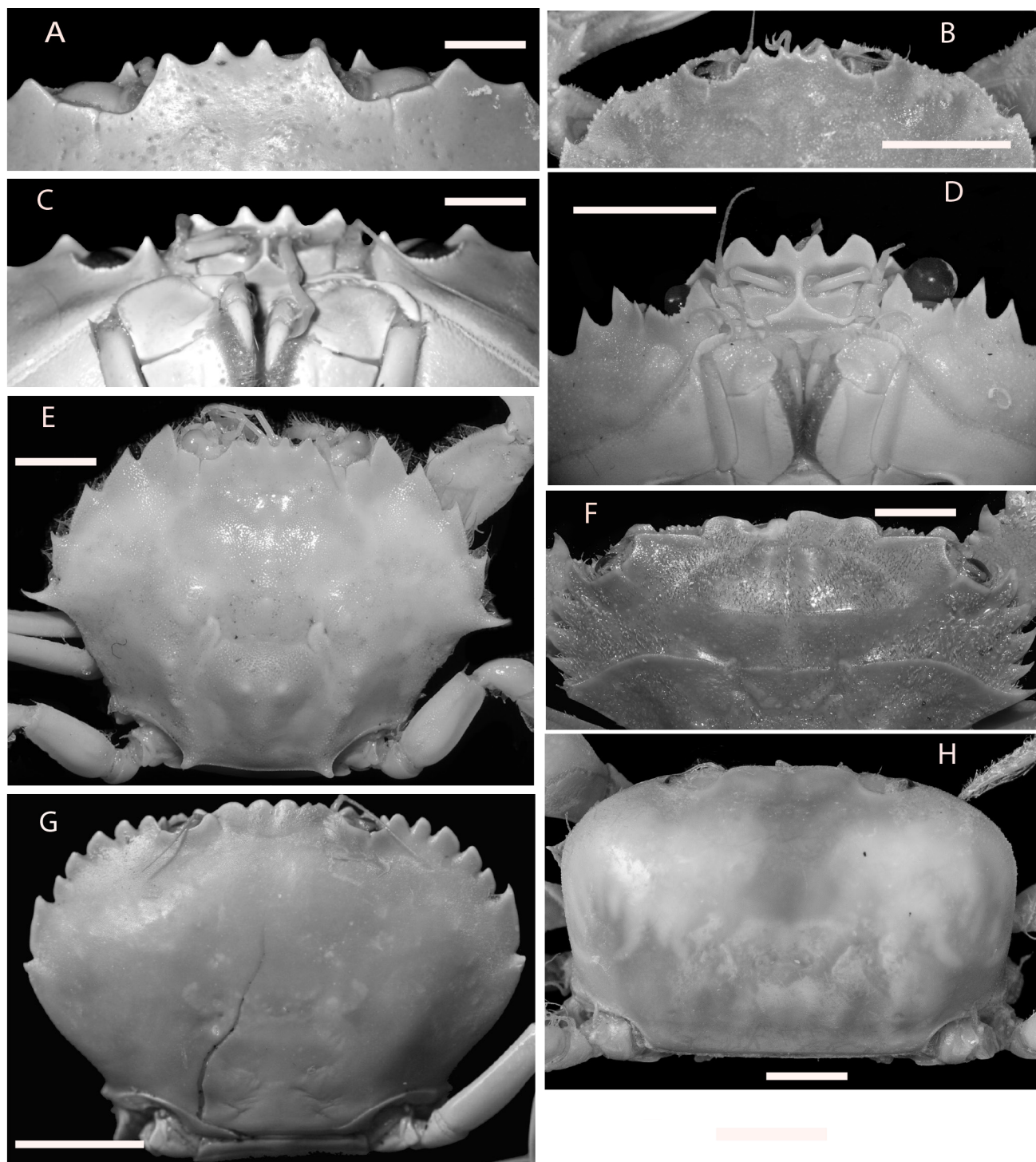


Fig. 5. Examples of frontorbital margins and carapaces. A. *Chaceon macphersoni* Manning & Holthuis, 1988, southwestern Indian Ocean, ZMMU Ma 4044, dorsal view; B. *Nectocarcinus bennetti* Takeda & Miyake, 1969, Maquarie Islands, ZMMU Ma 2301; C. *Chaceon macphersoni* Manning & Holthuis, 1988, ZMMU Ma 4044, ventral view; D. *Bathynectes longispina* Stimpson, 1871, Amper Seamount, Atlantic Ocean, ZMMU Ma 2392; E. *Parathranites orientalis* Miers, 1886, ZMB, without catalogue number; F. *Thalamita savignyi* A. Milne-Edwards, 1861, Gulf of Aden, ZMB 15592; G. *Carupa tenuipes* Dana, 1851, Japan, SMF, without catalogue number; H. *Libystes nitidus* A. Milne-Edwards, 1867, Maldives Islands, NHM 1991-156-1. Scale bars equal 10 mm (A, B, C, G), 5 mm (D, E, F) and 2 mm (H).

separated from the 1st anterolateral tooth, is also present. In some portunoids belonging to taxa that otherwise have numerous plesiomorphies (Spiridonov et al., 2014), one (in *Nectocarcinus*; Fig. 5B here; in *Zariquieyon* Manning & Holthuis, 1989, figs. 18, 19) or both supraorbital fissures (in *Gery-*

on; Fig. 3A) are strongly reduced. In the *Ovalipes iridescens* group only a single fissure is present: this is morphogenetically correlated with a transformation of the front with paired median teeth to a single tooth condition (Fig. 6). Finally, *Brusinia* (Fig. 4C), *Catoptrus* and *Libystes* (Fig. 5H) lack

supra- and infraorbital fissures, while in *Portumnus* only a single strongly reduced supraorbital fissure is present (Fig. 4D). These groups are morphologically different and apparently belong to different phylogenetic lineages (except for the relatively closely related *Catoptrus* and *Libystes*). Forms with reduced fissures or an entire supraorbital margin in many cases belong to deep-water (Geryonidae) or burrowing (*Ovalipes*) species or are inhabitants of reef cavities and underwater caves (*Catoptrus*). They are characterised by a reduction of orbits, which may be achieved by fusion of orbital lobes. An opposite case also leading to the disappearance of the orbital fissure is a long but open and shallow orbit of the Podophthalminae where their long eyestalks are held. Thus, it is very likely that portunoid crabs originally had a 3-lobed supraorbital margin but in particular lineages transformation of morphogenetic pattern took place, thus leading to formation of a bilobed or an entire margin.

Derived conditions from the 3-lobed supraorbital margin involve modifications of lobes. The outer and inner lobes have various relative sizes and shapes, and may be modified to teeth, such as in *Pirimela* which has a long and sharp median supraorbital tooth (Fig. 3C). An unusually looking infraorbital margin in *Bathynectes* is subdivided into three denticulated teeth (Fig. 5E), although this condition may be a derivation of the typical 3-lobed one.

Where the details of orbit morphology can be recognised, fossil taxa often show a condition that is characteristic for extant portunoids. Two or one supraorbital fissures. In one of the earliest, Cretaceous portunoids, *Eogeryon elegius* Ossó, 2016, the supraorbital margin closely resembles that of *Benthochascon* (Fig. 3B), while the infraorbital margin appears to be 3-lobed (Ossó, 2016, figs 5A, B). Orbits of some Cretaceous portunoid families (Carcineretidae, Longusorbiidae) are markedly broad at the expense of a narrow front and are similar in that respect to the orbits of the Podophthalminae. *Carcineretes* is diagnosed as having a sinuous orbit, “with two or three intra-orbital spines and notches (Schweitzer et al., 2007, 19). The original reconstruction of *Carcineretes woolacotti* Withers, 1922 shows four lobes of different width and shape and three notches (Withers, 1922; pl. 16). Protuberances and spines without fissures are characteristic of the orbits of *Longusorbis* (Schweitzer et al., 2007). The other Cretaceous genus with a narrow front, wide orbits and long eyestalks, *Ophthalmoplax*, also has three supraorbital lobes and two intra-orbital

spines (Schweitzer et al., 2007; Vega et al., 2013, figs. 3, 13). The median orbital tooth similar to the one in Recent Pirimelidae is seen in the Miocene *Pirimela lorentheyi* Müller, 1984 (Müller, 1984, pl. 60, fig. 3). Some extinct portunoid taxa are also reported to have an entire supraorbital margin, e.g., *Psammocarcinus* A. Milne-Edwards, 1860 (see Desmarest, 1822, pl. V, fig. 5; A. Milne-Edwards, 1860). The most unusual orbit with a completely denticulated supraorbital margin is found in *Pheophthalamus mochaensis* Feldmann, Schweitzer & Encinas, 2010 (assigned to the Podophthalminae) from the Neogene of South America (Feldmann et al., 2010, fig. 11), although most of the taxa included in this subfamily have a relatively simple supraorbital margin. Thus, the orbits of portunoids provide an important set of characters that may be used at various levels of taxonomic hierarchy.

Anterolateral carapace margin

The anterolateral margin of the carapace is subdivided into several teeth, the first corresponding to the outer orbital lobe. The functional significance of the anterolateral teeth was first interpreted by Garstang (1897a), who considered them as part of the apparatus preventing entering sediment particles to the branchial cavity in burrowing crabs. Brusiniidae, Geryonidae and Carcinidae do not have more than five teeth. In geryonids their number varies from three (*Geryon*, *Raymanninus*) to five (Ovalipiinae). In *Chaceon*, which typically has five anterolateral teeth, some teeth become obsolete with age. *Benthochascon*, *Nectocarcinus* and *Echinolatus*, which are tentatively referred to this family (but are considered by me as genera *incertae sedis*) are characterised by four large teeth. Some species of the last-named genus possess a unique character of additional denticles on the anterior margin of the anterolateral teeth or bifid teeth (Davie & Crosnier, 2006, fig. 3). Most of the Carcinidae have five anterolateral teeth. Important examples of reduction of anterolateral teeth in the Carcinidae are *Coenophthalmus* with three teeth and *Thia* with a nearly entire anterolateral margin, although one can see four notches on this margin which mark the position of five reduced teeth. A very dense belt of setae bordering the lateral margin in this burrowing species probably plays the role of branchial cavity protection in the absence of anterolateral teeth (Fig. 4E).

The number of anterolateral teeth in the Portunidae varies from two to nine and is largely a taxonomic character used at the generic level.

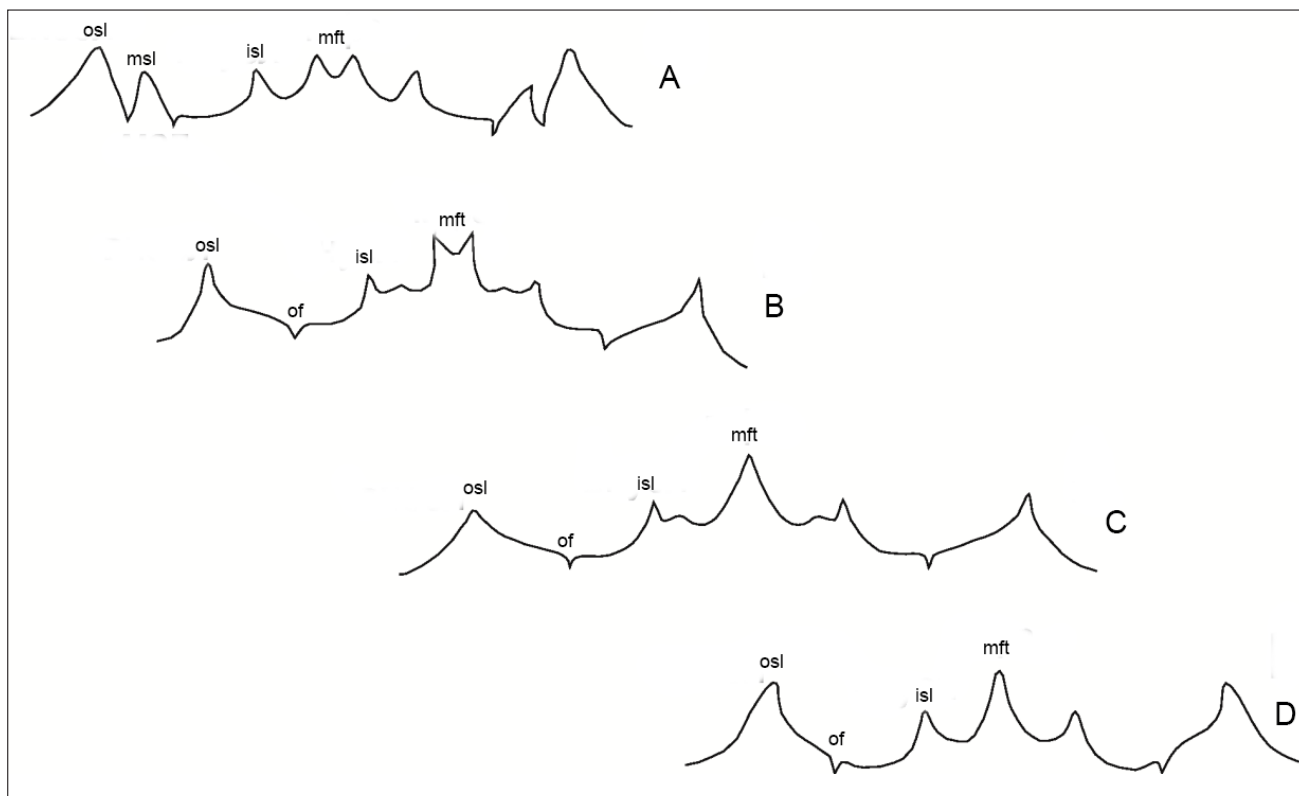


Fig. 6. Frontorbital margin of carapaces in *Ovalipes* spp. A. *O. trimaculatus* (De Haan, 1833), Patagonia, ZMMU, without catalogue number. B. *O. molleri* (Ward, 1933) (drawn on basis of photograph in Davie & Short, 1989, fig. 14B). C. *O. iridescens* Miers, 1886, southwestern Indian Ocean, ZMMU Ma 2300. D. *O. ocellatus*, northwest Atlantic, coast of Georgia, USA, SMF 7325. Abbreviations: isl: inner supraorbital lobe; mft: median frontal teeth (tooth); msl: medial supraorbital lobe; of: orbital fissure; osl: outer supraorbital lobe.

Spiridonov et al. (2014) argued that the nine teeth corresponded to a plesiomorphic condition for this family and the number of teeth showed various patterns of reduction in particular genera. Evans (2018) provided additional evidence for this in the Thalamitinae (which generally have a reduced number of teeth, from six to three) and suggested a nomenclature of teeth based on their general pattern and presumed homologies. Some oval forms, such as *Libystes*, have anterolateral teeth that are strongly reduced to nearly completely absent (see Apel & Spiridonov, 1998, figs. 5, 6a). Podophthalmiines also show a reduction of teeth (up to two), which is apparently connected to their habits and a characteristic shortening of the anterolateral margin. Noteworthy, the single extinct portunoid taxon that is characterised by nine anterolateral teeth, but not referred to the Portunidae is *Archaeoportunus* Artal, Ossó & Domínguez, 2010, for which a separate family was introduced (Artal et al., 2010). Otherwise, fossil taxa do not show such morphological peculiarities of the anterolateral margin that remarkably exceed variation observed in extant portunoids (see e.g., Internet 2). Although the

number of lateral teeth is subject to change in particular groups of portunoids, the major taxa have a distinct pattern of variation of this character.

Posterolateral and posterior carapace margin

A supra-dorsal position of the 5th pair of pereopods is morphologically correlated with the development of the posterolateral reentrant which extends motion possibilities for the last pair of legs, used for burrowing and swimming. Although this reentrant is feebly developed in the non-swimming Geryonidae (Figs. 3A–B), or carcinids like *Carcinus* (not swimming, and not commonly burrowing) and *Portumnus*, *Thia*, *Nautilocorystes* and *Brusinia*, presumably using all legs for burrowing (Figs. 4B–D).

The posterior carapace margin is bordered by a cuticular “wall” touching the 1st pleonal tergite. This margin is usually straight or gently convex (e.g., Figs. 3, 4). Much rarely, for instance in *Benthochascon*, this margin is concave (Fig. 3B). The majority of portunoids have rounded transitions between the posterolateral and posterior carapace margins. In some groups these

corners are angled (e.g., subgenera *Goniohellenus* and *Gonioneptunus* of the genus *Charybdis*; see Türkay & Spiridonov, 2006) or even spined, as in *Xiphonectes* (see Spiridonov, 2016) in the Portunidae. The only Recent carcinoid genus having angled, or spiny posterolateral corners is *Parathranites* (Fig. 5E; see also Crosnier, 2002). Most fossil portunoids studied that have variously expressed posterolateral reentrants are characterised by rounded posterolateral corners (Karasawa et al., 2008; see also examples via Internet 3). There are few exceptions, e.g., *Psammocarcinus* which shows an angled posterolateral corner (see Desmarest, 1822, pl. 5, fig. 3). A unique morphology of the posterolateral margin with a series of teeth is seen in *Styracocarcinus meridionalis* (Secretan, 1961), a Campanian crab considered within the Portunoidea but not assigned to any family (see Ossó, 2016, fig. 6A, B). The characters associated with the posterior part of the carapace are thus important for the diagnosis of genus-level taxa within portunoid families.

Pterygostomial and subhepatic regions

Surfaces of the carapace regions located ventral to the anterolateral margin determine both an absolute and a relative height of the carapace, which is a taxonomically important character at higher levels. In most groups these surfaces are smooth, granular or markedly setose. Particular taxa such as not closely related *Ovalipes* and *Laeonectes* are characterised by the presence of granular lines and other cuticular armature constituting parts of the stridulating apparatus which counterparts constitute processes of chelipeds. The construction of this apparatus is a set of characters at the species level, for instance in *Ovalipes* (see Stephenson & Rees, 1968). In the deep-water species of this genus a reduction of the stridulatory apparatus occurs, which is correlated with the development of an optical communication system on the basis of iridescent surfaces reflecting polarised light under conditions of practical darkness (Parker et al., 1998).

Sternal part of cephalothorax

Sternites and episternites are sclerites of the sternal part of the cephalothorax. The latter join the former in their posterolateral part by distinct or partly interrupted sutures. The hollow space between the lateral margin of the sternite and the respective episternite houses the condyle of the pereopod coxa, and the entire structure forms a sterno-coxal articulation. The major part

of episternites 4 to 6 is usually sickle shaped; it is extended posteriorly, touching the lateral margin of the next sternite over more than half of its extension. The shape of episternites 7 and 8 usually strongly deviates from the sickle-shaped one and may characterise taxa at family and subfamily levels (Fig. 7). In most portunoid crabs the width of episternites is several times less than the width of sternites but in *Thia* sternites are less than twice wider than episternites (Fig. 7B).

Sternites and episternites of thoracomeres 1–4 is consolidated as a thoracic sternum, the parts of which may be separated by furrows of various distinctness. This has taxonomic significance for diagnosing particular families, subfamilies and genera. The longitudinal median groove is characteristic of most Portunoidea, although may be present in other taxa as well.

Sutures between sternites 4–8 may be interrupted in various ways that usually characterise particular genera and subfamilies. The Portunidae have secondary sulci between sternites 6 and 7, which are considered as their unique synapomorphy, although *Libystes* lacks this character (Karasawa et al., 2008). Sternal characteristics are relatively well preserved and have been widely used in the taxonomy of fossil portunoids (Schweitzer et al., 2007; Karasawa et al., 2008).

Antennules and antennae

Antennules of most portunoids are relatively short, transversely folded and generally similar even in such distant groups as geryonids and portunids. In completely folded conditions, the antennules are concealed under the frontal margin and not seen dorsally. Only in podophthalmines, with their very narrow front, folded antennules cannot be completely hidden in dorsal view.

Antennae differ first of all by a so-called basal antennal segment which is interpreted as a fusion of the original segments 2 and 3 of the antennae (Ng et al., 2008). In a number of portunoid crabs this segment tends to form a distolateral process entering the orbital hiatus. Size and form of this process are important taxonomic characters. The tendency for enlargement reaches a maximum in the Thalamitinae: the process contacts the orbital margins and isolates the antennal flagellum from the orbital hiatus. The enlarged basal antennal segment itself often bears armature, e.g., granules, ridges and spines, the pattern of which is an important taxonomic character at the species level in thalamitines (Stephenson & Hudson, 1957; Apel & Spiridonov,

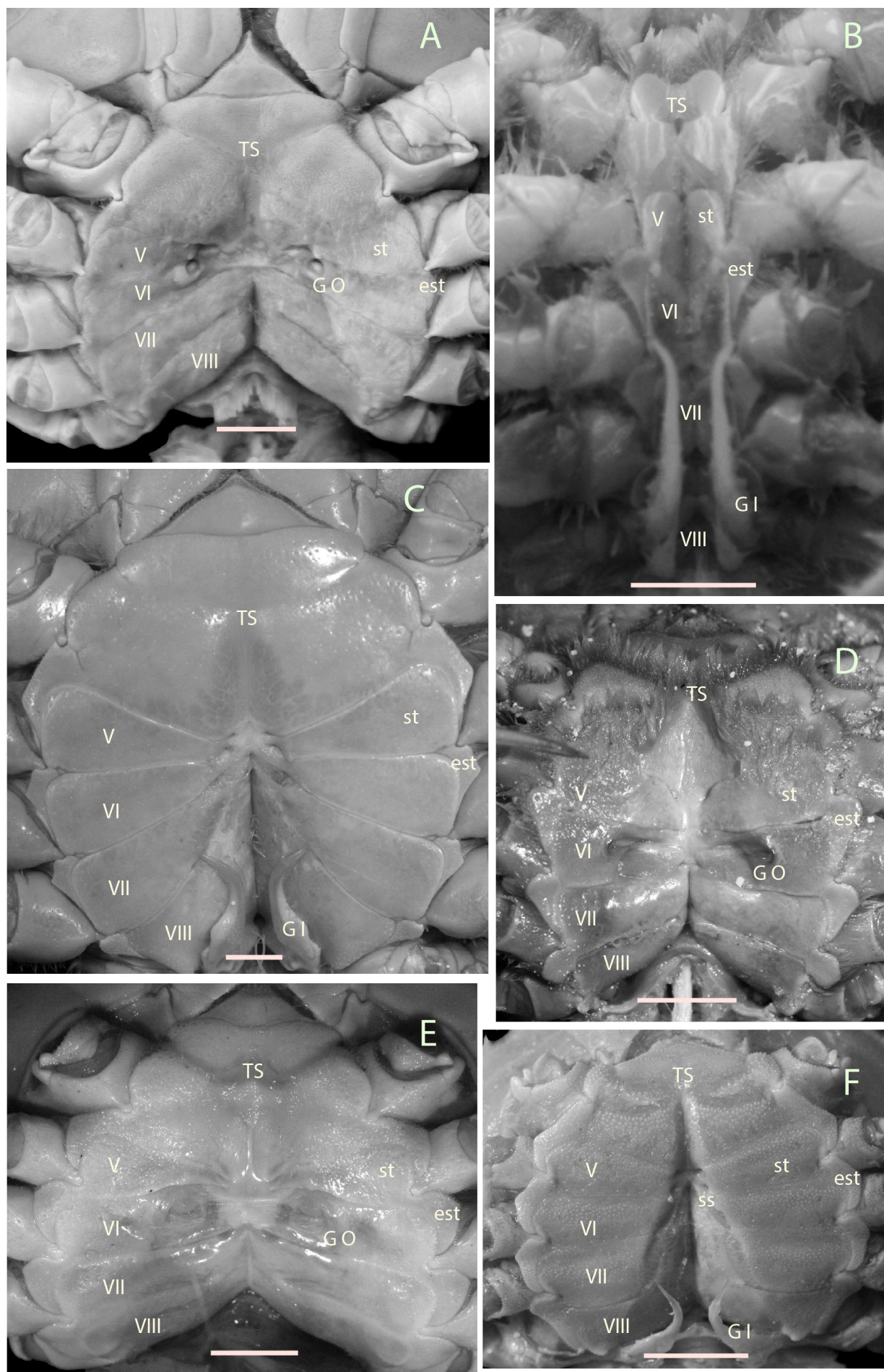


Fig. 7.

1998). A highly unusual antennular morphology for portunoids is seen in *Nautilocorystes*, which has long setose antennae (Fig. 4D), similar to the ones of *Corystes* Bosc, 1802 that are in turn associated with the burrowing habit of this crab (Schäfer, 1954: fig. 28). The details of antennae and antennules are rarely enough preserved to be considered for fossil taxa.

Maxillipeds

Although mouthparts including mandibles, maxillae and maxillipeds 1 and 2 are usually not preserved, maxilliped 1 should be mentioned here as having particular significance in portunoid taxonomy. The upper part of its endopod has a quasi-triangular or quasi-trapezoidal shape. Antero-mesially the so-called “portunoid lobe” is attached; this usually is dentiform, stick-shaped or finger-shaped. This lobe is present in all Portunidae but also in some carcinids, for example in *Bathynectes*, *Liocarcinus* and *Macropipus*, although absent in the Carcininae, Geryoninae and Ovalipinae along with *Nectocarcinus* (Spiridonov et al., 2014). In *Benthochascon*, the lobe is morphologically different from the one observed in other portunoids (Spiridonov et al., 2014). Currently, it is difficult to judge if the observed pattern is a result of parallel origin of lobes or reduction of this structure takes place independently in particular families. Functional properties of the maxilliped 1 lobe have not been studied.

Maxillipeds 3 are of similar construction in all Portunoidea. The shape of the meropodite, which covers the mouth cavity anteriorly is about as long as wide, quasi-quadrilateral, with a convex setose mesial margin and is not much different in geryonids and carcinids, except for some burrowing species in which it is more elongated. In the Thalamitinae and Portuninae, meropodites of maxilliped 3 are most diverse and may have a different shape, with rounded or angular anterior margins and varying setal coverage and granulation. These usually are characters that are taxonomically important at lower taxonomic level (species, species groups and small genera).

Chelipeds

The relative length of the chelipeds is a character that marks taxa at the family level. While relatively short, not exceeding in length pereopods 2 and 3, chelipeds are most probably a plesiomorphy, characteristic of Carcinidae and most Geryonidae (Figs. 3A–C), except for some species of *Ovalipes*, for instance the *Ovalipes iridescens* group. Chelipeds of the Portunidae are the longest pair of pereopods, on account of their long meri and chelae (Figs. 3D–F).

Meri of chelipeds may be smooth or possess spines. Geryonines possess a solitary spine on the posterior surface of merus. Nearly all Portunidae and few non-portunid portunoids (*Bathynectes*, *Parathranites* and species of the *Ovalipes iridescens* group) have spines on the anterior face of the merus (Figs. 3D–F). Long and spiny chelipeds are advantageous for defence (in particular, in typical defensive reaction), prey capture, courtship and mating behaviour (Schäfer, 1954; Spiridonov et al., 2014).

Carpi of chelipeds may have various shapes, although the respective taxonomic characters are associated mostly with carpal spines. All portunoid crabs, along with several other heterotreme taxa, have an inner spine on the after carpus its length is varying between taxa but is particularly significant in some species of *Achelous*. On the other hand, this is obsolete, in *Callinectes* spp. The taxa referred to the Geryonidae with reservation, such as *Echinolatus* (see Davie & Crosnier, 2006) and some *Nectocarcinus*, e.g., *Nectocarcinus beneti* Takeda & Miyake, 1969 are characterised by double carpal spines, similar to the ones seen in the Mathildellidae (Goneplacoidea).

Spines on the outer face of carpus are characteristic, first of all, of the Portunidae, but are also present in *Parathranites* (see Crosnier, 2002). They may undergo reduction; in particular, one of the differences between related species of *Xiphonectes*, *X. tenuipes* (De Haan, 1835) and *X. pseudotenuipes* (Spiridonov, 1999) is the reduced spines in the latter (Spiridonov, 1990, figs 2E, 3B). An important character in *Thalamita* and related genera is an additional spinule on the upper face of the cheliped carpus. It appears to have a parallel origin in several groups of species and genera (Spiridonov & Neumann, 2008; Evans, 2018).

Fig. 7. Sternal regions. A. *Benthochascon hemingi* Alcock & Anderson, 1899, South China Sea, ZIN-RAS 88509; B. *Thia scutellata* Fabricius, 1793, North Sea, SMF 38490. C. *Ovalipes iridescens* Miers, 1886, southwestern Indian Ocean, ZMMU Ma 2300. D. *Carcinus aestuarii* Nardo, 1848, Black Sea, Ma 5181. E. *Bathynectes longispina* Stimpson, 1871, Atlantic, Amper Seamount, ZMMU Ma 2392; F. *Achelous spinimanus* (Latreille, 1819), Gulf of Mexico, ZMMU Ma 4848. Abbreviations: G I – gonopod 1; G O – genital opening; TS – thoracic sternum; st – sternite; est – episternite; V – VIII – number of sternites. Scale bar equals 5 mm.

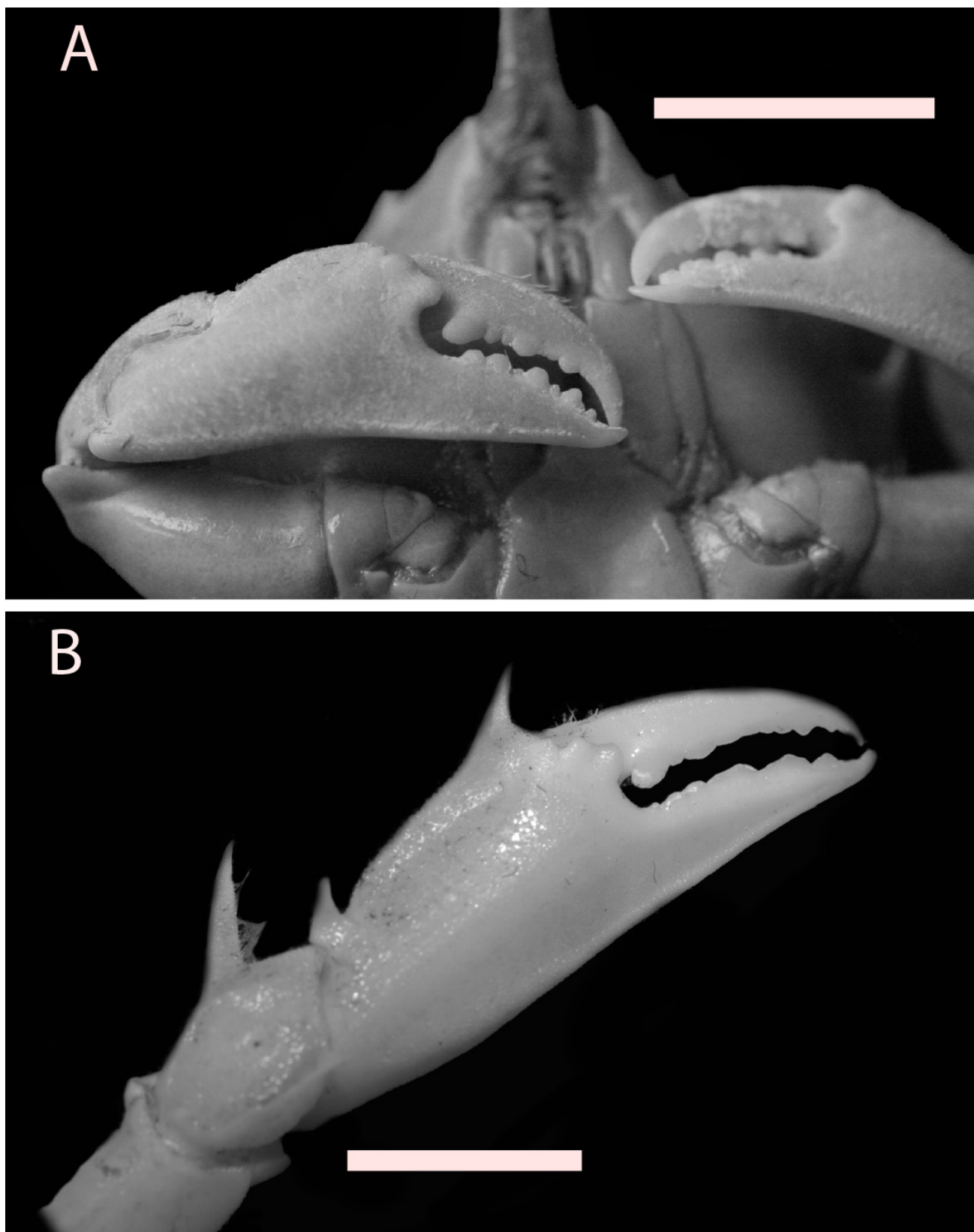


Fig. 8. Chelae. A. *Nauticorystes ocellatus*, NHMW, from the collection of the frigate “Novara” Expedition, # 83. B. *Patrathranites orientalis* Miers, 1886, ZMB, without catalogue number. Scale bar equals 5 mm.

Chela morphology and patterns of heterochely

Chela morphology is essential for morphological characterisation of the Portunoidea (Schäfer, 1954; Manning & Holthuis, 1981; Spiridonov et al., 2014), the presence of a large proximal mo-

lariform tooth on the dactylus of one of the chelae (heterodonty) along with serial bi- and trilobed conical teeth on the dactylus and the pollex of both chelae. Serial teeth separated into lobes increase the cutting edge and work as scissors.

The presence of a massive molariform tooth allows the portunoid chelae to maintain significant crushing capacity and perform various crushing techniques when feeding on molluscs. Various modifications from this basic plan and symmetrisation of chelae construction have been described by Spiridonov et al. (2014, figs. 2, 3) and interpreted in terms of belonging to particular ecomorphs: burrowers, walkers and swimmers. Reference is made to that paper for a detailed description. Typical portunoid heterodont chelae are found in *Nautilocorystes* (Fig. 8), which otherwise has a very peculiar “non-portunoid” general appearance which possibly is associated with a burrowing habit (Fig. 4D). Surprisingly, this chela is very similar to the that of the Polybiinae with a very different habit (see Spiridonov et al., 2014, fig. 2). Chelae are usually well preserved in fossil taxa which can often be recognised as portunoids by the characteristic morphological features of their palms (Müller, 1984; Schweitzer & Feldmann, 2000, 2011; Schweitzer et al., 2007; Karasawa et al., 2008; Phillips et al., 2013).

Pereopods 2–4 (ambulatory legs)

In portunoid crabs, pereopods 2–4 are usually similar but differ in size from front to rear, P2 or P3 being the longest. The orientation of the sterno-coxal articulation allow for the parallel position of pereopods which become in that case somewhat inclined in relation to the transverse axis of the body. Meri, carpi and propodi are compressed so that the morphologically dorsal face is exposed anteriorly. In most geryonids an anterodistal process or lobe is present in meri; in *Ovalipes* only low lobes can be traced there. Other processes and spines are rare on pereopods 2–4 and, usually, are characters used at intermediate hierarchical levels (e.g., groups of species and genera), such a series of spines on the anterior face of the merus is seen in *Coenophthalmus* (Steudel, 1998, figs. 37c–d).

In most portunoids, dactyli (fingers) of pereopods 2–4 are relatively similar, piercer shaped, or narrow knife-shaped, costate, often setose on the flexor margin. Active natatory species, such as *Callinectes* spp., *Portunus pelagicus* (Linnaeus, 1758) and related species, *Polybius henslowii* Leach, 1820, *Euphylax dovii* Stimpson, 1860 and *Charybdis smithii*, have leaf-shaped leg fingers, which are used in swimming. However, the morphology of dactyli in the the overwhelming majority of cases does not differ between pereopods. Heterodactyly (differing between pereopods 2–4 shape of fingers) is characteristic of a few taxa

known or presumed for their burrowing habits (*Brusinia*, *Thia*, *Nautilocorystes*, *Ovalipes*, *Portumnus*) (Fig. 4). However, the pattern of heterodactyly in these groups differs, which makes it a taxonomic character of a relatively high level (subfamily or family).

In fossil portunoid taxa, the morphology of ambulatory legs varies significantly, although this mostly refers to the more proximal segments of legs, while dactyli are less frequently preserved. In particular, in the Carcineretidae, pereopod 4 has a flattened carpus and merus (Schweitzer et al., 2007).

Pereopod 5

The dorsal position of the last pair of pereopods that is typical of portunoid crabs is achieved by a higher position of their coxae in relation to other legs (the so-called dorsal coxal shift). The fewer differences in the plane where the coxae of the 5th and other pereopods are located are known for *Brusinia* and *Portumnus*. The highest dorsal coxal shift is characteristic of such taxa as *Coenophthalmus* (non-swimming ecomorph), *Liocarcinus*, *Portunus*, *Thalamita* (all swimming or at least lifting over substrate) and *Caphyra* (non-swimming symbionts of cnidarians). A peculiar morphology of a modified pereopod 5 is an important portunoid character, used for swimming, burrowing and attaching to a host. The modification affects a shortening and broadening of the merus, flattening of the propodus, and ensiform, ovate, lanceolate, or hook shape of the dactylus. This construction, however, is not shared by all portunoid taxa, in particular *Chaceon* and *Geryon* have the last pair of pereopods not particularly different from others (Fig. 3A). This is probably also the case for such fossil family as the Icriocarcinidae (Phillips et al., 2013) of Cretaceous age.

The shape of segments of pereopod 5 provides a number of taxonomic characters which are used at various hierarchical levels. It is of interest to note that within a single (although probably non-monophyletic) genus *Liocarcinus* both broad (for instance in *L. vernalis*; see Fig. 1C) and relatively narrow dactyli of the last pair of legs are known (e.g., in *L. navigator*). Even greater variation is known for symbiotic *Lissocarcinus* spp. (an apparently monophyletic group; see Evans, 2018), where the dactyli are variously modified, possibly depending on the relationships of a particular species with its host.

Wherever preservation conditions enable an examination of the last pair of ambulatory legs in

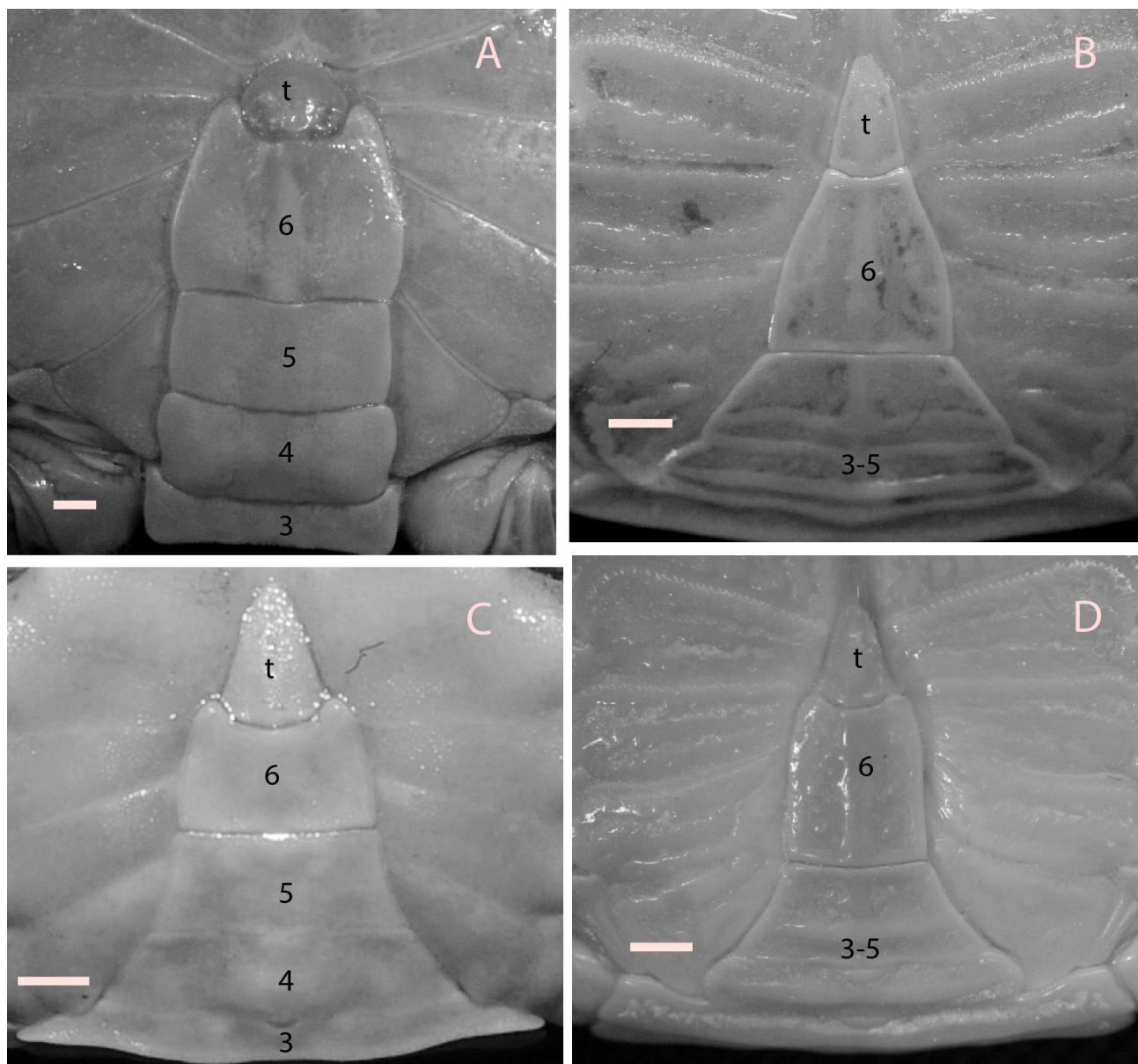


Fig. 9. Male pleons. A. *Ovalipes iridescens* Miers, 1886, southwestern Indian Ocean, ZMMU Ma 2300. B. *Achelous hastatus* (Linnaeus, 1767), Mediterranean, ZMMU Ma 1910; C. *Parathranites orientalis* Miers, 1886, Indo-Pacific, ZMB, without catalogue number; D. *Monomia petrea* Alcock, 1899, western Indian Ocean, ZMMU 2294. Abbreviations: 1–6 – pleomeres; t – telson. Scale bar equals 1 mm.

fossil crabs assigned to the Portunoidea, we see modified propodi and dactyli. While the Recent Geryoninae have the segments of pereopod 5 not much different from the anterior legs, *Chaceon peruvianus* (d'Orbigny, 1842) from the Miocene of South America clearly possessed broadened propodi and narrow-lanceolate dactyli of pereopod 5 (Schweitzer & Feldmann, 2000, fig. 10-1). This indicates that a characteristic construction of pereopod 5 can undergo evolutionary reversal and/or evolve as a parallelism (Simpson, 1961) in various groups of portunoids.

Pleon

A nearly universal characteristic of the portunoid pleon is the presence of a transverse keel on the tergite of the 3rd pleomere (Figs. 9B–D) (absent in *Brusinia*, *Ovalipes* [Fig. 9A] and *Carupa*). Male pleons are characterised by a tendency for fusion of pleomere terga 3 to 5, which is, however, not a universal characteristic of the group. Six separate pleomeres and the telson are apparently a plesiomorphic condition typical of most Heterotremata (Guinot, 1979; Davie et al., 2015).

In *Geryon*, *Chaceon*, *Benthochascon*, *Ovalipes* (Fig. 9A), *Echinolatus*, *Nectocarcinus*, and *Brusinia* pleomeres 3–5 are separated, although an ability of individual motion may be lost. In most carcinids and portunids they are fused, while some sutures or their traces may remain (Figs. 9B–D).

It is of interest to note that similar, possibly convergent or parallel fusion of the pleomeres is known for the American freshwater brachyuran family Trichodactylidae (Rodriguez, 1992). The functional significance of the pleomere fusion is unknown. It is possible that it is correlated with particular mechanisms of copulation (Karasawa et al., 2008). All portunoids with fused pleomeres also have short gonopods 2 (see below). Geryonids that have separated pleomeres possess also long gonopods 2 (Spiridonov et al., 2014).

A unique condition is observed in the males of *Thia*, where separated pleomeres (a unique character of carcinids) are associated with short gonopods 2. Since *Thia* is a quite specialised and not a basal taxon to the Carcinidae, it is unclear how this condition could originate and whether a reversal to non-fused pleonal segments is possible.

Males of most portunoids have a triangular or (in the Portunidae) T-shaped pleon (Figs. 9B–D), although a different condition is observed in *Ovalipes* with its quasi-rectangular pleon (Fig. 9A). In most fossil portunoids male pleons are also triangular, while in *Proterocarcinus* it is quasirectangular (Feldmann et al., 2005, fig. 5E), in some respect similar to that of *Ovalipes*.

Not all fossil taxa can be characterised by pleon morphology owing to preservation conditions. However, separated pleomeres 3–5, although probably immovable, are known for ancient geryonines (e.g., Schweitzer & Feldmann, 2000, fig. 9), Longusorbiidae (Karasawa et al., 2008), Icriocarcinidae (Philips et al., 2013), Lithophylacidae (Guinot & Breton, 2006) and the genus *Ophthalmoplax* (Schweitzer et al., 2007; Vega et al., 2013; Ossó-Morales et al., 2010). Surprisingly, separation of pleomeres is also characteristic of such genus as *Archaeoportunus*, which in several other respects is similar to the Portunidae (Artal et al., 2013, fig. 4b), although such Cretaceous taxa as *Carcineretes* had fused pleomeres (Schweitzer et al., 2007). The shape of the male pleon and the pattern of pleomere fusion can thus be regarded as important taxonomic characters for higher-level portunoid taxa, in most cases of family/subfamily rank.

Discussion

Recent morphological and molecular phylogenetic studies have indicated that several high-level extant taxa of portunoid crabs (families and subfamilies) are much more diverse morphologically than had been intuitively expected, although possible morphogenetic transitions between different character states may be inferred in many cases, as in the case of the frontal margin of *Ovalipes* (Fig. 6). Furthermore, each internally diverse taxon of portunoid crabs is characterised by a core suit of characters, which may be even called an “archetype” (I use this term only instrumentally, without a reference to essentialism; see Lyubarskiy, 1995) and peripheral conditions. This is a result of mosaic evolution and leads to polythetic diagnoses of taxa in many eukaryotic groups (see Mayr & Bock, 2002; Takhtajan, 2009) and varying resolution of particular taxonomic characters (Zarenkov, 1974). A proper description and understanding of this “archetype” may help to classify extinct taxa using a comparative approach to extant ones.

Firstly, several families established earlier by palaeontologists and redefined by Karasawa et al. (2008), such as the Carcineretidae, Lithophylacidae, Longusorbiidae and Psammocarcinidae, appear to have a distinct suit of characters that do not fit even peripheral conditions of extant portunoid families.

Similarities of these families to extant portunoid taxa may be the result of parallelism rather than of common origin. Although testing this is currently hardly possible, and the Portunoidea that contain the above-mentioned families should be considered as an evolutionary taxon in Simpson’s (1961) sense. The composition of the Portunoidea, including the extant families along with the Carcineretidae, Lithophylacidae, Longusorbiidae and Psammocarcinidae, appears to be appropriate and can be only rejected if a completely convergent origin of the core portunoid character suit in extant and extinct families is demonstrated.

Ossó (2016) established the family Eogeryonidae based on *Eogeryon elegius*. This family apparently has an affinity to portunoids, in particular to the Geryonidae, although shows some important differences. However, taking the significant variability of taxa combined in the Geryonidae (e.g., Geryoninae, Benthochasconinae and Ovalipiinae, possibly *Echinolatus* and *Nectocarcinus*), it would not be surprising to find additional support for considering *Eogeryon* as a taxon close to the ancestral geryonid. The sub-

rectangular male pleon of *Eogeryon* is indeed similar to the one of *Ovalipes*, while the general carapace outline of this fossil portunoid resembles that of *Benthochascon*.

Karasawa et al. (2008) performed a morphological cladistic analysis of Recent and extinct genera of portunoids and some other taxa, showing affinity to this group. To make classification compatible with reconstructed phylogenies they redefined the family Macropipidae Stephenson & Campbell, 1960 and included in this several fossils (Cretaceous to Neogene) genera (e.g., *Ophthalmoplax*), along with Recent taxa. This resulted in a quite broad diagnosis of the taxon. The extant Macropipidae (*sensu* Karasawa et al., 2008) turned out to be incompatible with molecular phylogenetic reconstructions (Schubart & Reuschel, 2009; Spiridonov et al., 2014; Evans, 2018). This indicated the necessity of splitting them between various groups of the newly defined Carcinidae (*Bathynectes*, *Macropipus*, *Parathranites*) and Geryonidae (*Raymanninus*, and possibly *Echinolatus* and *Nectocarcinus*). In this case, extinct genera return to an uncertain status, which is not a desirable situation. Briefly commenting on this, I can suggest to examine the relationships of the genera that have numerous plesiomorphies, such as *Proterocarcinus* to the Geryonidae in the broad new concept, and others such as *Portunites* to the Parathranitinae. *Ophthalmoplax* apparently does not have affinities to the Geryonidae, but it is also different from the Carcinidae. The general quasi-guadrate outline of the carapace, well-developed carapace regions and transverse ridges, narrow bilobed frontal margin, orbits and the construction of chela (Vega et al., 2013) are not typical of any extant subfamily. Few taxa within the Recent Carcinidae have spines on the upper face of cheliped dactylus, e.g., *Parathranites* and *Bathynectes*. The former genus is also characterised by an odd number of frontal lobes, similar to *Ophthalmoplax*. However, in other respects they do not have anything in common to assume close relationships. *Ophthalmoplax* apparently shows a unique combination of plesiomorphic and apomorphic character states that makes close relationships with an unknown ancestor of the Recent Carcinidae unlikely, so it would be better considered within a separate family.

Several other well-preserved and relatively speciose genera, such as *Coeloma* A. Milne-Edwards, 1865, mostly of Eocene – Oligocene age, have been variously treated since their discovery (Karasawa et al., 2008; De Grave et al., 2009; Jagt et al., 2010). I would agree with Ossó (2016)

on their very likely affinity to the Geryonidae, particularly considering the new concept of this family. Another particular, but important, task is to revise the good fossil record of the carcinid genus *Liocarcinus* (Hyžný et al., 2015) in the light of its recently documented paraphyly (Plagge et al., 2016), its significant persistence in the geological time (Fig. 2) and the new concept of the Carcinidae.

Within the Portunidae there generally are fewer problems in interpreting and positioning fossil taxa, although the classification of extant taxa at the subfamily level is still far from perfect. Classification of extinct taxa could thus significantly benefit from the progress of taxonomic studies of contemporary faunas. A particularly important issue is the relatively numerous fossil examples of *Portunus* (*sensu lato*) which may, in fact, belong to other genera such as *Portunus* (*sensu stricto*), *Achelous*, *Monomia* and others. Distinguishing between them is not an easy task because many important characters are not available for study. For example, as stated above, the oldest species of the group, “*Portunus*” *kochi* resembles *Achelous* in several morphological characters. “*Portunus*” *atecuicilis* Vega, Feldmann, Villalobos-Hiriart & Gio-Argaez, 1999, a common species from the Lower and Middle Miocene of Mexico, also likely belongs to *Achelous* on account of the construction of the front and chelae (Vega et al., 2009). Another common Miocene species in the Tethys and Paratethys, “*Portunus*” *monspeliensis* A. Milne-Edwards, 1860, could be referred either to *Achelous* and *Monomia* on account of the single visible spine on the cheliped manus and well-developed sculpture of the carapace (see Marangon & De Angeli, 2009, fig. 3; Gašparič & Ossó, 2016, pl. I, E, G), although the shape of the front and orbits and the relative size of the 1st anterolateral tooth support assignment of this species to *Achelous*. “*Portunus*” *miocaenicus* Müller, 1984 was referred to *Monomia* (as a subgenus) by the author himself. Examination of the published photograph (Müller, 1984, pl. 62, fig. 5) does not disapprove nor approve this because several important characters, i.e. the sternum, pleon and merus of cheliped remain unavailable for study. A few other species may be relatively confidently referred to *Portunus* (*sensu stricto*), such as *Portunus neogenicus* Müller, 1979, which shows a similarity to the extant Indo-Pacific species *Portunus sanguinolentus* (Herbst, 1783) (Müller, 1984, pl. 62, figs. 3, 4). A complete revision of fossil “*Portunus*” spp. is a challenge but it is worth to undertake this task because these numerous

records may tell much more about the history of Cenozoic faunas when properly assigned to genera.

Conclusions

It is trivial to say that our understanding of evolution of any taxonomic group, including portunoid crabs, would strongly benefit from integration of knowledge of extant and fossil taxa. However, we should carefully and clearly define a background for successful integration. Combining extant and fossil groups of portunoid crabs into a coherent classification that is compatible with phylogenetic reconstructions implies an acceptance of the concept of vertical taxa (Simpson, 1961). That is what palaeontologists explicitly or implicitly do when referring fossils to particular genera or families established on extant material, even though they necessarily work with incomplete sets of characters. Some standard characters for extant taxa, such as genital structures, maxillipeds, even dactyli of pereopods 2–4 and others are rarely available for comparative study of fossil taxa. This calls for extension of comparative morphological studies of Recent groups in order to find new characters that can help to classify fossil forms.

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References

- Adams, A. & White, A. 1848: Crustacea. In: Adams A. (ed.): The Zoology of the voyage of H.M.S. "Samarang", under command of Captain Sir Edward Belcher, during the years 1843–46. Part 2. Reeve, Bentham & Reeve, London, 33–67, pls 7–13
- Alcock, A.W. 1899. Material for a carcinological fauna of India. No. 4: The Brachyura Cyclometopa. Part II: A revision of the Cyclometopa, with an account of the families Portunidae, Cancridae and Corystidae. Journal of the Asiatic Society of Bengal, 68/2: 1–104.
- Alcock, A.W. 1900: Material for a carcinological Fauna of India. No. 6: The Brachyura Catometopa, or Grapsoidea. Journal of the Asiatic Society of Bengal, 69/2: 279–456.
- Alcock, A. & Anderson, A.R.S. 1899: Natural history notes from H.M. Royal Indian marine survey ship Investigator, commander T.H. Heming, R.N., commanding. Series III, No. 2. An account of the deep-sea Crustacea dredged during the surveying season of 1897–98. Annals and Magazine of Natural History (ser. 7), 3: 1–27, 278–292.
- Apel, M. & Spiridonov, V.A. 1998: Taxonomy and zoogeography of the portunid crabs (Crustacea: Decapoda: Brachyura: Portunidae) of the Arabian Gulf and the adjacent waters. Fauna of Arabia, 17: 159–331, pls 1–12.
- Artal, P., Ossó, À. & Domínguez, J.L. 2013: *Archaeoportunus isabenensis*, a new genus and species of portunoid crab (Crustacea, Decapoda) from the lower Eocene of Huesca (Spain). Boletín de la Sociedad Geológica Mexicana, 65/2: 307–317.
- Beurlen, K. 1930: Vergleichende Stammesgeschichte Grundlagen, Methoden, Probleme unter besonderer Berücksichtigung der höheren Krebse. Fortschritte der Geologie und Palaeontologie, 8/26: 317–586.
- Binkhorst, J.T. van 1857: Neue Krebse aus der Maestrichter Tuffkreide. Verhandlungen des naturhistorischen Vereins im Preussischen Rheinland und Westfalen, 14: 107–110.
- Bittner, A. 1893: Decapoden des pannonischen Tertiärs. Sitzungsberichte der kaiserlichen Akademie der Wissenschaften zu Wien, 102: 10–37.
- Bosc, L.A.G. 1802: Histoire naturelle des crustacés contenant leur description et leurs mœurs; avec figures dessinées d'après nature. T. Deterville, Paris: 1–258, pls 1–8.
- Brockerhoff, A.M. & McLay, C.L. 2011: Human-mediated spread of alien crabs: 27–106. In: Galil, B., Clark, P.F. & Carlton, J.T. (eds.): In the wrong place - alien marine crustaceans: distribution, biology and impacts. Springer Science, Frankfurt am Main.

- Collins, J.S.H., Garvie, C.L. & Melish, C.J.T. 2014: Some decapods (Crustacea; Brachyura and Stomatopoda) from the Pleistocene Beaumont Formation of Galveston, Texas. *Scripta Geologica*, 147: 309–322.
- Colosi, G. 1923: Una specie fossile de Gerionide (Decapodi brachiuri). *Bolettino della Società dei Naturalisti in Napoli* (series 2, vol. 15) 37: 248–255.
- Crosnier, A. 1975: Sur les *Caphyra* (Crustacea Decapoda Portunidae) de l'Océan Indien occidental et de la Mer Rouge. *Bulletin du Muséum national d'Histoire naturelle Paris*, (3)304 (Zoologie 214): 743–764.
- Crosnier, A. 2002: Révision du genre *Parathranites* Miers, 1886 (Crustacea, Brachyura, Portunidae). *Zoosystema*, 4/4: 799–825.
- Crosnier, A. 2003: A new genus and species of portunid crab (Crustacea: Decapoda: Brachyura) from New Caledonia, South-west Pacific. *The Raffles Bulletin of Zoology*, 51/2: 315–321.
- Dana, J.D. 1851: On the classification of the Cancroidea (Cyclometopa). *American Journal of Science and Arts. Ser. 2*, 12: 121–131.
- Dana, J.D. 1852: Crustacea. Part I. United States Exploring Expedition during the years 1838–1842 under the command of Charles Wilkes, U.S.N., 13: C. Sherman, Philadelphia, I–VIII + 1–685, 96 pls.
- Davie, P.J.F. & Crosnier, A. 2006: *Echinolatus* n. gen. (Crustacea, Decapoda, Portunidae) with description of two new species from the South-West Pacific. In: Richer de Forges, B., Justine, J.-L. (eds.): *Tropical Deep-Sea Benthos. Mémoires du Muséum national d'Histoire naturelle Paris*, 24: 193: 393–410.
- Davie, P.J.F., Guinot, D. & Ng, P.K.L. 2015: Systematics and classification of Brachyura: 1049–1130. In: Castro, P., Davie, P.J.F., Guinot, D., Schram, F.R. & von Vaupel Klein, J.C. (eds.): *Treatise on Zoology–Anatomy, Taxonomy, Biology–The Crustacea* (complementary to the volumes translated from the French of the *Traité de Zoologie* 9(C)(I), Decapoda: Brachyura (Part 1)). Brill, Leiden.
- Davie, P.J.F. & Short, J.W. 1989. Deepwater Brachyura (Crustacea: Decapoda) from southern Queensland, Australia with descriptions of four new species. *Memoirs of the Queensland Museum*, 27: 157–187.
- 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 Museo di Storia naturale de Milano*, 45: 1–340.
- De Grave, S., Pentcheff, D.N., Ah Yong, S.T., Chan, T.-Y., Crandall, K.A., Dworschak, P.C., Felder, D.L., Feldmann, R.M., Fransen, C.H.J.M., Goulding, L.Y.D., Lemaitre, R., Low, M.E.Y., Martin, J.W., Ng, P.K.L., Schweitzer, C.E., Tan, S.H., Tshudy, D. & Wetzer, R. 2009: A classification of living and fossil genera of decapod crustaceans. *The Raffles Bulletin of Zoology*, 21(Supplement): 1–109.
- De Haan, W. 1833–1850: Crustacea. In: Siebold P.F. (ed.): *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*, I–XXXI + 1–244.
- Desmarest, A.G. 1822: Les crustacés proprement dits. In: *Histoire naturelle des crustacés fossiles, sous les rapports zoologique et géologique. Savoir: les trilobites*, par Alexandre Brongniart. Les Crustacés proprement dits, par Anselme-Gaëtan Desmarest. F.G. Levrault, Paris/Strasbourg: 67–154, pls V–IX.
- Edmondson, C.H. 1930: New Hawaiian Crustacea. *Bernice P. Bishop Museum Occasional Papers*, 9/10: 3–17.
- Estampador, E.P. 1949: Studies on *Scylla* (Crustacea: Portunidae). 1. Revision of the genus. *Philippine Journal of Science*, 78: 95–108.
- 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>
- Fabricius, J.C. 1798. *Supplementum entomologiae systematicae*. Proft et Stoch, Hafniae: 1–572.
- Feldmann, R.M., Schweitzer, C. E. & Encinas, A. 2005: New decapods from the Navidad Formation (Miocene) of Chile. *Journal of Crustacean Biology*, 25/3: 427–449. <https://doi.org/10.1651/C-2547>
- Feldmann, R.M., Schweitzer, C.E. & Encinas, A. 2010: Neogene decapod crustaceans from southern Chile. *Annals of Carnegie Museum*, 78/4: 337–366. <https://doi.org/10.2992/007.078.0404>
- Garstang, W. 1897a: Contribution to marine bionomics. II. The function of antero-lateral denticulation in sand-burrowing crabs. *Journal of the Marine Biological Association*

- of the United Kingdom, 4/4: 396–401. <https://doi.org/10.1017/S002531540000552X>
- Garstang, W. 1897b: Contribution to marine bionomics. III. The systematic features, habits and respiratory phenomena of *Portumnus nasutus*. Journal of the Marine Biological Association of the United Kingdom, 4/4: 402–407. <https://doi.org/10.1017/S0025315400005531>
- Gašparič, R. & Ossó, Á. 2016: New reports of decapod *Portunus monspeliensis* A. Milne-Edwards, 1860 from Miocene beds of eastern Slovenia with notes on palaeoecology and palaeobiogeography. Geologija, 59/1: 55–66. <https://doi.org/10.5474/geologija.2016.005>
- Gibbes, L.R. 1850: On the carcinological collections of the United States. Proceedings of American Association Advancement of Sciences, 3: 167–201.
- Gistel, J. 1848: Naturgeschichte des Thierreichs für höhere Schulen. Hoffmann'sche Verlags-Buchhandlung, Stuttgart: i–xvi, 1–216, pls 1–32.
- Glaessner, M.F. 1928: Die Dekapodenfauna des österreichischen Jungtertiärs. Jahrbuch der Geologischen Bundesanstalt, 78: 161–219, pls. 3–4.
- Glaessner, M.F. 1960: The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. New Zealand Geological Survey, Paleontological Bulletin, 31: 1–79.
- Gordon, I. 1953: On *Sirpus*, a genus of pigmy cancrroid crabs. Bulletin of The British Museum (Natural History), Zoology, 2/3: 43–65.
- Guérin, F.E. 1832: Notice sur quelques modifications á introduire dans les Notopodes de M. Latreille, et établissement d'un nouveau genre dans cette tribu. Annales des Science naturelles (Zoologie), 25: 285–286.
- Guinot, D. 1979: Données nouvelles sur la morphologie, la phylogénèse et la taxonomie des Crustacés Décapodes Brachyours. Mémoires du Muséum national d'Histoire naturelle Paris, A112: 1–354.
- Guinot, D. & Breton, G. 2006: *Lithophylax triggeri* A. Milne-Edwards & Brocchi, 1879 from the French Cretaceous (Cenomanian) and placement of the family Lithophylacidae Van Straelen, 1936 (Crustacea, Decapoda, Brachyura). Geodiversitas, 28: 591–633.
- Hartnoll, R.G. 1971: The occurrence, methods and significance of swimming in the Brachyura. Animal Behaviour, 19: 34–50.
- Herbst, J.F.W. 1782–1804. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten. G.A. Lange, Berlin & Stralsund, Vol. 1: 1–274, Vol. 2: 1–226, Vol. 3: 1–216, Atlas: pls 1–72.
- Holthuis, L.B. 1987: *Necora*, a new genus of European swimming crabs (Crustacea, Decapoda, Portunidae) and its type species *Cancer puber* L., 1767. Zoologische Mededelingen, 61/1: 1–13.
- Hyžný, M., Harzhauser, M. & Danninger, W. 2015: Decapod Crustacea of the Central Paratethyan Oligocene Stage (middle Burdigalian): implications for systematics and biogeography. Geologia Carpathica, 66/3: 217–233. <https://doi.org/10.1515/geoca-2015-0021>
- Jagt, J.W.M., Van Bakel, B.W.M. & Fraaije, R.H.B. 2010: *Coeloma rupeliense* (Crustacea, Decapoda, Brachyura) from the Bilzen Formation (Rupel Group, Lower Oligocene) in northeast Belgium. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 80: 245–252.
- Karasawa, H., Schweitzer, C.E. & Feldmann, R.M. 2008: Revision of Portunoidea Rafinesque, 1815 (Decapoda: Brachyura) with emphasis on the fossil genera and families. Journal of Crustacean Biology, 28: 82–127. <https://doi.org/10.1651/07-2882R.1>
- Krøyer, H. 1838: Conspectus Crustaceorum Groenlandiae. Naturhistorisk Tidsskrift, 2: 249–261.
- Lamarck, J.B. 1801: Systeme des Animaux sans Vertèbres. Deuxieme edition. Vol. 5. Deterville, Paris: i–viii, 1–432.
- Latreille, P.A. 1819: Nouveau Dictionnaire d'Histoire Naturelle, 28: 1–570.
- Latreille, P.A. 1829: Les Crustacés, les Arachnides et les Insectes distribués en familles naturelles. In: Cuvier G. La Règne Animal. Vol. 4. Paris. 1829 —. P. I–XXVII + 1–584.
- Leach, W.E. 1814: Crustaceology. In: Brewster's Edinburgh Encyclopaedia, 7: 383–437.
- Leach, W.E. 1815–1820: Malacostraca Podophthalmata Britanniae; or Description of the British Species of the Linnean Genus Cancer as Have Their Eyes Elevated on Footstalks. James Sowerby, London: 1–124, pls 1–45.
- Leene, 1938: The Decapoda Brachyura of the Siboga-Expedition. VII. Brachygnatha: Portunidae. Siboga Expeditie Monographien, 39c3: 1–156.
- Lenz, H. & Strunk, K. 1914: Die Dekapoden der Deutschen Südpolar-Expedition 1901–1903. I. Brachyuren und Macruren mit Ausschluss der

- Sergestiden. Deutsche Südpolar-Expedition, 1901–03, Zoologie, 15/7: 257–345, pls 12–22.
- Linnaeus, C. 1758: *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Edit. decima, reformata. L. Salvius, Stockholmiae: I–III, 1–823.
- Linnaeus, C. 1761: *Fauna Svecica. Sistens Animalia Sveciae Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per Classes & Ordines, Genera & Species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus Insectorum*. L. Salvius, Stockholmiae: 1–578.
- Lyubarskiy, G.Yu. 1996: Archetype, style and rank in biological systematics. KMK Scientific Press, Moscow: 1–432 (in Russian).
- MacLeay, W.S. 1838: On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: *Illustrations of the Zoology of South Africa*. 5. Invertebrata, 3. Smith, A. (ed.): Smith, Elder & Co, London: 53–71, pls 2–3.
- Manning, R.B. 1989: *Sanquerus*, a replacement name for *Posidon* Herklots, 1851 (Crustacea, Decapoda, Portunidae). *Proceedings of the Biological Society of Washington*, 102/3: 698–700.
- Manning, R.B. & Chace Jr. F.A. 1990: Decapod and stomatopod Crustacea from Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology*, 503: 1–91. <https://doi.org/10.5479/si.00810282.503>
- Manning, R.B. & Holthuis, L.B. 1989: Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). *Proceedings of Biological Society of Washington*, 102/1: 50–77.
- Mantelatto, F.L., Robles, R., Wehrtmann, I.S., Schuhbart, C.D. & Felder D.L. 2018: New insights into the molecular phylogeny of the swimming crabs of the genera *Portunus* Weber, 1795 and *Achelous* De Haan, 1833 (Brachyura: Portunidae) of the Americas. *Journal of Crustacean Biology*, 38: 190–197.
- Marangon, S. & De Angeli, A. 2009: Exceptionally preserved specimens of *Portunus monspeliensis* (A. Milne Edwards, 1860) (Brachyura, Portunidae) from the Miocene of Sardinia (Italy). *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano*, 150/I: 3–12.
- Maury, C.J. 1930 by O Cretaceo da Parahyba do Norte. *Monographias do Serviço Geológico e Mineralógico do Brasil* 8: 1–305.
- Mayr, E. & Bock, W.J. 2002 ali 2008: Classifications and other ordering systems. *Journal of Zoology, Systematics and Evolutionary Research* 40/4, 169–194. <https://doi.org/10.1046/j.1439-0469.2002.00211.x>
- Miers, E.F. 1886: Report on the Brachyura collected by H.M.S. Challenger during the years 1873 – 1876. Reports of the scientific results of the voyage of H.M.S. Challenger. *Zoology*. 17/I: 1–362, pls 1–29.
- Milne-Edwards, A. 1860: *Historie des Crustacés podophtalmiques fossiles*. *Annales des Sciences naturelles (Zoologie)*, 4/14: 129–353, pls 1–10.
- Milne-Edwards, A. 1861: *Etudes zoologiques sur les crustacés recents de la famille de Portuniens*. *Archives du Muséum national d'Histoire naturelle*, 10: 309–421, pls 28–38.
- Milne-Edwards, A. 1865: *Monographie des Crustacés fossiles de la famille des Cancériens (suite)*. *Annales des Sciences Naturelles, série 5*, 3: 297–351.
- Milne-Edwards, A. 1867: Descriptions de quelques espèces nouvelles de Crustacés Brachyures. *Annales de la Société entomologique de France*, 4/7: 263–288.
- Milne-Edwards, A. 1869: Description de quelques crustacés nouveaux de la famille portuniens. *Nouvelle Archives du Muséum national d'Histoire naturelle*, 5: 146–158, pl. 6
- Milne-Edwards, A. 1870: Note sur le *Catoptrus*, nouveau genre appartenant à la division des Crustacés Brachyures catometopes. *Annales des Sciences Naturelles, Zoologie, série 5*, 13: 80–86
- Milne-Edwards, A. 1873: *Recherches sur la faune carcinologique de la Nouvelle-Calédonie, II*. *Nouvelles Archives du Muséum d'histoire naturelle*, 9: 155–332, pls 4–18.
- Milne-Edwards, A. 1881: Note sur quelques Crustacés fossiles des environs de Biarritz. *Annales des Sciences Géologiques (Paris)*, 11/2: 1–8, pls. 21.
- Milne Edwards, H. 1834. *Histoire naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces animaux*. Vol. I. Librairie encyclopédique der Roret, Paris: I–XXXV + 1–468.
- Milne Edwards, H. 1837. *Histoire naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces animaux*. Vol. II. Librairie encyclopédique der Roret, Paris: 1–531, pls 1–42.

- Montgomery, S.K. 1931: Report on the Crustacea Brachyura of the Percy Sladen Trust Expedition to the Abrolhos Islands under the leadership of Prof. W.J. Dakin, in 1913 along with other crabs from the Western Australia. *Journal of the Linnean Society of London (Zoology)*, 37: 405–465, pls 24–30.
- Müller, P. 1974: Decapoda (Crustacea) fauna a budapesti miocénből (2). *Földtani Közlöny*, 104: 275–287 (in Hungarian).
- Müller, P. 1979: Crustacés décapodes du Badénien et Sarmatien de Bulgarie. *Palaeontology, Stratigraphy and Lithology*, 10: 3–8, pls.1–3.
- Müller, P. 1984: Decapod crustaceans of the Badenian. *Geologica Hungarica, Series Palaeontologica*, 42: 1–317.
- Nardo, G.D. 1869: Annotazioni illustranti cinquantaquattro specie di Crostacei poddotalmi, endotalmi e succhiatori del mare Adriatico, alcune delle quali nuove o male conosciute, accompagnate da trentare figure litographie, e precedute dalla storia della carcinologica Adriatica antica e recente. *Memorie del Reale Istituto di Scienze, Lettere ed Arti, Venezia*, 14: 217–340.
- Naruse, T. & Ng, P.K.L. 2012: *Kume tигра*, a new genus and new species of carupine swimming crab (Crustacea: Brachyura: Portunidae) from Kume Island, Ryukyu Islands, Japan. *Zootaxa*, 3367/1: 204 – 221. <https://doi.org/10.11646/zootaxa.3367.1.19>
- Ng, P.K.L. 2000: The deep-water swimming crabs of the genus *Benthochascon* (Decapoda: Brachyura: Portunidae), with description of a new genus for the American *B. schmitti*. *Journal of Crustacean Biology*, 20/5: 310–324. <https://doi.org/10.1163/1937240X-90000033>
- Ng, P.K.L. 2002: On the unusual swimming crab, *Coelocarcinus foliatus* Edmondson, 1930, with description of a new species from the Indian Ocean (Decapoda, Brachyura, Portunidae). *Crustaceana*, 75: 51–60. <https://doi.org/10.1163/156854002317373519>
- Ng, P.K.L. 2011: *Pele ramseyi*, a new genus and new species of anchialine swimming crab (Crustacea: Brachyura: Portunidae) from the Hawaiian Islands. *Zootaxa*, 2737/1: 34–48. <https://doi.org/10.11646/zootaxa.2737.1.3>
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. 2008: *Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world*. *The Raffles Bulletin of Zoology, Supplement 17*: 1–286.
- Ng, P.K.L. & Takeda, M. 2003: *Atoportunus*, a remarkable new genus of cryptic swimming crab (Crustacea; Decapoda; Brachyura: Portunidae), with descriptions of two new species from the Indo-West Pacific. *Micronesica*, 35–36: 417–430.
- Nguyen, T.S., Ng, P.K.L. 2010: A new genus of the family Portunidae (Crustacea: Decapoda: Brachyura) and the identity of *Portunus (Cycloachelous) yoronensis* Sakai, 1974. *Zootaxa*, 2677: 38–48.
- Noetling, F. 1881: Ueber einige Brachyuren aus dem Senon von Mastricht und dem Tertiär Norddeutschlands. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 33: 357– 371.
- Orbigny, A.D. d'. 1842: Voyage dans l'Amerique meridionale: (le Brésil, la république orientale de l'Uruguay, la République Argentine, la Patagonie, la république du Chili, la république de Bolivie, la république du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832, et 1833 (1835). *Paleontologie. Partie. 3/4. Pitois-Levraul, Paris*: 1–188.
- Ossó, Á. 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: 213–246.
- Ossó, Á. & Gagnaison, C. 2019: An appraisal of the Middle-Late Miocene fossil decapod crustaceans of the 'Faluns' (Anjou-Touraine, France). *Geodiversitas*, 41/9: 367–383.
- Ossó, Á. & Stalennuy, O. 2011: Description of the first fossil species of *Bathynectes* (Brachyura, Polybiidae) in the Badenian (middle Miocene) of the Medobory Hills (Ukraine, Central Parathetys), with remarks on its habitat ecology. *Treballs Museu Geologic Barcelona*, 18: 37–46. <https://doi.org/10.32800/tmgb.2011.18.0037>
- Ossó-Morales, Á., Artal, P. & Vega, F.G. 2010: New crabs (Crustacea, Decapoda) from the Upper Cretaceous (Campanian) of the Moyenne Moulouya, northeast Morocco. *Revista Mexicana de Ciencias Geológicas*, 27: 213–224.
- Ortmann, A.E. 1893: Die Dekapoden-Krebse des Strassburger Museums. VI-te Theil. Abteilung Brachyura. Unterabteilung Majoidea und Cancroidea, Section Portuninea. *Zoologische Jahrbucher. Abteilung für Systematik, Geographie und Biologie der Tiere*, 7: 23–88, pl. 3.
- Ortmann, A.E. 1899: Crustacea, Zweite Hälfte: Malacostraca. In: Bronn H.G. (ed.): *Klassen und Ordnungen des Thier-Reichs, Band 5*,

- Abtheilung II (Gliederfüßler: Arthropoda), Lieferung 53-56. C.F. Winter, Leipzig: 1169-1232.
- Parker, A.R., McKenzie, D.R., Ah Yong, S.T. 1998: A unique form of light reflector and the evolution of signalling in *Ovalipes* (Crustacea: Decapoda: Portunidae). *Proceedings of Royal Society of London B*, 265: 861-867.
- Paulson, O. 1862. Zur Anatomie von *Diplozoon paradoras*. *Mémoires de l'Académie Imperiale des Sciences de St.-Petersbourg*, 7/5, 1: 1-16, 1 pl. 1.
- Paulson, O. 1875: Studies on Crustacea of the Red Sea, with notes regarding other seas. Part I. Podophthalmata and Edriophthalmata (Cumacea), xv + 144 p. Kiev, S.V. Kulzhenko (in Russian; English translation published by Por, F.D. 1961, 164 p. Jerusalem, Israel Program for Scientific Translations).
- Phillips, G.E., Nyborg, T. & Vega, F.J. 2014: Icriocarcinidae: a family of portunoid crabs from the Upper Cretaceous of North America. *Paläontologische Zeitschrift*, 88: 139-158. <https://doi.org/10.1007/s12542-013-0190-4>
- Plagge, C., Son, N.T., Ng, P.K.L., Türkay, M., Streit, B. & Klaus, S. 2016: *Liocarcinus corrugatus* (Pennant, 1777) (Crustacea: Brachyura: Portunidae): a cosmopolitan brachyuran species? *The Raffles Bulletin of Zoology*, 4: 374-388.
- Prestandrea, N. 1833: Su di alcuni nuovi crustacei dei mari di Messina. *Effemeridi Scientifiche e Letterarie per La Sicilia*, April 1833: 3-14.
- Rafinesque, C.S. 1815: Rafinesque C.S. 1815. *Analyse de la Nature ou tableau de l'univers et des corps organisés, Aux depeus de l'Auteur*, Palerme: 1-223.
- Rathbun, M.J. 1897: A revision of the nomenclature of the Brachyura. *Proceedings of the Biological Society of Washington* 11: 153-167.
- Rathbun, M.J. 1898: The Brachyura collected by the U.S. Fish Commission steamer Albatross, on the voyage from Norfolk, Virginia, to San Francisco, California, 1887-1888. *Proceedings of United States National Museum*, 21: 567-616, pls 41-44.
- Rathbun, M.J. 1935: Fossil Crustacea of the Atlantic and Gulf Coastal Plain Geological Society of America, Special paper 2: 1-160.
- Richards, B.C. 1975: *Longusorbis cuniculosus*: a new genus and species of Upper Cretaceous crab with comments on the Spray Formation at Shelter Point, Vancouver Island, British Columbia. *Canadian Journal of Earth Sciences*, 12: 1850-1863.
- Risso, A. 1816: *Histoire naturelle des Crustacés de Nice*. Paris: 1-175, pls 1-3.
- Rodriguez, G. 1992: The freshwater crabs of America. Family Trichodactylidae and a Supplement to the family Pseudothelphusidae. *Faune Tropicale* 31: 1-178. ORSTOM, Paris.
- Rüppell, E. 1830. Beschreibung und Abbildung von 24 Arten kurzschwänzigen Krabben, als Beitrag zur naturgeschichte des rothen Meeres. H.L. Bröner, Frankfurt a.M.: 1-28, pls. 1-6.
- Schäfer, W. 1954: Form und Funktion der Brachyuren-Schere. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft*, 489: 1-65.
- Schubart, C.D. & Reuschel, S. 2009: A proposal for a new classification of Portunoidea and Cancroidea (Brachyura: Heterotremata) based on two independent molecular phylogenies. In: Martin, J.W., Crandall, K.A. & Felder, D.L. (eds.): *Decapod crustacean phylogenetics* [Crustacean Issues, 18]: 533-550. CRC Press, Boca Raton, FL.
- 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 the Carnegie Museum* 76/1: 15-37. [https://doi.org/10.2992/0097-4463\(2007\)76\[15:ROTCBD\]2.0.CO;2](https://doi.org/10.2992/0097-4463(2007)76[15:ROTCBD]2.0.CO;2)
- Schweitzer, C.E. & Feldmann, R.M. 2000: New fossil portunids from Washington, USA, and Argentina, and re-evaluation of generic and family relationships within the Portunoidea Rafinesque, 1815 (Decapoda, Brachyura). *Journal of Paleontology*, 74/4: 636-653. [https://doi.org/10.1666/0022-3360\(2000\)074<0636:N-FPFWU>2.0.CO;2](https://doi.org/10.1666/0022-3360(2000)074<0636:N-FPFWU>2.0.CO;2)
- Schweitzer, C.E. & Feldmann, R.M. 2011: Revision of some fossil podotrematous Brachyura (Homolodromiidae; Longodromitidae; Torynommidae). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 260/2: 237-256. <https://doi.org/10.1127/0077-7749/2011/01.38>
- Secretan, S. 1961: Une nouvelle espèce de Xanthidés au Maroc: *Titanocarcinus meridionalis* nov. sp. *Notes de Service Géologique de Maroc*, 20/152: 39-50.
- Simpson, G.G. 1961: *Principles of animal taxonomy*. Columbia University Press, New York: 247 p.
- Spiridonov, V.A. 1999: Results of the Rumphius Biohistorical Expedition to Ambon (1990). Part. 8. Swimming crabs of Ambon (Crustacea:

- Decapoda: Portunidae). Zoologische Mededelingen (Leiden), 73/4: 63–97.
- Spiridonov, V.A. 2016: *Xiphonectes tuerkayi* sp.n. from the Indian Ocean with notes on *Xiphonectes longispinosus* Dana, 1852 (Crustacea: Decapoda: Portunidae). *Arthropoda Selecta*, 25/4: 357–372.
- Spiridonov, V.A., Neretina, T.V. & Schepetov, D. 2014: Morphological characterization and molecular phylogeny of Portunoidea Rafinesque, 1815 (Crustacea Brachyura): implications for understanding evolution of swimming capacity and revision of the family-level classification. *Zoologischer Anzeiger*, 253/5: 404–429. <https://doi.org/10.1016/j.jcz.2014.03.003>
- Spiridonov, V. & Neumann, V. 2008: Coral-inhabiting swimming crabs (Crustacea, Decapoda, Portunidae) of the Sudanese Red Sea. *Organisms, Diversity and Evolution*, 8/3: 170e1–170e19. <https://doi.org/10.1016/j.ode.2007.06.005>
- Spiridonov, V.A. & Türkay, M. 2001: Deep sea swimming crabs of the *Charybdis miles* species group in the western Indian Ocean. *Journal of Natural History*, 35/3: 434–464. <https://doi.org/10.1080/002229301300009649>
- Stebbing, T.R.R. 1921: Some Crustacea of Natal. III. *Annals of the Durban Museum*, 3/1: 12–26, pls. 1–5.
- Stephenson, W. 1972: An annotated checklist and key to the Indo-West-Pacific swimming-crabs (Portunidae). *Royal Society of New Zealand Bulletin*, 10: 1–64.
- Stephenson, W. & Hudson, J. 1957: The Australian portunids (Crustacea: Portunidae). II. The genus *Thalamita*. *Australian Journal of Marine and Freshwater Research*, 8/3: 312–368, 6 pls.
- Stephenson, W. & Rees, M. 1968: A revision of the genus *Ovalipes* Rathbun, 1898 (Crustacea, Decapoda, Portunidae). *Records of the Australian Museum*, 27/11: 213–261, pls 35–42.
- Steudel, S.C. 1998: Über Schwimmkrabben und Krabbenschwimmen. Unpubl. PhD thesis, Johann Wolfgang Goethe-Universität, Frankfurt am Main: 183 p.
- Števcíć, Z. 1991: Note on some rare and aberrant Australian crabs. *The Beagle. Records of Northern Territory Museum of Arts and Sciences*, 8/1: 121–134.
- Števcíć, Z. 2005: Fauna Croatica. The reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica*, 4/1: 1–150.
- Stimpson, W. 1860. Notes on North American Crustacea, in the Museum of the Smithsonian Institution. No. II. *Annals of the Lyceum of Natural History of New York*, 7: 177–246, pls 2, 5
- Stimpson, W. 1871: Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L.F. de Pourtales, Assistant U.S. Coast Survey. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 2: 109–160.
- Takeda, M. & Miyake, S. 1969: A small collection of crabs from New Zealand. OHMU – Occasional Papers of Zoological Laboratory Faculty of Agriculture Kyushu University, 2/8: 157–193, pls 1–3.
- Takhtajan, A.L. 2009: Flowering plants. Springer Science, Berlin: 1–871
- Tien, D.D. 1969: New species of swimming crabs from the Tonkin Gulf and Hainan Island. *Zoologicheskii Zhurnal*, 48: 505–511 (in Russian).
- Türkay, M. & Spiridonov, V.A. 2006: Deep sea swimming crabs of the subgenus *Charybdis* (*Goniohellenus*) Alcock, 1899 of the western Indian Ocean (Crustacea: Decapoda: Portunidae). *Fauna of Arabia*, 22: 199–223.
- Van Straelen, V. 1936: Crustacés décapodes nouveaux ou peu connus de l'époque crétacique. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 12/45: 1–50.
- Vega, F.J., Feldmann, R.M., García-Barrera, P., Filkorn, H., Pimentel, F. & Avendaño, J. 2001: Maastrichtian Crustacea (Brachyura: Decapoda) from the Ocozocuahtla Formation in Chiapas, southeast Mexico. *Journal of Paleontology*, 75/2: 319–329. <https://doi.org/10.1017/S0022336000018126>
- Vega, F.J., Feldmann, R.M., Villalobos-Hiriart, J.L. & Gío-Argez, R. 1999: A new decapod fauna from the Miocene Tuxpan Formation, Eastern Mexico. *Journal of Paleontology*, 73/3: 407–413. <https://doi.org/10.1017/S0022336000027931>
- Vega, F.J., Nyborg, T., Coutiño, M.A., Solé, J. & Hernández-Monzón, O. 2009: Neogene Crustacea from south eastern Mexico. *Bulletin of the Mizunami Fossil Museum*, 35: 51–69.
- Vega, F.J., Phillips, C.E., Nyborg, T., Flores-Ventura, J., Clements, D., Espinosa, B. & Solís-Pichardo, G. 2013: Morphology and size variation of a portunoid crab from the Maastrichtian of the Americas. *Journal of South American Earth Sciences*, 47: 116–135.

- Ward, M. 1933: New genera and species of marine Decapoda Brachyura from the coasts of New South Wales and Queensland. *Australian Zoologist*, 7: 377–394, pls 21–23.
- Ward, M. 1942: Notes on the Crustacea of the Desjardins Museum, Mauritius Institute with descriptions of new genera and species. *Mauritius Institute Bulletin*, 2/2: 49–109.
- Weber, F. 1795: *Nomenclator entomologicus secundum entomologiam systematicum III. Fabricii adjectis speciebus recens detectis et varietabilis*. C.E. Bohn, Kiel & Hamburg: I–VIII + 1–172.
- Withers, T.H. 1922: On a new brachyurous crustacean from the Upper Cretaceous of Jamaica.
- Zarenkov, N.A. 1970: Crabs of the Portunidae family collected by Soviet Expeditions in the tropical waters of the Pacific and Indian Oceans. *Bulletin Moskovskogo Obshchestva Ispytatelei Prirody (Otdel Biologicheskii)*, 75/5: 42–47 (in Russian).
- Zarenkov, N.A. 1974: Lectures in theory of systematics. Moscow University Press, Moscow: 1–154 (in Russian).
- Internet sources:
- Internet 1: <http://www.mbfossilcrabs.com/portunoidea/Ophthalmoplax%20minimus.jpg3..jpg> (accessed 20 March 2020).
- Internet 2: <http://www.mbfossilcrabs.com/Portunoidea.html> (accessed 23 March 2020).
- Internet 3: <http://www.mbfossilcrabs.com/Portunoidea.html> (accessed 23 March 2020).