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Revision of the generic system for the swimming crab subfamily Portuninae (Decapoda: Brachyura: Portunidae) based on molecular and morphological analyses

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Swimming crabs of the genus *Portunus* are revised based on analysis of three genetic markers (*COI*, 16S and *H3*) and a morphological comparison. The analyses reveal the polyphyletic composition of *Monomia*, *Portunus* and *Xiphonectes* and the paraphyly of *Achelous*. *Portunus*, in our revised composition, is restricted to 13, *Monomia* to ten and *Xiphonectes* to 14 species. Other species are transferred to *Achelous* (28) and *Cycloachelous* (nine) or to newly established genera. Four new genera are separated from *Xiphonectes* and one new genus from *Monomia*. The systematic composition of the portunid subfamily Portuninae now comprises 11 genera: *Arenaeus*, ***Allomonomia* gen. nov.**, *Cavoportunus*, *Callinectes*, *Cycloachelous*, ***Eodemus* gen. nov.**, ***Incultus* gen. nov.**, *Monomia*, *Portunus*, ***Trionectes* gen. nov.** and *Xiphonectes*. The genus *Lupella* is synonymized with *Achelous* (Achelouinae). *Xiphonectes pulchricristatus* and *Xiphonectes spinipes* are placed in ***Alionectes* gen. nov.**, *Portunus ponticus* is transferred to *Lupocycloporus* (both Lupocyclinae), and *Monomia euglypha* is now placed in *Cycloachelous* (Portuninae). *Portunus mokyevskyi* is considered a junior synonym of *Scylla tranquebarica* (Necronectinae). *Xiphonectes leptocheles* is confirmed as a valid species. *Cycloachelous granulatus unispinosus* is also considered a valid species and is to be treated as *Cycloachelous unispinosus*.

ADDITIONAL KEYWORDS: Bayesian analysis – classification – Crustacea – maximum likelihood – molecular phylogeny – taxonomy.

INTRODUCTION

Swimming crabs of the family Portunidae Rafinesque, 1815 are remarkable in having unique swimming abilities. They are also one of the most species-rich groups of brachyuran crabs. The number of known species has recently been estimated to be > 360 extant species in 50 genera (Davie *et al.*, 2015c; Evans, 2018), and there are > 140 fossil records (Schweitzer *et al.*, 2010). The general biogeographical range of these crabs exhibits a pantropical distribution, in tropical and subtropical areas of the Atlantic, Indian and Pacific Oceans, with only a few species occurring in temperate waters. Their vertical distribution is from the intertidal zone to the edge of the continental shelf at ~200 m, and in deeper waters records are more sporadic. Portunid crabs are ecologically significant as predominantly benthic predators; although several, mainly larger-sized, species also have a high economic value (Stephenson & Campbell, 1959; Hartnoll, 1971; Apel & Spiridonov, 1998; Ng, 1998; Spiridonov *et al.*, 2014).

The systematics of Portunidae has developed from a basis established by 19th and 20th century authors (i.e. Dana, 1852; Milne-Edwards, 1861; Paulson, 1875; Miers, 1886; Alcock, 1899; Balss, 1922; Rathbun, 1930) to a modern classification largely based on the works of authors such as Crosnier (1962), Stephenson (1972a, b, and references therein), Apel & Spiridonov (1998) and Števčić (2005), with the last revisions of higher portunoid taxa provided by Karasawa *et al.* (2008), Ng *et al.* (2008),

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Schubart & Reuschel (2009), Spiridonov *et al.* (2014) and Evans (2018), and new additions provided by authors such as Mantelatto *et al.* (2009, 2018), Ng (2011), Windsor *et al.* (2019) and Spiridonov (2020).

The most comprehensive listing of all portunid taxa was presented by Ng *et al.* (2008), who divided the family Portunidae into seven subfamilies (including the subfamily Portuninae Rafinesque, 1815). Four of those (i.e. Caphyrinae Paulson, 1875, Carupinae Paulson, 1875, Podophthalminae Stimpson, 1860 and Thalamitinae Paulson, 1875) were also accepted by Karasawa *et al.* (2008), and Portuninae was subdivided in the latter study into four subfamilies (Atoportuninae Števčić, 2005, Lupocyclinae Paulson, 1875, Necronectinae Glaessner, 1928 and Portuninae), with two remaining subfamilies being cosnidered as full families: Carcinidae MacLeay, 1838 and Macropipidae Stephenson & Campbell, 1960. Spiridonov *et al.* (2014) supported Karasawa and colleague's eight-subfamily concept of the Portunidae, whereas Davie *et al.* (2015c) reduced that number to five (Caphyrinae, Carupinae, Podophthalminae, Portuninae and Thalamitinae), with Carcinidae and Polybiidae Ortmann, 1893 treated as separate families. Subsequently, based on molecular studies, Evans (2018) considered there to be six subfamilies (Carupinae, Lupocyclinae, Necronectinae, Podophthalminae, Portuninae and Thalamitinae) by synonymizing Atoportuninae with Carupinae and by placing some earlier portunine or caphyrine taxa into the subfamily Thalamitinae and the family Carcinidae.

Most recently, Spiridonov (2020) retained the general concept of Portunidae described by Evans (2018), with separation of *Achelous* into the seventh subfamily, Achelouinae Spiridonov, 2020. In the study by Spiridonov (2020), the subfamily Portuninae comprises only three genera, *Arenaeus* Dana, 1851, *Callinectes* Stimpson, 1860 and *Portunus* Weber, 1795, but tentatively also including *Cavoportunus* Nguyen & Ng, 2010, *Cycloachelous* Ward, 1942 and *Monomia* Gistel, 1848. Spiridonov (2020) regarded *Xiphonectes* A. Milne-Edwards, 1873 as polyphyletic and listed the genus as *incertae sedis* among Portunidae.

According to Ng *et al.* (2008), Portunidae contained at that time 38 genera, of which 14 were in the subfamily Portuninae. The nominotypic genus *Portunus* comprised > 90 species divided into five subgenera: *Achelous* De Haan, 1833, *Lupocycloporus* Alcock, 1899, *Monomia*, *Portunus* and *Xiphonectes*. It is worth noting that these subgenera were originally described as genera, and only subsequently were placed under the name *Portunus*, or *Neptunus* De Haan, 1833 (junior synonym of *Portunus*), by several authors in the 20th century (e.g. Rathbun, 1930; Sakai, 1939; Stephenson & Campbell, 1959; Crosnier, 1962; Stephenson, 1972a, b).

At present, all those subgenera of *Portunus* (*s.l.*, i.e. as listed by Ng *et al.*, 2008) have already been returned to their original generic level. The growing inclination to use the subgeneric names of portunids at full generic level was started by Mantelatto *et al.* (2009) with their elevation of *Achelous*. Nguyen & Ng (2010) revalidated *Cycloachelous*, resurrected earlier by Davie (2002) as a subgenus of *Portunus*, but again treated as a synonym of *Achelous* by Ng *et al.* (2008). *Monomia* was reinstated as a genus by Chertoprud *et al.* (2012) and, subsequently, *Lupocycloporus* with *Xiphonectes* by Spiridonov *et al.* (2014). In addition to those, Nguyen & Ng (2010) established the new genus *Cavoportunus* for *Neptunus* (*Achelous*) *dubius* Laurie, 1906.

The systematic changes mentioned above were based predominantly on morphological evidence. The molecular phylogenies in portunid crabs have, until now, only been analysed at higher taxon levels, by Schubart & Reuschel (2009), Spiridonov *et al.* (2014) and Evans (2018), or to support distinct species identities (e.g. Koch *et al.*, 2015a). Genetic analyses were also performed to support species separations in an analysis of the Indo-West Pacific *Portunus pelagicus* (Linnaeus, 1758) species complex by Lai *et al.* (2010) and for the American portunids by authors such as Robles *et al.* (2007), Zupolini *et al.* (2017) or Mantelatto *et al.* (2007, 2009, 2018), where was suggested the revalidation of the subgenus *Achelous* at generic level (see above).

Recently, based on a wider multigene phylogenetic analysis of the Portunoidea (Evans, 2018) that included 29 species of *Portunus* (*s.l.*), the genus *Portunus* was confirmed as polyphyletic, with species nested inside three clades of the subfamily Portuninae (Evans, 2018: fig. 11): (1) type species of *Portunus* (*Portunus*) and some related congeners, along with *Arenaeus* and *Callinectes*; (2) the remaining *P.* (*Portunus*) species, all *P.* (*Achelous*) species and the monotypic genus *Lupella*; and (3) the *Portunus* subgenera *Cycloachelous*, *Monomia* and a paraphyletic *Xiphonectes*, leaving the taxonomic status of those taxa unresolved.

The aim of the present study was to perform phylogenetic analysis of the taxa corresponding to the genus *Portunus* (*s.l.*), as listed by Ng *et al.* (2008), and to provide their systematic rearrangement based on molecular and morphological comparative analyses. The genera *Callinectes* and *Arenaeus*, being morphologically close to *Portunus* (*s.l.*), are also considered in the systematic part of this study. The monotypic *Carupella* Lenz in Lenz & Strunck, 1914 was not taken into consideration owing to doubts about its validity and lack of data for molecular analyses (Evans, 2018).

MATERIAL AND METHODS

Collected material

The examined specimens were obtained either by field collecting, by visiting museums or by direct loans of material from museums. Field collecting was undertaken by the authors in Vietnam (M.K., V.A.S. and Z.Ď.), the Red Sea, the Arabian Sea and the Gulf of Mexico (V.A.S.), by means of scuba diving, snorkelling, exploration of tidal pools or by examination of catches in local fishing ports in Vietnam. The majority of the specimens were examined and/or loaned from MNHN, Paris (from Madagascar, Guadeloupe), NHM, London and SMF, Frankfurt. Remaining material was loaned or deposited in: AM, Sydney; MV, Melbourne; AMNH, New York; SMF, Frankfurt; ZIN RAN, St. Petersburg; ZMMU Moscow; and others (see full list and Abbreviations, below).

Molecular data

DNA sequences were obtained from both fresh and/or museum specimens; additional sequences were obtained from GenBank. The combined dataset comprises 70 species (Table 1).

DNA was isolated using the Qiagen Blood and Tissue DNA kit. Fragments of the mitochondrial genes 16S rRNA and *COI* and the nuclear gene *H3* were amplified using the Bioline MyTaq Red Mix. Amplification of 16S rRNA was carried out using the primers 16Sar (5′-CGCCTGTTTATCAAAAACAT-3′) and 16Sbr (5′-CCGGTCTGAACTCAGATCACGT-3′) (Palumbi *et al.*, 1991) and the following polymerase chain reaction (PCR) profile: 94 °C for 150 s; ten cycles of 92 °C for 50 s, 40 °C for 30 s and 72 °C for 40 s; 36 cycles of 92 °C for 30 s, 40 °C for 40 s and 72 °C for 40 s; and 180 s at 72 °C. Amplification of *COI* was carried out using the primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer *et al.*, 1994) and the following PCR profile: 94 °C for 150 s; 42 cycles of 90 °C for 30 s, 44 or 48 °C for 1 min and 72 °C for 1 min; and 10 min at 72 °C. Amplification of *H3* was carried out using the primers H3aF (5′-ATGGCTCGTACCAAGCAGACVGC-3′) and H3aR (5′-ATATCC-TTRGGCATRATRGTGAC-3′) (Colgan *et al.*, 1998) and the following PCR profile: 94 °C for 180 s; 37 cycles of 94 °C for 30 s, 48 °C for 30 s and 72 °C for 50 s; and 180 s at 72 °C. Amplifications were purified using the Sigma GenElute PCR clean-up kit and sequenced bidirectionally by Macrogen Europe, The Netherlands.

Phylogenetic analyses

Thirty-nine species of *Portunus* (*s.l.*) were used for the molecular multigene analysis and 59 for the 16S rRNA analysis only. Contigs and consensus sequences were constructed using the program MEGA 6.0 (Tamura *et al.*, 2013). Sequences were uploaded to the GenBank database (Sayers *et al.*, 2009). Sequences were aligned using MUSCLE under default parameters in MEGA 6.0 (Tamura *et al.*, 2013). A concatenated alignment was created using FASconCAT v.1.0 (Kück & Meusemann, 2010). The alignment of 16S sequences was edited using G-block (Castresana, 2000; Talavera & Castresana, 2007). *COI* saturation was tested using DAMBE v.6.4.73 (Xia, 2013, 2017), and *COI* third positions were excluded. Partioned models for maximum likelihood (ML) and Bayesian information (BI) analyses were chosen using PartitionFinder v.2.1.1 (Stamakis, 2006; Guindon *et al.*, 2010; Lanfear *et al.*, 2017). The ML analyses were carried out using RAXML-ng, using a partioned model with the automatic bootstopping option and 0.03 cut-off (Kozlov *et al.*, 2018). Bayesian analyses were carried out using MrBayes-XSEDE for two million generations (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) as implemented on the Cipres Science Gateway (Miller *et al.*, 2010). Convergence was evaluated using TRACER v.1.6 (Rambaut *et al.*, 2014) Effective sample size (ESS) values of each run > 200. The phylogenetic trees (Figs 1, 2) were visualized using FigTree v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

Adult morphological characters

Most of the morphological characters included in the diagnoses have been used in previous studies (Crosnier, 1962; Apel & Spiridonov, 1998; Karasawa *et al.*, 2008; Ng *et al.*, 2008; Davie *et al.*, 2015a), with the terminology from those studies generally adopted here; for descriptions of the chelipeds, the terms suggested by Spiridonov *et al.* (2014) are used. Some characters have not previously received an extensive consideration. They particularly refer to the morphology of the male pleon and its contacts with neighbouring parts of the body. The second (separate) and the third (fused without or with sutures with the fourth and the fifth) pleomeres usually have crests, which in most cases are exposed ventrally and can be either laminar and ventrally visible at least on one (Fig. 3A, D) or both pleomeres (Fig. 3B), or low (Fig. 3E, F) and poorly expressed (Fig. 3C). The shape of the lateral and anterolateral margins of the third pleomere is also informative. These margins can be characterized as straight (Fig. 3A), slightly convex (Fig. 3B), convex (Fig. 3C) or concave (Fig. 3D). Pleomere crests are usually smooth, except in a few cases where they are serrated. The last thoracic episternite usually touches the pleon at its broadest part, and the morphology of the contact zone is variable. Usually, the terminal part of the episternite is thin and acute, and it fits in the narrow interspace between the exposed portion of the lateral margin of the third pleomere and the last

Table 1. Portunoid crabs used for molecular phylogenetic reconstruction and their GenBank accession numbers. Abbreviation: NA, not applicable.

Species (former name)	Genus	Subfamily	Voucher	*H3*	16S rRNA	*COI*
Achelous acuminatus	*Achelous*	Achelouinae	CCDB 1714	NA	MG515558[a]	NA
Achelous affinis	*Achelous*	Achelouinae	CCDB 3146	NA	MG515560[a]	NA
Achelous angustus	*Achelous*	Achelouinae	NHM[LA] 336-35	NA	MG515561[a]	NA
Achelous asper	*Achelous*	Achelouinae	ULLZ 9091	NA	MG515562[a]	NA
Achelous brevimanus	*Achelous*	Achelouinae	ULLZ 9078	NA	MG515566[a]	NA
Achelous depressifrons	*Achelous*	Achelouinae	ULLZ 4442	NA	DQ388064[b]	NA
Portunus floridanus	*Achelous*	Achelouinae	ULLZ 4695	NA	DQ388058[b]	NA
Achelous gibbesii	*Achelous*	Achelouinae	ULLZ 4565	NA	DQ388057[b]	NA
Achelous iridescens	*Achelous*	Achelouinae	CCDB 1624	NA	MG515567[a]	NA
Achelous minimus	*Achelous*	Achelouinae	ULLZ 8686	NA	MG515569[a]	NA
Achelous ordwayi	*Achelous*	Achelouinae	USNM 61174	NA	DQ388066[b]	NA
Achelous panamensis	*Achelous*	Achelouinae	CCDB 3145	NA	MG515570[a]	NA
Achelous pichilinquei	*Achelous*	Achelouinae	NHM[LA] 559-36	NA	MG515573[a]	NA
Achelous sebae	*Achelous*	Achelouinae	ULLZ 4527	NA	DQ388067[b]	NA
Achelous spinicarpus	*Achelous*	Achelouinae	MNHN-IU-2014-4014	NA	**OM388540**	**OM714490**
Achelous spinimanus	*Achelous*	Achelouinae	CCDB 4180	NA	MG515574[a]	NA
Achelous stanfordi	*Achelous*	Achelouinae	CCDB 1121	NA	MG515576[a]	NA
Achelous rufiremus	*Achelous*	Achelouinae	USNM 151568	NA	DQ388063[b]	NA
Achelous tuberculatus	*Achelous*	Achelouinae	CCDB 3147	NA	MG515577[a]	NA
Achelous tumidulus	*Achelous*	Achelouinae	UF32157	NA	KT365589[c]	KT365591[c]
Achelous xantusii	*Achelous*	Achelouinae	ULLZ 9077	NA	MG515579[a]	NA
Callinectes marginatus	*Callinectes*	Portuninae	UF11403	NA	KT365527[c]	KT365694[c]
Carcinus maenas	*Carcinus*	Carcininae	SMF32757	FM208811[d]	FM208763[d]	NA
Cavoportunus aff. *dubius*	*Cavoportunus*	Portuninae	MNHN-IU-2008-12565	**OM719714**	**OM388541**	**OM714491**
Cavoportunus dubius	*Cavoportunus*	Portuninae	MNHN-IU-2014-4099	**OM719715**	**OM388542**	**OM714492**
Charybdis feriata	*Charybdis*	Thalamitinae	UF3739	KT425051[c]	KT365538[c]	KT365712[c]
Charybdis variegata	*Charybdis*	Thalamitinae	ZRC2012.1115	KT425043[c]	KT365600[c]	KT365723[c]
Goniosupradens obtusifrons	*Charybdis*	Thalamitinae	UF16599	KT425007[c]	KT365544[c]	KT365720[c]
Cycloachelous euglyphus	*Cycloachelous*	Portuninae	MNHN-IU-2010-6249	**OM719716**	**OM388543**	**OM714493**
Cycloachelous granulatus	*Cycloachelous*	Portuninae	MNHN-IU-2014-10101	**OM719717**	**OM388544**	**OM714494**
Cycloachelous levigatus	*Cycloachelous*	Portuninae	MNHN-IU-2014-10093	**OM719718**	MZ127805[i]	**OM714495**
Cycloachelous orbitosinus	*Cycloachelous*	Portuninae	MNHN-IU-2010-6278	**OM719719**	MZ127809[i]	**OM714496**
Cycloachelous suborbicularis	*Cycloachelous*	Portuninae	MNHN-IU-2014-4061	**OM719720**	**OM388545**	**OM714497**
Geryon longipes	*Geryon*	Geryoninae	SMF32747	FM208828[d]	FM208776[d]	NA
Liocarcinus holsatus	*Liocarcinus*	Polybiinae	SMF32750	FM208817[d]	FM208766[d]	NA
Lupella forceps	*Achelous*	Achelouinae	USNM 284565	NA	FJ152155[e]	NA
Lupocycloporus gracilimanus	*Lupocycloporus*	Lupocyclinae	MNHN-IU-2014-10089	**OM719721**	KY524462[f]	**OM714498**
Lupocycloporus innominatus	*Lupocycloporus*	Lupocyclinae	MNHN-IU-2014-4124	**OM719722**	**OM388546**	**OM714499**
Macropipus tuberculatus	*Macropipus*	Polybiinae	MNHN B31440	FM208815[d]	FM208769[d]	NA

Table 1. Continued

Species (former name)	Genus	Subfamily	Voucher	*H3*	16S rRNA	*COI*
Monomia argentata	*Monomia*	Portuninae	MNHN-IU-2014-10076	**OM719723**	KY524480[f]	**OM714500**
Monomia calla	*Allomonomia*	Portuninae	MNHN-IU-2014-10105	**OM719724**	**OM388547**	**OM714501**
Monomia gladiator	*Monomia*	Portuninae	MNHN-IU-2014-10087	**OM719725**	KY524466[f]	**OM714502**
Monomia haani	*Monomia*	Portuninae	MNHN-IU-2014-10086	**OM719726**	KY524463[f]	**OM714503**
Monomia lecromi	*Allomonomia*	Portuninae	MNHN-IU-2014-4052	**OM719727**	**OM388548**	**OM714504**
Monomia petrea	*Monomia*	Portuninae	MNHN-IU-2014-4071	**OM719728**	**OM388549**	**OM714505**
Monomia lucida	*Monomia*	Portuninae	NHM[UK] 2017.402	**OM719729**	MG563792[g]	**OM714506**
Portunus anceps	*Achelous*	Achelouinae	UF32492	NA	KT365604[e]	NA
Portunus hastatus	*Achelous*	Achelouinae	SMF31989	FM208796[d]	FM208780[d]	NA
Portunus inaequalis	*Achelous*	Achelouinae	ULLZ 4756	NA	FM208752[d]	NA
Portunus pelagicus	*Portunus*	Portuninae	MNHN-IU-2014-1192	**OM719730**	**OM388550**	**OM714507**
Portunus sanguinolentus	*Portunus*	Portuninae	MNHN-IU-2014-1193	**OM719731**	NA	**OM714508**
Portunus sayi	*Portunus*	Portuninae	UF26156	NA	KT365607[e]	NA
Portunus ventralis	*Achelous*	Portuninae	UF32351	NA	KT365559[e]	KT365747[e]
Xiphonectes arabicus	*Eodemus*	Portuninae	UF7735	NA	KT365554[e]	KT365737[e]
Xiphonectes brockii	*Incultus*	Portuninae	MNHN-IU-2014-10102	**OM719732**	**OM388551**	**OM714509**
Xiphonectes guinotae	*Xiphonectes*	Portuninae	MNHN-IU-2014-4095	**OM719733**	NA	**OM714510**
Xiphonectes hastatoides	*Eodemus*	Portuninae	MNHN-IU-2014-10103	**OM719734**	**OM388552**	**OM714511**
Xiphonectes aff. *hastatoides*	*Eodemus*	Portuninae	MNHN-IU-2014-10104	**OM719735**	**OM388553**	**OM714512**
Xiphonectes iranjae	*Xiphonectes*	Portuninae	MNHN-IU-2014-4103	**OM719736**	**OM388554**	**OM714513**
Xiphonectes longispinosus	*Xiphonectes*	Portuninae	MNHN-IU-2014-4113	**OM719737**	**OM388555**	**OM714514**
*Xiphonectes*aff. *longispinosus*	*Xiphonectes*	Portuninae	MNHN-IU-2014-4064	**OM719738**	**OM388556**	**OM714515**
Xiphonectes pseudohastatoides	*Eodemus*	Portuninae	MNHN-IU-2014-10069	**OM719739**	KR026903[h]	**NA**
Xiphonectes pseudotenuipes	*Trionectes*	Portuninae	MNHN-IU-2013-15288	**OM719740**	**OM388557**	**OM714516**
Xiphonectes pulchricristatus	*Alionectes*	Portuninae	MNHN-IU-2014-10088	**OM719741**	KY524461[f]	**OM714517**
Xiphonectes rugosus	*Trionectes*	Portuninae	MV-J45389	**OM719742**	**OM388558**	**OM714518**
Xiphonectes spiniferus	*Trionectes*	Portuninae	MNHN-IU-2008-12615	**OM719743**	**OM388559**	NA
Xiphonectes macrophthalmus	*Xiphonectes*	Portuninae	MNHN-IU-2008-12584	**OM719744**	**OM388560**	**OM714519**
Xiphonectes tenuipes	*Trionectes*	Portuninae	MNHN-IU-2014-1191	**OM719745**	**OM388561**	**OM714520**
Xiphonectes tuberculosus	*Incultus*	Portuninae	MNHN-IU-2014-1187	**OM719746**	**OM388562**	NA
Xiphonectes unidens	*Eodemus*	Portuninae	MNHN-IU-2014-1190	**OM719747**	**OM388563**	**OM714521**

Sources of sequences:
[a]Mantelatto *et al.* (2018);
[b]Mantelatto *et al.* (2007);
[c]Evans (2018);
[d]Schubart & Reuschel (2009);
[b]Mantelatto *et al.* (2007);
[f]Koch *et al.* (2017);
[g]Koch & Ďuriš (2018);
[h]Koch & Ďuriš (2015a);
[i]Koch (2021); bold, present study.

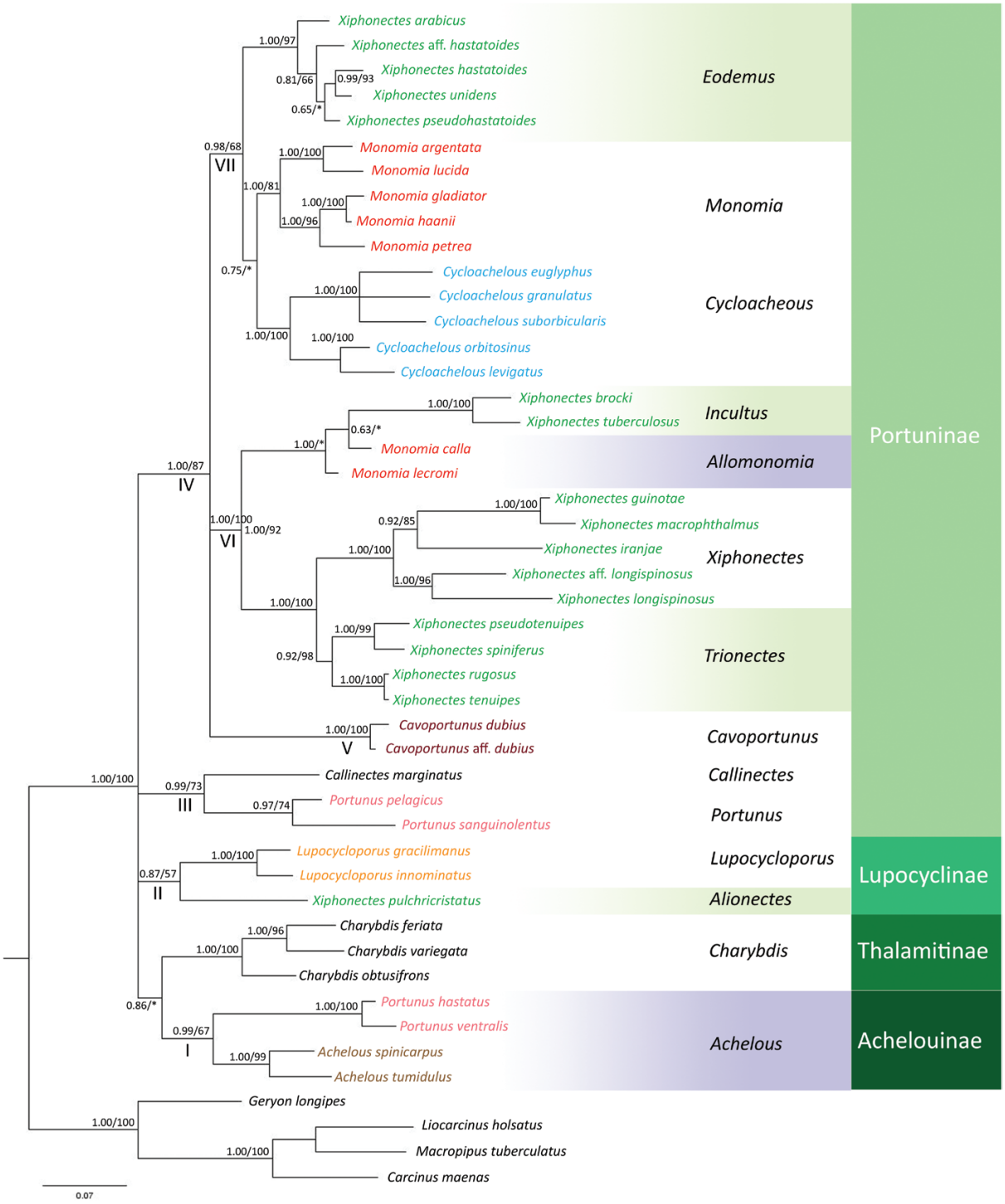

Figure 1. Bayesian inference phylogeny inferred from combined three gene sequences (histone *H3* nuclear gene and *COI* and 16S rRNA mitochondrial genes). Posterior probabilities and bootstrap support values (maximum likelihood/Bayesian inference) are shown at internodes. The colour of taxa names indicates generic affiliation.

(eighth) thoracic sternite (Fig. 3A, D). In less common cases, a broader terminal part of the episternite closely abuts the exposed part of the lateral margin of the third pleomere (Fig. 3E, F), sometimes forming a perfect coaptation (Lai *et al.*, 2010). Figure 3 illustrates also other characteristics used in the present study

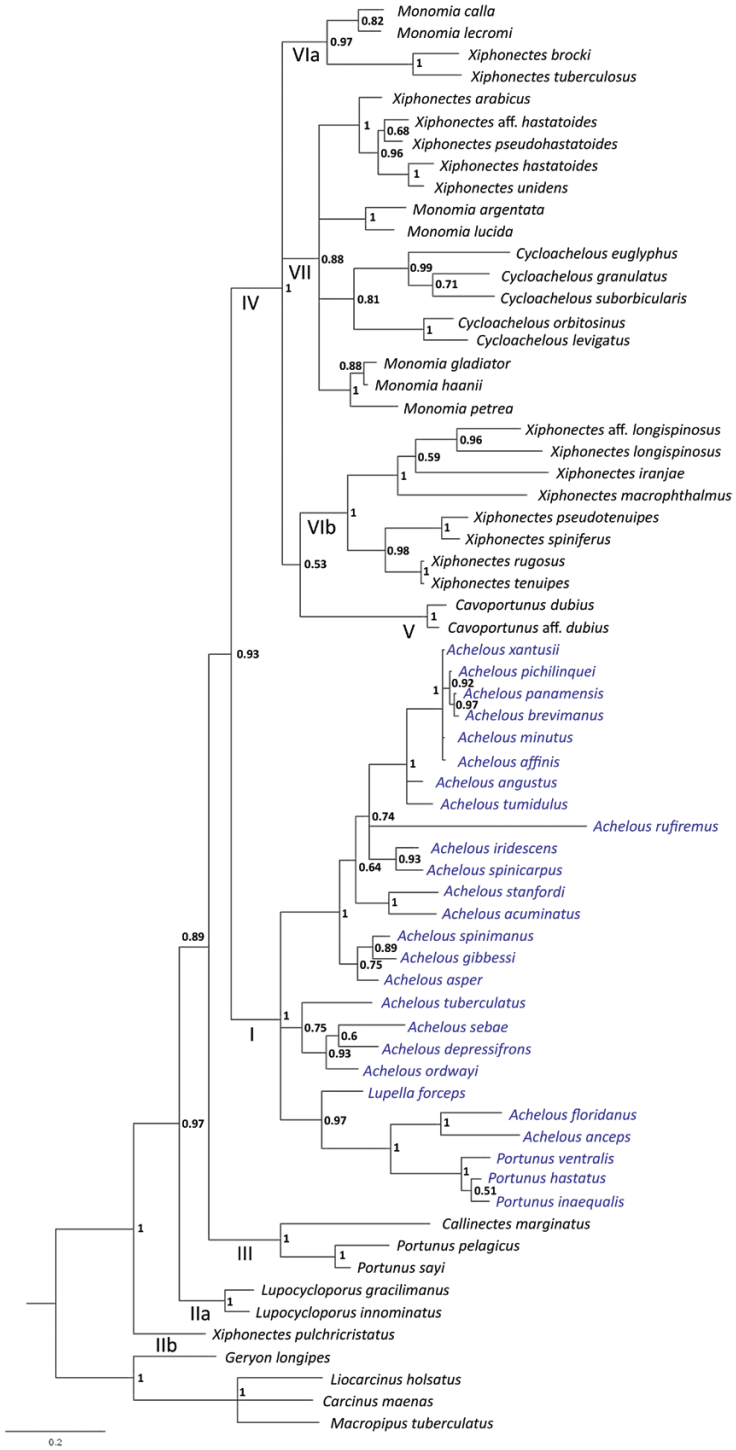

Figure 2. Bayesian phylogeny inferred from partial sequences of 16S rRNA mitochondrial gene. Posterior probabilities are shown at internodes. The blue colour of taxa names indicates geographical (Atlantic and eastern Pacific) affiliation comprising actual species in the genus *Achelous*.

for descriptions of the thoracic sternum and pleonal characters. However, the pleonal holding system, as reviewed in brachyuran crabs by Guinot & Bouchard (1998), was not examined closely in this study.

The first male gonopods, frequently used in carcinological literature (e.g. Stephenson & Campbell, 1959; Stephenson & Rees, 1967a, b; Williams, 1974; Sakai, 1976; Dai *et al.*, 1986; Dai & Yang, 1991; Yang *et al.*,

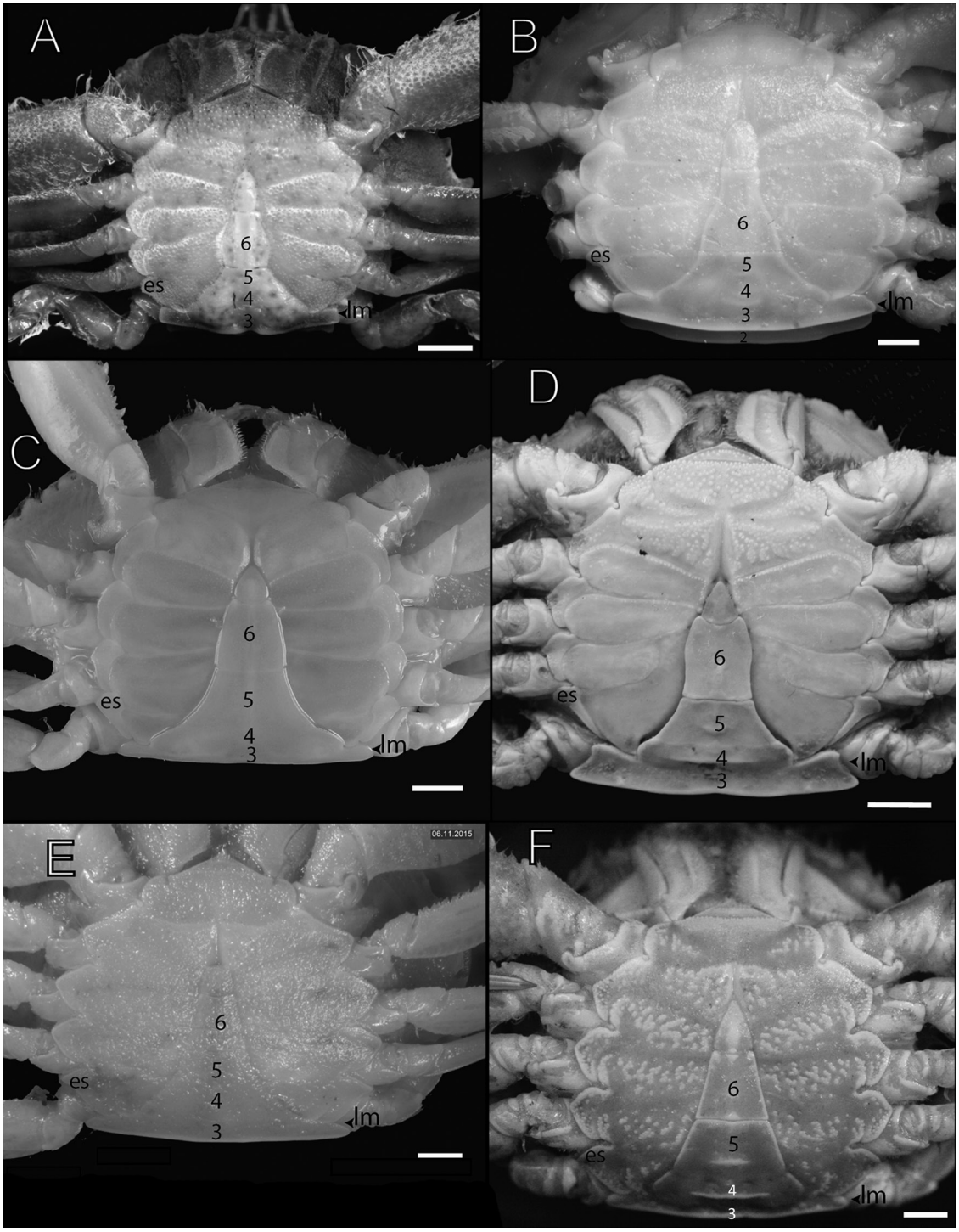

Figure 3. Characteristic examples of male pleon and surrounding sternal area. A, *Incultus alcocki* (Nobili, 1905), SMF 48040, Saudi Arabia, Red Sea. B, *Trionectes mariei* (Guinot, 1957), ZMMU Ma 3408, Egypt, Red Sea. C, *Portunus* aff. *sanguinolentus* (Herbst, 1783), NHCY148, Socotra I., Yemen, Arabian Sea. D, *Monomia haani* (Stimpson, 1858), ZIN RAN 71929, Vietnam, South China Sea. E, *Lupocycloporus gracilimanus* (Stimpson, 1858), ZMMU Ma 1974, Vietnam, South China Sea. F, *Lupocyclus rotundatus* Adams & White, 1848, ZMMU Ma 3451, Vietnam, South China Sea. Scale bars: 1 mm in A; 2 mm in B, C, E, F; 3 mm in D. Abbreviations: 2–6, pleonal segments 2–6; es, last thoracic episternite; lm, lateral margin of pleonal segment 3.

2012), were used in this study as an important tool to distinguish portunine taxa. The general gonopod shape and its relative size were recorded (e.g. long, slender; straight or curved; stout and hooked), but also the mutual position of the pair of the first gonopods in the pleonal cavity on the posterior thoracic sternum (e.g. subparallel, touching medially, overlapping each other medially by the bent region). The second male pleopods, varying in form among higher taxa (Davie *et al.*, 2015a), are scarcely commented on in the present study owing to their lower importance for portunine taxonomy.

The female vulvae (reviewed in detail by Guinot *et al.*, 2013) have already been used in portunid taxonomy by Apel & Spiridonov (1998). When describing these structures, we specifically point to the following characteristics: (1) the general shape, which can be rounded (Fig. 4A) or semi-rounded (Fig. 4E), elongately drop-like (Fig. 4B–D) or slit-like (Fig. 4E, G, H); (2) the relative size, which can be large, occupying a significant proportion of the proximal part of the genital sternite (Fig. 4A), medium (Fig. 4C–E) or small (Fig. 4B); (3) the orientation of the long axis, which can be subparallel (Fig. 4D) or subperpendicular (Fig. 4) to the anterior margin of the sternite, subparallel to the mesial margin of the sternite (Fig. 4G); and (4) the position inside the proximal part of the sternite (Fig. 4A–D) or on its margin, i.e. mesial or posteromesial (Fig. 4G, H).

Abbreviations

The following abbreviated terms are used in this report: CL, carapace length (in millimetres), measured as the median distance between the frontal border and the centre of the posterior border of the carapace; CW, the carapace width (i.e. the largest width, including the lateral teeth); ICZN, International Code of Zoological Nomenclature; IWP, Indo-West Pacific.

The abbreviated names of institutions are as follows: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; CCDB, Crustacean Collection, Department of Biology, University of São Paulo; MCZH, Museum of Comparative Zoology, Harvard University, Cambridge; MNHN, Muséum national d'Histoire naturelle, Paris; MV, Museum Victoria, Melbourne; NHCY, National History Collection of Yemen (deposited in SMF); NHM[LA], Natural History Museum of Los Angeles County; NHM[UK], Natural History Museum, London; NUS, National University of Singapore; OUMNH, Oxford University Museum of Natural History, Oxford; SMF, Senckenberg Museum, Frankfurt; UF, Florida Museum of Natural History, University of Florida, Gainesville; ULLZ, University of Louisiana, Lafayette; UO, University of Ostrava, Ostrava; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZIN RAN, Zoological Institute of Russian Academy of Sciences, St. Petersburg; ZMMU, Zoological Museum of Moscow State University, Moscow; ZMUC, Zoological Museum of University of Copenhagen, Copenhagen; ZRC, Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore.

RESULTS

Molecular analysis

The phylogenetic tree based on the combined dataset for three markers (Fig. 1) maintains all analysed species (43 spp. from seven up-to-date genera of Portuninae, one genus of Thalamitinae and one genus of Lupocyclinae) in a clade, clearly separated from the outgroup species of *Carcinus* Leach, 1814 (Carcininae), *Liocarcinus* Stimpson, 1858 and *Macropipus* Prestandrea, 1833 (Polybiinae) and *Geryon* Krøyer, 1837 (Geryonidae). The ingroup is composed of a basal polytomy of four major branches, with subsequent subdivisions of the latter to a total of 14 well-supported terminal clades, each representing a single traditional or newly established genus.

Clade I (Fig. 1) contains two subclades: (1) Atlantic species of *Portunus* [*Portunus hastatus* (Linnaeus, 1767) and *Portunus ventralis* (A. Milne-Edwards, 1879)] in a sister position to two representatives of the amphi-American portunine genus *Achelous*; and (2) three species of the thalamitine genus *Charybdis* De Haan, 1933. Clade II comprises species of *Lupocycloporus* (Lupocyclinae) and a single species of the portunine genus *Xiphonectes* (*Xiphonectes pulchricristatus* Gordon, 1931). Clade III contains two further species of *Portunus*, including *P. pelagicus*, the type species of the genus, together with one species of *Callinectes*.

The last clade (IV) of the basal polytomy is purely portunine and comprises the remaining majority of analysed species of the subfamily, divided into three subclades (V–VII). Subclade V contains a single genus, *Cavoportunus*. Subclade VI is predominantly composed of *Xiphonectes*, revealing two or three basally well-supported independent lineages; one of them [*Xiphonectes brockii* (De Man, 1887) and *Xiphonectes tuberculosus* (A. Milne-Edwards, 1861)] is in a sister position to two species of *Monomia* [*Monomia calla* Koch, Nguyen & Ďuriš, 2015 and *Monomia lecromi* (Moosa, 1996)], while the second clade contains *Xiphonectes longispinosus* (Dana, 1852), the type species of *Xiphonectes*. Subclade VII covers the remaining included *Xiphonectes* species and species of *Monomia* [including the type species *Monomia gladiator* (Fabricius, 1798)] and *Cycloachelous*.

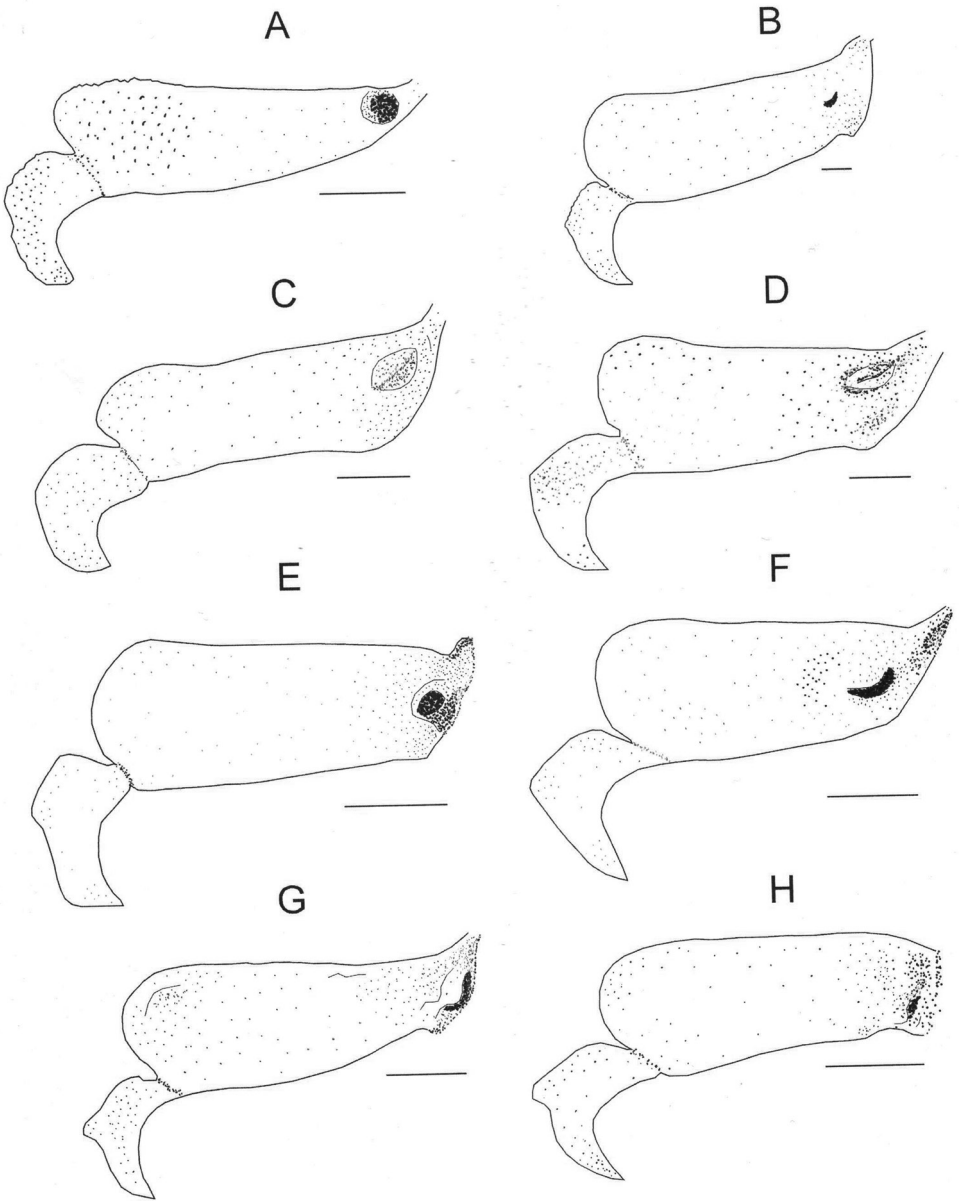

Figure 4. Characteristic examples of female genital sternites (with episternites) and genital openings. A, *Alionectes pulchricristatus* (Gordon, 1931), syntype NHM 1930.12.2.82/85, Hong Kong, China, South China Sea. B, *Portunus sanguinolentus* (Herbst, 1783), ZMMU Ma 3536, Vietnam, South China Sea. C, *Trionectes mariei* (Guinot, 1957), ZMMU Ma 3535, Vietnam, South China Sea. D, *Achelous spinimanus* (Latreille, 1819), ZMMU Ma 4848, Gulf of Mexico, Campeche Bank, Mexico. E, *Incultus tuberculosus* (A. Milne-Edwards, 1861), NHM 1925.2.25.14/16, Gulf of Oman, Oman. F, *Cycloachelous granulatus* (H. Milne Edwards, 1834), SMF 3852, Ternate I., Indonesia, Molucca Sea. G, *Monomia gladiator* (Fabricius, 1798), SMF 47994, Saudi Arabia, Red Sea. H, *Eodemus arabicus* (Nobili, 1905), ZMUC CRU-943, Bahrain, Persian Gulf. Scale bars: 1 mm.

Thus, the three-marker analysis performed here (Fig. 1) reveals the polyphyletic state of three current portunine genera: *Monomia*, *Portunus* and *Xiphonectes*. The analysed members of the non-portunine genera (i.e. *Achelous*, *Charybdis* and *Lupocyloporus*) are nested in a common polytomy with the apparently paraphyletic subfamily Portuninae.

The phylogenetic tree based on the single mitochondrial 16S rRNA marker (Fig. 2) includes a series of taxa not covered by the three-marker analysis, namely the majority of *Achelous* spp., *Lupella forceps* (Fabricius, 1793) and further species of *Portunus* [i.e. *Portunus inaequalis* (Miers, 1881) and *Portunus sayi* (Gibbes, 1850)], as currently defined. Most of

the established partial clades from the three-marker analysis, considered to be monophyletic groupings, are consistently revealed also in the 16S analysis. The Atlantic species *P. sayi* is here positioned together with its IWP congener *P. pelagicus*, the type species of the genus [*Portunus sanguinolentus* (Herbst, 1783) was not analysed in the 16S phylogeny], and both are in a sister position to the representative of *Callinectes*, *Callinectes marginatus* (A. Milne-Edwards, 1861). Also, the general clade of the main diversity of previous *Portunus* spp. (clade IV) comprises the majority of taxa revealed also by the three-marker tree, although clade VI is divided in the 16S analysis into two separate clades with an unresolved mutual relationship and placed in a common polytomy with clades V (*Cavoportunus*) and VII (*Cycloachelous*/*Monomia*/some *Xiphonectes* spp.).

In the 16S analysis, clade I containing the majority of taxa not covered in the three-gene phylogenetic reconstruction confirms the paraphyletic state of the amphi-American genus *Achelous*, which in the 16S study forms two basally supported clades positioned as a common polytomy with the third supported clade; the latter comprises *Lupella forceps* basally separated from *Achelous floridanus* and five further current *Portunus* species [i.e. *Portunus anceps* (de Saussure, 1857), *P. hastatus*, *P. inaequalis* and *P. ventralis*].

Both phylogenetic analyses consistently point to the polyphyletic character of *Portunus* [= the subgenus *Portunus* (*Portunus*), as listed by Ng *et al.* (2008)], and of *Monomia* and *Xiphonectes* (Portuninae), while the 16S analysis additionally indicates the paraphyletic composition of *Achelous* (Acheloiunae).

Morphological analyses

All the partial monophyletic assemblages revealed by our molecular analyses were compared for their morphological similarities or differences, with closer attention being paid to newly revealed groups of species separated from their currently assigned genera, but also to the remaining compositions of the current genera restricted here. The comparisons, mainly based on details of the carapace, chelae and secondary sexual structures, provided valuable morphological support for the multiple separated species complexes highlighted by the phylogenetic molecular analyses. The species composition of some earlier-established genera (i.e. *Achelous*, *Cavoportunus*, *Cycloachelous* and *Lupocycloporus*) has to be retained or even extended, whereas the previously species-rich *Monomia*, *Portunus* and *Xiphonectes* are here restricted in species number. Their diagnoses are revised, and new genera in the subfamilies Lupocyclinae and Portuninae are established. The application of molecular results, along with support from comparative morphological analyses of the new arrangement of portunid genera, is presented and discussed below.

SYSTEMATICS

Infraorder Brachyura Linnaeus, 1758

Superfamily Portunoidea Rafinesque, 1815

Family Portunidae Rafinesque, 1815

Subfamily Achelouinae Spiridonov, 2020

Achelous De Haan, 1833

(Figs 4D, 5)

= *Portunus* (*Achelous*) De Haan, 1833 (type species *Portunus spinimanus* Latreille, 1819, by monotypy; gender masculine).
= *Portunus* (*Hellenus*) A. Milne Edwards, 1874 (type species *Achelous spinicarpus* Stimpson, 1871, subsequent designation by Rathbun, 1930; gender masculine).
= *Lupella* Rathbun, 1897 (type species *Cancer forceps* Fabricius, 1793, by monotypy; gender feminine).

Included species: Twenty-eight.
Achelous acuminatus Stimpson, 1871
Achelous affinis Faxon, 1893
Achelous anceps (de Saussure, 1858) comb. nov.
= *Lupea anceps* de Saussure, 1858
= *Lupea duchassagni* Desbonne in Desbonne & Schramm, 1867
= *Neptunus sulcatus* A. Milne-Edwards, 1879
Achelous angustus (Rathbun, 1898)
= *Portunus* (*Achelous*) *angustus* Rathbun, 1898
Achelous asper (A. Milne-Edwards, 1861)
= *Neptunus asper* A. Milne-Edwards, 1861
= *Achelous transversus* Stimpson, 1871
= *Amphitrite paucispinis* Lockington, 1877
Achelous binoculus (Holthuis, 1969)
= *Portunus binoculus* Holthuis, 1969
Achelous brevimanus Faxon, 1895
Achelous depressifrons (Stimson, 1859)
= *Amphitrite depressifrons* Stimpson, 1859
= *Portunus* (*Achelous*) *bahamensis* Rathbun, 1930
Achelous floridanus (Rathbun, 1930)
= *Portunus* (*Achelous*) *floridanus* Rathbun, 1930
Achelous forceps (Fabricius, 1793) comb. nov.
= *Cancer forceps* Fabricius, 1793
= *Lupa leachii* De Haan, 1833
Achelous gibbesii (Stimpson, 1859)
= *Lupa gibbesii* Stimpson, 1859
Achelous guaymasensis (Garth & Stephenson, 1966)
= *Portunus guaymasensis* Garth & Stephenson, 1966
Achelous hastatus (Linnaeus, 1767) comb. nov.
= *Cancer hastatus* Linnaeus, 1767
= *Cancer ponticus* Herbst, 1790
= *Portunus dufourii* Latreille, 1819
= *Eriphia prismaticus* Risso, 1827
= *Neptunus hastatus* var. *rubromaculatus* Steinitz, 1932
Achelous inaequalis (Miers, 1881) comb. nov.

= *Neptunus* (*Amphitrite*) *inaequalis* Miers, 1881
Achelous iridescens (Rathbun, 1894)
= *Neptunus* (*Hellenus*) *iridescens* Rathbun, 1894
Achelous isolamargaritensis (Türkay, 1968)
= *Portunus* (*Achelous*) *floridanus isolamargaritensis* Türkay, 1968
Achelous minimus (Rathbun, 1898)
= *Portunus* (*Achelous*) *minimus* Rathbun, 1898
= *Portunus* (*Achelous*) *pichilinquei* Rathbun, 1930
Achelus ordwayi Stimpson, 1860
= *Neptunus cruentatus* A. Milne-Edwards, 1861
= *Portunus aurimanus* Gundlach & Torralbas, 1900
Achelous panamensis Stimpson, 1871
Achelous rufiremus (Holthuis, 1959)
= *Portunus rufiremus* Holthuis, 1959
Achelous sebae (H. Milne Edwards, 1834)
= *Lupea sebae* H. Milne Edwards, 1834
= *Lupa biocellata* Gundlach & Torralbas, 1900
Achelous spinicarpus Stimpson, 1871
Achelous spinimanus (Latreille, 1819)
= *Portunus spinimanus* Latreille, 1819
= *Lupa banksii* Leach, 1816
= *Achelous spinimanus smithii* Verrill, 1908
= *Portunus vossi* Lemaitre, 1991
Achelous stanfordi (Rathbun, 1902)
= *Portunus* (*Achelous*) *stanfordi* Rathbun, 1902
Achelous tuberculatus Stimpson, 1860
Achelous tumidulus Stimpson, 1871
Achelous ventralis (A. Milne-Edwards, 1879) comb. nov.
= *Neptunus ventralis* A. Milne-Edwards, 1879
Achelous xantusii Stimpson, 1860

Diagnosis: Carapace (Fig. 5A) approaching hexagonal shape, > 1.5 times as broad as long; dorsal surface finely granulate, with regions moderately demarcated, often with ridges or patches of granules in centre of regions; urogastric depression distinctly posterior to half-length of carapace. Front (Fig. 5B) with four triangular or rounded lobes. Orbit ellipsoidal; supraorbital margin with relatively deep median and reduced lateral fissures. Inner supraorbital lobe often truncate or subdivided into two teeth or lobes. Infraorbital margin with broad notch. Anterolateral margin with nine spiniform teeth: anterior eight ones subequal in size; last tooth lateral, large, in most cases two or more times longer than other teeth. Posterolateral junction of carapace usually rounded. Sutures (Fig. 5C) on thoracic sternum well developed; thoracic sternites partly granular. Chelipeds with merus bearing three to five spines on anterior border, unarmed or with one spine distally on posterior border; carpus with single spine on outer face and spine on inner face that can be extremely long; upper surface of palm with two or three teeth including usual tooth near articulation with carpus; chelae (Fig. 5D) costate, moderately unequal and heterodontic; in larger chela, molariform tooth present proximally on cutting edge of dactylus. Dactyli of pereiopods 2–4 ensiform or cultriform, rarely lanceolate, usually markedly costate; setose on ventral margin. Merus of pereiopod 5 distinctly longer than broad, posterodistal spine present but may be obsolete. Male pleon (Fig. 5C) narrowly triangular; crest on third pleomere moderately laminar; lateral margins of third pleomere straight or convex; terminal part of posterior thoracic episternite fills interspace between anterior margin of pleomere 3 and thoracic sternite 8; third to fifth terga fused but unclear sutures may remain, combined part usually with keels, subequal to sixth pleomere; sixth pleomere with lateral margins straight or sinuous, convergent distally. Telson elongately triangular. First male (Fig. 5E) gonopod of moderate length, arched or sinuous; basal part robust, lying obliquely inwards; distal part moderately slender, curved anterolaterally and tapering distally to slender tip; pair of first gonopods not touching medially in pleonal cavity. Female vulva (Fig. 4D) elongately drop-like, with long axis usually almost parallel to anterior margin of sternite.

Systematic position: The clade of four *Achelous* species analysed in the present three-marker study (Fig. 1; as *Achelous* or *Portunus*) is in a sister position to the thalamitine genus *Charybdis*. Their combined clade is nested within the basal polytomy of the four clades [i.e. together with the clade of the lupocycline *Lupocycloporus* and the new genus *Alionectes*, the clade of the portunine *Portunus* (*s.s.*) and *Callinectes*] and with the joint clade of all remaining IWP genera previously included in *Portunus* (*s.l.*). The true phylogenetic relationship of those four clades thus remains unresolved at present, and the subfamily composition of the family Portunidae remains provisional owing to the paraphyly or polyphyly of the subfamily Portuninae itself.

In none of the recent molecular phylogenetic reconstructions (Spiridonov *et al.*, 2014; Evans, 2018; Mantelatto *et al.*, 2018; present study) is *Achelous* shown as related to *Portunus*, the nominotypic genus of subfamily Portuninae. *Achelous* and *Lupella* (see discussion on the latter genus below) are distinguished by a peculiar set of morphological characters, with some apparent plesiomorphies (e.g. sutures still visible on fused male pleomeres 3–5) and apomorphies (e.g. a tendency for a long inner spine on the cheliped carpus). For these reasons, Spiridonov (2020) has recently separated these two genera into a new subfamily Achelouinae. This was also regarded as a step towards purifying the concept of Portuninae, which remains most probably paraphyletic, even with *Achelous* excluded.

In the present 16S analysis (Fig. 2), all *Achelous* species form a well-supported clade of mixed Atlantic

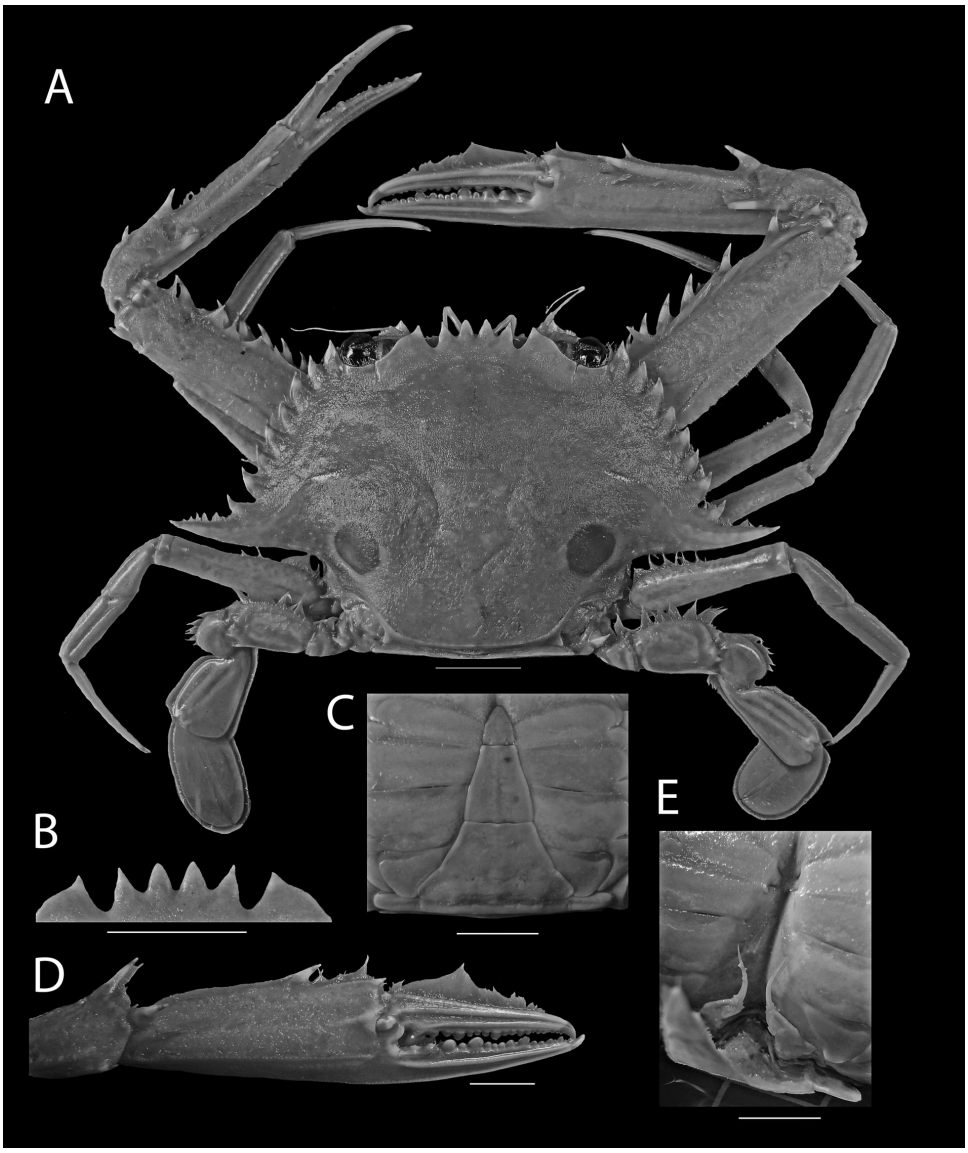

Figure 5. *Achelous sebae* (H. Milne Edwards, 1834), male, CW 71 mm, MNHN-IU-2014-4026, Guadeloupe, W. Atlantic. A, total view. B, front. C, pleon. D, right chela, outer view. E, first pair of gonopods, shape and position. Scale bars: 10 mm.

and eastern Pacific representatives together with *Lupella forceps* and some Atlantic '*Portunus*' species. This is consistent with the phylogenetic results in the studies of Evans (2018) and Mantelatto *et al*. (2007, 2009, 2018). The systematic position of those *Lupella* or '*Portunus*' taxa, however, remained unresolved in these papers.

Lupella forceps was considered to be a portunine crab with distinctively slender and long chelipeds in adult males (Rathbun, 1930; Taissoun, 1973), but otherwise not principally differing from *Achelous* (e.g. Rathbun, 1930; Monod, 1956; Garth & Stephenson, 1966) in either carapacial morphology or the shape of the male pleon and the first gonopods. The chelipeds of *Lupella forceps* bear uniquely long and slender ('filiform', see Rathbun, 1930: 133) fingers, about three times longer than the short palm in adult males, whereas in females those fingers are filiform too, but distinctly shorter, only slightly longer than the palm (Taissoun, 1973). Some *Achelous* species also possess chelae with fingers subequal to the palm length (e.g. *Achelous tuberculatus*, *Achelous spinimanus* and *Achelous xantusii*). The remarkable chelae of *Lupella forceps* are therefore best regarded as a species-specific apomorphy. Besides that character, *Lupella* does not differ materially from *Achelous*. The male first gonopods are short, basally stout and distally bent, slender and tapering; similar in shape to those of *Achelous spinicarpus* or *Achelous inaequalis*, for example, whereas

the gonopods might be more slender, sinuate and with the apex recurved in some other *Achelous* species (e.g. *Achelous gibbesii*, *Achelous hastatus* or *Achelous spinimanus*; see Monod, 1956; Taissoun, 1973). The male pleon is elongately triangular in *Lupella forceps*, with a feebly convex, distally tapering sixth segment, whereas in *Achelous* it is generally shorter, with convex sides of the sixth segment; the pleon of *Achelous anceps* is, however, similar to that of *Lupella* (see Rathbun, 1930; Taissoun, 1973). The general outline of the carapace is variable in *Achelous*, from subhexagonal, with long lateral teeth, to semicircular, with those teeth not noticeably larger than the preceding teeth (Rathbun, 1930). As is evident from published photographs and figures of the dorsal structures of a fairly flattened carapace (Monod, 1956; Rathbun, 1930; Taissoun 1973), the epibranchial ridge surrounding the somewhat swollen metagastric region is most prominent and is highly arched in most *Achelous* species; but in *Lupella forceps* the ridge is straight and slightly oblique.

In the present single-marker molecular analysis, *Lupella forceps* is nested in a clade with five species of *Portunus* [as listed by Mantellato *et al*. (2007, 2018)], all affiliated into *Achelous* (*Achelous anceps*, *Achelous floridanus*, *Achelous hastatus*, *Achelous inaequalis* and *Achelous ventralis*) in this study. These five species do not differ morphologically from the remaining *Achelous* species and are, to a similar extent, variable in carapace shape (hexagonal or semicircular), chelipeds or the male pleon. The male first gonopods in this group also are of both types (see Monod, 1956: figs 227–231) discussed above. Based on the morphological arguments (above) and the present molecular support, we propose here to transfer *Lupella forceps* to *Achelous*, with placement of the generic name *Lupella* into the synonymy of the genus. Nevertheless, the taxonomic position of *Lupella* and closer taxa might be tested in the future by means of wider molecular analyses.

A series of species up to now considered to be '*Portunus*' or '*Portunus* (*Portunus*)' [as listed by Mantelatto *et al.* (2018) or Evans (2018), respectively], and here transferred to *Achelous* (see below), are superficially similar to the genus *Portunus* (*s.s.*) in having a relatively broad carapace and a single tooth on the posterior border of the cheliped merus. *Portunus* (*s.s.*) differs from *Achelous* by the triangular pleon with a rounded telson apex (Fig. 15C) vs. with a sharp telson apex (Fig. 5C) and by the male gonopods, which are straight and thread-like (Fig. 15E) vs. distinctly shorter, arched (Fig. 5E).

Most *Achelous* spp. also have a distinct tooth on the posterior margin of the merus of the last pereiopods (Fig. 5A). Although reduced in some *Achelous* species, this character is shared by this genus and the taxa of the lupocycline clade in the present analyses consisting of *Alionectes* and *Lupocycloporus* (Figs 6A, 7A; see below).

Remarks: The current composition of *Achelous* consists of species distributed in the Atlantic and the eastern Pacific. Among them, some species from the previous nominotypic subgenus *Portunus* (as listed by Ng *et al.*, 2008) are also present. The support for separating most of them into a taxon distinct from the mostly IWP *Portunus* (*Portunus*) has already been highlighted by the molecular results of Mantelatto *et al*. (2007, 2009, 2018); the separate biogeographical affiliations also sustain such subdivision.

Mantelatto *et al.* (2009) elevated six species from the subgenus *Achelous* to generic level. Three others were transferred there from the subgenus *Portunus*, and one from the genus *Cronius* Stimpson, 1860. Mantelatto *et al.* (2009) suggested the position of a group of four Atlantic *Portunus* species (i.e. *Achelous anceps*, *Achelous floridanus*, *Achelous hastatus* and *Achelous ventralis*) to be unclear owing to their basal separation from the main assemblage of species of their genus. In a subsequent study, Mantelatto *et al.* (2018) revealed an isolated position for *Portunus anceps*, whereas in the former study it was placed among the other *Achelous* species mentioned above in this paragraph. This is also the case for our 16S analysis (Fig. 2), where these four species form an isolated but basally well-supported clade together with two other Atlantic species, *Achelous inaequalis* and *Achelous forceps* (= previously *Lupella forceps*). In the recent systematic account of the Brazilian portunids, Rodrigues *et al.* (2017) retained *Achelous anceps*, *Achelous floridanus* and *Achelous ventralis* in the genus *Portunus* based on a morphological distinction between *Achelous* and *Portunus* originally proposed by Verrill (1908): dactyli of pereiopods 2–4 ensiform or cultriform, markedly costate vs. relatively broad, lanceolate, leaf-like or cultriform, indistinctly costate. Given that there is no substantial morphological distinction between these three species and *Achelous hastatus* from the genus *Achelous*, we regard them as being congeneric.

Four species of *Portunus* (*Portunus*) or *Portunus* (*Achelous*) [as listed by Ng *et al.*, 2008; i.e. *P.* (*P.*) *acuminatus*, *P.* (*P.*) *affinis*, (*P.*) *P. xantusii* and *P.* (*A.*) *floridanus*] were originally affiliated with the genus *Achelous* (see: Stimpson, 1860, 1871; Faxon, 1893; Rathbun, 1930). Given that they agree with the main diagnostic characters of the genus, Mantelatto *et al.* (2018) resurrected their original generic name for the first three of these. Recently, Marco-Herrero *et al.* (2021) have also listed the remaining species, *P.* (*A.*) *floridanus*, under the generic name *Achelous* but left *Achelous gibbesii* under *Portunus*, despite its new affiliation already provided by Mantelatto *et al.* (2009).

A further *Portunus* species, the eastern Pacific *Achelous minimus*, has never before been included in *Achelous*, but was regarded as a subspecies of *Portunus xantusii* by Garth & Stephenson (1966), which was originally in

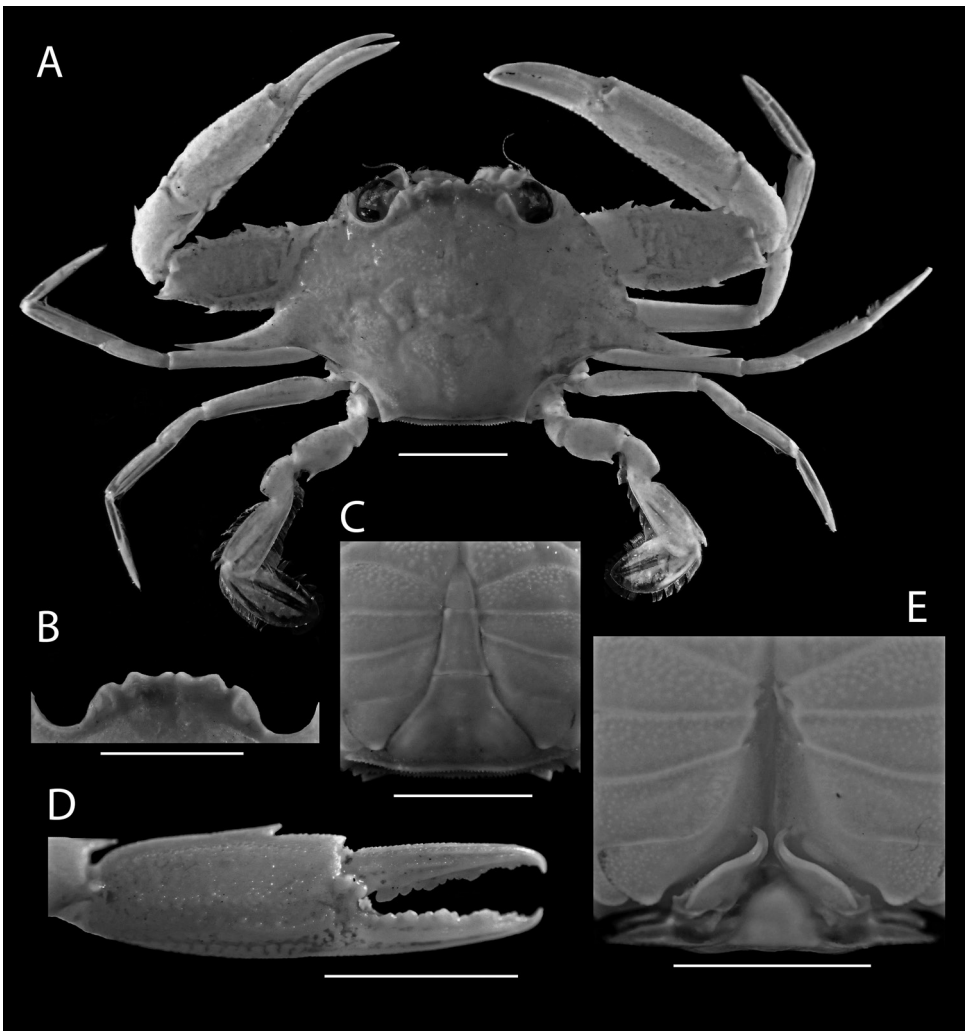

Figure 6. *Alionectes pulchricristatus* (Gordon, 1931), male, CW 26 mm, MNHN-IU-2014-10088, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, first pair of gonopods, shape and position. Scale bars: 5 mm.

Achelous (see Stimpson, 1860; above). It is transferred here to *Achelous* based on the morphology of its male pleon and gonopods (see Garth & Stephenson, 1966).

Size: Mostly medium-size portunids; maximum recorded size (CL × CW) ranges from 13.8 mm × 32.4 mm in *Achelous tuberculatus* to 65.0 mm × 110.0 mm in *Achelous spinimanus* (Verrill, 1908; Rathbun, 1930; Garth & Stephenson, 1966; Williams, 1984).

Ecological notes: *Achelous* spp. generally occur from the upper subtidal zone to a depth of 200 m, with most species having a relatively broad depth range [Verrill, 1908; Rathbun, 1930; Garth & Stephenson, 1966; Williams, 1984; de Melo, 1996; Rodrigues *et al.*, 2017; i.e. from 0 to 500–550 m in *Achelous spinicarpus* and *Achelous spinimanus* (see Holthuis, 1959; de Melo, 1996) or even to 640 m in *Achelous floridanus* (see Williams, 1984)]. They are not usually reported from estuaries, except for *Achelous inaequalis* in West Africa (Manning & Holthuis, 1981). These crabs prefer mostly soft, often mixed substrates and sometimes hard bottoms with algae or seagrass (in the upper subtidal zone) or sessile macrofauna (Garth & Stephenson, 1966; de Melo, 1996). Several species were found swimming in the water column or on flotsam (i.e. Sargasso seaweed; Verrill, 1908; Rathbun, 1930; Garth & Stephenson, 1966; Jerde, 1967), which implies an important role of swimming in their ecology.

Geographical range: Tropical and subtropical West and East Atlantic, Mediterranean and Tropical East

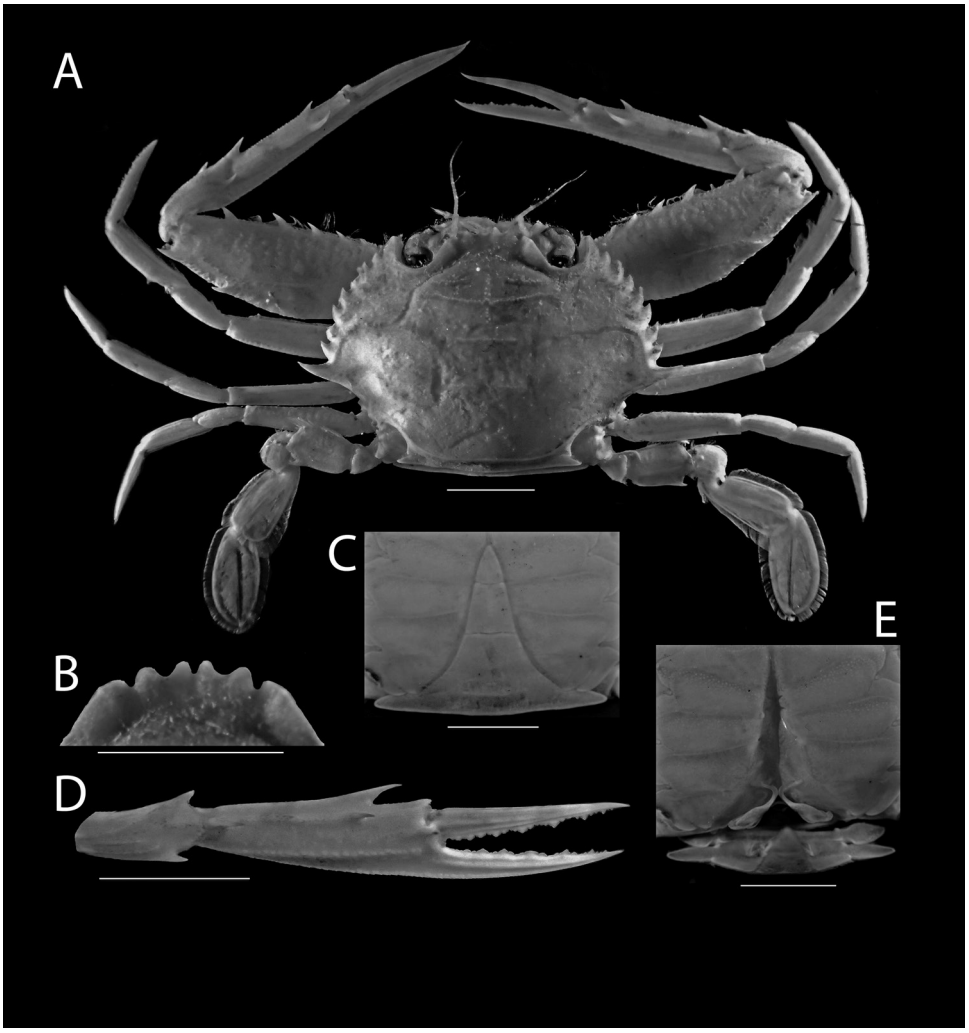

Figure 7. *Lupocycloporus gracilimanus* (Stimpson, 1858), male, CW 24.2 mm, MNHN-IU-2014-1184, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

Pacific (Rathbun, 1930; Garth & Stephenson, 1966; Manning & Holthuis, 1981; d'Udekem d'Acoz, 1999).

SUBFAMILY LUPOCYCLINAE PAULSON, 1875

***ALIONECTES* GEN. NOV.**

(FIGS 3A, 4A, 6)

Zoobank registration: urn:lsid:zoobank.org:act:5946851F-6789-4AF3-8DB9-B609146580ED
Type species: Neptunus (*Hellenus*) *pulchricristatus* Gordon, 1931, by present designation.

Included species: Two.
Alionectes pulchricristatus (Gordon, 1931) comb. nov.
= *Neptunus* (*Hellenus*) *pulchricristatus* Gordon, 1931
= *Neptunus* (*Hellenus*) *alcocki* Gordon, 1930 [preoccupied name, primary junior homonym of *Neptunus* (*Hellenus*) *alcocki* Nobili, 1906]
Alionectes spinipes (Miers, 1886) comb. nov.
= *Neptunus* (*Amphitrite*) *spinipes* Miers, 1886

Diagnosis: Carapace (Fig. 6A) broadly hexagonal, with outline of anterior half semicircular; width (without last lateral teeth) ~1.5 × length; dorsal surface convex; regions feebly developed. Front (Fig. 6B) with four blunt triangular lobes projecting beyond tip of inner supraorbital lobe. Orbits large, circular, with inner supraorbital lobe rounded; upper border of orbit deep, without fissures; infraorbital margin with subrectangular shallow lateral notch. Anterolateral margin of carapace with nine teeth: eight anterior ones low, triangular or almost reduced, unequal in size; last tooth distinctly larger, lateral. Posterolateral junction of carapace subrectangular, slightly produced, pointed. Sutures of thoracic sternum well expressed; suture between thoracic sternum 6 and 7 developed in males and interrupted in females;

suture 7/8 interrupted in males and almost fused in females. Thoracic sternites granular (Fig. 6C). Merus of third maxilliped rounded distally, not produced anterolaterally. Chelipeds relatively robust; merus bearing three spines on anterior border and two spines distally on posterior border; carpus with outer spine. Chelae (Fig. 6D) moderately unequal, heterodontic; palm with longitudinal serrated carinae, inner dorsal carina with one or two distal spines, proximal spine over articulation with carpus sharp or obsolete. In larger chela, well-developed molariform tooth present. Dactyli of pereiopods 2–4 cultriform, setose with fine plumose setae; merus of pereiopod 5 distinctly longer than broad; posterior margin with distal spine. Male pleon (Figs 3A, 6C) triangular, elongate, regularly tapering distally; pleomeres 2 and 3 forming low subequal crests, with at least second pleomere with crest marginally serrated. Lateral part of pleomere 3 in coaptation with terminal part of last thoracic episternite; third to fifth pleomere terga fused, without trace of sutures and keels; sixth pleomere elongate, tapering distally. First male (Fig. 6E) gonopod relatively short and robust proximally; arched and steeply tapering distally to the slender tip; pair of first gonopods lying obliquely directed inwards, touching subdistal parts, with apices directed anterolaterally. Female vulva (examined in *Alionectes pulchricristatus*; Fig. 3A) located in medial part of proximal portion of sternite, rounded, occupying more than one-third of sternite length, with long axis nearly perpendicular to anterior edge of sternite.

Etymology: An arbitrary combination of the suffix of the name '*Xiphonectes*' [from Greek, νεκτες, received] and the Latin *alio*, other, to point it out as 'another genus derived from *Xiphonectes*'; gender masculine.

Systematic position: The species of *Alionectes* were previously included in *Xiphonectes*, sharing with the latter, and with the new genera *Eodemus*, *Incultus* and *Trionectes*, a general body appearance with the carapace flattened and the similarly produced posterior anterolateral tooth, and the produced or subacute angle formed by the posterolateral and posterior margins. *Alionectes* is unique among these five genera mainly by the large circular orbits without dorsal fissures, by the distinct posterodistal tooth on the merus of the swimming leg and by the serrated margin of the transverse crest of the second (or also third) pleonal somites in males. The species of this genus, together with *Eodemus*, possess two posterodistal spines on the cheliped merus (vs. a single spine in *Incultus* and *Xiphonectes*, or one or two spines in *Trionectes*). The first male gonopods are, unlike those in the other four genera compared here, relatively short and proximally robust, and obliquely touch along their out-curved subdistal parts (for comparison of the gonopod shape and position, see the respective paragraph regarding *Incultus*).

In the present phylogenetic analysis (Fig. 1), the representative of *Alionectes* occupies a position remote from the morphologically similar genera listed above, but in a sister position to *Lupocycloporus*. Both genera share a posterodistal spine on the merus of the last pereiopod (a character possessed by *Lupocyclus* Adams & White, 1848 and, despite being reduced, also by *Achelous*, along with the subfamily Thalamitinae; see Apel & Spiridonov, 1998), the subtriangular shape of the male pleon, the coaptation of the terminal part of the last thoracic episternite and the anterolateral margin of the third pleomere (shared also with *Lupocyclus*, but in a perfect state in *Alionectes*), and the stout, strongly hooked first male gonopods. *Lupocycloporus* is clearly distinguishable by its remarkably slender chelipeds and by the carapace bearing transverse ridges dorsally (instead of granulate patches on the dorsal regions in *Alionectes*) and rounded corners distolaterally (see also: Stephenson & Campbell, 1959; Spiridonov, 2020). Based on both morphological and molecular evidence, *Alionectes* is thus placed here in the subfamily Lupocyclinae, which previously contained only two genera, *Lupocyclus* and *Lupocycloporus*.

Remarks: Although *Alionectes spinipes* was not included in the present molecular analysis, this species is easily included in the new genus because of its close morphological similarity to *Alionectes pulchricristatus*. Both species share orbits without any notch on the upper margin, the serrated margin of the blade-like ridge of the second pleonal somite, a spine on the merus of the swimming legs and almost identical gonopodes. *Alionectes spinipes* differs from *Alionectes pulchricristatus* by the triangular shape of the anterolateral teeth of the carapace (vs. reduced in size, tuberculiform), by the distinctly shorter lateral tooth (i.e. less than the width of the front; vs. distinctly longer than the width of the front in *Alionectes pulchricristatus*) and by a smooth, not serrated, ridge on the third pleonal somite (vs. serrated ridges on both the second and third pleomeres).

Size: Relatively small crabs; the maximum reported size (CW) in *Alionectes spinipes* (male) is 26 mm (Stephenson & Rees, 1967a) and in *Alionectes pulchricristatus* (female) 32 mm (Gordon, 1931).

Ecological notes: The existing information for *Alionectes pulchricristatus* indicates it to be a

subtidal species living mostly within the upper 100 m but known to a depth of ~290 m on various types of substrates (Stephenson & Rees, 1967a; Apel & Spiridonov, 1998).

Geographical range: Indo-West Pacific, so far known from the northern Indian Ocean (Gulf of Oman and eastwards) and in the western tropical Pacific from China and Vietnam to the Philippines, Indonesia and Australia (Stephenson, 1972a, b; Apel & Spiridonov, 1998; present study).

LUPOCYCLOPORUS ALCOCK, 1899
(FIGS 4E, 7)

= *Portunus* (*Lupocycloporus*) Alcock, 1899

Type species: Achelous whitei A. Milne-Edwards, 1861, by monotypy; gender masculine.

Included species: Eight.
Lupocycloporus aburatsubo (Balss, 1922)
= *Neptunus buratsubo* Balss, 1922
Lupocycloporus gracilimanus (Stimpson, 1858)
= *Amphitrite gracilimanus* Stimpson, 1858
= *Achelous whitei* A. Milne-Edwards, 1861
Lupocycloporus innominatus (Rathbun, 1909)
= *Neptunus* (*Lupocycloporus*) *innominatus* Rathbun, 1909
Lupocycloporus laevis (A. Milne-Edwards, 1861)
= *Neptunus laevis* A. Milne-Edwards, 1861
Lupocycloporus minutus Shen, 1937
= *Neptunus* (*Lupocycloporus*) *minutus* Shen, 1937
Lupocycloporus ponticus (Fabricius, 1798) comb. nov.
= *Portunus ponticus* Fabricius, 1798
= *Portunus ponticus* Weber, 1795 (*nomen nudum*)
Lupocycloporus sinuosodactylus (Stephenson, 1967)
= *Portunus sinuosodactylus* Stephenson, 1967
Lupocycloporus wilsoni (Moosa, 1981)
= *Portunus* (*Lupocycloporus*) *wilsoni* Moosa, 1981

Diagnosis: Carapace (Fig. 7A) ~1.5 times as broad as long, approaching quasi-hexagonal shape, but with arcuate anterolateral margin, dorsally convex. Regions feebly developed, marked by granular ridges and patches. Front (Fig. 7B) with four rounded or subtriangular lobes, median ones usually more producing than lateral ones; all lobes projecting beyond tips of inner supraorbital lobes, which are quasi-triangular in shape. Orbit nearly circular; supraorbital margin with two shallow, reduced fissures. Anterolateral margin armed with nine teeth: eight anterior ones increasing in size posteriorly or subequal, small, acute and projecting forwards; ninth tooth distinctly larger, lateral. Posterolateral angle of carapace broadly rounded. Sutures on thoracic sternum well developed (Fig. 7C). Merus of third maxilliped with anteroexternal angle rounded or subrectangular, not produced laterally. Merus of chelipeds robust, with four to seven spines on anterior margin and two distal spines on posterior margin; carpus with spine on outer face. Chelae slender (Fig. 7D), nearly equal, homoiodontic; palm with two subdistal spines on upper surface. Dactyli of pereiopods 2–4 cultriform, costate, weakly setose on ventral margin. Merus of pereiopod 5 distinctly longer than broad, with spine on posterior margin. Male pleon triangular (Figs 4E, 7C). Pleomeres 2 and 3 with low crests; lateral margins of pleomere 3 rounded, narrowing distally; posterior margin of last thoracic episternite touches most of anterolateral margin of pleomere 3. Pleomeres 3–5 fused, without sutures remaining but keeled. First male gonopod (Fig. 7E) relatively short and robust proximally, curved and tapering distally; pair of first gonopods lying obliquely, touching subdistal parts, with apices directed anterolaterally or laterally. Female vulva (examined in *Lupocycloporus gracilimanus*) elongate, rounded on ends, located along most of the mesial margin of the sternite.

Systematic position: Lupocycloporus has a distinct general morphology and extremely slender homoidontic chelae, similar to the chelae of *Lupocyclus*. Indeed, species of these genera exhibit sister-group relationships in recent phylogenetic reconstructions, and both genera were included in a separate subfamily Lupocyclinae Paulson, 1875 (Spiridonov *et al.*, 2014; Evans, 2018). In the present phylogenetic reconstruction (Fig. 1), *Lupocycloporus* spp. form a basally unsupported clade with *Alionectes pulchricristatus*. Given that *Lupocycloporus* and *Alionectes* share common apomorphies [i.e. the swimming leg merus with a distinct posterodistal acute tooth (below), elongately subtrianglar male pleon and laterally bent gonopods with a swollen basal part], these and other characters (see discussion under *Alionectes*) might support their close relationship.

Remarks: After an examination of photographs of the holotype of *Portunus ponticus* Fabricius, 1798, from the ZMUC (Jensen, 2006), we propose here to include it in *Lupocycloporus*. The type specimen (the type data from J. C. Fabricius were published by Zimsen, 1964) is consistent with species of the latter genus by the almost hexagonal carapace with transverse granular ridges on its dorsum and with two submedian frontal teeth most prominent (instead of patches of granules and small submedian frontal

teeth in *Monomia*) and slender chelae, which are comparatively stouter in *Monomia* spp. The merus of the swimming leg possesses a distinct posterodistal acute tooth, a character typical for *Lupocycloporus* and *Alionectes*, but lacking in *Monomia* (see Koch *et al.*, 2015b).

Size: Small to medium-sized crabs; known maximum size ranges from 12.5 mm × 22.0 mm (*Lupocycloporus innominatus*; Spiridonov, 1999) to 24.0 mm × 44.5 mm (*Lupocycloporus gracilimanus*, male specimen ZMMU Ma 1922).

Ecological notes: Scarce information indicates these crabs to be a subtidal species, generally occurring from the upper subtidal zone to a depth of ~100 m, on predominately soft substrates (Stephenson, 1972a, b; Moosa, 1981a, b; Spiridonov, 1999).

Geographical range: Indo-West Pacific: the known species are confined to the eastern Indian Ocean and the westernmost tropical Pacific; there are no records in the western Indian Ocean or in the Pacific to the east of the Philippines and New Caledonia (Alcock, 1899; Stephenson, 1972a, b; Moosa, 1981a, b; Spiridonov, 1999; Poupin, 2010).

Subfamily Portuninae Rafinesque, 1815

Arenaeus Dana, 1851

= *Arenaeus* Dana, 1851 (type species *Portunus cribrarius* Lamarck, 1818, by monotypy; gender masculine) [ICZN, 1922. Opinion 73]

Key to distinguish genera of subfamily Portuninae (Carupella not included)

1. Posterolateral junctions of carapace rounded (Fig. 15A); dorsal surface of carapace finely granulate, with regions feebly demarcated, sometimes with narrow rows of granules 2
- Posterolateral junctions of carapace rounded; dorsal surface of carapace with well-defined granulated regions (Figs 8A, 9A, 10A, 14A) 4
- Posterolateral junctions of carapace angular, pointed, often distinctly upturned; dorsal surface with well-defined granulated regions (Figs 12A, 13A, 16A, 17A) 7
2. Supraorbital fissures broadly open, V-shaped (Rathbun, 1930: pl. 58) ..... *Arenaeus*
- Supraorbital fissures narrow or fused 3
3. Merus of third maxilliped with anteroexternal angle rounded or subrectangular, not produced laterally; supraorbital fissures not broadly open (Fig. 15A); male pleon narrowly triangular, almost smooth (Fig. 15C) ..... *Portunus*
- Merus of third maxilliped with anteroexternal angle strongly produced laterally; male pleon reverse T-shaped (Rathbun, 1930: pl. 58) ..... *Callinectes*
4. Cheliped palm with two spines on upper face (excluding spine on articulation with carpus) (Fig. 9A) ..... *Cavoportunus*
- Cheliped palm with a single spine on upper face (excluding spine on articulation with carpus) (Fig. 14A) 5
5. Frontal teeth distinct; carpus of chelipeds usually with a sharp spine on outer surface (Fig. 8A, B) ..... *Allomonomia*
- Frontal teeth low, lobate; carpus of chelipeds with low spine or crest on outer face 6
6. Carapace semicircular or circular (Fig. 10A), except for *Cycloachelous euglyphus*: hexagonal, inner convex carapacial part, excluding depressed lateral teeth semicircular; Serène, 1969: fig. 2) ..... *Cycloachelous*
- Carapace broadly hexagonal (Fig. 14A) ..... *Monomia*
7. Frontal teeth low, indistinct (Figs 12A, B, 13A, B) 8
- Frontal teeth distinctly produced, lobate or acute (Figs 16A, B, 17A, B) 9
8. Merus of third maxilliped anterolaterally produced to elongate triangular projection; merus of chelipeds with two posterodistal teeth; anterolateral teeth of carapace sharp (Fig. 12A) ..... *Eodemus*
- Merus of third maxilliped without elongate distolateral projection; merus of chelipeds with single posterodistal tooth; anterolateral teeth of carapace blunt (Fig. 13A) ..... *Incultus*
9. Three frontal teeth (Fig. 16B); male pleon elongately trapezoid (Fig. 16C); infraorbital margin deep, 'V'-shaped notch ..... *Trionectes*
- Four frontal teeth (Fig. 17B); sixth male pleomere distinctly constricted subdistally (Fig. 16C); infraorbital margin with narrow lateral notch ..... *Xiphonectes*

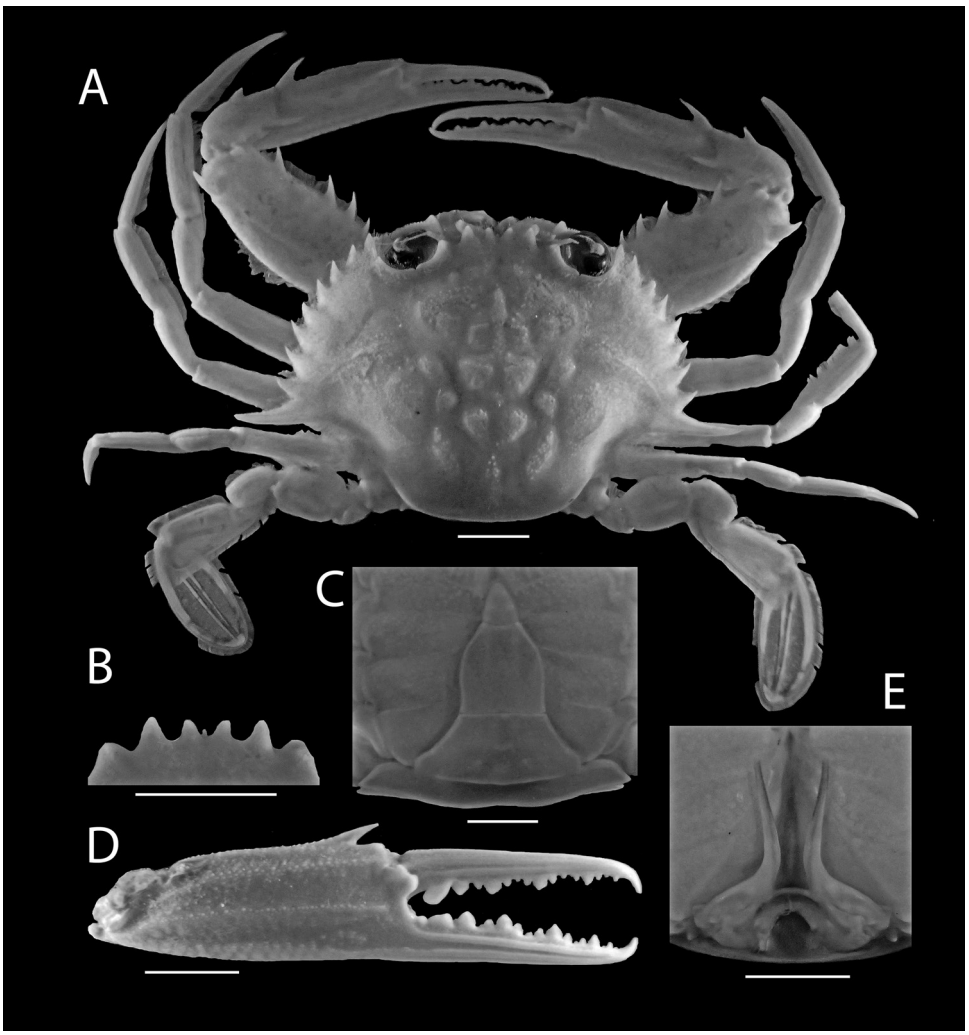

Figure 8. *Allomonomia lecromi* (Moosa, 1986), male holotype, CW 35 mm, MNHN-IU-2008-11268, Chesterfield Islands (A, B, E), and male, CW 37.7 mm, MNHN-IU-2014-4052, New Caledonia (C, D). A, total view, dorsal. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

= *Euctenota* Gerstaecker, 1856 (type species *Euctenota mexicana* Gerstaecker, 1856, by monotypy; gender feminine)

Included species: Two.
Arenaeus cribrarius (Lamarck, 1818)
= *Portunus cribrarius* Lamarck, 1818
= *Lupa maculata* Say, 1818
= *Arenaeus websteri* H.G. Jones, 1968
Arenaeus mexicanus Gerstaecker, 1856
= *Euctenota mexicana* Gerstaecker, 1856
= *Arenaeus bidens* Smith, 1871

Diagnosis (modified from Williams, 1984): Carapace more than twice as wide as long, finely granulate. Front not so far advanced as outer orbital angles, with six teeth including inner orbitals; submedian pair of teeth at either side of central notch coalesced. Superior margin of orbit with two deep fissures dividing it into three lobes; inferior margin of orbit with wide external fissure, inner angle much advanced. Lower surface of carapace densely setose. Anterolateral margin with nine strong teeth, somewhat acuminate, heavily setose beneath; most posterior produced into strong lateral tooth. Chelipeds of moderate size; merus with three spines on anterior border and short tuberculiform one near distal end of posterior border; carpus with lateral ridges and inner spine, outer spine present or absent; palm with five longitudinal granulose ridges and two spines, one at articulation with carpus and another above base of dactylus. Walking legs rather short and broad, densely fringed with short setae. Swimming legs stout, unarmed. Pleomere 2 produced on each side into strong, sharp, slightly upcurved spine. Male pleon

broadly triangular on segments 3–5, sixth segment elongate, telson narrowly triangular. First male pleopod long, slender, filiform, with short, swollen basal part.

Remarks: No specimen was analysed in this study. Spiridonov *et al.* (2014) suggested *Arenaeus* to be the closest relative of *Portunus* (in the present restricted extent, below) and *Callinectes*, all relatively large swimming forms with a lack of conspicuous granular patches on the carapace, slender gonopods and leaf-like walking dactyli. Evans (2018) subsequently confirmed their close, but somewhat unresolved phylogenetic relationship.

Size: Both males and females reach a width of 153 mm (Camp *et al.*, 1977; Williams, 1984).

Geographical range: Western Atlantic, from Massachusetts to Argentina; eastern Pacific, from Mexico to Peru (Rathbun, 1930; Zupolini *et al.*, 2017).

ALLOMONOMIA GEN. NOV.

(FIG. 8)

Zoobank registration: urn:lsid:zoobank.org:act:98CEC882-F852-4A87-88C6-99AB5FDC0C51

Type species: Portunus lecromi Moosa, 1996, by present designation.

Included species: Two.

Allomonomia calla (Koch, Nguyen & Ďuriš, 2015) comb. nov.
= *Monomia calla* Koch, Nguyen & Ďuriš, 2015

Allomonomia lecromi (Moosa, 1996) comb. nov.
= *Portunus lecromi* Moosa, 1996

Diagnosis: Carapace (Fig. 8A) subhexagonal, with anterior outline semicircular; width (without lateral teeth) ~1.3 × length; dorsal surface with well-defined granulate regions. Front (Fig. 5B) with four sharp triangular teeth, submedian teeth narrower than lateral teeth, all distinctly projecting beyond tip of inner supraorbital lobe. Epistome apophysis well developed and may be visible between median frontal lobes. Orbit relatively large, ellipsoidal, with supraorbital margin granulate, with two well-developed fissures in middle and on base of first anterolateral tooth; infraorbital margin strongly granulated, with narrow, deep lateral notch, with tooth-like elevation mesially and on ventral side of first anterolateral tooth. Anterolateral margin convex, longer than posterolateral margin, armed by nine teeth: eight anterior ones subequal, small, acutely forward projecting; ninth tooth distinctly larger, lateral. Posterolateral angle of carapace rounded. Sutures of thoracic sternum well expressed (Fig. 8C); thoracic sternites partly granular. Merus of third maxilliped with anterolateral lobe subrectangular. Chelipeds moderately stout; merus with four spines on anterior and one spine distally on posterior border; carpus with usual sharp spine on outer face. Upper surface of palm with two granular crests, inner one ending by spine distally; outer surface with two granular crests ending on level of finger joint. Chelae (Fig. 8D) nearly symmetrical but heterodontic; flattened molariform tooth present proximally at cutting edge of dactylus of one of the chelae. Dactyli of pereiopods 2–4 cultriform, costate, setose on ventral margin. Merus of pereiopod 5 a little longer than broad, without spine on posterior margin. Male pleon (Fig. 8C) 'T'-shaped. Posterior pleonal margin forming a pair of subparallel transverse laminar crests on both second and third pleomeres. Lateral margins of pleomere 3 straight, terminal part of posterior thoracic episternites narrow, fits in interspace between anterior margin of pleomere 3 and thoracic sternite 8. Pleomeres 3–5 fused, without sutures, but with elevated submarginal ridge posteriorly on fourth pleomere; telson narrowly triangular. First male (Fig. 8E) gonopod moderately robust; distal half slender, held subparallel to each other; tip with wide opening. Female vulva remains undescribed.

Etymology: Derived from the generic name *Monomia* [from Greek, meaning 'only one'], to which the new genus is generally similar, and the prefix *allo-* (Greek ἄλλο, other), alluding to the superficial morphological similarity but different systematic position of the new genus to the former; gender feminine.

Systematic position: The two known species of *Allomonomia* were members of the subgenus/genus *Monomia* in earlier concepts (Ng *et al.*, 2008; Koch *et al.*, 2015b). They share some general morphological characters (i.e. the carapace with a rounded posterolateral angle, the third meri of the maxillipeds with a triangular anterodistal projection, and the chelae with two teeth on the upper surface of the palm). *Allomonomia* differs from *Monomia* by the semicircular shape of the carapace (vs. more widened, semi-elliptic or hexagonal), the front with four subequal triangular teeth projecting distinctly beyond the inner supraorbital angle (vs. low and subequal ones with submedians lower than laterals, projecting slightly beyond the tip of the inner supraorbital angle), an indistinct median epistomial spine (vs. reaching distinctly beyond front), only one posterodistal spine on the cheliped merus (vs. predominantly two spines) and by the first male gonopods lying in a subparallel position, with broadened apical openings (vs. gonopods generally overlapping each other by bent region medially, with narrow terminal opening).

In the present 16S molecular analysis (Fig. 2), both species of *Allomonomia* are in a sister position to *Incultus*, whereas the three-marker analysis (Fig. 1)

revealed paraphyly of *Allomonomia*, with the latter genus positioned as sister to *Allomonomia calla*. However, morphological characters provide proper support to an independent generic status of both genera. Both of them are very similar in the bent shape of the first male gonopods, which are lying in a pair with subparallel distal parts in *Allomonomia* (Fig. 8E) but overlapping each other by the bent regions in *Incultus* (Fig. 13E). Both these genera are also characterized by the presence of only a single posterodistal tooth on the cheliped merus. Together with this, *Allomonomia* species are different in the general appearance of the body from the species of *Incultus*, with a distinctly convex dorsal carapace with a semicircular anterior outline and rounded posterolateral angles (vs. hexagonal, deeply depressed, with elevated, swollen regions and with posterolateral angles acutely produced).

The sister clade to the *Allomonomia–Incultus* clade in the present three-marker analysis (Fig. 1) is a branch composed of *Xiphonectes* and *Trionectes* (see below). The *Allomonomia* spp. were previously included in *Monomia*, whereas the species now included in *Incultus* and *Trionectes* were all previously included in the genus/subgenus *Xiphonectes* (as listed by Ng *et al.*, 2008; Spiridonov *et al.*, 2014). All species of the large, combined clade have the first male gonopod consisting of a robust basal part and bent distal part. The species of the *Xiphonectes–Trionectes* clade have the distal part short and hooked (Figs 16E, 17E), whereas species belonging to the *Allomonomia–Incultus* genera have the distal part of the first gonopod distinctly more sharply bent, more slender and longer (Figs 8E, 13E). *Trionectes* is also easily distinguished by having three frontal teeth on the carapace.

Size: Although few specimens have been available for measurements, *Allomonomia* spp. appear to be medium-sized portunids, ranging from 20 mm × 30 mm in *Allomonomia lecromi* (Moosa, 1996) to a maximum CW of 38.4 mm in *Allomonomia calla* (Koch *et al.*, 2015b).

Ecological notes: The two known species of the genus have been collected from relatively deep waters: *Allomonomia lecromi* at 120–150 m from the Chesterfield Islands (Moosa, 1996), *Allomonomia calla* at 106–111 m and from a tangle net deeper than 50 m, from the Philippines (Koch *et al.*, 2015b).

Geographical range: Indo-West Pacific: known from Madagascar, the Philippines and New Caledonia.

CALLINECTES STIMPSON, 1860

= *Callinectes* Rathbun, 1896 (type species *Callinectes sapidus* Rathbun, 1896, subsequent designation by Rathbun, 1896, under plenary powers; gender masculine) [ICZN, 1964. Opinion 712]

Included species: Sixteen.
Callinectes affinis Fausto-Filho, 1980
Callinectes amnicola Rochebrune, 1883
= *Neptunus amnicola* Rochebrune, 1883
= *Neptunus edwardsi* Rochebrune, 1883
= *Neptunus marginatus* var. *truncata* Aurivillius, 1898
= *Callinectes latimanus* Rathbun, 1897
Callinectes arcuatus Ordway, 1863
= *Callinectes pleuriticus* Ordway, 1863
= *Callinectes dubia* Kingsley, 1879
= *Callinectes nitidus* A. Milne-Edwards, 1879
Callinectes bellicosus Stimpson, 1859
= *Callinectes ochoterenai* Contreras, 1930
Callinectes bocourti A. Milne-Edwards, 1879
= *Callinectes cayennensis* A. Milne-Edwards, 1879
= *Callinectes maracaiboensis* Taissoun, 1972
Callinectes danae Smith, 1869
Callinectes exasperatus (Gerstaecker, 1856)
= *Lupea exasperata* Gerstaecker, 1856
= ?*Lupa trispinosa* Leach, 1816
= *Callinectes tumidus* Ordway, 1863
Callinectes gladiator Benedict, 1893
= *Lupa smythiana* White, 1847 (*nomen nudum*)
Callinectes larvatus Ordway, 1863
Callinectes marginatus (A. Milne-Edwards, 1861)
= *Neptunus marginatus* A. Milne-Edwards, 1861
= *Callinectes africanus* A. Milne-Edwards, 1879
Callinectes ornatus Ordway, 1863
= *Callinectes humphreyi* H. G. Jones, 1968
?*Callinectes pallidus* (Rochebrune, 1883)
= *Neptunus pallidus* Rochebrune, 1883
Callinectes rathbunae Contreras, 1930
Callinectes sapidus Rathbun, 1896 [ICZN, 1964. Opinion 712]
= *Portunus diacantha* Latreille, 1825 [name suppressed; ICZN, 1964. Opinion 712]
= *Callinectes sapidus acutidens* Rathbun, 1896
Callinectes similis Williams, 1966
Callinectes toxotes Ordway, 1863
= *Callinectes robustus* A. Milne-Edwards, 1879

Diagnosis (modified from Rathbun, 1930): Similar to *Portunus*, distinguished by narrow, reversed 'T'-shaped male pleon, and merus of third maxillipeds strongly produced outwards at anteroexternal angle. Body usually of large size; front formed by two or four teeth; dorsum of carapace with four dorsal carinae formed of single granules; two transverse, usually curved and subparallel lines on gastric region and one sinuous oblique line on branchial region leading inward from lateral tooth; nine strong anterolateral teeth, with posteriormost tooth at lateral angle; chelipeds stout; palm with five external carinae, with

dorsodistal spine and proximal spine at articulation with carpus; carpus without inner spine, outer spine at widest part of article; merus with three (exceptionally four) stout spines on inner margin and small spine at posterodistal end; swimming legs without spines. Pleon of immature female triangular from fourth segment to telson.

Remarks: As Spiridonov *et al.* (2014) noted, *Callinectes* is closely related to *Portunus* (in its herein redefined scope) and Atlantic *Arenaeus*, as is evident from their general appearance being relatively large swimming forms, sharing leaf-like walking dactyli, the lack of conspicuous granular patches on their carapace and slender gonopods. This view is confirmed by other recent cladistic (Karasawa *et al.*, 2008) and molecular (Mantellato *et al.*, 2009, 2018; Evans, 2018) studies of portunids. In the present study, a well-supported clade is formed by two species of *Portunus* and a single *Callinectes* (*Arenaeus* was not included in the present analysis). The infrageneric molecular diversity of American *Callinectes* analysed by Robles *et al.* (2007) revealed two major clades among 12 of 16 currently valid species included in that analysis: the '*bocourti*' clade including *Callinectes affinis*, *Callinectes bocourti*, *Callinectes rathbunae*, *Callinectes sapidus* and *Callinectes toxotes*; and the '*danae*' clade composed of *Callinectes arcuatus*, *Callinectes bellicosus*, *Callinectes danae*, *Callinectes exasperatus*, *Callinectes larvatus*, *Callinectes ornatus* and *Callinectes similis*. Morphological distinctions between these lineages are mainly in the relative length of the first gonopods (reaching the fourth thoracic sternite in the '*bocourti*' group; see Williams, 1974).

Size: Generally, in adult males and females the CW is between 100 and 150 mm (Rathbun, 1930); the largest males in low-salinity waters might reach even > 230 mm (Williams, 1965).

Ecological notes: Species of *Callinectes* inhabit a variety of substrate types in estuaries and shallow oceanic waters, from the upper sublittoral zone to a depth of 40 m (Williams, 1965).

Geographical range: The native range of the genus is along the Atlantic and Pacific coasts of America (Rathbun, 1930) and western Africa (Monod, 1956); recently introduced to European waters, including the Baltic, Mediterranean and Black seas (Nehring, 2011).

Cavoportunus Nguyen & Ng, 2010

(Fig. 9)

= *Cavoportunus* Nguyen & Ng, 2010: 41.

Type species: Neptunus (*Achelous*) *dubius* Laurie, 1906, by monotypy; gender masculine.

Included species: One.
Cavoportunus dubius (Laurie, 1906)
= *Neptunus* (*Achelous*) *dubius* Laurie, 1906
= *Portunus* (*Cycloachelous*) *yoronensis* Sakai, 1974

Diagnosis (after Nguyen & Ng, 2010): Carapace hexagonal in shape, width ~1.3 × length, dorsal surface glabrous; frontal margin slightly upturned; surface microscopically granular with distinct regions; metagastric ridge distinctly visible, other ridges indistinct, dorsal surface with numerous small granules. Front with four teeth, slightly projecting beyond tip of internal supraorbital angle. Orbit relatively large, with moderate dorsal inclination; inner supraorbital margin rounded; upper border of orbit with single fissure. Infraorbital margin straight, with forward-directed tooth. Anterolateral margin with nine teeth: first tooth largest; second to ninth teeth smaller, subequal in size. Posterolateral junction of carapace rounded. Basal antennal article with lobe-like process. Merus of third maxilliped produced anterolaterally. Cheliped length ~1.8 × width of carapace; manus slightly less massive than merus; fingers relatively long, slender. Adult male with two prominent deep depressions on sternite eight inside sternopleonal cavity, anterior being larger, in which first gonopod sits. First male gonopod short, relatively stout, 'S'-shaped; basal part relatively slender; subdistal part prominently dilated, lobiform; distal part with distinct folds on tip. Second gonopod elongate, tapering, about four-fifths length of first gonopod. Penis coxal, long, slender, proximally lodged between two raised processes of sternite 8. Female vulva mostly surrounded by thick, whitish, crescent-shaped rim; salient, short sternal cover on outer margin; separate, small, round operculum.

Systematic position: In the present three-marker phylogenetic reconstruction (Fig. 1), *Cavoportunus* is resolved as an independent branch within a large clade of IWP genera previously belonging to *Portunus* (*s.l.*), in a sister position to two multigenera branches (i.e. the *Allomonomia–Incultus–Trionectes–Xiphonectes* clade and the *Cycloachelous–Eodemus–Monomia* clade).

As pointed out by Nguyen & Ng (2010), *Cavoportunus* is morphologically most similar to *Cycloachelous*. Both taxa share some important synapomorphies, in particular a tendency to a decreasing carapace width-to-length ratio and approaching a circular carapace shape (Figs 9A, 10A), the secondary symmetrization and homoiodonty of the chelipeds (Spiridonov *et al.*, 2014), and a short and stout first gonopod (Fig. 9E), but which is morphologically complex and exhibits coaptation of the median groove. The deep depression

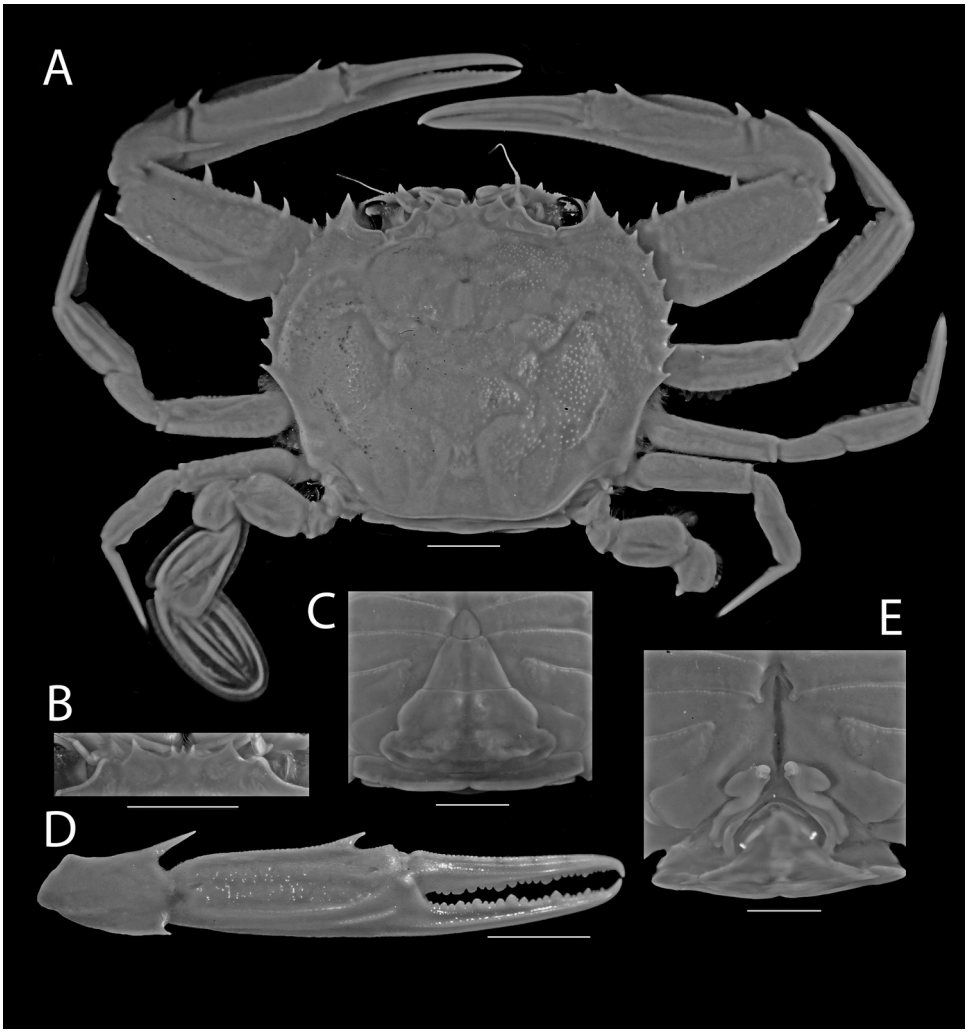

Figure 9. *Cavoportunus* aff. *dubius* (Laurie, 1906), male, CW 28 mm, MNHN-IU-2014-1186, Madagascar. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

(Fig. 9E) on each side on the eighth thoracic sternite (to accommodate the lateral flange of the gonopod apex) is a unique autapomorphy for *Cavoportunus* (Nguyen & Ng, 2010). *Cavoportunus* can also be distinguished easily from *Cycloachelous* by the presence of a single fissure (vs. two shallow ones) on the supraorbital margin of the carapace and by a single distal spine (vs. two spines) on the posterior margin of the cheliped merus (Figs 9A, 10A).

Remarks: Currently, *Cavoportunus* is monotypic, containing only the species *Cavoportunus dubius*. In the present study, the genus is represented by two specimens: a male *Cavoportunus* aff. *dubius* (MNHN-IU-2008-12565) from the Marquesas Islands, and an ovigerous female *Cavoportunus dubius* (MNHN-IU-2014-4099) from the Philippines. The size of the female (CW 15 mm) is close to the upper limit known for *Cavoportunus dubius* (see Nguyen & Ng, 2010), but except for sexual dimorphism there are no noticeable differences between the specimens. Those two specimens seem genetically different [3.0% (*COI*) or 5.2% (16S)], hence the former might represent an undescribed species.

Size: Small crabs; maximum reported size of *Cavoportunus dubius* (female) is 14.3 mm × 18.5 mm (Nguyen & Ng, 2010).

Ecological notes: The single representative of the genus is a low subtidal species occurring between 20–30 and 245 m (Spiridonov & Zhadan, 1999; Nguyen & Ng, 2010).

Geographical range: Indo-West Pacific: from the Gulf of Aden (Neumann & Spiridonov, 1999) and Madagascar (present study, MNHN) to Japan, the Philippines,

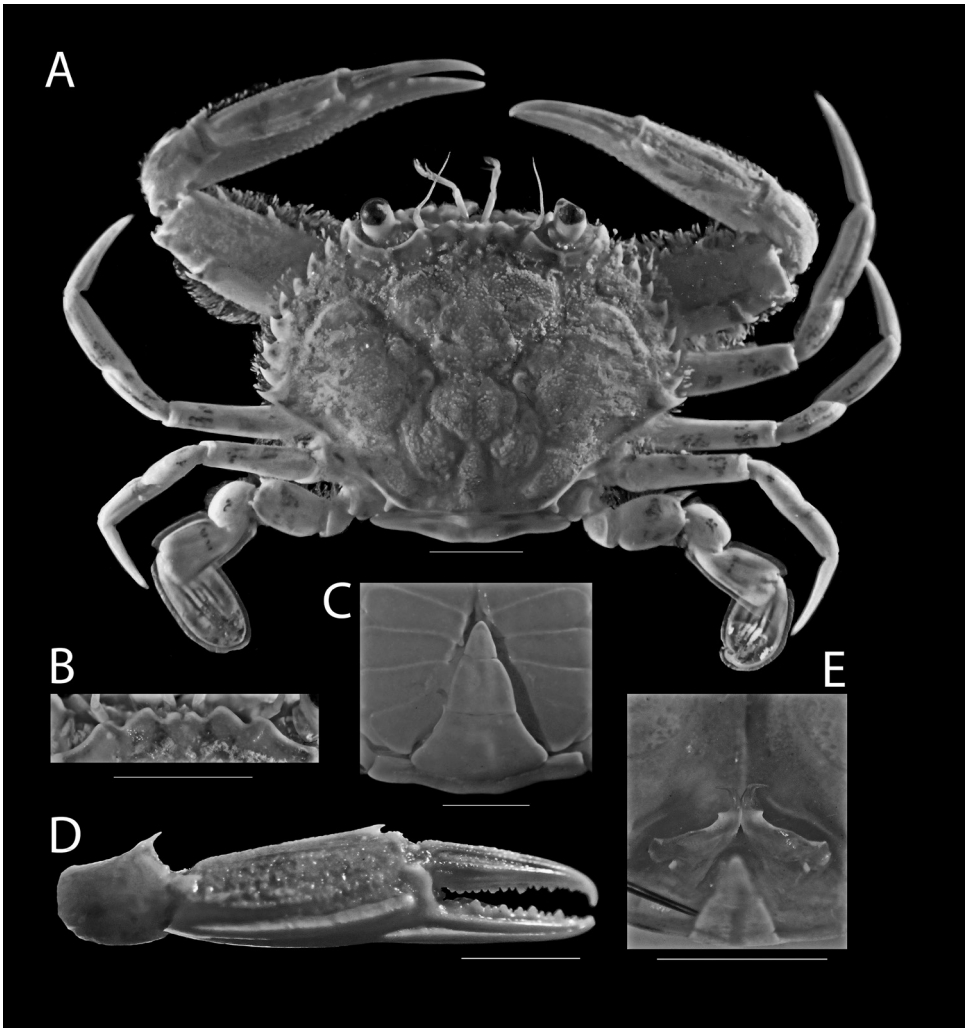

Figure 10. *Cycloachelous granulatus* (H. Milne Edwards, 1834), male, CW 22.5 mm, MNHN-IU-2014-10101, Vietnam, South China Sea (A–D) and *Cycloachelous euglyphus* (Laurie, 1906), male, CW 23.6 mm, NHM 1907.5.22.297, India (E). A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

New Caledonia and French Polynesia (Spiridonov & Zhadan, 1999: fig. 1A; Nguyen & Ng, 2010).

Cycloachelous Ward, 1942

(Figs 4F, 10, 11)

= *Cycloachelous* Ward, 1942 (type species *Lupea granulatus* H. Milne Edwards, 1834, by original designation; gender masculine).

Included species: Nine.
Cycloachelous elongatus (A. Milne-Edwards, 1861)
= *Achelous elongatus* A. Milne-Edwards, 1861
Cycloachelous euglyphus (Laurie, 1906) comb. nov.
= *Neptunus* (*Amphitrite*) *euglyphus* Laurie, 1906
Cycloachelous granulatus (H. Milne Edwards, 1834)
= *Lupea granulatus granulatus* H. Milne Edwards, 1834
= *Amphitrite speciosa* Dana, 1852
Cycloachelous levigatus Koch, 2021
Cycloachelous octodentatus (Gordon, 1938)
= *Neptunus* (*Achelous*) *octodentatus* Gordon, 1938
Cycloachelous orbicularis (Richters, 1880)
= *Achelous orbicularis* Richters, 1880
Cycloachelous orbitosinus (Rathbun, 1911)
= *Portunus* (*Achelous*) *orbitosinus* Rathbun, 1911
Cycloachelous suborbicularis (Stephenson, 1975)
= *Portunus suborbicularis* Stephenson, 1975
Cycloachelous unispinosus (Miers, 1884)
= *Achelous granulatus unispinosus* Miers, 1884

Diagnosis: Carapace (Fig. 10A) quasi-hexagonal or almost circular in shape, usually < 1.5 times

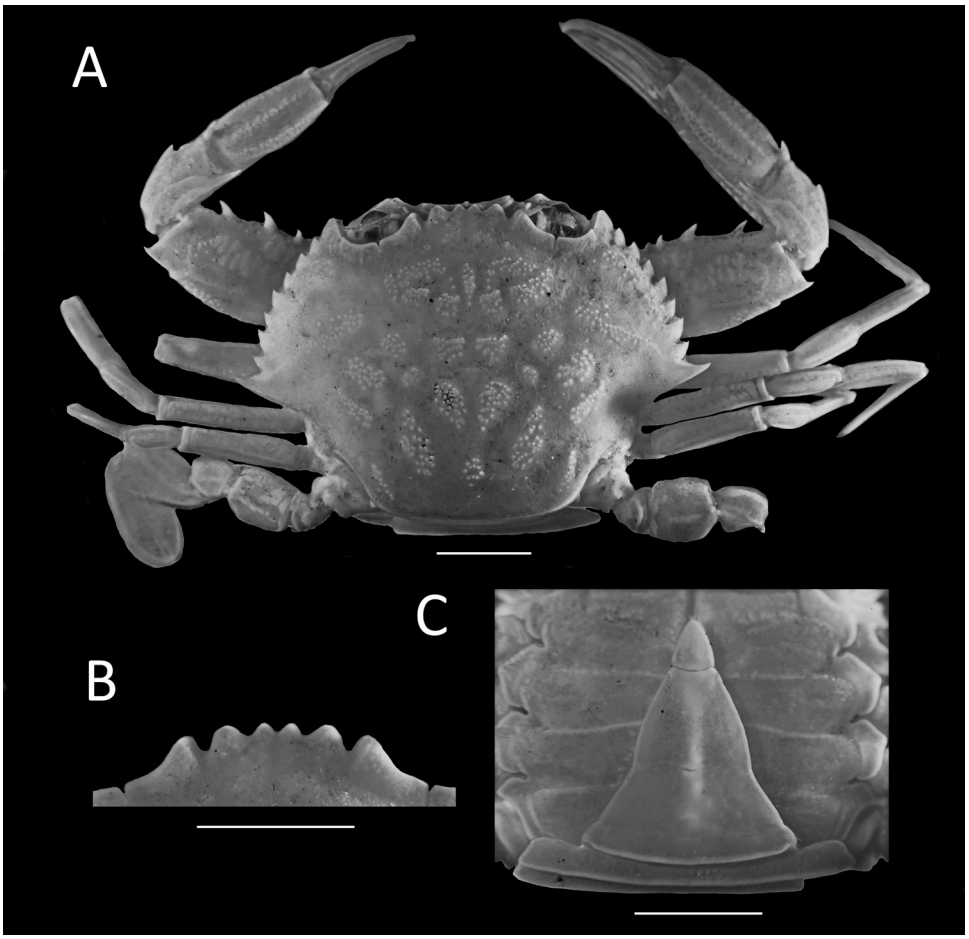

Figure 11. *Cycloachelous unispinosus* (Miers, 1884), male, CW 25.2 mm, NHM 1882.7, Prince of Wales Channel, Australia. A, total view. B, front. C, pleon. Scale bars: 5 mm.

broader than long, flattened, with granular ridges and/or patches or entirely covered with granules. Regions moderately developed. Orbit ellipsoidal, with two shallow fissures on supraorbital margin. Infraorbital margin visible in dorsal view, with pronounced notch; outer infraorbital lobe appressed to ventral side of outer supraorbital lobe (= first anterolateral tooth). Frontal margin (Fig. 10B) consisting of four low lobes. Nine well-developed anterolateral teeth: first to eighth subequal; ninth somewhat longer than others or of similar size. Posterolateral junction of carapace rounded. Sutures on thoracic sternum distinct (Fig. 10C); suture between thoracic sternites 6 and 7 nearly complete in males and interrupted in females; thoracic sternites usually smooth. Anterolateral angle of maxilliped 3 merus strongly produced laterally or auriculate. Chelipeds relatively slender; merus with three or four spines on anterior margin and two distal spines on posterior margin; carpus with single spine on anterior margin of outer face. Chelae (Fig. 10D) usually of nearly equal size and homoiodontic, without proximal molariform tooth on cutting edge of dactylus; palm with two carinae and single spine on upper face (excluding spine at articulation with carpus) and three carinae on outer face. Dactyli of pereiopods 2–4 cultriform, costate, weakly setose on ventral margin. Merus of pereiopod 5 distinctly longer than broad, without spine on posterior margin. Male pleon (Fig. 10C) quasi-triangular or with lateral margin of sixth pleomere markedly convex. Lateral margins of pleomere 3 straight or slightly concave; terminal part of posterior thoracic episternite fills interspace between anterior margin of pleomere 3 and thoracic sternite 8. Pleonal terga 3–5 fused, without remaining sutures; keels usually absent. Gonopod 1 (Fig. 10E) short and stout, distally hooked, or moderately slender, curved. Female vulva (Fig. 4F) a narrow, oblique fissure, relatively distant from margins.

Systematic position: In our three-marker phylogenetic reconstruction (Fig. 1), *Cycloachelous* forms a sister

group to *Monomia* and *Eodemus*, with unsupported internal relationships. *Cycloachelous*, together with *Cavoportunus* (see above), shares with these genera some morphological apomorphies, such as the female vulva in the form of a narrow slit, and (mostly) two distal spines on the posterior margin of the cheliped merus. However, *Cycloachelous* spp. are distinct in overall appearance from other genera of the former *Portunus* (*s.l.*) owing to their carapace shape and symmetrical chelipeds.

Remarks: Cycloachelous granulatus has been considered to comprise two subspecies: the nominotypic one and *Cycloachelous granulatus unispinosus*, originally *Achelous granulatus* var. *unispinosus* Miers, 1884. The latter subspecies was described based upon a single type specimen from Prince of Wales Channel, Queensland, Australia (Miers, 1884: 230, pl. 23B). Later, Miers (1886: 180) considered it as a separate species, *Neptunus* (*Achelous*) *unispinosus*. Miers (1884: 230) suggested it could be distinguished from *Cycloachelous granulatus* 'in wanting the submedian spine of the posterior margin of the arm of the chelipedes', meaning by a single spine on the posterior margin of the cheliped merus, vs. two spines (a generic character of *Cycloachelous*). In the subsequent description, he added an important character of the frontal teeth or lobes: 'the median teeth smaller, but not less prominent than submedian teeth' (Miers, 1886: 180). However, in *Cycloachelous granulatus* the median frontal teeth are distinctly less prominent than submedians (laterals in the present terminology). This indicates that Miers' variety *unispinosus* is indeed a separate species, probably not even belonging to *Cycloachelous*. We (M.K. and Z.Ď.) examined the holotype specimen of *Achelous granulatus* var. *unispinosus* Miers, 1886 (NHM 82.7); the distinctions mentioned by Miers (above) were confirmed. In addition, the male pleons also differ in both the crabs, in that the penultimate somite is shorter, but wider anteriorly in *Cycloachelous granulatus* (vs. longer, but narrower distally) and the telson is respectively larger (vs. smaller).

The morphology of *P.* (*Monomia*) *euglyphus* (as listed by Ng *et al.*, 2008) shows some characters typical for *Cycloachelous*, the most significant being the unique shape of the male gonopods, which are similar to those of the type species, *Cycloachelous granulatus* (compare: Serène, 1969: fig. 6; Nguyen & Ng, 2010: fig. 5D). The present analysis confirms the inclusion of *Neptunus* (*Amphitrite*) *euglyphus* Laurie, 1906 in *Cycloachelous*.

Size: Small to medium-sized crabs: maximum recorded size ranges from 12 mm × 22 mm (*Cycloachelous euglyphus*; present study, ZIN RAN 1/37447 male specimen) to 22.6 mm × 33.0 mm (*Cycloachelous orbitosinus*).

Ecological notes: The most frequently recorded species are the intertidal to subtidal *Cycloachelous granulatus* (down to the depth of 120 m) and the upper to lower subtidal *Cycloachelous orbitosinus* (45–77 m) and *Cycloachelous laevigatus* 20–120 m) (Stephenson, 1972a, b; Apel & Spiridonov, 1998; Spiridonov, 1999; Neumann & Spiridonov, 1999; Yang *et al.*, 2012; Koch, 2021).

Geographical range: Throughout the entire IWP from the Red Sea and south-east Africa to the Hawaiian Islands and French Polynesia.

EODEMUS GEN. NOV.

(FIGS 4H, 12)

Zoobank registration: urn:lsid:zoobank.org:act:0676E050-17EF-4030-8605-BB6D580EC7D7

Type species: Portunus pseudohastatoides Yang & Tang, 2006, by present designation.

Included species: Six.

Eodemus arabicus (Nobili, 1905) comb. nov.
= *Neptunus* (*Hellenus*) *arabicus* (Nobili, 1905)
= *Portunus acerbiterminalis* Stephenson & Rees, 1967

Eodemus hastatoides (Fabricius, 1798) comb. nov.
= *Portunus hastatoides* Fabricius, 1798
= *Portunus hastatoides* Weber, 1795 (*nomen nudum*)

Eodemus pseudohastatoides (Yang & Tang, 2006) comb. nov.
= *Portunus pseudohastatoides* Yang & Tang, 2006

Eodemus subtilis (Nguyen & Ng, 2021) comb. nov.
= *Xiphonectes subtilis* Nguyen & Ng, 2021

Eodemus unidens (Laurie, 1906) comb. nov.
= *Neptunus* (*Hellenus*) *unidens* Laurie, 1906
= *Portunus dayawanensis* H.-L. Chen, 1986
= *Portunus trilobatus* Stephenson, 1972
= *Neptunus* (*Hellenus*) *tweediei* Shen, 1937

Eodemus vassilyi (Nguyen & Ng, 2021) comb. nov.
= *Xiphonectes vassilyi* Nguyen & Ng, 2021

Diagnosis: Cephalothorax and chelipeds with fine, hair-like marginal setae. Carapace (Fig. 12A) hexagonal, more than two times as broad as long (including lateral teeth); dorsal surface tomentose, regions feebly defined by patches of fine granules. Front (Fig. 12B) with three or four lobes slightly projecting beyond tip of inner orbital lobe; median tooth or pair distinctly smaller than laterals. Orbit relatively large, approaching circular; inner

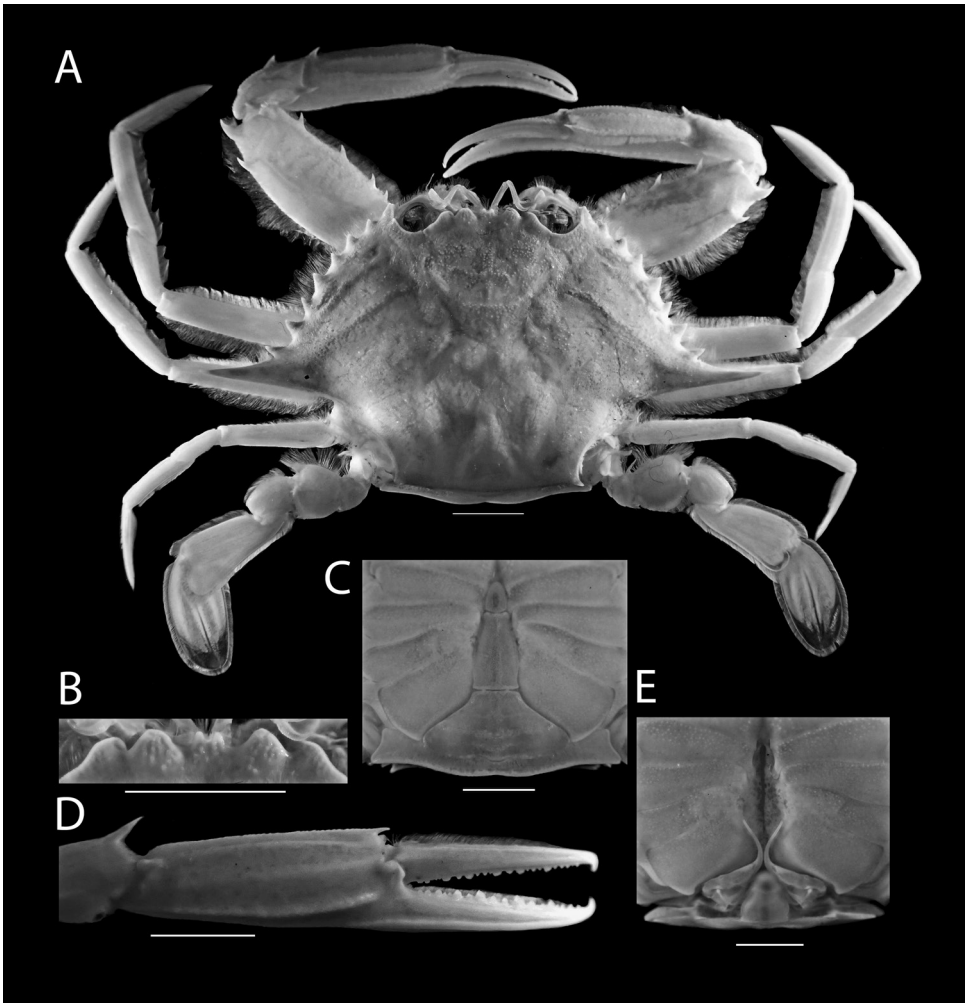

Figure 12. *Eodemus pseudohastatoides* (Yang & Tang, 2006), male, CW 39 mm, MNHN-IU-2014-10067, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

supraorbital lobe rounded; supraorbital margin with two narrow fissures with appressed walls; infraorbital margin with broad, 'Y'-shaped lateral notch. Anterolateral margin with nine sharp teeth: first to eighth teeth subequal in size; eighth tooth arising anteriorly from base of ninth tooth; ninth tooth large, directed laterally. Posterolateral junction of carapace produced to distally upturned spiniform tooth. Sutures of thoracic sternum well expressed (Fig. 12C); thoracic sternites usually smooth or sparsely granular. Merus of third maxilliped anterolaterally produced to elongate projection. Chelipeds relatively robust; merus with four spines on anterior and two spines distally on posterior border; carpus with usual outer spine. Chelae (Fig. 12D) slightly unequal, heterodontic; in larger chela, molariform tooth present proximally at cutting edge of dactylus; fingers densely setose distomedially. Dactyli of pereiopods 2–4 cultriform, costate, setose on ventral margin. Merus of pereiopod 5 distinctly longer than broad, without spine on posterior margin. Male pleon 'T'-shaped (Fig. 12C), with sixth pleomere elongate, narrow. Lateral margins of pleomere 3 markedly concave; pleomere terga 3–5 fused, without remaining sutures. First gonopod (Fig. 12E) relatively long, arched, tapering distally; pair of first gonopods not overlapping, only touching each other in median body plane, with distal parts directed anteriorly. Female vulva (Fig. 4H) in form of a narrow slit located close to mesial margin of sternite.

Etymology: Derived from Latin *eodem*, 'to the same place', alluding to the similar outer appearance of included species; gender masculine.

Systematic position: The species of the portunine *Eodemus* and of the newly established genera *Incultus* and *Trionectes*, plus the lupocycline *Alionectes*, were previously affiliated in the genus (or subgenus) *Xiphonectes* (as listed by Ng *et al.*, 2008; Spiridonov *et al.*, 2014). These genera are similar in their overall appearance, with a more or less strongly depressed carapace, usually with a long pair of lateral teeth and elevated patches of granules on the dorsum, and with produced or subacute posterolateral angles.

Their morphological distinction, together with *Xiphonectes* in its present reduced extent (below), is discussed under those genera. *Eodemus* can be distinguished easily by the more distinct 'T'-shape of the male pleon, concave lateral margins of the third male pleomere and the distinctly laterally produced anterolateral lobe of the third maxilliped merus.

Based on our three-marker analysis, *Eodemus* is closely related to the species of *Monomia* (*s.s.*, below) and *Cycloachelous*. Those genera share, among other features, the overall shape of the carapace, with granular patches on regions of the dorsum, and four frontal teeth, with the submedian pair smaller (in some *Eodemus* spp., the submedians are fused to a single tooth; see also Wong *et al.*, 2010). Other potential synapomorphies are the produced anterolateral lobe of the third maxilliped merus, two posterodistal spines on the cheliped merus, the 'T'-shaped male pleon, concave lateral margins of the third pleomere (at least in most *Monomia*) and a slit-shaped female vulva located close to the mesial margin of the sternite. The first gonopods are relatively long, usually bent and distally slender in *Eodemus* and *Monomia* (*s.s.*), whereas they are stout or moderately slender and curved in *Cycloachelous*.

All examined specimens of *Eodemus* are relatively small (CW usually ≤ 41 mm), whereas the species of *Monomia* are represented by distinctly larger specimens (see below). The posterior lateral tooth of the carapace is of variable length in both genera, but generally longer in *Eodemus*. The posterolateral junction of the carapace is produced to a distally upturned spine in the new genus, whereas it is greatly rounded in *Monomia* spp. In the latter, the epistome is medially produced to a long median spine distinctly overreaching the front, whereas such a structure is not recognizable from the dorsal view in *Eodemus* spp. The first male gonopods, despite the generally similar shape in both genera, touch in the median body plane along their bent parts in *Eodemus* spp., but in the majority of *Monomia* spp. they overlap each other (except for some Australian species with subparallel, not overlapping, distal parts of the gonopods).

Remarks: For *Monomia argentata*, the iridescence of the cuticle had been incorporated as a typical character to its specific name by White (1847; as *Amphitrite argentata*; a *nomen nudum*). The name was subsequently also accepted by A. Milne-Edwards (1861; as *Neptunus argentatus*). This remarkable phenomenon of iridescence was also observed by us in *E. pseudohastatoides* (see Koch *et al.*, 2015a), which also contributes to the hypothetical relationship of *Eodemus* and *Monomia* indicated by the molecular analysis (Fig. 1).

Among all other species of the genus, *E. arabicus* (types examined, MNHN B5926, B5927) can be distinguished by the posterolateral junction of the carapace not as upturned as in the former two species. *Neptunus* (*Hellenus*) *tweediei*, *P. trilobatus* and *P. dayawanensis* have recently been synonymized with *Xiphonectes unidens* (now *E. unidens*) by Nguyen & Ng (2021). Two new *Xiphonectes* species described in the latter study, *X. subtilis* and *X. vassilyi*, as formerly belonging to the *X. hastatoides* species complex (Nguyen & Ng, 2021), are now also affiliated in *Eodemus*.

Size: Maximum reported size ranges from CW 25 mm [*E. unidens*, in Stephenson & Rees, 1967a (as *Portunus tweediei*)] to 19.4 mm × 41.0 mm [*E. hastatoides*, in Apel & Spiridonov, 1998 (as *Portunus hastatoides*)].

Ecological notes: Some species appear to be mostly shallow-water living species, such as *E. arabicus* recorded in the intertidal to the upper subtidal zone down to 55 m (Red Sea, ZMMU Ma 3295) or *E. hastatoides* with a depth range from 7 to 100 m (Stephenson & Rees, 1967a; Stephenson, 1972a, b; Moosa, 1981a; Apel & Spiridonov, 1998; Yang *et al.*, 2012; Nguyen & Ng, 2021).

Geographical range: Indo-West Pacific: from the Red Sea and the western Indian Ocean to Japan, the Philippines, Indonesia, Australia, the Chesterfield Islands and New Caledonia (Crosnier, 1962; Stephenson, 1972a, b; Moosa, 1996; Apel & Spiridonov, 1998; Neumann & Spiridonov, 1999; Poupin, 2010).

INCULTUS GEN. NOV.

(FIGS 3A, 4E, 13)

Zoobank registration: urn:lsid:zoobank.org:act:2B1B6DEC-6146-4A5B-A77B-4340C140CDF5

Type species: Neptunus tuberculosus A. Milne-Edwards, 1861, by present designation.

Included species: Three.

Incultus alcocki (Nobili, 1905) comb. nov.
= *Neptunus* (*Hellenus*) *alcocki* Nobili, 1906

Incultus brockii (De Man, 1887) comb. nov.
= *Neptunus brockii* De Man, 1888
Incultus tuberculosus (A. Milne-Edwards, 1861) comb. nov.
= *Neptunus tuberculosus* A. Milne-Edwards, 1861

Diagnosis: Carapace (Fig. 13A) flattened, broadly hexagonal, > 1.5 times as long as broad (including lateral teeth). Dorsal surface granulated; regions conspicuously elevated, with pair of closely set cardiac elevations most prominent; distinct wide depressions present behind orbits. Front (Fig. 13B) with three or four subequal low or obsolete lobes distinctly projecting beyond inner supraorbital lobe. Orbit relatively large, ellipsoidal, with inner supraorbital lobe rounded; upper border of orbit with two short fissures. Infraorbital margin granulated, with broad lateral notch. Anterolateral margin with nine blunt or lobiform teeth; ninth distinctly larger, lateral. Posterolateral angles of carapace produced, distinctly upturned over posterior margin. Sutures (Fig. 13C) and grooves of thoracic sternum poorly to moderately distinct; thoracic sternites partly granular. Antennal flagellum long, more than twice orbital width. Merus of third maxilliped elongate, anterolaterally produced to rounded lobe. Chelipeds stout; merus with three or four spines on anterior border, one distal spine on posterior border, followed more basally with distinct, obliquely elevated sulcus forming small tuberculate lobe and continuing as transverse groove or crossing distal merus. Carpus with short spine on outer face. Chelae (Fig. 13D)

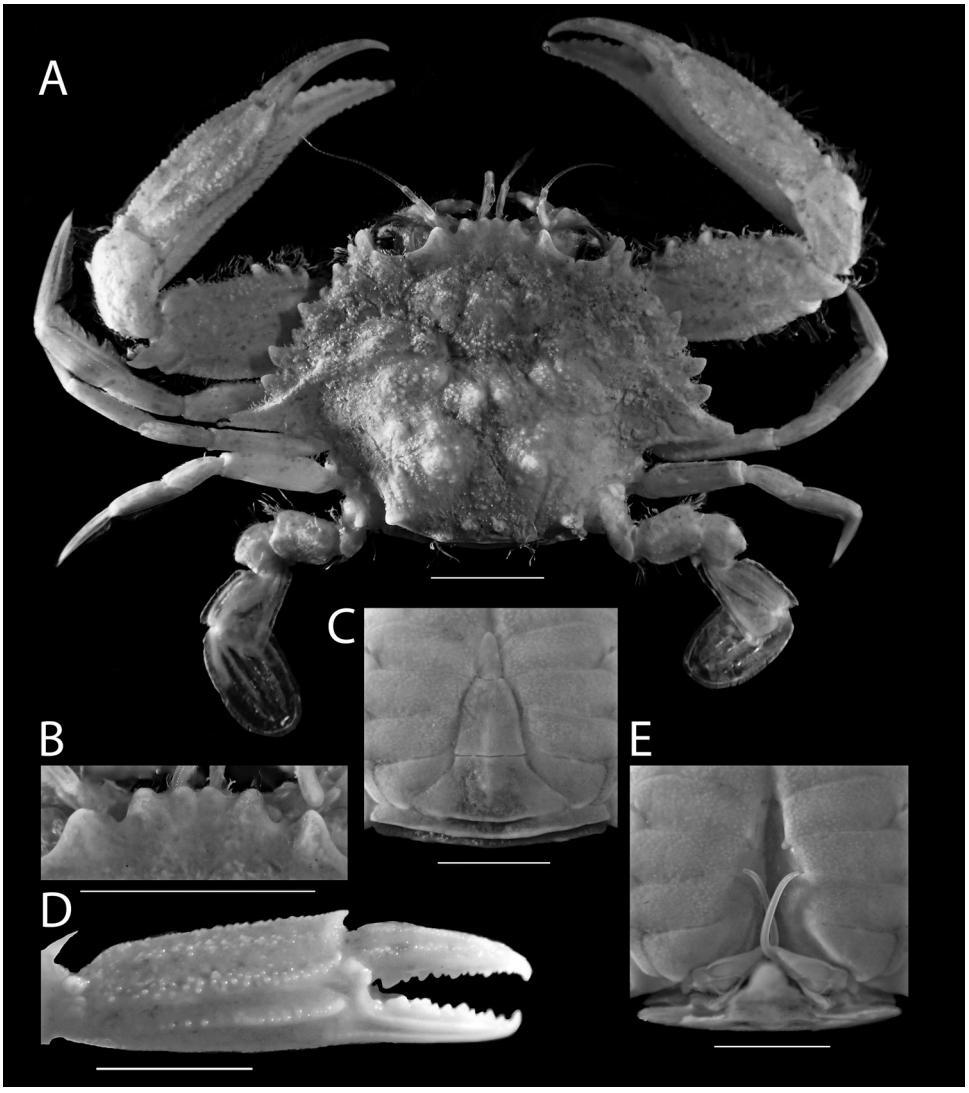

Figure 13. *Incultus tuberculosus* (A. Milne-Edwards, 1861), male, CW 22 mm, MNHN-IU-2014-1187, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

moderately unequal, heterodontic, with flattened molariform tooth located proximally at cutting edge of dactylus; palm unarmed or with small spine distally over dactylar articulation, two distinct longitudinal crests on outer surfact and two on upper surfaces of palm; fingers distinctly shorter than palm. Dactyli of pereiopods 2–4 cultriform, costate, setose on ventral margin. Merus of pereiopod 5 distinctly longer than broad, without spine on posterior margin. Male pleon (Fig. 13C) quasi-triangular; crests on second and third pleomeres low. Lateral margins of third pleomere straight; apex of thoracic episternite 7 fills in interspace between anterior margin of pleomere 3 and episternite 8; third to fifth somites fused, without remaining sutures, crests or keels on them may be present; last pleomere elongate. First male gonopod (Fig. 13E) stout or moderately slender distally, arched or almost rectangularly bent; tip rounded, with moderately wide subterminal opening; gonopods in pair overlapping each other by bent regions (not obvious in *I. alcocki* possessing relatively short gonopods). Female vulva (Fig. 4E) elliptic, located at mesial or posteromesial margin of sternite.

Etymology: The genus name is derived from the Latin adjective '*incultus*', meaning rough, unkempt, but is here treated as a masculine noun in apposition. It alludes to the somewhat untidy external appearance of the known species; gender masculine.

Systematic position: All three included species were listed in the subgenus *Xiphonectes* by Ng *et al.* (2008), but later accepted at generic level following Spiridonov *et al.* (2014). The included species are similar to *Xiphonectes* (as restricted in this study) and to *Eodemus*, *Trionectes* and the lupocycline *Alionectes*, in general appearance of the body. The carapace in all these genera is flattened, with a similarly long posterior tooth of the anterolateral series and with an angulate junction of the posterolateral and posterior margins.

Incultus bears a morphologically close relationship to *Xiphonectes* and *Trionectes*. It differs from these genera by: (1) distinctly elevated dorsal regions on the carapace (vs. feebly demarcated in both); (2) lobate anterolateral teeth on the carapace (vs. predominantly sharply triangular in both); (3) the front with three or four low and often indistinct subequal teeth (vs. four distinct triangular or rounded teeth, with submedian ones smaller in *Xiphonectes*, and three subequal triangular or blunt teeth, with the median one more slender in *Trionectes*); (4) the infraorbital margin with a broad lateral notch (vs. narrow in *Xiphonectes* and deep, 'V'-shaped in *Trionectes*); (5) the male pleon with second and third somites each bearing a low transverse crest (vs. second high, laminar and third shallow; the latter might also be high in some *Xiphonectes* spp.); (6) the male pleon with the sixth somite elongately trapezoid (vs. similar in *Trionectes*, but distinctly constricted subdistally in *Xiphonectes*); (7) the stout chelipeds (vs. comparatively slender in *Xiphonectes*), with fingers distinctly shorter than the palm (vs. subequal in both other genera); and (8) the first male gonopod with a rounded tip, being relatively long, almost rectangularly bent at the midlength at least in *I. brockii* and *I. tuberculosus*; the pair of gonopods overlap each other by the bent regions (vs. gonopods slender, smoothly out-curved distally, not meeting medially in *Xiphonectes*; similar but shorter and stouter in *Trionectes*).

Eodemus is distinguishable from *Incultus* by deep orbits, with two incisions with fully appressed walls, and with the inferior margin bearing a broad 'Y'-shaped lateral notch. The cheliped merus bears two spines distally on the posterior border. The male pleon is almost 'T'-shaped, with the sixth somite elongate, narrow (vs. pleon subtriangular in *Incultus*, with the sixth pleomere trapezoid). The first gonopods are relatively long, arched, distally slender; the pair of first gonopods are touching in the median body plane at the bent parts.

Based on the present molecular analyses, *Incultus* is closely related to *Allomonomia*. Species of both taxa have the first male gonopods bent in a similar way; those lie in a pair overlapping each other by their bent regions in *Incultus* gen. nov., while being subparallel with distal parts in *Allomonomia*. Both genera are also characterized by the presence of only a single posterodistal tooth on the cheliped merus. Additionally, *Incultus* is different from *Allomonomia* in having a hexagonal and deeply depressed carapace with elevated swollen regions and the posterolateral angles acutely produced; whereas in *Allomonomia*, the carapace is distinctly convex dorsally, with a semicircular anterior outline and with rounded postrolateral angles.

In addition to the general shape of the body mentioned above, *Alionectes* differs from *Incultus* mainly by large circular orbits without dorsal fissures (vs. with small, 'Y'-shaped fissures in *Incultus*) and by a distinct posterodistal tooth on the merus of the swimming legs. The cheliped merus bears two spines distally on the posterior border (vs. a single distal spine and an oblique keel more proximally). The male pleon has the second and third somites with subequally low crests, marginally serrated on the second pleomere. The first male gonopods are relatively short and robust proximally, tapering distally to the out-curved tip; the pair of first gonopods lies obliquely inwards, touching at their subdistal parts.

Remarks: *Neptunus* (*Hellenus*) *alcocki* Nobili, 1905 (= *Portunus alcocki*; see: Stephenson, 1972a, b; Neumann & Spiridonov, 1999) has until recently been included in the subgenus *Portunus* (*Xiphonectes*). It is known from the holotype male and a single female from the Gulf of Aden (Neumann & Spiridonov, 1999); it has also been recorded in the Red Sea [Laurie, 1915; and present material, SMF (V.A.S.)]. The species was not included in the present molecular analyses. Based on the holotype, illustrated by Guinot (1957: figs 3, 4, 9, 10) and examined by us (M.K. and Z.Ď.), the species possesses three low frontal lobes, a character typical for *Trionectes* or some species of *Eodemus* and *Xiphonectes*. However, it shows a closer morphological affinity to *Incultus* rather than to other portunine genera. Its median frontal tooth is evidently derived from the fusion of two small submedian teeth and it has low lateral frontal teeth, similar to *I. brockii*, with four obsolescent teeth forming a shallowly undulating margin (in *I. tuberculosus*, the two submedians are distinct but small). In contrast, in the other three genera the frontal teeth are triangular. The stout arched first male gonopods are also distinct from those of *Trionectes*, which distally are strongly bent and slender, with a minute terminal opening, whereas in *I. alcocki* they only feebly taper distally to a moderately wide opening (see Guinot, 1957: figs 8–10). Furthermore, *I. alocki* shares with other *Incultus* spp. the unique morphology of the rounded female vulva located at the mesial or posteromesial margin of the sternite (compare Neumann & Spiridonov, 1999: fig. 2C; Apel & Spiridonov, 1998: fig. 117d) and is herein thus transferred to *Incultus*.

Size: Small to medium-sized species; maximal recorded size range from 7.8 mm × 16.3 mm in *I. alcocki* (Neumann & Spiridonov, 1999) to 20.5 mm × 35.0 mm in *I. brockii* (Yang *et al.*, 2012) and 29.0 mm × 49.0 mm in *I. tuberculosus* (Stephenson & Rees, 1967a).

Ecological notes: The included species show different depth ranges, with *I. brockii* being an intertidal to upper subtidal species (Spiridonov, 1999), whereas *I. tuberculosus* occurs on various substrates from the upper subtidal to continental slope, ranging from 7–9 to 580 m in depth (Stephenson, 1972a, b; Apel & Spiridonov, 1998; Yang *et al.*, 2012). *Incultus alcocki* appears to be an upper subtidal species occurring mostly on sand (Laurie, 1915; Neumann & Spiridonov, 1999; present material, SMF).

Geographical range: Indo-West Pacific: *I. tuberculosus* has the broadest range, from the Red Sea and East Africa to the Hawaiian Islands (Stephenson, 1972a, b; Apel & Spiridonov, 1998); *I. brockii* is restricted to the eastern Indian Ocean and the western Pacific; and *I. alcocki* is currently known only from the Red Sea and the Gulf of Aden (see above).

MONOMIA GISTEL, 1848

(FIGS 3D, 4G, 14)

= *Portunus* (*Amphitrite*) De Haan, 1833 {type species *Portunus gladiator* Fabricius, 1798, subsequent designation by Miers (1886); name pre-occupied by *Amphitrite* Müller, 1771 [Polychaeta]; gender feminine.

= *Portunus* (*Monomia*) Gistel, 1848 (replacement name for *Amphitrite* De Haan, 1833; gender feminine).

Included species: Ten.

Monomia argentata (A. Milne-Edwards, 1861)
= *Amphitrite argentata* White, 1847 (*nomen nudum*)
= *Neptunus argentatus* A. Milne-Edwards, 1861
Monomia australiensis (Stephenson & Cook, 1973)
= *Portunus australiensis* Stephenson & Cook, 1973
Monomia curvipenis (Stephenson, 1961)
= *Portunus curvipenis* Stephenson, 1961
Monomia gladiator (Fabricius, 1798)
= *Portunus gladiator* Fabricius, 1798
= *Cancer menestho* Herbst, 1803
Monomia glareosa (Alcock, 1899)
= *Neptunus* (*Amphitrite*) *argentatus* Alcock, 1899
Monomia haani (Stimpson, 1858)
= *Amphitrite haanii* Stimpson, 1858
= *Portunus pseudoargentata* Stephenson, 1961
Monomia lucida Koch & Ďuriš, 2018
Monomia petrea (Alcock, 1899)
= *Neptunus* (*Amphitrite*) *petrea* Alcock, 1899
Monomia rubromarginata (Lanchester, 1900)
= *Achelous rubro-marginatus* Lanchester, 1900
Monomia samoensis Ward, 1939

Diagnosis: Carapace (Fig. 14A) quasi-hexagonal; ~1.6–1.8 times as broad as long; margins setose, dorsal surface tomentose, with well-defined granulate regions. Front (Fig. 14B) with four subtriangular blunt teeth, submedian teeth usually distinctly lower than lateral ones, all teeth projecting slightly beyond tip of inner orbital lobe; median epistomial apophysis well developed, reaching distinctly beyond front. Orbit relatively large, ellipsoidal, with upper margin granulate and two well-developed fissures, in middle and near base of first anterolateral tooth; lower orbital margin with large lateral notch, one or two strong obtuse mesial teeth, and outer infraorbital lobe appressed to ventral side of outer supraorbital lobe (= first anterolateral tooth). Anterolateral margin of carapace convex, slightly longer than posterolateral margin, armed by nine teeth: eight anterior ones

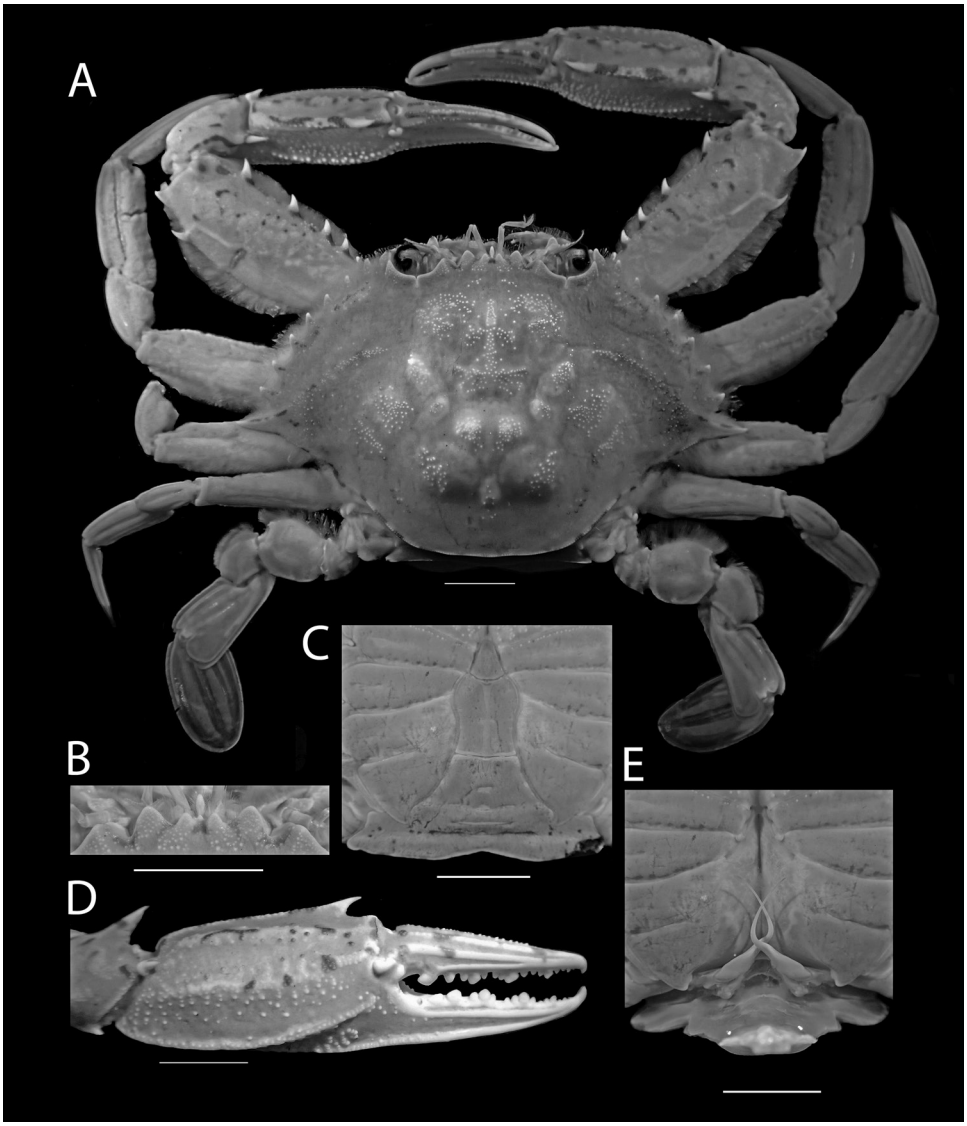

Figure 14. *Monomia gladiator* (Fabricius, 1798), male, CW 75 mm, MNHN-IU-2014-1188, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 10 mm.

subequal, small, acute and projecting forwards; ninth tooth distinctly larger, lateral. Posterolateral angle of carapace broadly rounded. Sutures on thoracic sternum well developed (Fig. 14C). Merus of third maxilliped with anterolateral lobe subtriangular. Chelipeds moderately stout; merus with four or five spines on anterior border and two (rarely one) spine on posterior border; carpus with spine on outer face, which may be reduced; upper surface of palm with two granular crests, inner one strong, ending by spine distally; outer surface with two granular crests ending at level of finger joint, lower arched, creating outer ventral, sharply produced margin. Chelae (Fig. 14D) slightly unequal, weakly heterodontic, with molariform tooth on cutting edge of dactylus (this molariform tooth may be reduced in large specimens). Dactyli of pereiopods 2–4 styliform, densely setose on ventral margin. Merus of pereiopod 5 a little longer than broad, without spine on posterior margin. Male pleon 'T'-shaped (Figs 3D, 14C). Pleomeres 2 and 3 forming transverse laminar crests; lateral margins of pleomere 3 usually distinctly concave; apex of posterior thoracic episternite fills interspace between anterior margin of pleomere 3 and thoracic sternite 8. Pleomeres 3–5 fused, but a groove remains at place of suture between pleomeres 3 and 4; usually keels and crests present on these pleomere terga. Pleomere 6 as long as broad or longer, sometimes with a small median spine directing backwards on distal part; with telson narrowly triangular. First male gonopods (Fig. 14E)

long, bent; gonopods in pair overlapping each other by bent regions, with distal parts directed anterolaterally, or subparallel and touching only medially. Female vulva (Fig. 4G) slit-shaped, located at anteromesial margin of sternite, often covered with cuticular cup.

Systematic position: The genus is morphologically similar to the newly established genus *Allomonomia* (see discussion under that genus). They share the following morphological features: rounded posterolateral angles of the carapace, third maxilliped merus with a triangular anterodistal projection and the chelae with two teeth on the upper surface of the palm. *Monomia* differs from *Allomonomia* by the front having four low and subequal teeth, with the submedians lower than the laterals, projecting slightly beyond the tip of the inner supraorbital angle, the median epistomial spine reaching distinctly beyond the front, predominantly two posterodistal spines on the cheliped merus and by the first male gonopods in a pair usually overlapping each other along their bent parts.

The three-marker phylogenetic analysis (Fig. 1) shows *Monomia* as most closely related to *Cycloachelous* and *Eodemus* (see above), together forming a basal well-supported clade. As already discussed, these three genera are similar in the presence of granular patches on the dorsal regions of the carapace, four frontal teeth with the submedian pair smaller, a produced anterolateral lobe of the third maxilliped merus, two posterodistal spines on the cheliped merus (rarely single in *Monomia* spp.), the 'T'-shaped male pleon, concave lateral margins of the third male pleomere, and the first gonopods relatively long, usually bent, distally slender, and a slit-shaped female vulva. They differ, as discussed above for *Eodemus*, in mostly larger body sizes in *Monomia*, usually longer posterior lateral tooth and acutely produced posterolateral angle of the carapace in *Eodemus* (latter rounded in *Monomia*) and the medially produced epistome in *Monomia*. The first male gonopods overlap each other along their bent parts in the majority of *Monomia* spp. (except for some Australian spp. with subparallel, not overlapping, distal parts of the gonopods), whereas they only touch at their bent parts in *Eodemus*.

Cycloachelous shares with the aforementioned taxa some apparent morphological apomorphies, such as a slit-shaped female vulva and (generally) two distal spines on the posterior margin of the cheliped merus. However, *Cycloachelous* spp. are distinct in their general appearance from other genera owing to their circular carapace shape, stout gonopods with unique shapes and symmetrical chelipeds (see Remarks for the respective genera).

Remarks: Monomia now contains ten species. Previously, 14 species were included in *Monomia* (see Ng *et al.*, 2008; Koch *et al.*, 2015b; Koch & Ďuriš, 2018). Four species are herein removed and transferred to different genera: two species, *P.* (*M.*) *lecromi* and *M. calla*, are placed in the new genus *Allomonomia*; *P.* (*M.*) *euglyphus* is transferred to *Cycloachelous*; and *P.* (*M.*) *ponticus* is transferred to *Lupocycloporus*.

There has been substantial confusion regarding the nomenclature of the type species of the genus *Monomia*, *Portunus gladiator* Fabricius, 1798. It has been considered as a secondary homonym of *Cancer gladiator* Fabricius, 1793, a junior subjective synonym of *P. sanguinolentus* (Stephenson & Cook, 1973; Chertoprud *et al.*, 2012). Stephenson & Cook (1973) then suggested *Amphitrite haani* Stimpson, 1858 as the next available synonym of *P. gladiator*. However, there is current agreement that this suggestion of homonymy is based on a misinterpretation of the International Code of Zoological Nomenclature (Ng *et al.*, 2008; Spiridonov *et al.*, 2014; Windsor *et al.*, 2019). Furthermore, both morphological and molecular genetic evidence (Windsor *et al.*, 2019) clearly indicate that *M. gladiator* and *M. haani* are distinct species and that *M. pseudoargentata* (Stephenson, 1961) is a junior subjective synonym of *M. haani*.

The morphological examination of the Australian species, *M. curvipenis* (one male, AM P.80096) and *M. rubromarginata* (1 female, MV J45390; four males, MV J45533) showed some characteristics such as the small median spine directed backwards on the distal part of the sixth male pleomere and a different shape of the first gonopods compared with the rest of the species. The generic affiliation of these species needs to be confirmed by further molecular analyses.

Size: These are medium to large portunid crabs, with the maximum size (CL × CW) ranging from 22.0 mm × 38.0 mm (*M. argentata*; Yang *et al.*, 2012) to 61.0 mm × 111.6 mm (*M. haani*, this study; ZIN RAN male).

Ecological notes: This group comprises predominantly lower subtidal crabs occurring to depths not exceeding 100 m, with soft, mainly sandy bottoms (Sakai, 1939, 1976; Crosnier, 1962; Dai & Yang, 1991; Apel & Spiridonov, 1998; Chertoprud *et al.*, 2012), but *M. argentata* seems to be a deepwater species known from depths down to 400–402 m (four males, MNHN-IU-2018-4942).

Geographical range: Indo-West Pacific: from the Red Sea and south-eastern Africa to Japan, the Philippines, Australia, New Caledonia and Samoa (Sakai, 1939, 1976; Stephenson, 1972a, b; Apel & Spiridonov,

1998; Poupin, 2010); there is a questionable record of *M. argentata* from the Hawaiian Islands (Castro, 2011).

PORTUNUS WEBER, 1795

(FIGS 3C, 4B, 15)

= *Portunus* Weber, 1795 (type species *Cancer pelagicus* Linnaeus, 1758, designation by Rathbun, 1926; gender masculine) [Opinion 394]; see Holthuis (1952).

Full synonymy: see Ng *et al.* (2008): 152 [*Portunus* (*Portunus*)].

Included species: Thirteen.

Portunus armatus (A. Milne-Edwards, 1861)
= *Neptunus armatus* A. Milne-Edwards, 1861
Portunus convexus De Haan, 1835
= *Neptunus sieboldi* A. Milne-Edwards, 1861
Portunus hawaiiensis Stephenson, 1968
Portunus madagascariensis (Hoffman, 1874)
= *Neptunus madagascariensis* Hoffmann, 1874
Portunus pelagicus (Linnaeus, 1758)
= *Cancer pelagicus* Linnaeus, 1758 [Opinion 394]
= *Cancer pelagicus* Forskål, 1775 [pre-occupied name, primary junior homonym of *Cancer pelagicus* Linnaeus, 1758]
= *Cancer cedonulli* Herbst, 1794
= *Portunus denticulatus* Marion de Procé, 1822
= *Portunus* (*Portunus*) *pelagicus* var. *sinensis* Shen, 1932
Portunus pubescens (Dana, 1852)
= *Lupa pubescens* Dana, 1852
= *Neptunus tomentosus* Haswell, 1881
Portunus reticulatus (Herbst, 1799)
= *Cancer reticulatus* Herbst, 1799
Portunus rufiarcus Davie, 1987
Portunus sanguinolentus (Herbst, 1783)
= *Cancer sanguinolentus* Herbst, 1783
= *Cancer gladiator* Fabricius, 1793
= *Callinectes alexandri* Rathbun, 1907
= ?*Cancer raihoae* Curtiss, 1938
Portunus serratifrons (Montrouzier, 1865)
= *Neptunus serratifrons* Montrouzier, 1865
Portunus sayi (Gibbes, 1850)
= *Lupa sayi* Gibbes, 1850
= *Portunus tropicalis* Marion de Procé, 1822
= *Lupea pudica* Gerstaecker, 1856
= *Lupea parvula* Desbonne, in Desbonne & Schramm, 1867
Portunus segnis (Forskål, 1775)
= *Cancer segnis* Forskål, 1775
= *Portunus mauritianus* Ward, 1942
Portunus trituberculatus (Miers, 1876)
= *Neptunus trituberculatus* Miers, 1876

Diagnosis: Carapace (Fig. 15A) usually broadly hexagonal, much broader than long, width (without lateral teeth)-to-length ratio > 1.5. Dorsal surface finely granulated, with regions feebly demarcated, sometimes with narrow rows of granules in their centres. Urogastric depression distinctly anterior (rarely slightly posterior) to half length of carapace. Front (Fig. 15B) with four triangular or rounded teeth; median ones may be extremely reduced. Supraorbital margin with two short fissures; infraorbital margin with shallow lateral notch. Epistome apophysis well developed, may be producing medially as prominent spine far overreaching submedian frontal teeth. Anterolateral margin with nine spiniform teeth; teeth of anterior series (except last tooth) short, subequal in size; last tooth distinctly larger, lateral. Posterolateral junction of carapace rounded. Most of the sutures on thoracic sternum indistinct (Fig. 15C), thoracic sternites generally smooth. Merus of third maxilliped with anteroexternal angle rounded or subrectangular, not produced laterally. Chelipeds usually stout; merus with posterior border subparallel to anterior (or convex), bearing three or four spines on anterior border, and unarmed or with one spine distally on posterior border. Carpus with a spine and carinae on outer face; in a few cases, carina ends in an additional spinule. Chelae (Fig. 15D) slightly inaequal, heterodontic upper surface of palm with two distal teeth; molariform tooth present proximally at cutting edge of dactylys of larger chela. Dactyli of pereiopods 2–4 relatively broad, lanceolate, leaf-like or cultriform, indistinctly costate, densely setose on ventral margin. Merus of pereiopod 5 subquadrate, only little longer than broad or, more rarely, elongate, distinctly longer than broad, without a spine on posterior margin. Male pleon (Figs 3C, 15C) narrowly triangular, almost smooth. Pleomeres 2 and 3 with low keels, in some species not visible in ventral view; lateral margins of pleomere 3 straight or concave; terminal part of posterior thoracic episternite fills interspace between anterior margin of pleomere 3 and thoracic sternite 8; third to fifth pleomeres fused, without remaining sutures but with indistinct transverse keels; combined part distinctly longer than sixth pleomere, the latter with lateral margins convergent distally; telson triangular and rounded, subequal or shorter than sixth pleomere. First male gonopod (Fig. 15E) with short and robust transverse base and long, string-like distal part, basally curved and broadly arching anteriorly, touching medially; apices straight, reaching telson basis. Female vulva (Fig. 4B) in form of a transverse slit or rounded, located in medial part of proximal portion of sternite, with long axis subparallel or oblique to anterior margin of sternite.

Systematic position: Based on the present molecular results and a morphological comparison, *Portunus* is closely related to *Callinectes*. Spiridonov *et al.* (2014)

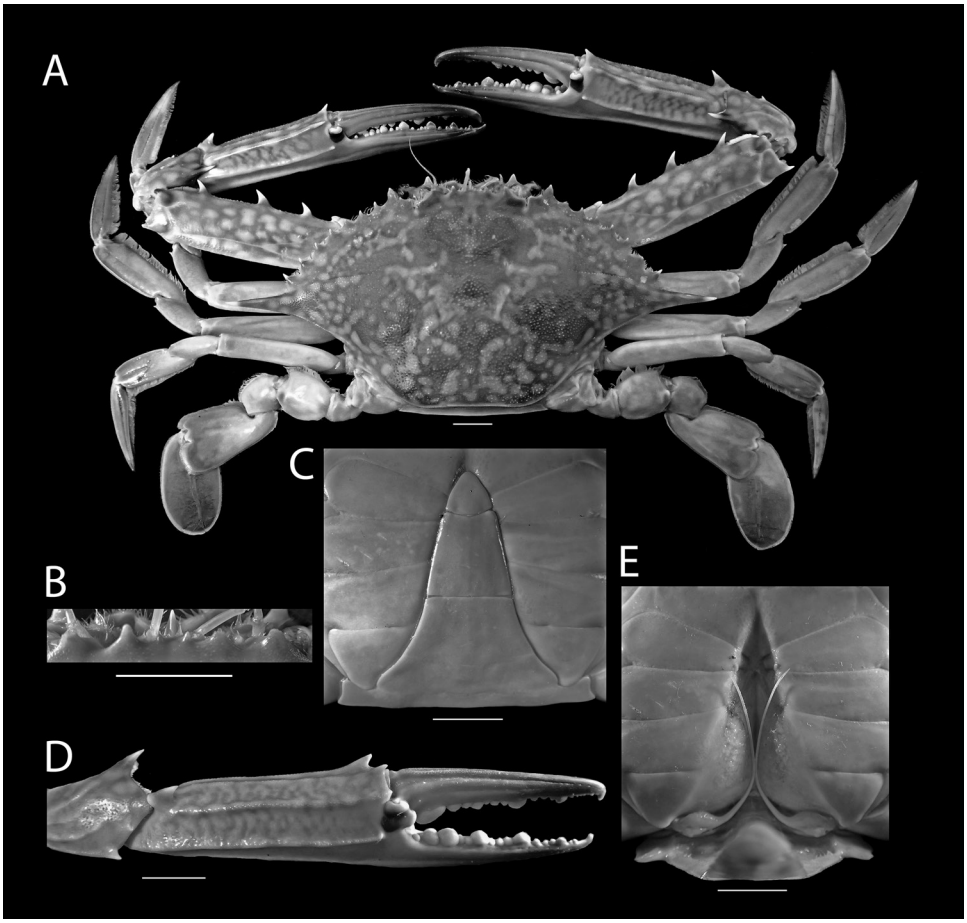

Figure 15. *Portunus pelagicus* (Linnaus, 1758), male, CW 128 mm, MNHN-IU-2014-1189, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 10 mm.

presented *Portunus*, *Callinectes* and Atlantic *Arenaeus* as key members of the subfamily Portunidae, with unresolved positions for other species of *Portunus* (*s.l.*) diagnosed by being relatively large swimming forms sharing leaf-like walking dactyli, the lack of conspicuous granular patches on the carapace and slender gonopods. The other '*Portunus*' species were separated into multiple subgenera (see listing by Ng *et al.*, 2008), some of which have since been raised to generic level (Mantelatto *et al.*, 2009; Nguyen & Ng, 2010; Chertoprud *et al.*, 2012; Spiridonov *et al.*, 2014). Here, they are all nested inside a major monophyly as part of an unresolved basal polytomy together with *Portunus–Callinectes*, *Achelous*, Lupocyclinae and the Thalamitinae clades (Fig. 1).

Remarks: From 24 species of *Portunus* (*Portunus*) as listed by Ng *et al.* (2008), the present generic reassignment reduces this to 13 species. *Portunus mauritianus* Ward, 1942 had already been synonymized with *P.* (*P.*) *segnis* by Ng *et al.* (2008); three species (*P. asper*, *P. gibbessi* and *P. rufiremus*) were transferred to *Achelous* by Mantelatto *et al.* (2009) and four others (*P. acuminatus*, *P. affinis*, *P. minimus* and *P. xantusii*) by Mantelatto (2018); and *P. floridanus* has recently been transferred to *Achelous* by Marco-Herrero *et al.* (2021). The remaining four species (*P. anceps*, *P. hastatus*, *P. inaequalis* and *P. ventralis*) are assigned to *Achelous* in this study (see above). *Portunus serratifrons* (Montrouzier, 1865) was already suggested to be a juvenile *Scylla serrata* by A. Milne-Edwards (1873), but it is still listed herein as a valid species of *Portunus*, albeit rather provisionally. The generic affiliation of *P. madagascariensis* (Hoffmann, 1877) needs to be re-examined owing to its close similarity to *P. sanguinolentus*. The species is thus here provisionally regarded as valid.

Portunus mokyevskyi Zarenkov, 1970 was listed in the subgenus *Portunus* by Ng *et al.* (2008) on the basis of the original description (Zarenkov, 1970). The holotype of this species, a juvenile male measuring 19.0 mm × 29.2 mm (ZMMU Ma 2177, Indonesia, North Sulawesi, Amurang, littoral, 18 December 1962, O. B.

Mokievsky lgt.), was examined by one of us (V.A.S.). The general morphology and smoothness of the carapace, the presence of two spines on the posterior margin of the cheliped merus and the pattern of heterodonty (i.e. Keenan *et al.*, 1998; Spiridonov *et al.*, 2014) undoubtedly indicate that it belongs to *Scylla* De Haan, 1833 (Necronectinae); the shape of the frontal lobes and the pattern of spines on the carpus and palm of chelipeds allow us to identify it as *Scylla tranquebarica* (Fabricius, 1798) (*sensu* Keenan *et al.*, 1998), under which species we here formally synonymize it.

Except for *P. madagascariensis* and *P. serratifrons*, for which original descriptions were too brief (Montrousier, 1865; Hoffman, 1874), two groups of species may be recognized among the remaining ten species of *Portunus* based on their morphology [i.e. the *P. convexus* group (together with *P. pubescens*, *P. rufiarcus* and *P. sayi*) and the *P. pelagicus* group (with the six remaining species)]. There are differences in the shape of the morphology of the carapace and chelipeds. Given that our molecular analysis does not cover members of the *P. convexus* group, the congeneric status of its three species needs to be confirmed in the future.

Size: The genus includes the group of medium-sized species *P. pubescens* (maximum size CL × CW 25.0 mm × 45.0 mm; Crosnier, 1962), *P. convexux* (30.4 mm × 51.6 mm; our data, SMF male), *P. rufiarcus* (CW 27.1 mm, the only known specimen, holotype; Davie, 1987) and *P. sayi* (37.1 mm × 76.1 mm; Rathbun, 1930). The maximum known sizes of the remaining larger species reach distinctly higher values, e.g. CL × CW: 61.5 mm × 136.0 mm in *P. sanguinolentus* (see Apel & Spiridonov, 1998), 77.2 mm × 163.4 mm in *P. reticulatus* (see Lai *et al.*, 2010), 82.0 mm × 188.0 mm in *P. trituberculatus* (see Yang *et al.*, 2012) and CW 173 mm in *P. armatus* (female MNHN-IU-2018-1413).

Ecological notes: Portunus spp. are generally shallow-water dwellers, confined mostly to the intertidal and upper subtidal zones, preferring sandy substrates but also occurring on other types of substrates, notably seagrass meadows; larger-sized species are known for their complex migration pattern and frequent occurrence in the outer parts of estuaries. *Portunus sanguinolentus* and especially *P. sayi* are commonly associated with flotsam, thus travelling large distances over deep waters (reviewed by Spiridonov, 2013). *Portunus sayi* is likely to reproduce when living on floating sargassum (Verrill, 1908; Rathbun, 1930).

Geographical range: Indo-West Pacific (majority of spp.); tropical western Atlantic (*P. sayi*); Mediterranean Sea (*P. segnis*, Lessepsian migrant from the Red Sea, now common Mediterranean species; Lai *et al.*, 2010).

TRIONECTES GEN. NOV.

(FIGS 3B, 4C, 16)

Zoobank registration: urn:lsid:zoobank.org:act:BCC68580-6F16-44F1-8DDC-D41241E34F7B

Type species: Portunus (*Amphitrite*) *tenuipes* De Haan, 1835, by present designation.

Included species: Seven.

Trionectes andersoni (De Man, 1887) comb. nov.
= *Neptunus* (*Hellenus*) *andersoni* De Man, 1887

Trionectes mariei (Guinot, 1967) comb. nov.
= *Portunus* (*Hellenus*) *mariei* Guinot, 1957

Trionectes pseudotenuipes (Spiridonov, 1999) comb. nov.
= *Portunus pseudotenuipes* Spiridonov, 1999

Trionectes rugosus (A. Milne-Edwards, 1861) comb. nov.
= *Neptunus rugosus* A. Milne-Edwards, 1861

Trionectes spiniferus (Stephenson & Rees, 1967) comb. nov.
= *Portunus spiniferus* Stephenson & Rees, 1967

Trionectes tenuipes (De Haan, 1835) comb. nov.
= *Amphitrite tenuipes* De Haan, 1835)

Trionectes tridentatus (Yang, Dai & Son, 1979) comb. nov.
= *Portunus tridentatus* Yang, Dai & Song, 1979

Diagnosis: Carapace (Fig. 16A) broadly hexagonal, width ~1.5 times as long as broad (without lateral teeth); dorsal surface variously granulate, with regions moderately demarcated. Front (Fig. 16B) with three distinct triangular or rounded lobes, median lobe subequal but more slender than lateral ones, all three lobes distinctly projecting beyond tip of inner supraorbital lobe. Orbit with inner supraorbital angle truncated, with oblique distal margin; dorsal orbital margin with two short fissures; infraorbital margin with deep 'V'-shaped lateral notch. Anterolateral margin with nine spiniform, triangular or lobiform teeth, irregular in size; last tooth distinctly larger, lateral. Posterolateral junction of carapace angular, pointed, often distinctly upturned, sharp. Sutures of thoracic sternum unclear (Fig. 16C); thoracic sternites may be granular. Merus of third maxilliped elongate, distally markedly produced to triangular, trapezoidal or rounded lobe. Chelipeds robust, with merus bearing three or four spines on anterior border and one or two spines distally on posterior border; carpus with single spine on outer face, which, in some species (*T.*

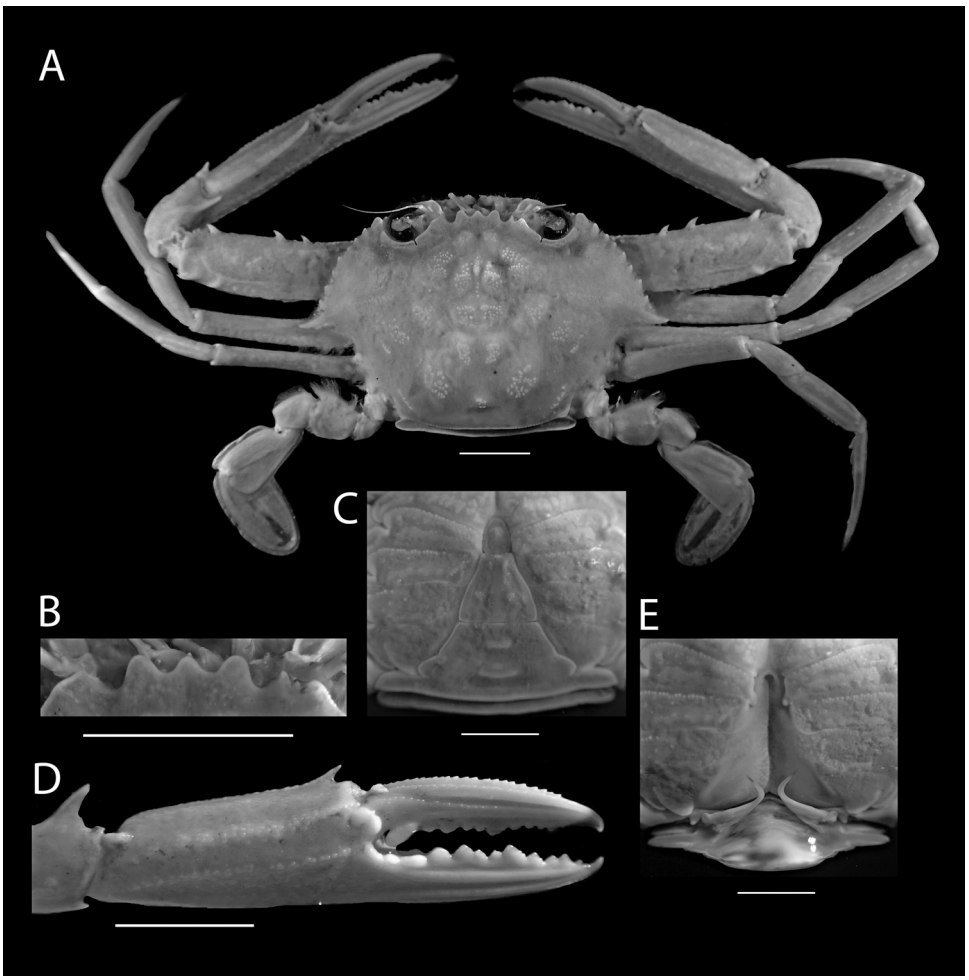

Figure 16. *Trionectes tenuipes* (De Haan, 1835), male, CW 39 mm, MNHN-IU-2014-1185, Vietnam, South China Sea. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 10 mm.

pseudotenuipes), is obsolete; upper surface of palm with one or two distal teeth. Chelae (Fig. 16D) slightly inaequal, heterodontic, with moderate molariform tooth at cutting edge of dactylus in larger chela. Dactyli of pereiopods 2–4 cultriform or styliform, costate, with short setose emargination on ventral margin. Merus of pereiopod 5 a little longer than broad, without posterodistal spine. Male pleon (Figs 3B, 16C) quasi-triangular. Pleomeres 2 and 3 with laminar crests. Lateral margins of pleomere 3 straight or convex; terminal part of posterior thoracic episternite fills interspace between anterior margin of pleomere 3 and thoracic sternite 8. Pleomeres 3–5 fused without remaining sutures, but indistinct keels may be present. Pleomere 6 with lateral margins sinuate. First male gonopod (Fig. 16E) short, curved, tapering distally to slender tip; pair of first gonopods lying obliquely directed inwards but isolated, not touching medially, with apices curved anterolaterally. Female vulva (Fig. 4C) (examined in *T. mariei* and *T. tenuipes*) in form of an oblique widened slit, located in medial part of proximal portion of sternite.

Etymology: Given that species were previously included in *Xiphonectes*, the new generic name is a combination of the Greek 'τρί', three (pointing on trilobed front) and 'νήκτης', swimmer, thus a 'trilobed swimmer'; gender masculine.

Systematic position: All species of *Trionectes*, together with the new genera *Eodemus*, *Incultus* and the lupocycline genus *Alionectes*, were previously considered members of *Xiphonectes* (see listing by Ng *et al.*, 2008). All these taxa are similar in overall appearance, with a more or less strongly depressed carapace, usually with a long pair of lateral teeth and elevated patches of granules on the dorsum and with a produced or subacute posterolateral angle.

Based on the morphological comparison and the present molecular analysis, *Trionectes* is most closely

related to *Xiphonectes* (*s.s.*; present paper), and *Incultus* is more basal (see remarks for *Xiphonectes*, below). *Trionectes* differs from these genera by: (1) the front with three subequal triangular or blunt teeth in *Trionectes* (vs. four distinct triangular or rounded teeth, with submedian ones smaller in *Xiphonectes*, or four shallow subequal teeth in *Incultus*); (2) feebly demarcated dorsal regions of the carapace (vs. distinctly elevated in *Incultus*); (3) predominantly sharply triangular anterolateral teeth on the carapace (vs. lobate in *Incultus*); (4) the infraorbital margin deep, 'V'-shaped, in *Trionectes* (vs. with narrow lateral notch in *Xiphonectes*, or with broad lateral notch in *Incultus*); (5) the male pleon elongately trapezoid (vs. same in *Incultus*, but with the sixth pleomere distinctly constricted subdistally in *Xiphonectes*); (6) the chelipeds stout (vs. same in *Incultus*, but comparatively slender in *Xiphonectes*), with fingers subequal to palm length (vs. same in *Xiphonectes* but distinctly shorter in *Incultus*); (7) the first male gonopods short, stout, subdistally bent, not meeting medially (vs. similar but more slender, smoothly out-curved in midlength in *Xiphonectes*, but relatively long, bent in midlength, with pair of gonopods overlapping each other medially in *Incultus*); and (8) the female vulva, which is located at the mesial or posteromesial margin of the sternite in *Incultus* and has a different position in *Trionectes* and *Xiphonectes*.

From the lupocycline *Alionectes*, *Trionectes* can be distinguished easily by the tridentate front, the presence of a dorsally incised orbital margin, which is entire in *Alionectes*, the posterodistally unarmed merus of the swimming leg, and by the smooth, entire margin of the transverse crest on the second pleonal somite in males (vs. serrated on the second pleomere in *Alionectes*).

Trionectes is also easily distinguished from *Eodemus* by the tridentate front, but also by the subtriangular male pleon (vs. a 'T'-shaped pleon) and by the distally produced triangular or circular rounded, not distolaterally produced, third maxilliped merus (vs. a distinctly laterally produced anterolateral lobe). The genera also differ by the position and shape of the female vulva, which is in the form of a widened slit in *Trionectes* and somewhat distant from the margin of the sternite, and chinking located close to the mesial margin in *Eodemus*.

Remarks: Three species differ from the remaining ones in the genus. The examined MNHN and ZMMU specimens of *T. mariei* and MNHN specimens of *T. spiniferus* and the species *T. tridentatus*, based on published reports (Dai & Yang, 1991; Yang *et al.*, 2012), all have distinct unequal and sharp anterolateral teeth on the carapace, the third maxillipeds with a rounded distal projection, more robust chelipeds and three spines on the upper surface of the chela palm, but they all share the trilobed front, and the pleon bears a distinct laminar crest on the second pleomere typical for *Trionectes*. Only *T. spiniferus* was available for the present molecular analysis but, based on the morphological similarity of all three species and its deeply nested position in the *Trionectes* clade (Fig. 3), the inclusion of *T. mariei* and *T. tridentatus* in the genus appears to be well founded.

Size: Small to medium-sized crabs; maximum known size ranges from CW 16 mm in *T. rugosus* (A. Milne-Edwards, 1861) to CL × CW: 24.5 mm × 53.3 mm in *T. tridentatus* (Yang *et al.*, 2012).

Ecological notes: The species with better-documented records (i.e. *T. tenuipes* and *T. pseudotenuipes*), occur mostly in the upper subtidal zone, to a depth of 35 m, on sand or muddy sand (Ramadan, 1936; Monod, 1938; Spiridonov, 1999). The few known records of *T. mariei* are also from upper subtidal sand patches on reefs (Guinot, 1957; present study: ZMMU Ma 3408 and SMF 47928 specimens).

Geographical range: Indo-West Pacific: from the Red Sea (Ramadan, 1936; Monod, 1938; present study) and the western Indian Ocean to the Philippines and New Caledonia (Stephenson, 1972a, b; Spiridonov, 1999; Poupin, 2010; Yang *et al.*, 2012).

XIPHONECTES A. MILNE EDWARDS, 1873 (FIG. 17)

= *Xiphonectes* A. Milne-Edwards, 1873 [type species *Amphitrite vigilans* Dana, 1852, subsequent designation by Rathbun (1930); gender masculine].

Included species: Fourteen.
Xiphonectes aculeatus Koch & Ďuriš, 2019
Xiphonectes bidens (Laurie, 1906)
= *Neptunus* (*Hellenus*) *bidens* Laurie, 1906
Xiphonectes gracillimus (Stimpson, 1858)
= *Amphitrite gracillimus* Stimpson, 1858
Xiphonectes guinotae (Stephenson & Rees, 1961)
= *Portunus guinotae* Stephenson & Rees, 1961
Xiphonectes hainanensis (H.-L. Chen, 1986)
= *Portunus hainanensis* H.-L. Chen, 1986
Xiphonectes iranjae (Crosnier, 1962)
= *Portunus iranjae* Crosnier, 1962
Xiphonectes latibrachium (Rathbun, 1906)
= *Parathranites latibrachium* Rathbun, 1906
Xiphonectes leptocheles A. Milne-Edwards, 1873
Xiphonectes longispinosus (Dana, 1852)

= *Amphitrite longispinosus* Dana, 1852
= *Amphitrite vigilans* Dana, 1852
= *Xiphonectes vigilans* var. *obtusidentatus* Miers, 1884
Xiphonectes macrophthalmus (Rathbun, 1906)
= *Portunus* (*Xiphonectes*) *macrophthalmus* Rathbun, 1906
Xiphonectes paralatibrachium (Crosnier, 2002)
= *Portunus paralatibrachium* Crosnier, 2002
Xiphonectes stephensoni (Moosa, 1981)
= *Portunus stephensoni* Moosa, 1981
= *Portunus emarginatus* Stephenson & Campbell, 1959 [pre-occupied name, primary junior homonym of *P. emarginatus* Leach, 1814, = synonym of *Macropipus arcuatus* (Leach, 1814)]
Xiphonectes tenuicaudatus (Stephenson, 1961)
= *Portunus tenuicaudatus* Stephenson, 1961
Xiphonectes tuerkayi Spiridonov, 2016
= *Portunus longispinosus* forma *longimera* Spiridonov, 1994 (*nomen nudum*)

Diagnosis: Carapace (Fig. 17A) broadly hexagonal, about twice as broad as long when lateral spines are included, width (without lateral teeth) ~1.5 × length; dorsal surface variously granulate, with regions moderately demarcated, with patches of granules, sometimes in some species projecting to centre, forming elevated tubercles. Front (Fig. 17B) with four triangular or rounded lobes; submedian lobes distinctly smaller than laterals, sometimes fused, projecting beyond tip of inner supraorbital lobe. Orbit nearly circular, with inner supraorbital lobe small, angulate, often merged to inner supraorbital margin, latter with two short fissures; infraorbital margin clearly visible in dorsal view, with narrow lateral notch. Anterolateral margin with six to nine spiniform teeth; particular teeth may have a tendency to reduction; teeth of anterior series (except last tooth) short, irregular in size, last tooth distinctly larger, lateral. Posterolateral junction of carapace angular, pointed, often distinctly upturned, sharp. Thoracic sternites partly granular, with sutures (Fig. 17C) well demarcated. Merus of third maxilliped elongate, distally produced to rounded lobe, rarely angulate. Chelipeds usually relatively slender; with merus bearing three to five spines on anterior border and one spine or obtuse lobe distally on posterior border; carpus with a sharp spine on outer face; upper surface of palm with two (rarely one) distal teeth. Chelae (Fig. 17D) slightly inaequal, heterodontic, with a moderate molariform tooth at cutting edge of dactylus in larger chela. Dactyli of pereiopods 2–4 cultriform, costate, with short, hairy emargination on ventral margin. Merus of pereiopod 5 a little longer than broad. Male pleon quasi-triangular (Fig. 17C). Pleomeres 2 and 3 with low transverse smooth crests, that on pleomere 2 higher; lateral margins of pleomere 3 convex or acuminated; terminal part of posterior thoracic episternite fills interspace between anterior margin of pleomere 3 and thoracic sternite 8. Pleomeres 3–5 fused without apparent sutures, but feeble keels may be present. Pleomere 6 with lateral margins sinuate, constricted subdistally, rarely elongate, simple. First male gonopod (Fig. 17E) in most cases elongate, curved, tapering distally to slender tip; pair of first gonopods lying obliquely directed inwards but not touching medially, apices curved anterolaterally. Female vulva relatively large, located in medial part of proximal portion of sternite, drop-shaped or ovoid, with long axis subparallel or oblique to anterior margin of sternite.

Systematic position: Xiphonectes (as listed by Ng *et al.*, 2008; Spiridonov *et al.*, 2014) is subdivided here, based on the present molecular analyses, into five genera, of which four (i.e. *Eodemus*, *Incultus*, *Trionectes* and the lupocycline *Alionectes*] are newly established. The four new genera are nested inside three unrelated clades, and two of them occupy sister positions with other currently known or new portuniine genera. All these taxa are similar by their overall appearance, with a more or less strongly depressed carapace, usually with a pair of long lateral teeth, elevated patches of granules on the dorsum, and produced or subacute posterolateral angles.

Of the above new taxa, *Trionectes* is sister positioned in the present molecular analysis to the newly restricted *Xiphonectes*, whereas *Incultus* is more basal. *Xiphonectes* differs from these by: (1) feebly demarcated dorsal regions of the carapace (vs. distinctly elevated in *Incultus*); (2) predominantly sharply triangular anterolateral teeth on the carapace (vs. lobate in *Incultus*); (3) frequent cases of reductions in the number of anterolateral teeth (vs. a full set of nine teeth in *Incultus* and *Trionectes*); (4) the front with four distinct triangular or rounded teeth, with submedian ones smaller (vs. four shallow subequal teeth in *Incultus* and three subequal triangular or blunt teeth in *Trionectes*); (5) the infraorbital margin with a narrow lateral notch (vs. a broad lateral notch in *Incultus* and deep, 'V'-shaped notch in *Trionectes*); (6) the male pleon with the sixth somite distinctly constricted subdistally (vs. elongately trapezoid in *Incultus* and *Trionectes*); (7) the chelipeds comparatively slender in *Xiphonectes* (vs. stout in the other two), with fingers subequal to the palm length (vs. distinctly shorter in *Incultus*); (8) the first male gonopods slender, smoothly out-curved distally, not meeting medially in *Xiphonectes* (vs. short and stout in *Trionectes*, but relatively long, bent in midlength, with the pair of gonopods overlapping each other

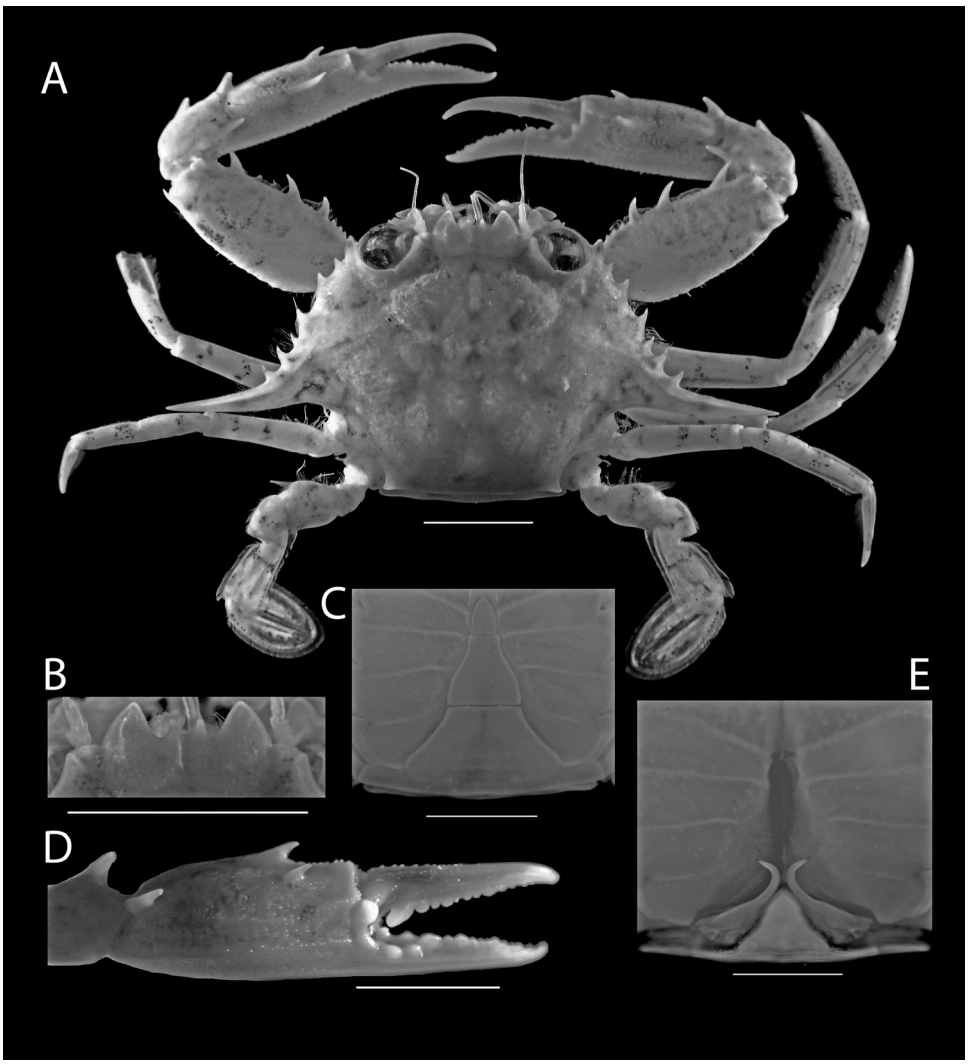

Figure 17. *Xiphonectes iranjae* (Crosnier, 1962), male, CW 29 mm, MNHN-IU-2014-4103, Réunion, W. Indian Ocean. A, total view. B, front. C, pleon. D, right chela, outer view. E, pair of first gonopods, shape and position. Scale bars: 5 mm.

medially in *Incultus*); and (9) by the female vulva being located relatively distant from the sternite margins, vs. located at the mesial margin or posteromesial in *Incultus*.

Xiphonectes is distinguishable from *Alionectes* by the presence of a dorsally incised orbital margin, which is entire in *Alionectes*, by a single posterodistal spine on the cheliped merus (vs. two spines in *Alionectes*) and by a smooth laminar crest on the second pleonal somite of males, whereas the margin is serrated in the latter genus.

Eodemus is distinguishable easily from *Xiphonectes* by the 'T'-shaped male pleon (vs. subtriangular) and by the distinctly laterally produced anterolateral lobe of the third maxilliped merus (vs. distally produced, rounded or angular, not distolaterally produced) and by a slit-like female vulva.

Remarks: Since *Xiphonectes* was raised to full generic status by Spiridonov *et al.* (2014), it has become one of the most species-rich portunid genera, containing, according to Ng *et al.* (2008), 28 species, with *X. longispinosus* composed of four subspecies. Ng *et al.* (2008) include *X. longispinosus longimerus* Spiridonov, 1994, which they consider to be an available name for the species. This name was originally introduced as *Portunus longispinosus* forma *longimera* by one of us (Spiridonov, 1994). When introducing this name, Spiridonov (1994: fig. 5) used an infrasubspecific rank with the status of 'forma', intentionally making this name unavailable (ICZN, 1999: Articles 10.2 and 15.2); the reason for this was to introduce the forms of *X. longispinosus* as a preliminary step towards the revision of this species complex. Recently, this species was described by Spiridonov (2016) as *X. tuerkayi* Spiridonov, 2016.

The list by Ng *et al.* (2008) does not include *X. leptocheles*. This species was described and illustrated by A. Milne-Edwards (1873: 159, pl. 4, fig. 1), but was synonymized, without particular discussion, with *X. longispinosus* by Stephenson & Campbell (1959). Later, this name disappeared even from major portunid accounts (i.e. Stephenson, 1972a, b; Sakai, 1939, 1976; Crosnier, 2002), but was listed in *Xiphonectes* (*s.l.*) in the studies by Spiridonov (2016) and Nguyen & Ng (2021) as a synonym of *X. longispinosus*. The photograph of the type specimen of *X. longispinosus* from HMCZ was previously kindly sent by A. Baldinger to one of us for another study (Spiridonov, 2016: fig. 1). Its current re-examination and comparison with the description and illustration of *X. leptocheles* confirms a separate status of the latter species.

As a result of the present revision, only 14 species currently remain in *Xiphonectes*, with the four former *X. longispinosus* subspecies all elevated to species level. The remaining species are herein transferred to the newly established *Eodemus* (six species), *Incultus* (three species), *Trionectes* (eight species) and to the new lupocycline *Alionectes* (two species). Two species that were not included in our molecular analysis, *X. latibrachium* and *X. paralatibrachium*, show some morphological differences; they have the median frontal teeth projecting beyond the lateral ones, indistinct supraorbital notches and more robust chelipeds. Their inclusion in *Xiphonectes* should be confirmed by future genetic analyses.

During the examination of the MNHN material in Paris, additional morphotypes of the *X. longispinosus* complex, with some potentially new species, were recognized by one of us (M.K.). A further revision of this group may therefore be necessary.

Size: Small crabs; maximum reported size ranges from CL × CW: 8.8 mm × 17.0 mm in *X. guinotae* (Apel & Spiridonov, 1998) to 14.0 mm × 30.3 mm in *X. iranjae* (Yang *et al.*, 2012).

Ecological notes: The genus includes both upper subtidal species (e.g. *X. guinotae*, *X. iranjae* and *X. longispinosus*; see Apel & Spiridonov, 1998; Spiridonov, 1999, 2016) and lower subtidal species (e.g. *X. tuerkayi* from the western Indian Ocean; Spiridonov, 2016) occurring mostly on sandy substrates.

Geographical range: Indo-West Pacific: from the Red Sea and the western Indian Ocean to Japan, Australia, the Hawaiian Islands and French Polynesia (Stephenson, 1972a, b; Poupin, 2010; Castro, 2011).

DISCUSSION

The classification of Portunidae has undergone substantial changes during the last two centuries. The history has recently been reviewed in detail by Karasawa *et al.* (2008) and Davie *et al.* (2015b, c) and was mentioned cursorily in the Introduction of this study. Despite the infrafamilial variations of the number and composition of subfamilies revised in recent studies (e.g. Karasawa *et al.*, 2008; Ng *et al.*, 2008; Schubart & Reuschel, 2009; Spiridonov *et al.*, 2014; Davie *et al.*, 2015c; Evans, 2018; Spiridonov, 2020), Portuninae remains among the most species-rich portunid subfamilies.

The last comprehensive listing of extant genera and species of the subfamily Portuninae was undertaken by Ng *et al.* (2008) and included ten genera and > 140 species. Of these, the single genus *Portunus* (*s.l.*, with five subgenera) itself included almost 100 species. The taxonomic history of *Portunus* has been complicated and was discussed extensively by Holthuis (1952). The five subgenera listed in *Portunus* by Ng *et al.* (2008; i.e. *Achelous*, *Lupocycloporus*, *Monomia*, *Portunus* and *Xiphonectes*) have since all been formally elevated or re-elevated to generic status (Mantelatto *et al.*, 2009; Spiridonov *et al.*, 2014; Evans, 2018). Additionally, *Cycloachelous*, established by Ward (1942) for *Lupea granulata* H. Milne Edwards, 1834, was subsequently largely ignored by most later authors, who mostly preferred not to use subgenera. It was treated as a possible subgenus of *Portunus* by Stephenson & Campbell (1959), but *Cycloachelous granulata* was referred back into *Portunus* (*Achelous*) by Utinomi (1969: 86), thus synonymizing it again under *Achelous*. *Cavoportunus* Nguyen & Ng, 2010 was established as new by Nguyen & Ng (2010) to accommodate *Portunus* (*Achelous*) *dubius* (Laurie, 1906).

Although it is clear from morphology that the relationships between species and subgenera of *Portunus* are complex, previous molecular analyses of a limited number of taxa had already begun to shed more light on the phylogenetic groupings within the Portunidae and *Portunus* (*s.l.*). Following Mantelatto *et al.* (2007), the polyphyly of *Portunus* (*s.l.*) was also suggested by Spiridonov *et al.* (2014), indicating the necessity for a wider revision of the genus. Mantelatto *et al.* (2007) pointed to the variously allied relationships of IWP *P. pelagicus* and *P. trituberculatus* and the Atlantic *P. sayi* to *Callinectes*. Stephenson *et al.* (1968) suggested a series of species of the predominantly IWP '*P. pelagicus* group' as a distinct group within *Portunus*, with the Atlantic *P. sayi* possibly being the closest relative to both *Callinectes* and *Arenaeus*. This is consistent with the molecular analysis performed here (Figs 1, 2), wherein *P. sayi* and the type species of *Portunus*, *P. pelagicus*, are members of the restricted

genus *Portunus* (*s.s.*); the latter, compared with other previous *Portunus* subgenera or new genera, is here most closely related to *Callinectes*.

The most basal portunine taxa remain unresolved in the present three-gene phylogenetic reconstruction (Fig. 1). The basal polytomy is created by four clades, i.e. (1) the above-mentioned *Portunus* (*s.s.*) and *Callinectes* lineage [Portuninae]; (2) *Alionectes* and *Lupocycloporus* [Lupocyclinae]; (3) *Achelous* [Achelouinae]; and (4) *Charybdis* [Thalamitinae]; while the basally well-supported 'major clade' covers all the remaining portunine taxa: *Cavoportunus*, *Cycloachelous*, *Monomia* (*s.s.*), *Xiphonectes* (*s.s.*) and the new genera *Allomonomia*, *Eodemus*, *Incultus* and *Trionectes*. Although the relationship of Portuninae to the other portunid subfamilies remains unresolved, the respective individual portunine genera themselves are basally well supported, thus allowing the comfirmation of their separate systematic position.

The wide diversity of Atlantic *Portunus* species examined genetically by Mantelatto *et al.* (2007, 2009, 2018), also incorporated into the 16S rRNA phylogenetic reconstruction here (Fig. 2), revealed a common clade of species (as listed by Ng *et al.* 2008) in the subgenera *Portunus* or *Achelous*, but also containing *Lupella forceps*. Mantelatto *et al.* (2009, 2018) proposed a major change in the classification of the taxa *Cronius* Stimpson, 1860 and *Portunus* (*Achelous*) De Haan, 1833. They recommended that *Achelous* be recognized as a distinct genus and that *Cronius tumidulus* (Stimpson, 1871) should be transferred there with nine other species: *Neptunus asper* A. Milne-Edwards, 1861, *Portunus binoculus* Holthuis, 1969, *Amphitrite depressifrons* Stimpson, 1859, *Lupa gibbesii* Stimpson, 1859, *Achelous ordwayi* Stimpson, 1860, *Portunus rufiremus* Holthuis, 1959, *Lupea sebae* H. Milne Edwards, 1834, *Achelous spinicarpus* Stimpson, 1871 and *Portunus spinimanus* Latreille, 1819. Of these, three species (*Neptunus asper*, *Lupa gibbesii* and *Portunus rufiremus*) had previously been placed in the subgenus *Portunus* (*Portunus*) Weber, 1795.

Although this classification is possible, the status and generic affinities of the other 17 species that had been placed in *Portunus* (*Achelous*) by other workers [as listed by Ng *et al.* (2008)] was not addressed in studies by Mantelatto *et al.* (2007, 2009, 2018). The American *P.* (*A.*) *floridanus* Rathbun, 1930 was allied with three species in the subgenus *Portunus* (*Portunus*) [*P.* (*P.*) *anceps* (Saussure, 1858), *P.* (*P.*) *hastatus* (Linnaeus, 1767) and *P.* (*P.*) *ventralis* (A. Milne-Edwards, 1879)], but their generic status was deemed uncertain. The generic affiliation of seven other American species previously placed in *Portunus* (*Achelous*) [i.e. *P.* (*A.*) *angustus* Rathbun, 1898, *A. brevimanus* Faxon, 1895, *P.* (*A.*) *guaymasensis*, *Neptunus* (*Hellenus*) *iridescens*, *P.* (*A.*) *isolamargaritensis*, *P.* (*A.*) *stanfordi* and *A. tuberculatus*] was not discussed. For the time being, these seven species are retained in *Achelous*, although with some doubt. Also not treated were the nine IWP species: *Neptunus* (*Achelous*) *dubius*, *Achelous elongatus*, *Lupa granulatus granulatus*, *Achelous granulatus unispinosus*, *Neptunus octodentatus*, *Achelous orbicularis*, *Portunus* (*A.*) *orbitosinus*, *P.* (*A.*) *suborbicularis* and *P.* (*Cycloachelous*) *yoronensis*.

Following Stephenson & Campbell's (1959: 117) comments on *Portunus granulatus*, Davie (2002: 463) had 'suggested that the distinctive male first gonopod and the narrow carapace of *P. granulatus* may be sufficient to place it in a separate subgenus'. However, he opted to keep the morphologically similar *P. orbitosinus* in the subgenus *Achelous*. On the basis of their similar carapace shapes and features (rounded carapaces with low anterolateral teeth that are all subequal in size), all the IWP species can be referred easily to *Cycloachelous*. The only two species with such features but having different male thoracic sterna and gonopods are *Neptunus* (*Achelous*) *dubius* and *Portunus* (*Cycloachelous*) *yoronensis*, which are subjective synonyms (see Crosnier, 1984). They have been referred to a new genus, *Cavoportunus*, by Nguyen & Ng (2010) and are confirmed as members of that genus in the present study.

The present 16S analysis allowed us also to compare the GenBank sequences of *Lupella forceps*. Based on the present results (Fig. 1), a morphological comparison of available material and published reports (e.g. Garth & Stephenson, 1966), we confirm the placement of all Atlantic and eastern Pacific *P.* (*Achelous*) and *P.* (*Portunus*) taxa [except *P.* (*P.*) *sayi*] in *Achelous*, as proposed by Mantelatto *et al.* (2009, 2018), with inclusion of the eastern Pacific *Lupella forceps* in that genus too. *Achelous* differs morphologically from *Portunus* (as currently defined) particularly by details of the shape of the male pleon and the first gonopods (e.g. Garth & Stephenson, 1966; Lai *et al.*, 2010; present report) and is also genetically distinct. Owing to the closer resemblance to members of the subfamily Thalamitinae than to Portuninae, as tentatively indicated by Mantelatto *et al.* (2018) and by the present analyses (Figs 1, 2), a separate systematic position of *Achelous* within its own portunid subfamily Achelouinae, as proposed by Spiridonov (2020), has been confirmed in this study.

From *Xiphonectes* (*s.l.*), recently treated as a full genus by Spiridonov *et al.* (2014), three monophyletic portunine genera (*Eodemus*, *Incultus* and *Trionectes*) have been separated. From those, *Incultus* shows a close phylogenetic relationship to *Allomonomia* (ML topology of the three-marker analysis; Fig. 1), separated from *Monomia* (*s.l.*). The relationship of those two new genera is also well supported by morphological characteristics, such as the short and basally stout first male gonopods with their distal part bent, long

and slender (Stephenson & Campbell, 1959; Dai *et al.*, 1986; Dai & Yang, 1991; Koch *et al.*, 2015b). Both those genera are positioned as sister to *Xiphonectes* (*s.s.*) and *Trionectes*, both of which also possess basally stout and distally bent first male gonopods, although the distal part of these is short and stout. However, all four genera mentioned here differ in details of the male gonopod, carapace or male pleon, thus confirming their separate positions highlighted by the molecular resolutions presented here.

The fourth new portunine genus separated in this study from *Xiphonectes* (*s.l.*) (i.e. *Eodemus* gen. nov.) is genetically distant from *Xiphonectes* (*s.s.*) and the new genera mentioned above. It is a member of the clade including the here-restricted genus *Monomia*; both in a broader clade with *Cycloachelous* and *Cavoportunus*. *Eodemus* gen. nov. and *Monomia* consistently possess, among other characters, granular patches on the dorsal carapace and the shape of frontal teeth, the third maxilliped merus, the male pleon and gonopods and the posterodistal armament of the cheliped merus (see, e.g. Stephenson & Campbell, 1959; Dai *et al.*, 1986; Dai & Yang, 1991; Wong *et al.*, 2010). The *Cycloachelous–Cavoportunus* clade is distinguishable from the *Eodemus–Monomia* clade by having, among other features, relatively stouter and hooked first male gonopods (Nguyen & Ng, 2010).

Two further *Xiphonectes* species are now transferred to the lupocycline genus *Alionectes*. Both species share with *Xiphonectes* (*s.l.*) their general body shape, with a flattened carapace and a produced lateral tooth. Nevertheless, the new genus occupies a sister position to *Lupocycloporus*, with both genera sharing a posterodistal spine on the merus of the last pereiopod (a character also possessed by *Lupocyclus*), a subtriangular male pleon, the coaptation of the last thoracic episternite with the third pleomere, and the stout, strongly hooked first male gonopods (Stephenson & Campbell, 1959; Apel & Spiridonov, 1998; Spiridonov, 2020).

As noted above, *Monomia* is also divided here into two taxa. *Allomonomia*, currently containing two species, *Allomonomia lecromi* and *Allomonomia calla* (recently compared by Koch *et al.*, 2015b). *Monomia* is subdivided into two well-supported partial subclades, not named herein. The *Monomia argentata* species complex contains here two species, *M. argentata* and *M. lucida*, distinguishable by the iridescence of various parts of the cuticle (Koch & Ďuriš, 2018), whereas the second group around *M. gladiator* consists of somewhat robust and non-iridescent forms. We did not observe further noticeable morphological differences between those subclades.

Full revision of portunid crabs cannot be complete without clarifying the remaining problematic taxa. Among species *incertae sedis* listed in the present list (above), at least two species might be, even based on laconic original descriptions by J. C. Fabricius, species of *Portunus* (*s.l.*; see Ng *et al.*, 2008; i.e. *Cancer defensor* Fabricius, 1787 and *Cancer armiger* Fabricius, 1787, both from Australia). Their types are lost (Zimsen, 1964: 647). The identities of those species and their affiliation to any of the currently revised portunine genera therefore remain uncertain.

Conclusion

The new rearrangement of the subfamily Portuninae presented here leads to a reduction of the number of genera from the previous 17 to the current 11, namely *Arenaeus*, *Allomonomia*, *Callinectes*, *Cavoportunus*, *Cycloachelous*, *Eodemus*, *Incultus*, *Monomia*, *Portunus*, *Trionectes* and *Xiphonectes* (with the position of *Carupella* remaining unresolved; Evans, 2018). This reduction was mainly attributable to previous or current transfers of separate taxa (*Achelous*, *Alionectes*, *Cronius*, *Lupocycloporus*, *Lupocyclus*, *Sanquerus*, *Scylla*, *Atoportunus* and *Laleonectes*) to other subfamilies.

Further studies need to consider whether *Alionectes*, *Lupocycloporus* and *Lupocyclus* deserve separation into their own (Lupocyclinae) subfamily, and *Achelous* into its own subfamily (Achelouinae). This will require a more comprehensive molecular and morphological comparison of *Achelous* and Thalamitinae (and other taxa not included herein), which share with the above three genera important morphological characters, such as the presence of a posterodistal tooth on the merus of the last pereiopods. Our revision here also calls for the reconsideration of the generic affinity of exclusively fossil species currently assigned to *Portunus* (more than one-third of known fossil species of Portunidae), which might eventually make possible a realistic reconstruction of the evolutionary history of Portuninae and portunids in general.

Regarding the key morphological characters frequently used in diagnoses and differential analyses of crab taxa and widely discussed in the systematic sections above, we have applied one more important character in this study (i.e. the mutual position of the first male gonopods in the male pleonal cavity on the posterior thoracic sternum). The gonopods, although often generally similar between related taxa, may lie subparallel or distally bent outwards, being well spaced in both cases; they also may touch each other along their bent regions or at parallel distal parts; or they may overlap each other medially along their bent regions, with distal parts directed outwards. The stouter basal part may lie subparallel to each other and to the median body plane or obliquely inwards, with their distal parts variously bent or hooked.

One of the other morphological characters used in this study, the shape and position of the female vulvae, appears to correspond to male gonopod types only in part. However, studies on mating behaviour and functional morphology of genital structures are required to understand fully the taxonomic and phylogenetic significance of characters associated with gonopods and female vulvae.

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