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Research article

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A new cryptic species of Polybiidae (Crustacea: Decapoda: Portunoidea) from the East Atlantic, with considerations on the genus *Polybius*

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Abstract. The use of integrative taxonomy has confirmed the existence of a new distinct crab species, cryptic, within the group of the former genus *Liocarcinus*, now *Polybius*, closely related to *P. holsatus*, *P. vernalis* and *P. marmoreus*. Previous reports have considered it to be the Atlantic form of *P. vernalis*, or as a species "affinis" or "comparable to" *P. holsatus*. Diagnostic morphological characters are presented for identification and the morphological variability in these species, mainly within *P. vernalis* (the most related) is analysed. Furthermore, based on molecular and other previous data, a new combination (genus change) is proposed. This new species, *Polybius dioscurus* sp. nov., lives on infralittoral sandy bottoms, coexisting with the other species mentioned, in the temperate and subtropical zone of the North Atlantic Ocean, including the Alboran Sea (westernmost Mediterranean).

Keywords. New species, integrative taxonomy, morphological variability.

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Introduction

Integrative taxonomy, and especially its molecular advances, are leading to increasing changes in the taxonomy and systematics of many groups and species of crabs. The swimming crabs of the superfamily Portunoidea Rafinesque, 1815, are an example of a classification that has been in a state of flux for decades, without reaching a consensus (Passamonti *et al.* 1997; Schubart & Reuschel 2009; Spiridonov *et al.* 2014; Evans 2018; Poore & Ahyong 2023).

Within the superfamily Portunoidea, morphological and genetic variability in many species along a geographic cline (e.g., Guerao *et al.* 2006) and the existence of cryptic or pseudocryptic species have been reported (e.g., Lai *et al.* 2010).

The genus *Liocarcinus* Stimpson, 1871 has 13 extant species (WoRMS Editorial Board 2023), with an Atlantic and Indo-Pacific distribution (Ingle 1980; Poore 2004) and 7 extinct species (Schweitzer & Feldmann 2010). However, some current species show a certain morphological variability that has caused confusion when identifying them (Palmer 1927; d'Udekem d'Acoz 1986, 1989; Moukrim *et al.* 2010).

Within the *Liocarcinus*/*Polybius* complex, species like *Liocarcinus corrugatus* (Pennant, 1777) and *L. strigilis* (Stimpson, 1858) are genetically different, although they appear morphologically similar (Plagge *et al.* 2016). In less frequent cases, there are species easily separable on a morphological basis that cannot be distinguished by comparing classical barcoding mtDNA gene fragments. For example, Schubart & Reuschel (2009) have shown that the species *Polybius henslowii* Leach, 1820 [in Leach, 1815–1875] (of the mono-specific genus *Polybius* Leach, 1820) and *Liocarcinus holsatus* (Fabricius, 1798, type species of the genus *Liocarcinus*) are genetically indistinguishable for two mitochondrial genes, and are closely related to *L. depurator* (Linnaeus, 1758) and *L. vernalis* (Risso, 1827) [in Risso, 1826–1827]. Nevertheless, as suggested by these authors and Plagge *et al.* (2016), we consider them both to be different and valid species, with *P. henslowii* being the result of a very recent speciation from a common ancestor with *L. holsatus*. The cause of this genetic similarity between two morphologically different species, living in different habitats and with different biological behaviours, has yet to be established. The apparent lack of genetic separation is probably due to the use of genes that are not variable enough, DNA sequences that are too short or mitochondrial introgression (see Cannicci *et al.* 2017; Shahdadi *et al.* 2021). In any case, these genetic data (and ours in this study) can be seen as an argument for synonymising the two genera in order to avoid paraphyly within of the genus *Liocarcinus* (see also the arguments in d'Udekem d'Acoz 1999).

On the other hand, species identification problems have been cited (Palmer 1927; d'Udekem d'Acoz 1986; Moukrim *et al.* 2010) that show morphological variability between species, which raises doubts about whether we are dealing with more than one species (cryptic species) or whether it is simply a case of intraspecific biogeographic variability. That is why the morphological variability of the species *L. vernalis*, the closest to the new species (sibling species), must be analysed.

The objectives of this study are: (1) describe a new cryptic species of *Polybius*, (2) clarify the taxonomic status of some Polybiidae Ortmann, 1893, and (3) show the morphological variability of some species from European waters, mainly *P. vernalis*, which are responsible for misidentifications.

Material and methods

Morphology

All the specimens used for the morphological study are listed in the description of the new species and in the section Other material studied.

The following morphological characters were analysed: the maximum carapace width (CW) measured between the fifth anterolateral teeth; maximum carapace length (CL) between the tip of the rostrum (central tooth) and posterior margin of the carapace; anterolateral margin length (AB) as the distance between the tip of the external orbital (1st) and the 5th anterolateral teeth; postero-lateral margin length (PB) as the distance between the tip of the 5th teeth to the curvature of the posterior margin; and the maximal length (ML) and length/height (ML/MH) of the meri of the walking legs from the lateral view.

The studies by Palmer (1927), Zariquiey Álvarez (1968), Ingle (1980) and d'Udekem d'Acoz & Rappé (1991) were mainly used for identification of species, in addition to other papers mentioned in the discussion.

Both conventional and stacked photography were used for the images. For stacked photography, Canon EOS 600D camera with a resolution of 18 MP in 'large' image mode was mounted on a tripod equipped with a rail system. The camera was equipped with a Canon 50 mm macro lens. The photographs were taken in a photo studio softbox and no flash was used. Individual photographs were calibrated and generated using Helicon Focus software. Focus stacking was carried out with the Zerene Stacker software (zerenesystems.com/cms/home).

Repositories

CCDB	=	Crustacean Collection of the Department of Biology (CCDB) of FFCLRP, University of São Paulo, Ribeirão Preto, Brazil
Crust 18094V	=	codes given by the authors, they mention: Collections, Gothenburg Natural History Museum, Gothenburg, Sweden
ICMAN	=	Instituto de Ciencias Marinas de Andalucía (ICMAN-CSIC), Puerto Real, Cádiz, Spain
ICMC or ICMCBR	=	Institut de Ciències del Mar (ICM), Colecciones Biológicas de Referencia (CBR), Barcelona, Spain.
JSD and JSDUK	=	codes given by the authors, they mention: Institution Storing: University of Bangor
MNHN	=	Muséum national d'Histore naturelle, Paris, France
NHMUK	=	Natural History Museum, London, UK
MT	=	code assigned by the authors in GenBank, but apparently the specimens are not deposited (not mentioned) in a specific collection.
RBINS	=	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
SMF	=	Senckenberg Museum Frankfurt, Frankfurt, Germany
USC MHN	=	Universidade de Santiago de Compostela, Museo de Historia Natural
ZMG	=	Zoologisches Museum, Universität Greifswald, Germany

Molecular analysis

Total genomic DNA of the specimens of *Polybius* and *Liocarcinus* used for the molecular analyses (see Table 1 and Supp. file 1) were extracted from pereiopod muscle tissue following a modified Chelex 10% protocol by Estoup *et al.* (1996). Partial sequences of the mitochondrial 16S rRNA and cytochrome c oxidase subunit I (COI) genes were amplified. The cycling conditions of the polymerase chain reaction (PCR) were: 2 min at 95°C, 35 cycles of 30s at 95°C, 30s (16S) or 45s (COI) at 48°C (16S) or 45°C

Table 1 (continued on next two pages). Specimens of *Polybius* Leach, 1820 and *Liocarcinus* Stimpson, 1871 used for molecular analyses in the present work. Museum and collection accession codes (MC), localities, GenBank accession codes for 16S and GenBank or BOLD accession codes for COI sequences (new sequences obtained in this study in bold), and references; (–) no data. The specimens that were in Christoph Schubart´s laboratory when he passed away could not be deposited in Museums (Specimen not available, SNA), for this reason their sequences cannot be upload to GenBank and are available in Supp. file 1.

Specimen	Locality	MC	16S	COI	References
Liocarcinus navigator	Roscoff, France	SMF44087	KU560475	KP795939	Plagge *et al.* (2016)
Liocarcinus navigator	Cádiz Bay, Spain	ICMCBR000216	**OR555902**	**OR557380**	Present study
Liocarcinus navigator	Isla Canela, Spain	ICMCBR000252	**OR555903**	**OR557381**	Present study
Liocarcinus navigator	Isla Canela, Spain	CRUST_ICMAN/3771	**OR555904**	(–)	Present study
Polybius bolivari	Mallorca, Spain	ICMCBR000256	**OR555892**	**OR557372**	Present study
Polybius depurator	Helgoland, Germany	SMF44080	KU560480	(–)	Plagge *et al.* (2016)
Polybius depurator	North Sea, UK	(–)	GQ268545	(–)	Kirby & Lindley (unpubl.)
Polybius depurator	Alboran Sea, Spain	MNHN:uncatalogued	FM208767	(–)	Schubart & Reuschel (2009)
Polybius depurator	Mediterranean, Spain	ICMCBR000247	**OR555897**	(–)	Present study
Polybius depurator	Mediterranean, Spain	ICMCBR000248	**OR555898**	**OR557375**	Present study
Polybius depurator	Sicily, Italy	JSDMe01	(–)	JQ305906	Matzen *et al.* (2011)
Polybius depurator	North Sea, UK	MT04040	(–)	KT209530	Raupach *et al.* (2015)
Polybius depurator	Oeresund, Sweden	Crust 18094V	(–)	MG935260	Lundin (unpubl.)
Polybius depurator	UK	JSDUK53	(–)	JQ306013	Matzen *et al.* (2011)
Polybius dioscurus sp. nov.	Armação, Portugal	(SNA)	**XX06**	**XX14**	Present study
Polybius dioscurus sp. nov.	Isla Canela, Spain	ICMCBR000238	**OR555885**	**OR557367**	Present study
Polybius dioscurus sp. nov.	Isla Canela, Spain	CRUST_ICMAN/3764	**OR555886**	(–)	Present study
Polybius dioscurus sp. nov.*	Cádiz Bay, Spain	CRUST_ICMAN/3759	**OR555887**	**OR557369**	Present study
Polybius dioscurus sp. nov.	Cádiz Bay, Spain	CRUST_ICMAN/3760	(–)	**OR557368**	Present study
Polybius dioscurus sp. nov.	off Cádiz Bay, Spain	CRUST_ICMAN/3761	**OR555888**	(–)	Present study
Polybius dioscurus sp. nov.	Agadir, Morocco	CRUST_ICMAN/3763	**OR555889**	(–)	Present study
Polybius dioscurus sp. nov.	Agadir, Morocco	CRUST_ICMAN/3762	**OR555890**	**OR557370**	Present study
Polybius dioscurus sp. nov.	Oostduinkerke, Belgium	(SNA)	**XX07**	**XX13**	Present study

Table 1 (continued). Specimens of *Polybius* Leach, 1820 and *Liocarcinus* Stimpson, 1871 used for molecular analyses in the present work. Museum and collection accession codes (MC), localities, GenBank accession codes for 16S and GenBank or BOLD accession codes for COI sequences (new sequences obtained in this study in bold), and references; (–) no data. The specimens that were in Christoph Schubart´s laboratory when he passed away could not be deposited in Museums (Specimen not available, SNA), for this reason their sequences cannot be upload to GenBank and are available in Supp. file 1.

Specimen	Locality	MC	16S	COI	References
Polybius dioscurus sp. nov.	Marbella, Spain	CRUST_ICMAN/3765	**OR555891**	**OR557371**	Present study
Polybius dioscurus sp. nov.**	Roscoff, France	(–)	KU560482	KP795929	Plagge *et al.* (2016)
Polybius henslowii	Santander, Spain	(SNA)	**XX09**	(–)	Present study
Polybius henslowii	Alboran Sea, Spain	(SNA)	**XX10**	(–)	Present study
Polybius henslowii	Portugal	SMF32759	FM208765	(–)	Schubart & Reuschel (2009)
Polybius henslowii	Portugal	SMF32759	(–)	KP795932	Plagge *et al.* (2016)
Polybius henslowii	Ceuta, Spain	ICMCBR000251	**OR555901**	**OR557379**	Present study
Polybius henslowii	Ceuta, Spain	ICMCBR000250	(–)	**OR557378**	Present study
Polybius henslowii	UK	JSDUK103	(–)	JQ306042	Matzen *et al.* (2011)
Polybius holsatus	Portugal	(SNA)	**XX8**	(–)	Present study
Polybius holsatus	Helgoland, Germany	SMF32750	FM208766	(–)	Schubart & Reuschel (2009)
Polybius holsatus	North Sea, UK	(–)	GQ268540	(–)	Kirby & Lindley (unpubl.)
Polybius holsatus	North Sea, UK	MT05438	(–)	KT208934	Raupach *et al.* (2015)
Polybius holsatus	North Sea, UK	MT08117	(–)	KT209350	Raupach *et al.* (2015)
Polybius holsatus	Helgoland, Germany	SMF44051	(–)	KP795928	Plagge *et al.* (2016)
Polybius holsatus	Skagerrak, Sweden	Crust19201V	(–)	MG934891	Lundin (unpubl.)
Polybius marmoreus	Azores, Portugal	SMF36275	KU560483	KP795933	Plagge *et al.* (2016)
Polybius marmoreus	North Sea, UK	(–)	GQ268547	(–)	Kirby & Lindley (unpubl.)
Polybius marmoreus	Belgium	(SNA)	**XX11**	(–)	Present study
Polybius marmoreus	North Sea, UK	(–)	(–)	GQ268535	Kirby & Lindley (unpubl.)
Polybius marmoreus	North Sea	MT05400	(–)	KT208606	Raupach *et al.* (2015)
Polybius marmoreus	North Sea, UK	MT05439	(–)	KT209516	Raupach *et al.* (2015)
Polybius vernalis	Istanbul, Turkey	SMF2991	KU560481	KP795930	Plagge *et al.* (2016)

Table 1 (continued). Specimens of *Polybius* Leach, 1820 and *Liocarcinus* Stimpson, 1871 used for molecular analyses in the present work. Museum and collection accession codes (MC), localities, GenBank accession codes for 16S and GenBank or BOLD accession codes for COI sequences (new sequences obtained in this study in bold), and references; (–) no data. The specimens that were in Christoph Schubart´s laboratory when he passed away could not be deposited in Museums (Specimen not available, SNA), for this reason their sequences cannot be upload to GenBank and are available in Supp. file 1.

Specimen	Locality	MC	16S	COI	References
Polybius vernalis	Varna, Bulgaria	(SNA)	**XX01**	(–)	Present study
Polybius vernalis	Lesbos, Greece	(SNA)	**XX05**	(–)	Present study
Polybius vernalis	Istria, Croatia	(SNA)	**XX04**	(–)	Present study
Polybius vernalis	Livorno, Italy	(SNA)	**XX03**	(–)	Present study
Polybius vernalis	Fusaro, Italy	SMF32761	FM208768	(–)	Schubart & Reuschel (2009)
Polybius vernalis	Almeria, Spain	CRUST_ICMAN/3766	**OR555894**	(–)	Present study
Polybius vernalis	Almeria, Spain	CRUST_ICMAN/3767	**OR555896**	(–)	Present study
Polybius vernalis	Fuengirola, Spain	(SNA)	**XX02**	(–)	Present study
Polybius vernalis	Marbella, Spain	CRUST_ICMAN/3768	**OR555895**	**OR557374**	Present study
Polybius vernalis	Marbella, Spain	CRUST_ICMAN/3769	**OR555893**	(–)	Present study
Polybius vernalis	Grosseto, Italy	CCDB1739	(–)	JX123455	Zupolini *et al.* (2017)
Polybius vernalis	Mediterranean, Spain	(SNA)	**XX12**	(–)	Present study
Polybius vernalis	Almeria, Spain	CRUST_ICMAN/3770	(–)	**OR557373**	Present study
Polybius zariquieyi	Italy	SMF36278	KU560477	KP795940	Plagge *et al.* (2016)
Polybius zariquieyi	Italy	ZMG1083	KU560478	KP795941	Plagge *et al.* (2016)
Polybius zariquieyi	Balearic Islands, Spain	ICMCBR000262	**OR555899**	**OR557377**	Present study
Polybius zariquieyi	Balearic Islands, Spain	ICMCBR000265	**OR555890**	(–)	Present study
Polybius zariquieyi	Balearic Islands, Spain	ICMCBR000261	(–)	**OR557376**	Present study

* = Holotype; ** = as *P. marmoreus* in Plagge *et al*. (2016).

(COI), and 30s (16S) or 45s (COI) at 72°C, and finally 5 min at 72°C. The primers 1472 (5´–AGA TAG AAA CCA ACC TGG–3´) (Crandall & Fitzpatrick 1996) and 16L2 (5´–TGC CTG TTT ATC AAA AAC AT–3´) (Schubart *et al.* 2002) were used to amplify a maximum of 540 bp of the 16S, and the primers COH6 (5´–TAD ACT TCD GGR TGD CCA AAR AAY CA–3´) and COL6b (5´–ACA AAT CAT AAA GAT ATY GG–3´) (Schubart & Huber 2006) allowed amplification of a maximum of 670 bp of COI. PCR products were sent to Stab-Vida laboratories to be purified and then bidirectionally sequenced.

Sequences were edited using the software Chromas Lite ver. 2.6.4 (Technelysium Pty Ltd 2017) and aligned with BioEdit Sequence Alignment Editor ver. 7.2.6.1 (Hall 1999). The final DNA sequences obtained were compared with sequences retrieved from the GenBank database. New sequences have been deposited in GenBank under the accession number OR555885–OR555904 (16S) and OR557367–OR557381 (COI).

Phylogenetic and molecular evolutionary analyses were conducted using MEGA ver. X (Kumar *et al.* 2018) on the new sequences obtained for *Polybius* spp. and *Liocarcinus* spp. and including other sequences of these species downloaded from GenBank. The best-fitting nucleotide substitution model for 16S and COI were obtained with the tools implemented in MEGA X, using the corrected Akaike information criterion. The analysis for 16S and COI were carried out separately because of the composition of different species for each gene. The phylogenetic reconstruction analyses for 16S were inferred from Neighbour-Joining using the p-distance method. Blocks of ambiguous data were identified and excluded using Gblocks (Talavera & Castresana 2007). The nodal confidence of the topologies obtained was assessed via 2000 Bootstrap replicates. The phylogenetic analysis of the COI sequences database was performed with Maximum Likelihood (ML) analysis using MEGA X. Topological robustness was tested using 2000 nonparametric Bootstrap replicates. In the analysis of both genes, *Carcinus aestuarii* Nardo, 1847 and *Carcinus maenas* (Linnaeus, 1758) were used as outgroup.

Results

Molecular analysis

After applying Gblocks (Talavera & Castresana 2007) and eliminating any ambiguous data, the 16S alignment consisted of 502 bp (78% of the initial 642 positions). The best-fitting nucleotide substitution model was Tamura 3-parameter with invariant sites and gamma-distributed rates for the variable sites (T92+G+I). In the COI analysis, the final alignment consisted of 658 bp, and the best-fiting nucleotide substitution model was the general-time-reversible model with invariant sites and gamma-distributed rates for the variable sites (GTR+G+I). All sequences included in both analyses are listed in Table 1.

The results of the 16S and COI analyses show a clearly separate and well-supported clade for *Polybius dioscurus* sp. nov. that is mainly related with the clade of the *P. marmoreus* (Leach, 1814) representatives (Figs 1–2). The relationships with *P. vernalis*, *P. holsatus*, *P. henslowii*, *P. bolivari* (Zariquiey Álvarez, 1948), *P. depurator* and *P. zariquieyi* (Gordon, 1968) are slightly differently resolved in 16S and COI analyses, and more species and genes of *Polybius* must be included in the analyses for a better resolution, but this is beyond the objectives of the present study.

Polybius henslowii and *P. holsatus* share the same clade in both analyses as was previously shown by Schubart & Reuschel (2009) and Plagge *et al.* (2016), which justifies their grouping in the same genus.

Concerning to *Liocarcinus navigator* (Herbst, 1794), its long genetic distances with other *Polybius* spp. included in this study (similarity: 90–93% -16S and <86% -COI) suggests that it should be removed from *Polybius/Liocarcinus* and that a new genus will have to be created for it. Christoph D. Schubart was studying several of the species currently in *Liocarcinus* (*L. corrugatus*, *L. maculatus* (Risso, 1827), *L. navigator*, *L. pusillus* (Leach, 1816), and *L. strigilis*) and considering new grouping in order to propose

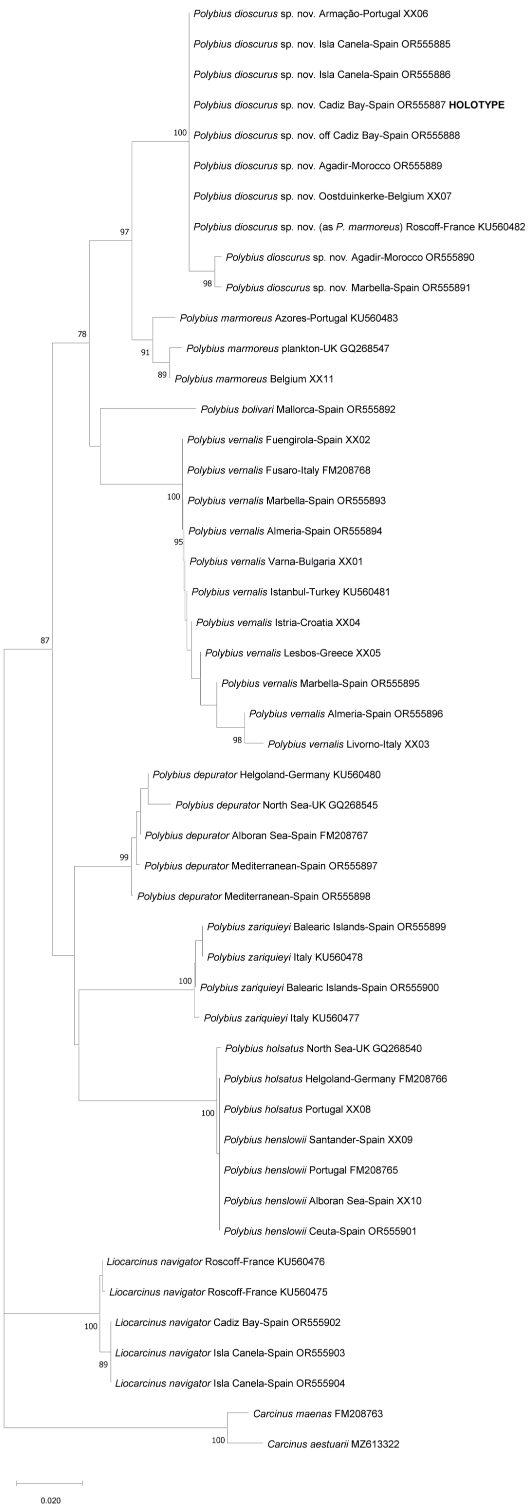

Fig. 1. Neighbor-Joning (NJ) phylogenetic tree based on mitochondrial 16S rRNA sequences of species of *Polybius* Leach, 1820 and *Liocarcinus* Stimpson, 1871, using 2000 Bootstrap replicates. Number on nodes represent NJ Bootstrap values, only values >70 are included. *Carcinus aestuarii* Nardo, 1847 and *C. maenas* (Linnaeus, 1758) are used as outgroup. GenBank accession codes are indicated for each species, except those with codes XX## which sequences are listed in Supp. file 1.

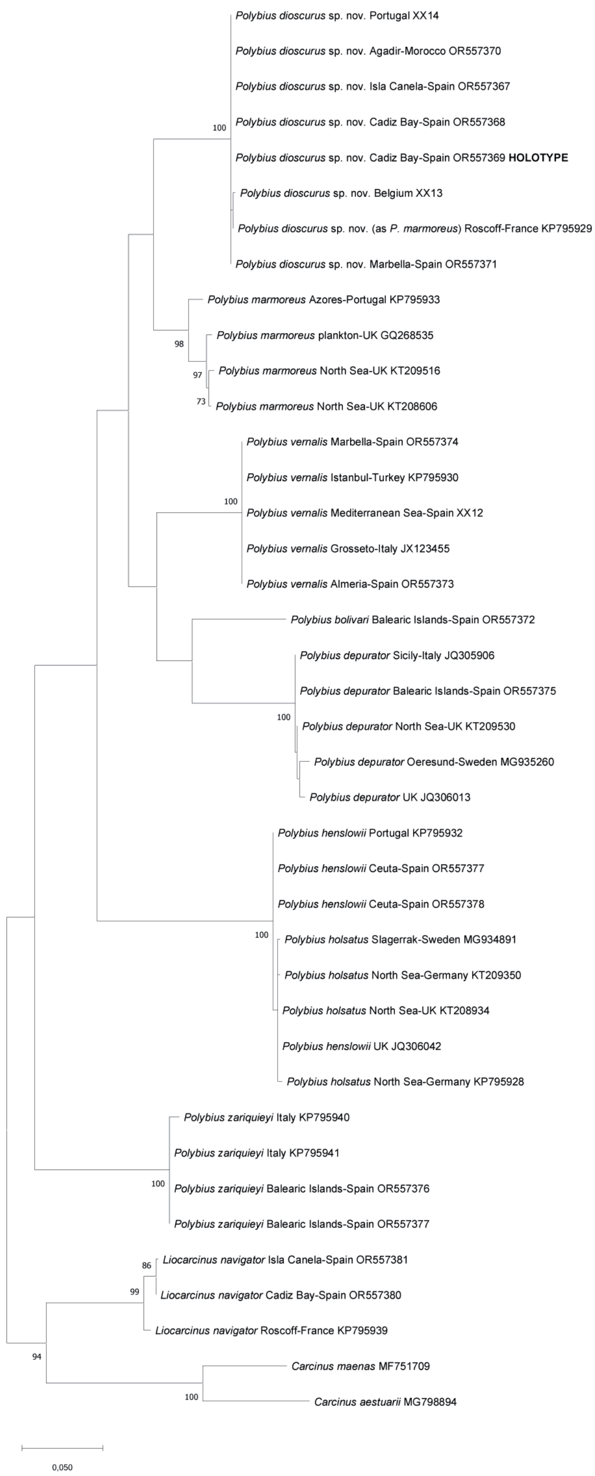

Fig. 2. Maximum likelihood (ML) phylogenetic tree based on mitochondrial cytochrome c oxidase subunit I sequences of species of *Polybius* Leach, 1820 and *Liocarcinus* Stimpson, 1871, using 2000 Bootstrap replicates. Number on nodes represent ML Bootstrap values, only values > 70 are included. *Carcinus aestuarii* Nardo, 1847 and *C. maenas* (Linnaeus, 1758) are used as outgroup. GenBank accession codes are indicated for each species, except those with codes XX## which sequences are listed in Supp. file 1.

new genera for them based on both morphological and genetic data. He commented the initial results of this study with some of the co-authors of the present study before his sudden death.

Systematic account

Phylum Arthropoda von Siebold, 1848
Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Superfamily Portunoidea Rafinesque, 1815
Family Polybiidae Ortmann, 1893

Genus ***Polybius*** Leach, 1820 [in Leach, 1815–1875]

Modified diagnosis

Carapace circular or suboval, slightly or clearly broader than long, often convex longitudinally; generally with well-defined regions; smooth, or ornamented with transverse ridges or granules; naked or with short hairiness. Frontal margin tri-lobulated or tridentate. Anterolateral margins with five teeth, including external orbital, somewhat flattened, more or less equal or decreasing in size, from third to fifth, with pointed or rounded apices; the first four teeth are directed forwards, the last one may be directed laterally or anterolaterally. Marked posterolateral reentrants. Orbits with two fissures on upper orbital margin, ventral outer orbital margin with a broad to narrow longitudinal incision. With a gap between the ventral internal orbital margin and the second antenal peduncle segment that is in contact with the lower-lateral margin of the frontal region. Chelipeds generally shorter than pereiopods; merus without distal ventral tooth, carpus of cheliped with large spine on inner angle. Propodus of pereiopod 2 to 4 each with a ventral ridge. Dactylus of pereiopod 5 compressed, paddle-like or broadly lanceolate.

Remarks

Within this genus, and according to our data and the previous information provided by Schubart & Reuschel (2009), Spiridonov *et al.* (2014), Plagge *et al.* (2016) and Evans (2018), the following species should be included: *Polybius henslowii*, *Liocarcinus holsatus*, *L. marmoreus*, *L. vernalis*, *P. dioscurus* sp. nov. (which constitute a group of species morphologically and molecularly very closely related, Figs 1–2, this study), *L. bolivari* (Zariquiey Álvarez, 1948), *L. depurator* and *L. zariquieyi* (Gordon, 1968). The species *L. maculatus* and *L. pusillus* must be confirmed by DNA genetic analysis. As it is further separated, we suggest that *L. navigator* should be transferred to a different genus as mentioned above. In addition, the species and genera *Liocarcinus corrugatus*, *Liocarcinus strigilis*, *Necora* Holthuis, 1987, *Macropipus* Prestandrea, 1833 and *Bathynectes* Stimpson, 1871 are morphologically and genetically more different (see first references of this paragraph) and their position-statuses need to be analysed and justified in more detail (Schubart pers. comm. to other co-authors before his death).

Furthermore, Ng *et al.* (2008) and WoRMS Editorial Board (2023) also included *Liocarcinus subcorrugatus* (A. Milne-Edwards, 1861) and *Liocarcinus rondeletii* (Risso, 1816) within *Liocarcinus*, for which there is no genetic information. The former is apparently endemic of the Red Sea (Spiridonov *et al.* 2013), but its status is doubtful (d'Udekem d'Acoz 1999; Noël 2016). The latter, which is similar to *L. navigator*, is separated by Risso (1816: 26) from its congeners by the presence of only four anterolateral teeth on the margins of the carapace "bords latéraux à quatre dents" (also in Risso 1826–1827: 2), while all the species in this genus have five (e.g., Manning & Holthuis 1981: 83, diagnosis here). However, in the related *P. navigator* the fourth is smallest, sometimes almost obsolete (Ingle 1980) and Risso's descriptions are known to be sometimes inaccurate (Holthuis 1977). Palmer (1927), Miranda y Rivera

(1933) treated it as a synonym of *Liocarcinus arcuatus* (= *L. navigator*). However, Zariquiey Álvarez (1968: 369), due to the morphological differences he observed between the Atlantic and Mediterranean populations, considered that the Mediterranean specimens belonged to a different subspecies (*L. arcuatus rondeletii*). Ng *et al.* (2008) and WoRMS Editorial Board (2023) accept *Liocarcinus rondeletii* as a valid species, but we are not aware of recent genetic or morphological studies to support this new status. The validity of this taxon cannot be accepted without in-depth studies (as in for *L. subcorrugatus*), as it is known that within some species of this genus, e.g., *P. vernalis*, there is considerable morphological variability between populations (see below).

The following new species is described based on morphological and molecular evidence.

Polybius dioscurus sp. nov.
urn:lsid:zoobank.org:act:E3FB5F11-959A-43C0-85A4-9A9FB88ED7C8
Figs 3–5, 6A, C, 7B, 8C–D, 9

Portunus marmoreus – ? Bell 1844–1853: 105, in part, not unnumbered fig. — ? White 1857: 50, in part. — ? Palmer 1927: 889, in part (second abnormal specimen). — Nobre 1931: 66, figs 31–32; 1936: 36, pl. 11 fig. 19.
Portunus barbarus – Monod 1956: 173, 179, in part.
Macropipus barbarus – Forest & Guinot 1956: 37, in part (Atlantic specimens only), not fig. 5.
Macropipus holsatus – Cardona Bendito 1965: 152, pl. 2 fig. d.
Macropipus marmoreus – ? Bourdon 1965: 29 (in part).
Macropipus vernalis – Neves 1975: 32, in part, figs 10, 11c.
Liocarcinus vernalis – García Raso 1984: 107 in part. — González Gurriarán & Méndez 1986: 43 (key), 96, fig. 30, 210, foto 19. — d'Udekem d'Acoz 1989: 184, in part, fig. 16, not fig. 17; 1991: 84, fig. 1; 2011: 78, fig. 1. — Adema 1991: 111, figs 1–2. — d'Udekem d'Acoz & Rappé 1991: 95, figs 3, 6, 9, 12. — Fransen 1991: 124. — Ingle 1996: 57, 138, fig. 37. — Ingle & Clark 1998: 224, figs 1c, 2c, 2f. — Livory 1998: 49. — López de la Rosa *et al.* 2002: 87. — McCarthy *et al.* 2005: 20. — Ashelby 2006: 1341. — Martin 2011: 221, unnumbered colour photographs. — De Blauwe & Decleer 2017: 173, unnumbered colour photographs.
Liocarcinus sp. aff. *holsatus* – d'Udekem d'Acoz 1986: figs 17, 20.
Polybius (*Polybius*) *vernalis* – d'Udekem d'Acoz 1999: 222, in part, unnumbered fig. p.1.
Liocarcinus cf. *holsatus* – Moukrim *et al.* 2010: fig. 2f.

Diagnosis

Carapace glabrous, wider than long, smooth. Frontal region with three slightly protruding blunt triangular teeth, with a tuberculate rim, continued by the inner-orbital angle, middle tooth rounded, subacute and does not reach same proportions as the lateral ones, which are more developed (wider and rounded), the curvature between rostral teeth is rounded. Anterolateral margins of the carapace curved with five teeth (including the external orbital), the fifth and the fourth being somewhat larger, the third and fourth with a rectilinear outer face. Chelipeds (P1) subequal; propodus outer face of the palm with 3 longitudinal keels along entire length; dorsal edge with a smooth rounded keel ending in a blunt distal tooth; internal face without keels; dactyl externally with a central depression, between two rounded ridges; dorsally, three rounded longitudinal ridges with depressions between them; merus smooth; carpus with one strong and protruding tooth on antero inner dorsal margin, on the anterior outer upper part one well-marked and rounded projection and two others below. Walking legs with merus, carpus and propodus smooth; dactylus quite rectilinear dorsally (P2 wider, robust and with a slightly more curved tip), with a more or less quadrangular section, and with angles defined by rounded longitudinal edges, the dactylus of P4 has a dense row of short setae in the basal third (or a little more), in P5 the dactyl is strongly flattened, paddle-like, oval, ending in a point. First sexual male pleopod (gonopod) with curved distal part, which forms an angle of almost 90° (more curved in large specimens) and ends in a small point.

Etymology

The name of the species is derived from the Greek mythology. Castor and Pollux are twin half-brothers in Greek and Roman mythology, known together as the Dioscuri (plural). The singular form is Dioscurus. The name, which is a noun in apposition, refers to the great similarity between the new species and *Polybius vernalis* (Risso, 1827).

Material examined

Holotype

SPAIN • ♂ (26.4 mm CW); outer Bay of Cádiz, Cádiz, Valdelagrana; 36°43′ N, 06°14′ W; 3.3–6.6 m depth; 31 Oct. 1996; I. López de la Rosa leg.; fine sand bottoms; GenBank: OR555887–16S, OR557369–COI; CRUST_ICMAN/3759.

Paratypes

BELGIUM – **Southern North Sea** • 3 ♂♂, 2 ♀♀; Groenendijk; 51°08′30″ N, 2°41′ E; 1 m depth; 10 Nov. 1990; C. d'Udekem d'Acoz leg.; sandy beach, net refuse of shrimp fishermen; RBINS, INV. 187227 • 1 ♂ (illustrated); between Nieuwpoort and Oostduinkerke; 51°09′ N, 2°42′ E; 1 m depth; 13 Oct. 2018; d'Udekem d'Acoz leg.; sandy beach, net refuse of shrimp fishermen; RBINS, INV. 187223 • 4 ♂♂, 6 ♀♀ (colour in life photographed); between Nieuwpoort and Oostduinkerke; 51°09′ N, 2°42′ E; 1 m depth; 13 Oct. 2018; d'Udekem d'Acoz leg.; sandy beach, net refuse of shrimp fishermen; RBINS, INV. 187230 • 20 ♂♂; between Oostduinkerke and Koksijde; 51°08′ N, 2°39′ E; 1 m depth; 27 Sep. 2019; d'Udekem d'Acoz leg.; sandy beach, net refuse of shrimp fishermen; RBINS, INV. 187229 • 1 ♂; same collection data as for preceding; RBINS, INV. 187226.

FRANCE – **Brittany** • 1 ♂; Saint Lunaire; 48°38′ N, 2°06′ W; 18 Mar. 1988; d'Udekem d'Acoz leg.; RBINS, INV. 187222 • 9 ♂♂, 7 ♀♀; W of Crozon Peninsula, Anse de Dinant; 48°15′ N, 4°33′ W; 1 m depth; 30 Mar. 2010; d'Udekem d'Acoz leg.; net refuse of *Donax* fishermen; RBINS, INV. 187228.

MOROCCO – **Agadir Bay** • 1 ♂ (36.7 CW); from Pte. d'Anza to South of Oued Souss; 30°26′ N, 09°40′ W – 30°18′ N, 09°37′ W; 6–25 m depth; May 1999; Gofas and Moukrim leg.; sandy bottoms; GenBank: OR555890–16S, OR557370–COI; CRUST_ICMAN/3762 • 1 ♂ (40.6 mm CW); same collection data as for preceding; GenBank: OR555889-16S; CRUST_ICMAN/3763 • 6 ♂♂; same collection data as for preceding; CRUST_ICMAN/3777 • 1 ♂, 1 ♀; same collection data as for preceding; MNHN-IU-2022-4081 • 1 ♂, 1 ♀; same collection data as for preceding; NHMUK 2024.3, 2024.4.

PORTUGAL – **Algarve** • 107 ♂♂ (one with *Sacculina*); Praia de Cabanas; 37°08′ N, 7°35′30″ W; 1 m depth; 20 Jul. 1988; d'Udekem d'Acoz leg.; net refuse of *Donax* fishermen; RBINS, INV. 187232 • 67 ♀♀ (some ovigerous); same collection data as for preceding; RBINS, INV. 187233.

SPAIN • 1 ♀ (19.3 mm CW); same collection data as for holotype; GenBank: OR557368–COI; CRUST_ICMAN/3760 • 2 ♀♀, 1 ♂; inner part of the Cádiz Bay; 1994–1995; fine muddy sand bottoms with *Caulerpa prolifera*; CRUST_ICMAN/3778 • 8 ♀♀, 6 ♂♂ (30.0 mm max CW); Cádiz, Chipiona; CRUST_ICMAN/3779 • 1 ♂; Gulf of Cádiz, Huelva, Isla Canela; 14 Jan. 2021; Helena Marco-Herrera leg.; FEMP-04: stn 10C; CRUST_ICMAN/3772 • 1 ♀; same collection data as for preceding; CRUST_ICMAN/3773 • 1 ♀; same collection data as for preceding; GenBank: OR555886–16S; CRUST_ICMAN/3764 • 3 ♀♀; Gulf of Cádiz, Huelva, Doñana National Park; 12 Apr. 2021; FEMP-04: stn 6; CRUST_ICMAN/3774 to CRUST_ICMAN/3776 • 4 ♀♀, 1 ♂; same collection data as for preceding; CRUST_ICMAN/3780 • 6 ♀♀; same collection data as for preceding; 12 Jan. 2021; 0.5–1 m depth;

FEMP-04: stns 10C, 6 and 2; fine sandy bottoms; CRUST_ICMAN/3781 • 1 ♀; W Mediterranean, Alboran Sea, Málaga, Marbella; 2–4 m depth; 24 Mar. 2021; García Raso leg.; from *Donax trunculus* Linnaeus, 1758 fisheries; GenBank: OR555891–16S, OR557371–COI; CRUST_ICMAN/3765 • 1 ♂; Málaga, Fuengirola; 2–4 m depth; Aug. 1983; García Raso leg.; from *Donax trunculus* fisheries; CRUST_ICMAN/3782 • 18 ♀♀ (smallest ovigerous ♀: 16.4 mm width), 14 ♂♂; Málaga; 1979–1981, García Raso leg., from *Donax trunculus* fisheries; CRUST_ICMAN/3783.

Comparative material examined

***Polybius henslowii* Leach, 1820**

FRANCE • 2 ♂♂, 3 ♀♀; Bay of Biscay, cruise PELGAS 10, stn O.0627, chalut 68; 2 Jun. 2010; Jocelyne Martin leg., RBINS, INV. 187237.

SPAIN • 1 ♂; Málaga, Fuengirola; 10 Jun. 1978; 2 m depth; García Raso leg.; sandy bottoms of *Donax trunculus*; CRUST_ICMAN/3784 • 1 ovigerous ♀; Málaga, Fuengirola; 14 Sep. 1979; 4 m depth; J.E. García Raso leg.; sandy bottoms; CRUST_ICMAN/3785 (in Málaga is caught in benthic and pelagic fisheries, from 2 m onwards).

***Polybius holsatus* (Fabricius, 1798)**

BELGIUM – **Southern North Sea** • 6 ♂♂, 1 ♀; Duinbergen (municipality of Knokke-Heist); 1 m depth; Jul. 1986; d'Udekem d'Acoz leg.; sandy beach; RBINS, INV. 187221.

SPAIN • 1 ♂, 1 ♀; Galicia, Ría de Arousa; Victoriano Urgorri leg.; USC MHN 102060.

***Polybius marmoreus* (Leach, 1814)**

BELGIUM – **Southern North Sea** • 1 ♂, 2 ♀♀; between the Grote Bank and the Thorton Bank, trawler 029; 22 and 26 Feb. 1991; Eddy Eneman leg.; RBINS, INV. 187225 • 3 ♂♂, 7 ♀♀; Heist (municipality of Knokke-Heist); 9 Mar. 2012; Hans De Blauwe leg.; beach suppletion; RBINS, INV. 187218 • 1 ♂; Wenduine; 22 Mar. 2012; beach suppletion; Hans De Blauwe leg.; RBINS, INV. 187231.

FRANCE • 2 ♂♂; net refuse at Boulogne-sur-Mer; 17 Aug. 1985; d'Udekem d'Acoz leg.; RBINS, INV. 187224 • 1 ♂; southern North Sea or eastern English Channel, RV Thalassa, JBTS 2010, stn Ø0162; 7 Feb. 2010; Jocelyn Martin leg.; RBINS, INV. 187220.

SPAIN • 4 ♂♂, 1 ♀; Málaga, Fuengirola, Las Chapas de Marbella; 2–6 m depth; 14 Sep. 1979; García Raso leg; sandy bottoms; CRUST_ICMAN/3786.

***Polybius vernalis* (Risso, 1827)**

BULGARY • 2 ♂♂, 2 ♀♀; Varna Bay; 1 Jun. 2005; C. Schubart and S. Rauschel leg.; from fishermen, RBINS, INV. 187236.

ITALY • 1 ♂, 2 ♀♀; Fusaro beach, near mouth of lagoon; 40°49′20″ N, 14°03′03″ E; 0.5 m depth; 12 Oct. 2006; C. Schubart and Jesse Ragioneri leg.; digging sand; RBINS, INV. 187234.

SPAIN • 1 ♂; Málaga, Marbella; 2–4 m depth; 24 Mar. 2021; García Raso leg.; from *Donax trunculus* fisheries; GenBank: OR555895–16S, OR557374–COI; CRUST_ICMAN/3768 • 1 ♂; same collection data as for precding; GenBank: OR555893–16S; CRUST_ICMAN/3769 • 16 ♂♂, 6 ♀♀; same collection data as for preceding CRUST_ICMAN/3789 (in this sample the proportion *P.v.*/*P.d.* sp. nov. was: 24/1) • 2 ♂♂; Málaga Bay; 2–6 m depth; Jul. 1979; García Raso leg.; from *Donax trunculus* fisheries; CRUST_ICMAN/3787 • 2 ♂♂; Fuengirola; 2–4 m depth; 10 Jun. 1978; García Raso leg., from bivalves fisheries; CRUST_ICMAN/3788 • 13 ♂♂, 14 ♀♀; Málaga; 1978–1981; from *Donax trunculus* fisheries; CRUST_ICMAN/3790 • 6 ♂♂, 5 ♀♀; Fuengirola; about 5–6 m depth; 2 Oct. 2007; García Raso leg.; RBINS, INV. 187238 (one registration number for all these specimens).

TUNISIA • 1 ♂; Bay of Tunis; Feb. 2007; Jeanne Zaouali leg.; DNA extr. 21.04.08 R168-10; RBINS, INV. 187235.

Description

Maximum size. CL/CW: 30.7/40.6 mm.

Habitus. Carapace glabrous, wider than long (length/width relationships, CL/CW = 0.75 to 0.84 (holotype: 0.78) (Figs 3A, 4A, 5A), somewhat domed (convex), nearly smooth, but with some small tubercles especially located in the protogastric areas (in small aggregations) and in the anterior regions of the branchial areas (forming striae). Frontal region flat, with three slightly protruding blunt triangular teeth (Figs 3A, F, 4A, 5A, 6A, C, 7B), with a tuberculate rim, continued by the inner-orbital angle (Fig. 6A, C). This region is antero-dorsally delimited by a clear band; the middle tooth is rounded, subacute and does not reach the same proportions as the lateral ones, which are more developed (wider and rounded). Relative distance between external orbital teeth (apex to apex) and the distance between lateral rostral teeth (apex to apex) = 3.21 to 3.56 in males (holotype: 3.23; mean: 3.38), 3.44–3.56 in females (mean 3.50). Orbital area circular, concave, dorsally with two short longitudinal incisions, the internal longer (Figs 3A, F, 4A, 5A, 6A, 7B); ventral face with a very pronounced outer incision and a well protruding antero-internal lobe. Anterolateral borders of the carapace (Figs 3A, 4A, 5A) well curved, with a length more or less similar than the postero-lateral ones (0.95 to 1.17), which are converging. Anterolateral edges with five teeth (including the external orbital), the fifth and the fourth being somewhat larger, the third and fourth with a rectilinear outer face. Ventrally, the anterior margins (anterolateral teeth region) are delimited by a dense row of short setae; with a fringe of setae behind the pterygostomial sulcus. Branchial regions slightly domed, like the protogastric and centrogastric ones; concave urogastric region (depressed); cardiac region, with two tuberculate protruding areas anteriorly (and sometimes with two smaller ones behind) and flattened intestinal region.

Epistome. With two inclined longitudinal keels, one on each side.

Antennule (A1). With a broad transversely folded basal segment in a fossa below the frontal area, with the ventral edge showing a projecting lobe located towards the third of the outer half.

Antenna (A2). Basal segments narrow, with a flagellum of about 26 segments, longer than the orbital concavity, reaching the basal half of the first anterolateral tooth (outer orbital).

Chelipeds (P1) (Figs 3A–C, 4A–C, 5A, D). Subequal. Propodus with a rounded ventral rim on its outer face, extending from the apex of the fixed finger to approximately the middle of the palm. Outer face of the palm with 3 longitudinal keels along entire length (one towards the middle zone and two in the dorsal zone, slightly more separated from each other, the upper one ends in the propo-carpal articular condyle); dorsal edge with a smooth rounded keel ending in a blunt distal tooth; internal face without keels, with the central area bulging (longitudinally) leaving two depressions (upper and lower). The palm (without the fixed finger) is 1.7 times as long as high and 1.48 times as long as the dactyl. Dactyl (mobile finger) with the distal part curved, externally presenting a central longitudinal depression, between two rounded and projecting ridges; dorsally, three rounded longitudinal ridges can be seen: an upper external one (which is the upper rounded edge of the external face), a central dorsal (somewhat more protruding, especially in its basal part) and an upper internal one, with depressions between them; inner face with a central longitudinal depression delimited by two rounded edges. Carpus (Figs 3C, 4C, 5D) with one strong and protruding tooth on antero inner dorsal margin; on the anterior outer upper part (coinciding

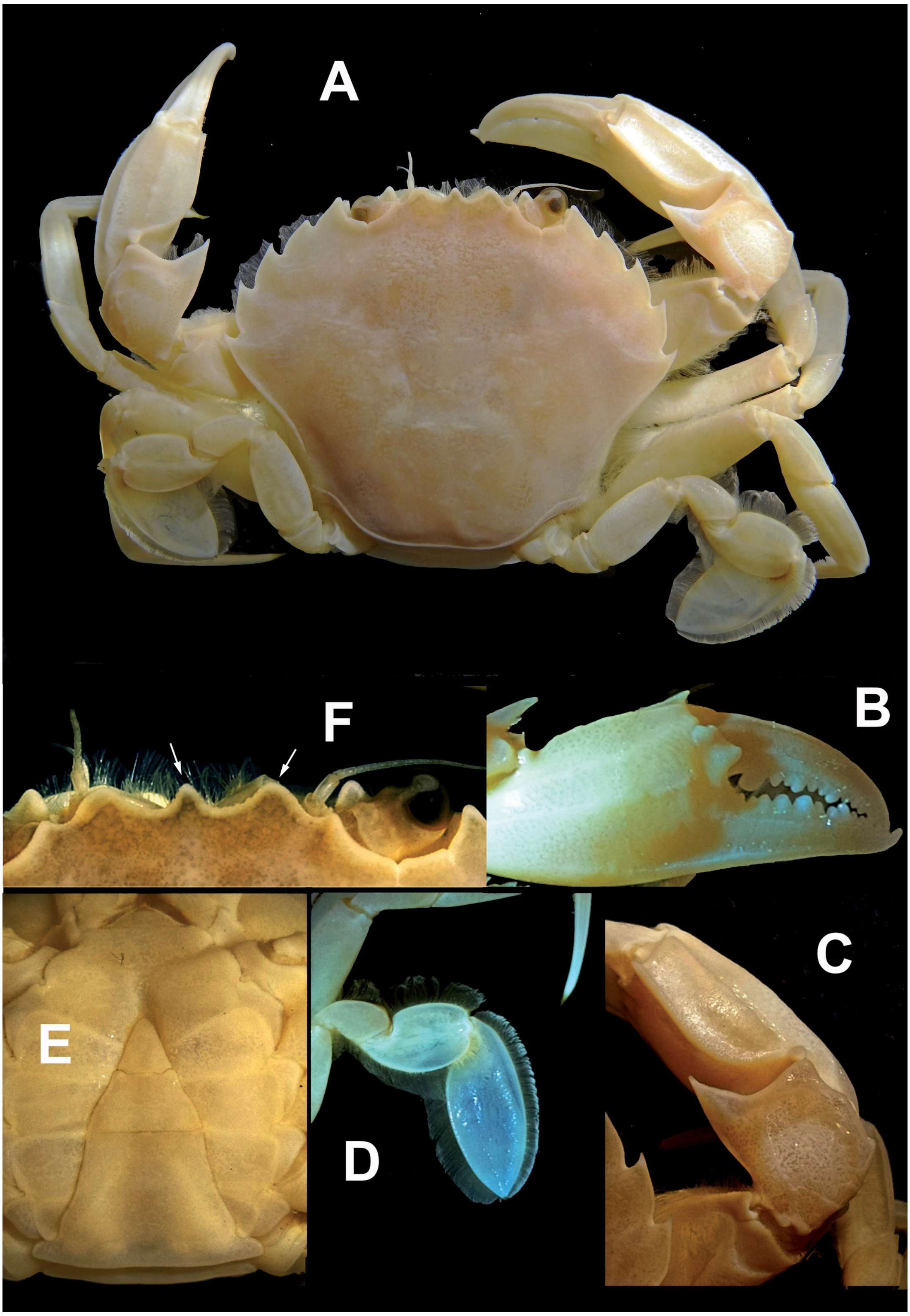

Fig. 3. *Polybius dioscurus* sp. nov., holotype, ♂, 26.4 mm CW, from Valdelagrana, Cádiz, Spain, 36°43′ N, 06°14′ W, 3.3–6.6 m depth, 31 Oct. 1996 (CRUST_ICMAN/3759). **A**. Dorsal habitus. **B**. Right cheliped, facial view. **C**. Carpus of left cheliped. **D**. Carpus to dactylus of right pereiopod 5. **E**. Body in ventral view, abdomen view.

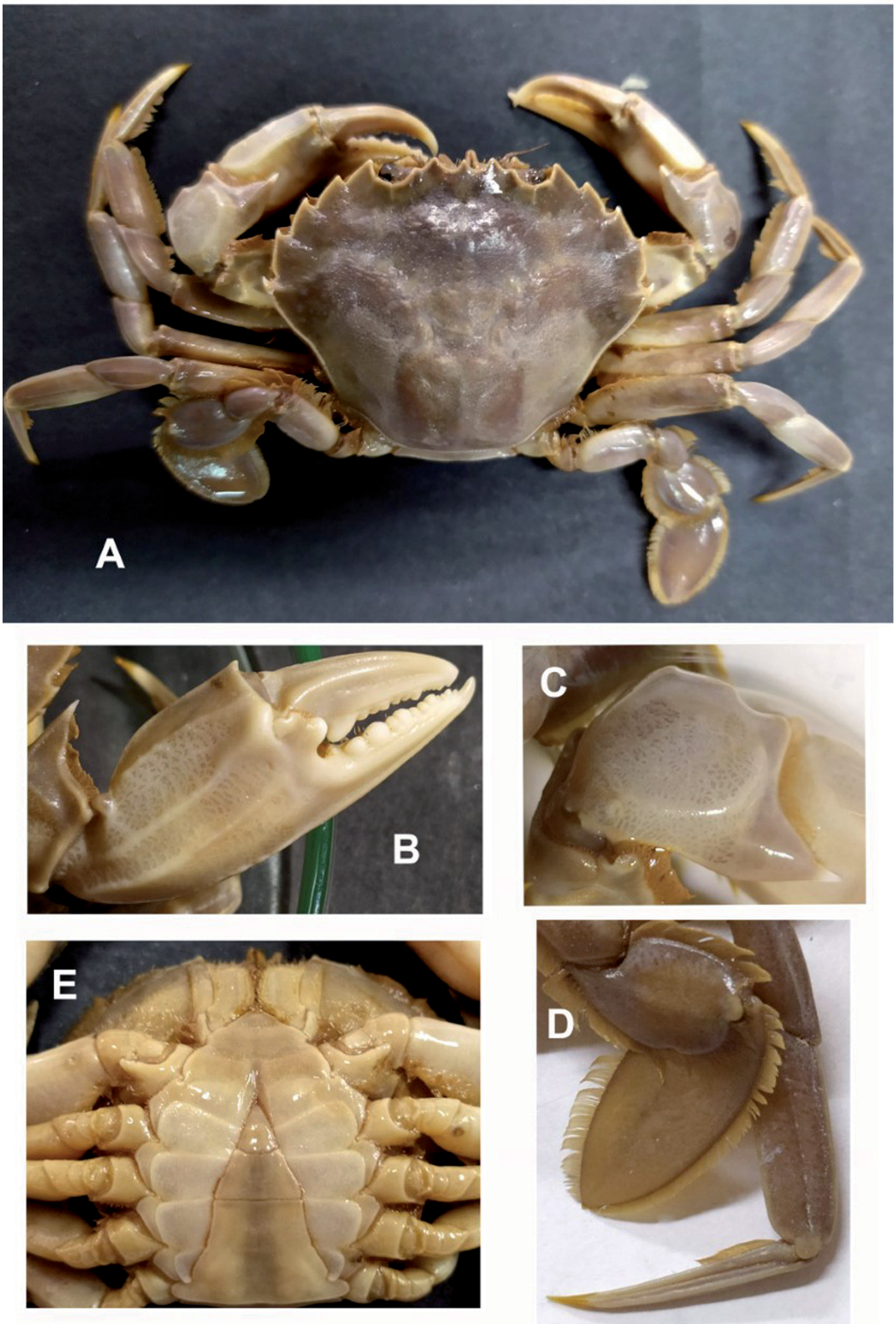

Fig. 4. *Polybius dioscurus* sp. nov., paratype, ♂, 36.7 mm CW, from Agadir Bay, Morocco. 30°26′ N, 09°40′ W – 30°18′ N, 09°37′ W, 6 to 25 m depth, May 1999 (CRUST_ICMAN/3762). **A**. Dorsal habitus. **B**. Right cheliped, facial view. **C**. Carpus of left cheliped. **D**. Dactylus of right pereiopods 5 and 4. **E**. Body in ventral view.

Fig. 5. *Polybius dioscurus* sp. nov., paratype, ♂ from Belgium, between Nieuwpoort and Oostduinkerke (RBINS, INV. 187223). **A**. Dorsal habitus. **B**. Facial habitus. **C**. Ventral habitus. **D**. Carpus of right cheliped.

with the superior articulation with the propodus) there is one well-marked and rounded projection and two others below: a not very prominent middle one and a bit more prominent posterior one. The external face ornamented with slightly raised areas and soft depressions. Merus smooth, with short setae along the entire upper edge (less in the most distal area) and inner edge of lower face (more developed in the distal area).

Walking legs. Morphometric values: merus length (ML): P3 ≈ 2 ≈ 4 > 5. The ML/MH (merus length/height) ratio of P2–P3–P4 is between 2.9 to 3.1 and about 1.8 in P5. The ratio MLP2/P5, MLP3/P5 and MLP4/P5 is 1.82–1.88–1.8, respectively. Propodus length (PL): P3 slightly > P4 slightly > P2. Dactylus length (DL): P2 somewhat > P3 ≈ P4. The dactylus of all walking legs (P2 to P4) are longer than their respective propodus.

Second pereiopods (P2). Merus smooth, with setae along the basal half of the dorsal margin, ventral margin without setae. Carpus and propodus smooth. Both segments with two dorsal ridges. On the propodus, external (anterior) face delimited ventrally by a row of very short setae, not extending onto carpus, and another row on internal (posterior) face, both separated by a dorsal longitudinal depression (wider in carpus). On the ventral edge of both segments, and along their entire length, there is a dense row of short setae. Inner face of carpus smooth and that of the propodus with a slight central longitudinal depression at anterior part. Dactylus of P2 quite rectilinear dorsally, and morphologically similar to those of P3 and P4, but wider, robust and with a slightly more curved tip; with a more or less quadrangular section, and with angles defined by rounded longitudinal edges, which leave a central longitudinal depression on dorsal, ventral and lateral sides (external and internal). Two dense rows of short setae are present on the anterior (external) face: one ventral (on the ventral edge) that exceeds half the length of the dactyl, up to approximately ⅔ basal, and another dorsal, somewhat shorter (on the dorsal edge) row, which runs from the basal part of the dactyl to half or little more.

Third and fourth pereiopods (P3 and P4). Similar to the second one (P2) and to each other. Both present setae on the basal half (P3), or on the entire (P4) dorsal (or superior) edge of the merus, and are glabrous on the ventral edge. Carpus and propodus smooth (without setae on the dorsal and ventral faces). The dactyli are morphologically similar to those of P2, but somewhat less robust and narrower ($2^{nd} > 3^{rd} > 4^{th}$). In P3 the row of short ventral setae goes from the basal part to half the length of the dactyl, or little more; while in P4 they are only found in the basal third (or a little more) (Fig. 4D), not reaching half of the dactyl, the row of dorsal setae is like that of P2.

Fifth pereiopods (P5). Merus smooth, with long setae all over the dorsal border, and in the distal fourth of the ventral outer part; ML/MH ratio: 1.63–1.85 (males), 1.76–2.0 (females). Smooth carpus, with long setae all over the dorsal and ventral edge. Propodus and dactylus flattened, with long setae on all edges (dorsal and ventral). Dactyl strongly flattened, paddle-like, oval (Figs 3A, D, 4A, D, 5A, C) (2.11 to 2.37 L/W), ending in a point.

First sexual male pleopod (gonopod). With curved distal part, which forms an angle of almost 90° (Fig. 8C–D), more curved in large specimen, and ends in a small point.

Pleon. Male pleon embedded in the sternum (Figs 3E, 4E, 5C), with the 3^{rd} to 5^{th} segments fused, narrowing strongly from the beginning of the 6^{th} and ending in a triangular telson. Rounded female abdomen.

Colour pattern (Fig. 9). Body and legs usually greyish with a finely speckled motive; a large white, brown or black mark is occasionally present on the anterior part of carapace. Some specimens have a marbled colour pattern. The legs never exhibit the orange hue, which is usual in *P. holsatus*.

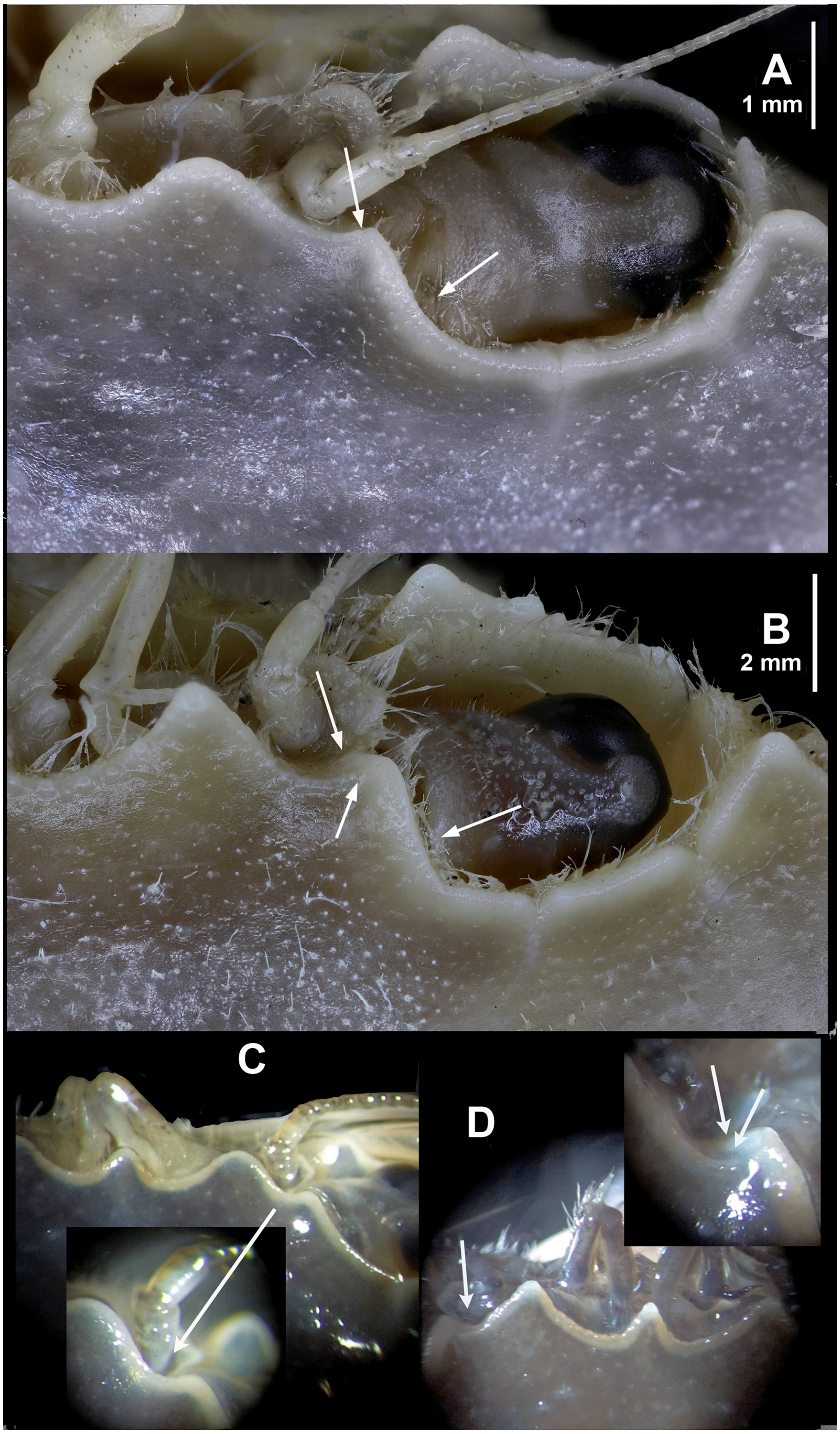

Fig. 6. Dorsal view of orbital region and adjacent lateral rostral teeth. **A**. *Polybius dioscurus* sp. nov., paratype, ♂ from Belgium, between Nieuwpoort and Oostduinkerke (RBINS, INV. 187223). **B**. *Polybius vernalis* (Risso, 1827), ♂ from Tunisia, Bay of Tunis (RBINS, INV. 187235). **C**. *Polybius dioscurus* sp. nov., ♀ from Málaga (CRUST_ICMAN/3765) **D**. *Polybius vernalis*, ♂ from Málaga (CRUST_ICMAN/3789). Arrows show differences in the orbital region between both species.

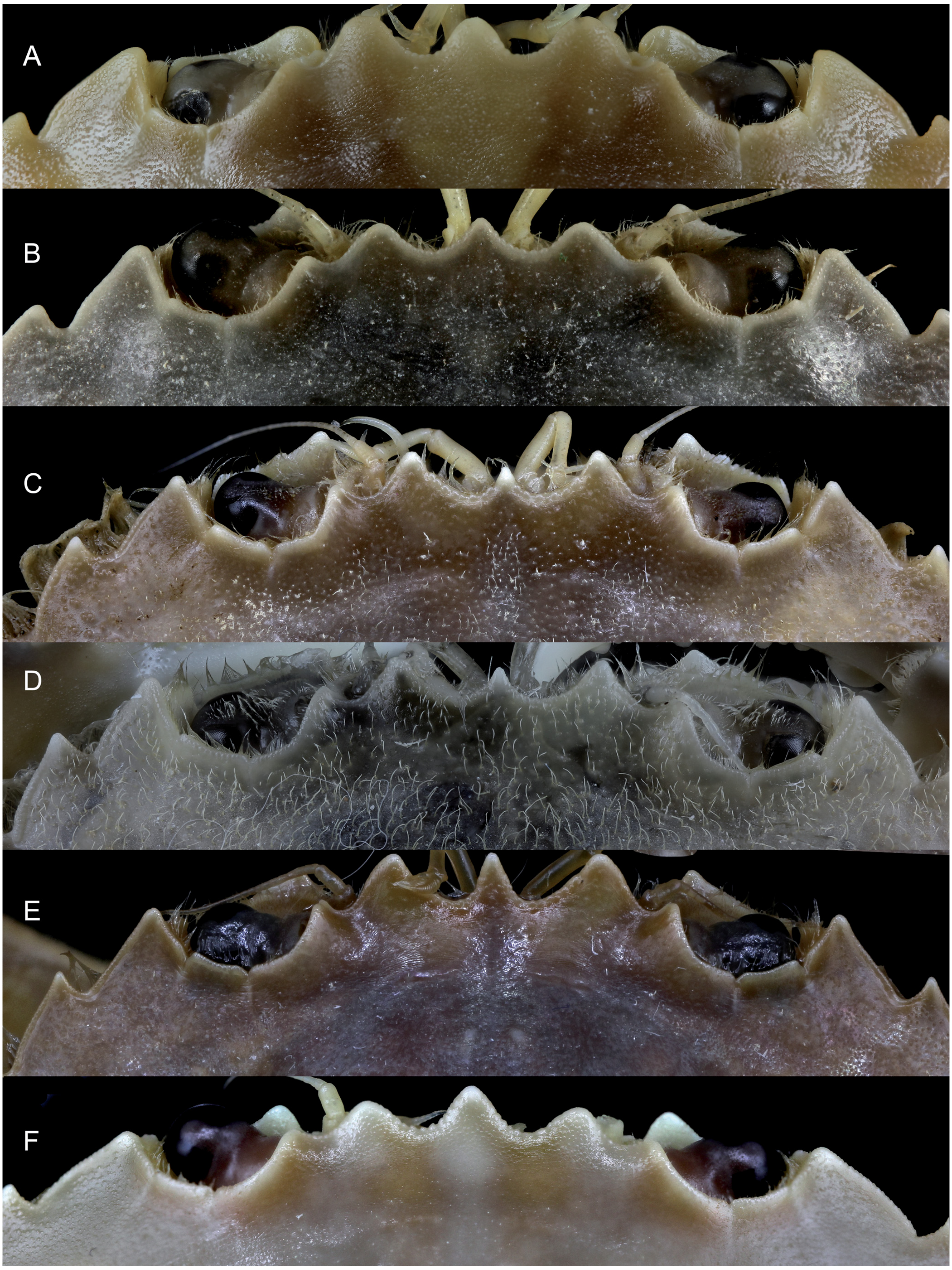

Fig. 7. Frontal region in dorsal view, male. **A**. *Polybius marmoreus* (Leach, 1814) from Belgium, Heist (RBINS, INV. 187218). **B**. *Polybius dioscurus* sp. nov., paratype, ♂ from Belgium, between Nieuwpoort and Oostduinkerke (RBINS, INV. 187223). **C–E**. *Polybius vernalis* (Risso, 1827). **C**. Specimen from Tunisia, Bay of Tunis (RBINS, INV. 187235). **D**. Specimen from Spain, Málaga, Fuengirola (RBINS, INV. 187238). **E**. Specimen from Bulgaria, Varna Bay (RBINS INV. 187236). **F**. *Polybius holsatus* (Fabricius, 1798), ♂ from Belgium, Duinbergen (RBINS, INV. 187221).

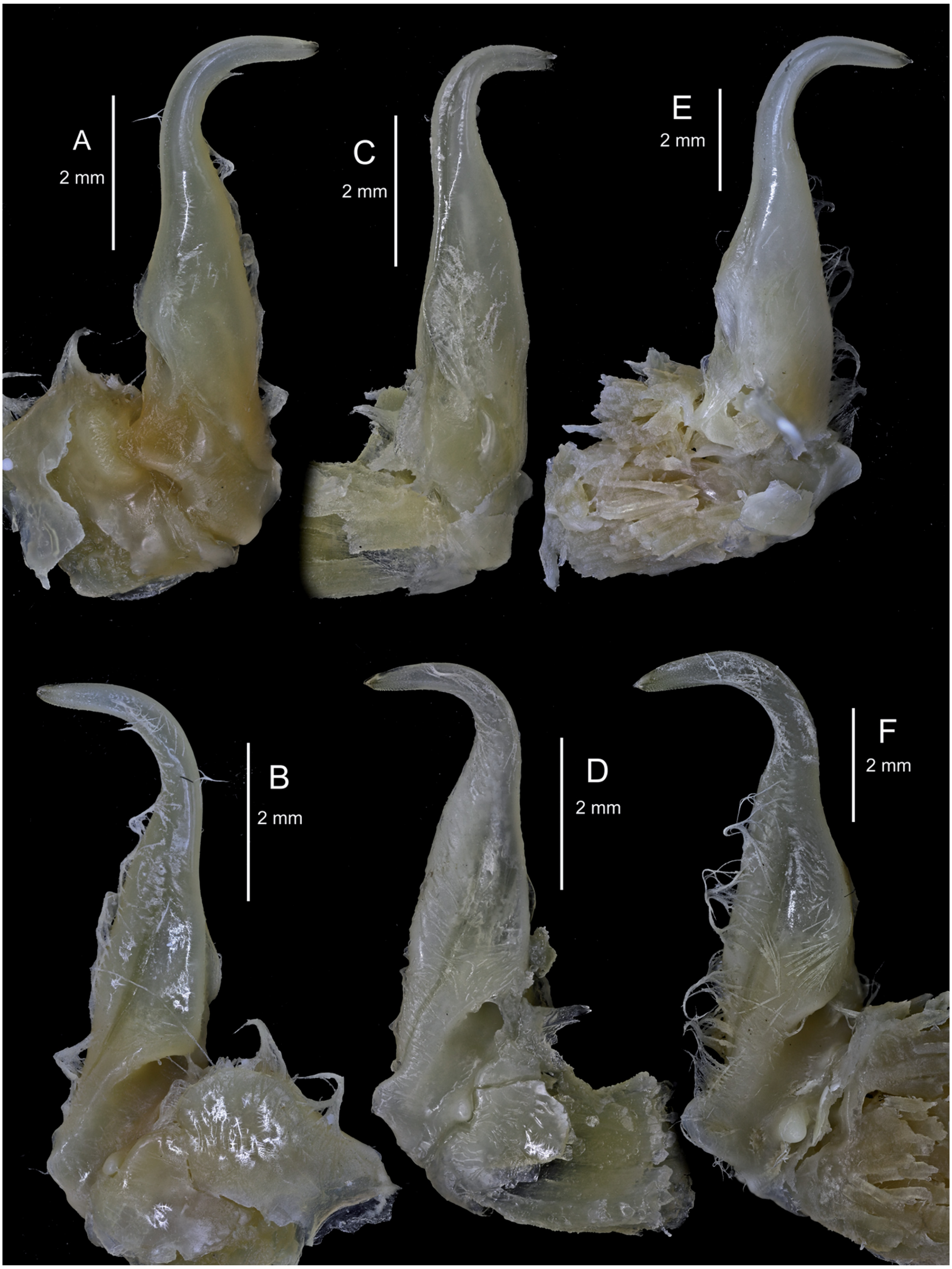

Fig. 8. Left gonopod 1 of male. **A–B**. *Polybius marmoreus* (Leach, 1814) from Belgium, Heist (RBINS, INV. 187218). **A**. Ventral view. **B**. Dorsal view. **C–D**. *Polybius dioscurus* sp. nov., paratype, ♂ from Belgium, between Nieuwpoort and Oostduinkerke (RBINS, INV. 187223). **C**. Ventral view. **D**. Dorsal view. **E–F**. *Polybius vernalis* (Risso, 1827) from Tunisia, Bay of Tunis (RBINS, INV. 187235). **E**. Ventral view. **F**. Dorsal view.

Distribution

Its exact geographical distribution is not well known, since in the papers (taxonomic, genetic and ecological) the identification of the species of *Polybius* is not at all clear (there is a lot of confusion between *P. holsatus*, *P. marmoreus*, *P. vernalis* and *P. dioscurus* sp. nov.). According to our data, it is present in the Atlantic Ocean: British Isles (Ingle & Clark 1998; McCarthy *et al.* 2005; Ashelby 2006; d'Udekem d'Acoz 2011), the Netherlands (Adema 1991), Belgium (d'Udekem d'Acoz & Rappé 1991), Normandy (Livory 1998), Bretagne (d'Udekem d'Acoz 1986: fig. 10), Bay of Biscay (González Gurriarán & Ménez 1986), Portugal (Nobre 1931, 1936; Neves 1975), Gulf of Cádiz (López de la Rosa *et al.* 2002, as *Liocarcinus vernalis*), Morocco: Bay of Agadir (Moukrim *et al.* 2010; fig. 2f), "Maroc atlantique" (materiel examine by d'Udekem d'Acoz), Western Sahara (Monod 1956 as *Portunus barbarus*), Mauritania and Canary Islands (Fransen 1991, as *L. vernalis* ?) and in the Mediterranean Sea: Alboran Sea, and Málaga (Marbella and Fuengirola) (García Raso 1984 in part).

Habitat

It lives between 5 to 25 m, on bottoms of fine sand (range of median 0.17–0.32), with a low pelite content near the shore which increases to ca 10% at 20 m off Morocco, although at Oued Souss the pelite content was higher at a shallow depth (30% at 10 m). In Spain, it inhabits the Gulf of Cádiz on sandy bottoms with *Callista chione* (Linnaeus, 1758) (0.5–10 m) and on fine muddy sand bottoms with *Caulerpa prolifera* (Forsskål) J.V.Lamouroux (3.3–6.6 m) and at Málaga it lives on sandy bottoms and has been caught during the harvesting of "coquina" (*Donax trunculus* Linnaeus, 1758) at 2–6 m. In Belgium, it lives on fine sand just below the tide marks and in shallow waters. So far, it has not been recorded in enclosed bays and environments of reduced salinity.

Remarks

The new species, *Polybius dioscurus* sp. nov., belongs to the group formed by *P. holsatus*, *P. vernalis* and *P. marmoreus*, which are morphologically and genetically related (Figs 1–2), but with significant differences. They have often been misidentified, because they share a combination of morphological characters, including some variability. Palmer (1927) analyzed the morphology of *Polybius holsatus* (as *Portunus holsatus*) and compared it with that of *P. marmoreus*, showing a variability, which in some cases may correspond to characters of the new species. In 1986, d'Udekem d'Acoz raised the possibility that it was a new species, naming it *Liocarcinus* aff. *holsatus*, although he later considered it to be an Atlantic form of *Polybius vernalis*, with small population differences (d'Udekem d'Acoz 1989). These considerations were not mentioned in later reports (d'Udekem d'Acoz 1999), with the only exception of the existence of a glabrous versus a pubescent carapace. In the same broad period, d'Udekem d'Acoz & Rappé (1991) and Ingle & Clark (1998) carried out two very useful studies on the morphological differences between the three species considered valid in this group: *P. holsatus*, *P. vernalis* [in using material of *P. dioscurus* sp. nov.] and *P. marmoreus* (all as *Liocarcinus*). This group was genetically validated by Passamonti *et al.* (1997), who also showed that there are some genetic differences among the populations of *P. depurator* and proposed the possible creation of subspecies. Ojeda *et al.* (2022) also cited differences between Atlantic and Mediterranean populations. Moukrim *et al.* (2010) captured specimens of the new species on bottoms of fine sand between 5 and 25 m, off Agadir (Morocco), citing it as *Liocarcinus* cf. *holsatus*, since its morphology was considered close to *P. holsatus*, but still different.

This variability and the combination of morphological features is the reason for misidentifications, including records in GenBank and BOLD, where molecular sequences have been assigned to *P. marmoreus*, for example a specimen from Roscoff (France) obtained by Plagge *et al.* (2016) (COI sequence KP795929) (see Fig. 2) and another from Portugal (sequence not available from BOLD, only early-release). Also, it has been assigned to *P. holsatus*, just like three specimens from Portugal (sequences not available from BOLD, only early-release); but all of them actually correspond to *P. dioscurus* sp. nov.

The **rostrum** of the new species (Figs 3A, F, 4A, 5A, 7B) is similar to that of *P. vernalis*, since the middle tooth is somewhat narrower either not, or only barely reaching the lateral ones, which are wider, rounded and more protruding; the central one is usually somewhat more rounded wide and somewhat longer in *P. dioscurus* sp. nov. (Figs 6C, 7B vs 6D, 7C–E). In *P. vernalis* a greater variability is observed,

Fig. 9. *Polybius dioscurus* sp. nov., paratypes from Belgium, between Nieuwpoort and Oostduinkerke (RBINS, INV. 187230), colour variation (in life) (sex not recorded during photo session).

mainly in specimens from the Black Sea in which the central rostral tooth is longer (Figs 7E, 12). It differs from that of *P. marmoreus* because the middle tooth is similar to the lateral ones, rounded, and with equal length and width in this species (Figs 7A, 13A). In *P. holsatus* the median tooth overreaches the lateral ones (Figs 7F, 14A), as in *P. henslowii* (Fig. 15A). The **rostral area** of *P. vernalis* differs from that of *P. dioscurus*. The inner orbital angles are more projected in *P. vernalis*, while the curvature between the rostral teeth is more rounded in *P. dioscurus* (in *P. vernalis* the deepest zone is displaced towards the median tooth, not centred, Figs 6D, 7C–E vs 7B); however, there is some variability in this character. In addition, the tuberculate rostral rim is continuous with that of the inner orbital angle in *P. dioscurus*, while in *P. vernalis* it is not so clear because it is projected anteriorly and flexes slightly downward (Fig. 6), and the inner side of the orbital socket shows a steeper slope in *P. vernalis*. The **carapace** in *P. vernalis* is frequently covered by short setae (e.g., Fig. 11), while in the others species it is glabrous, although we have seen specimens that were only almost glabrous. In addition, the carapace of *P. vernalis* from the Black Sea (Fig. 12) is nearly smooth and hairless and their frontal teeth are a bit longer, different from those of the Mediterranean Sea (Figs 10–11); but no genetic differences were detected, and the shape of their orbital region (the most important character separating them from *P. dioscurus*) exhibits no difference in relation to the Mediterranean specimens. The **anterolateral margin** of the carapace is clearly curved, but in *P. holsatus* it is slightly shorter than the posterolateral one (Fig. 14A) (AB/PB: 1.17–1.23). In *P dioscurus* (Figs 3A, 4A, 5A) both are more or less similar in length (0.95–1.17) and in *P. vernalis* the posterolateral margin is slight shorter (1.07–1.17), but there are no clear differences between these two species. In *P. marmoreus* this ratio is 1.04–1.16. The anterolateral fifth tooth in *L. vernalis* projects slightly more outward than in *P. dioscurus* (with the tips pointing forwards) (Figs 10A, 11–12 vs 3A, 4A, 5A). The **posterolaterals borders** are convergent, particularly in *P. holsatus* (Fig. 14A).

Other features that could be used are: **the anterior outer border of the carpus of chelipeds**, that in *P. dioscurus* sp. nov. shows protruding lobes that are slightly less marked than those of *L. holsatus* (Figs 3C, 4C, 5D vs 14D), but closer to those of *L. vernalis*. However, in large specimens of *P. dioscurus* these lobes are less developed (Fig. 4C) (while in medium-small specimens they are more similar to those of *P. vernalis*). In *L. marmoreus* the outer border is rounded and without any protrusions (Fig. 13D) (see Palmer 1927; d'Udekem d'Acoz 1986; d'Udekem d'Acoz & Rappé 1991). The **ventral setae of dactyl P4** occupy approximately ⅓ basal in *L. dioscurus* and *L. vernalis* (Fig. 4D), while in *L. holsatus* they exceed half their length (d'Udekem d'Acoz & Rappé 1991). In *L. marmoreus* they almost reach ½. However, this character remains somewhat variable. The **merus of P5** is distinctly shorter in *L. holsatus* (ratio ML/MH: 1.1–1.3; 1.4–1.6 according d'Udekem d'Acoz & Rappé 1991) than those of *P. dioscurus* (1.63–1.89), *P. vernalis* (1.51–1.76) and *L. marmoreus* (1.65–1.87), whose ratio values overlap. D'Udekem d'Acoz & Rappé (1991) and d'Udekem d'Acoz (1991) found different ratios for the last two species (2.0–2.5, and 1.8–2.1, respectively). The datcylus and propodus are similar in *P. vernalis* and *P. dioscurus* but somewhat different from those of *P. holsatus*. The posterodistal lobe of the propodus is more developed and broader in *P. holsatus* than in other species (Ingle & Clark 1998) and the dactylus is usually broader in *P. holsatus*.

The distal part of the **first male pleopod** is slightly more curved in *P. vernalis* (Fig. 8E–F; in larger specimens even somewhat hooked) than in *P. dioscurus* sp. nov., in which it tends to form an angle of approximately 90° (Fig. 8C–D).

Discussion

There are 18 species within the family Polybiidae in European waters, 11 in the former genus *Liocarcinus* (or 12, if *Liocarcinus rondeletii* is accepted as a species and not as a subspecies of *L. navigator*), whose taxonomic-phylogenetic relationships have begun to be analysed, but no definite conclusion has yet been reached (Passamonti *et al.* 1997; Schubart & Reuschel 2009; Spiridonov *et al.* 2014). The extant

Fig. 10. *Polybius vernalis* (Risso, 1827), ♂ from Tunisia, Bay of Tunis (RBINS, INV. 187235). **A**. Dorsal habitus. **B**. Facial habitus. **C**. Ventral habitus.

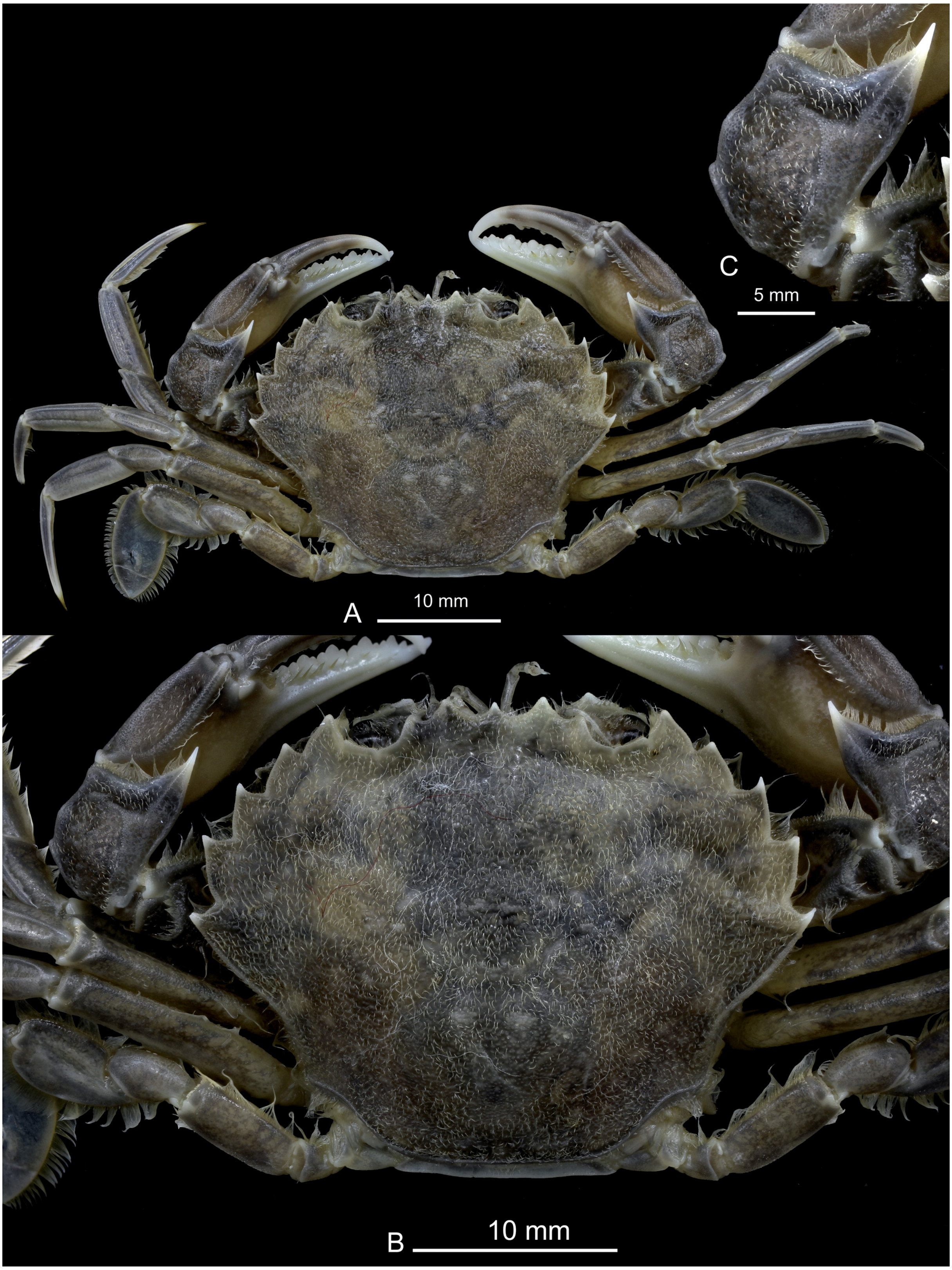

Fig. 11. *Polybius vernalis* (Risso, 1827), ♂ from Spain, Málaga, Fuengirola (RBINS, INV. 187238). **A**. Dorsal habitus. **B**. Carapace. **C**. Carpus of right pereiopod.

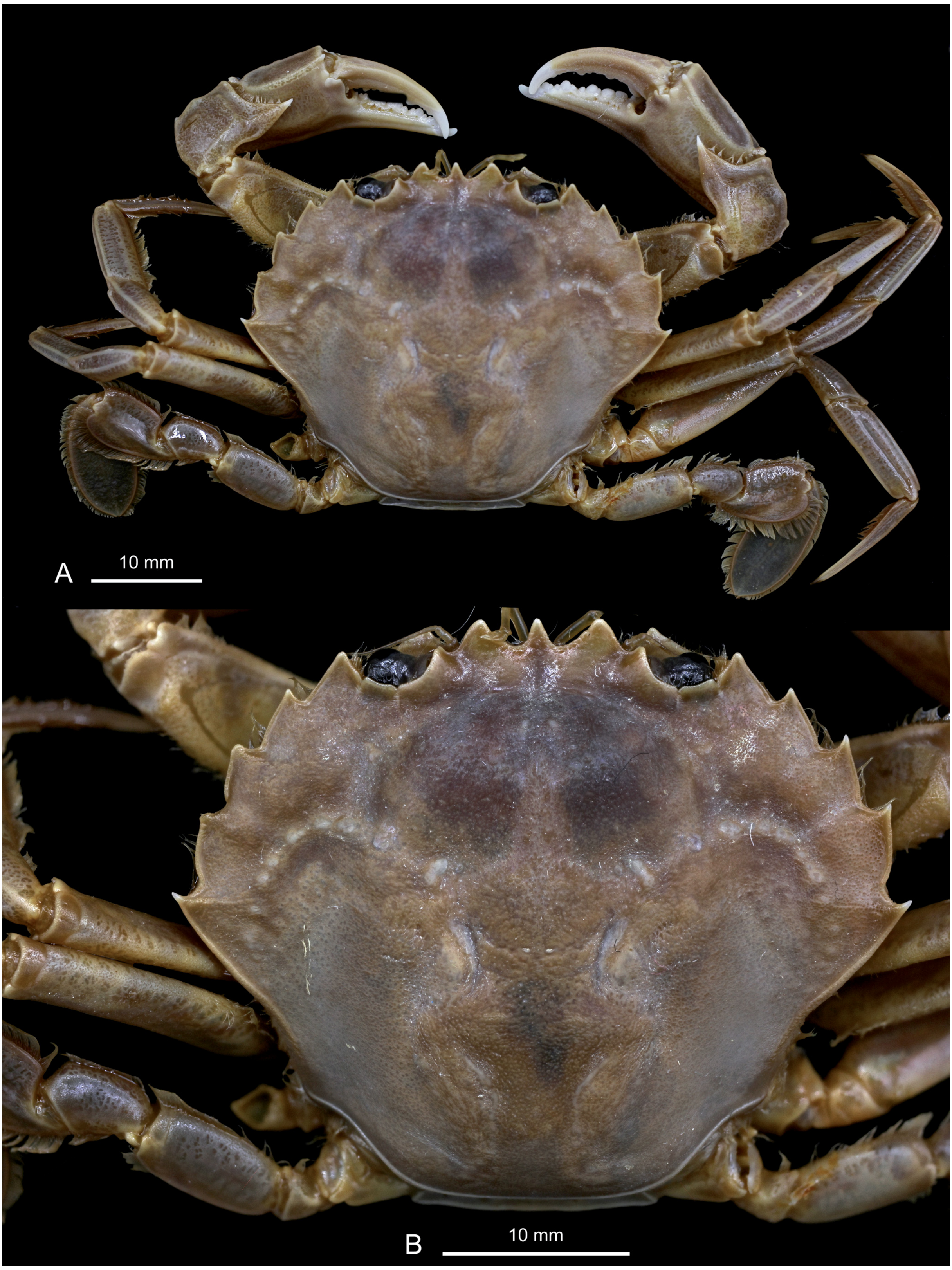

Fig. 12. *Polybius vernalis* (Risso, 1827), ♂ from Bulgaria, Varna Bay (RBINS INV. 187236). **A**. Dorsal habitus. **B**. Carapace.

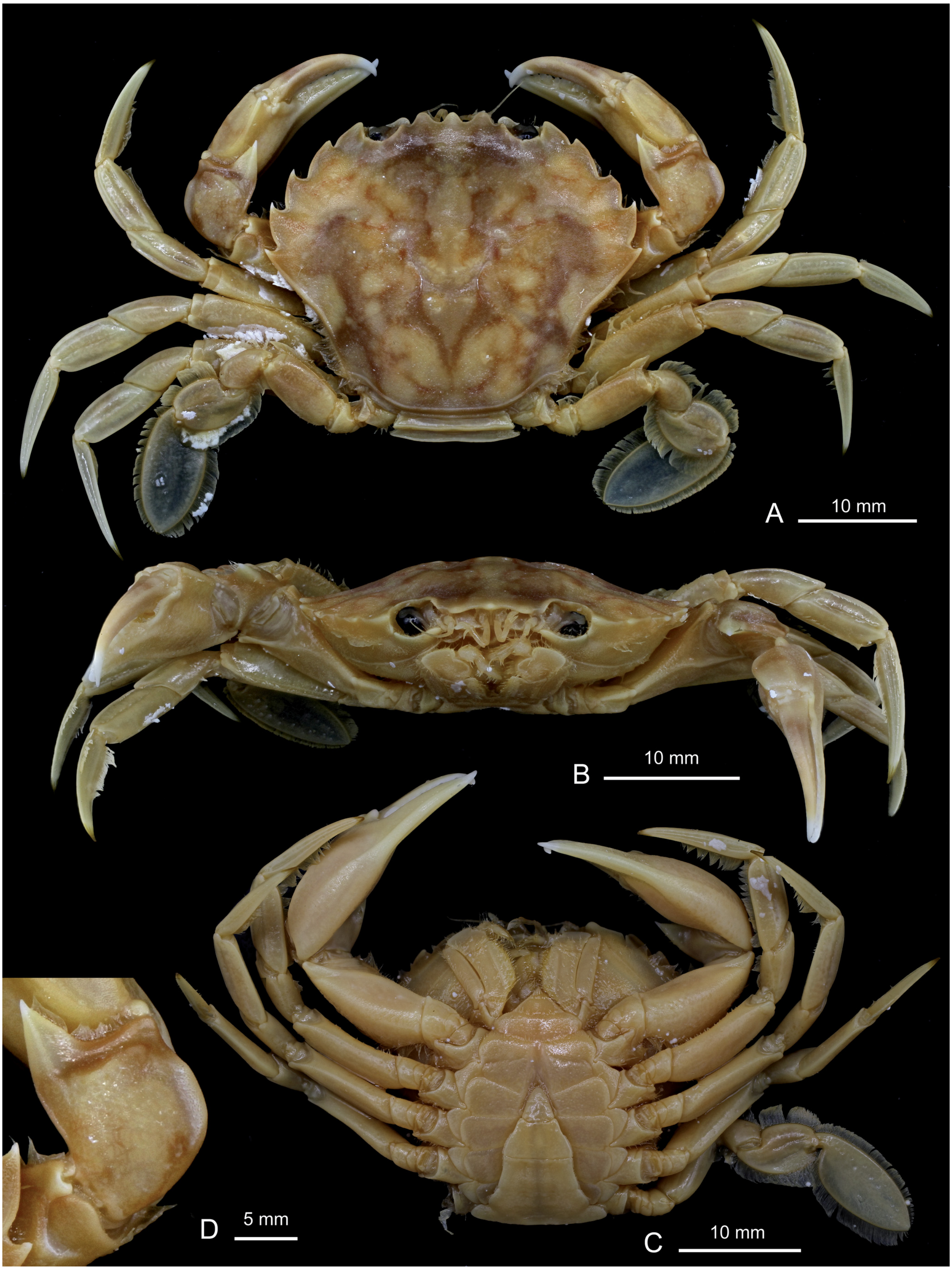

Fig. 13. *Polybius marmoreus* (Leach, 1814), ♂ from Belgium, Heist (RBINS, INV. 187218). **A**. Dorsal habitus. **B**. Carapace facial view. **C**. Carpus of right pereiopod. **D**. Ventral view.

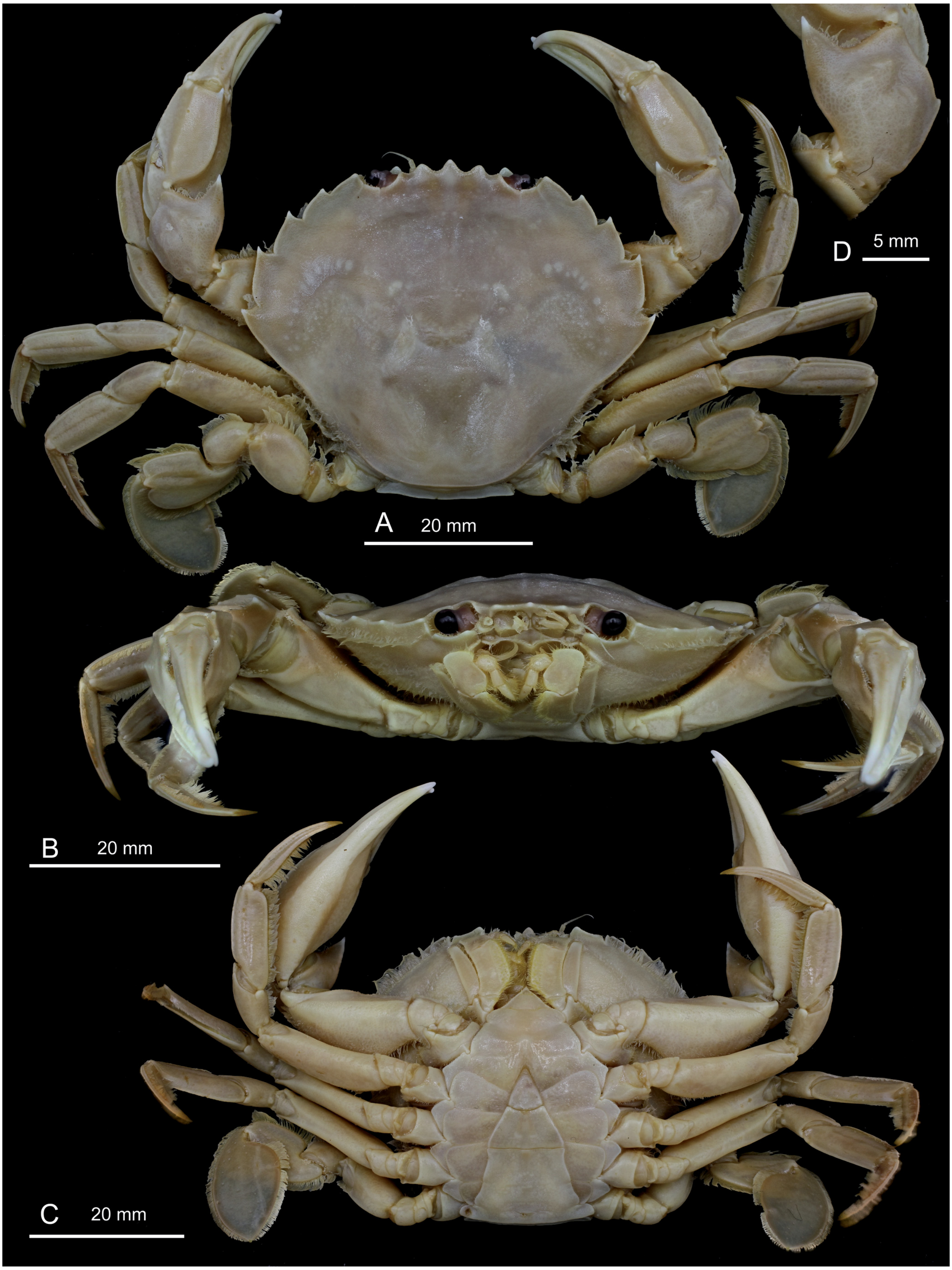

Fig. 14. *Polybius holsatus* (Fabricius, 1798), ♂ from Belgium, Duinbergen (RBINS, INV. 187221). **A**. Dorsal habitus. **B**. Facial habitus. **C**. Ventral habitus. **D**. Carpus of right pereiopod.

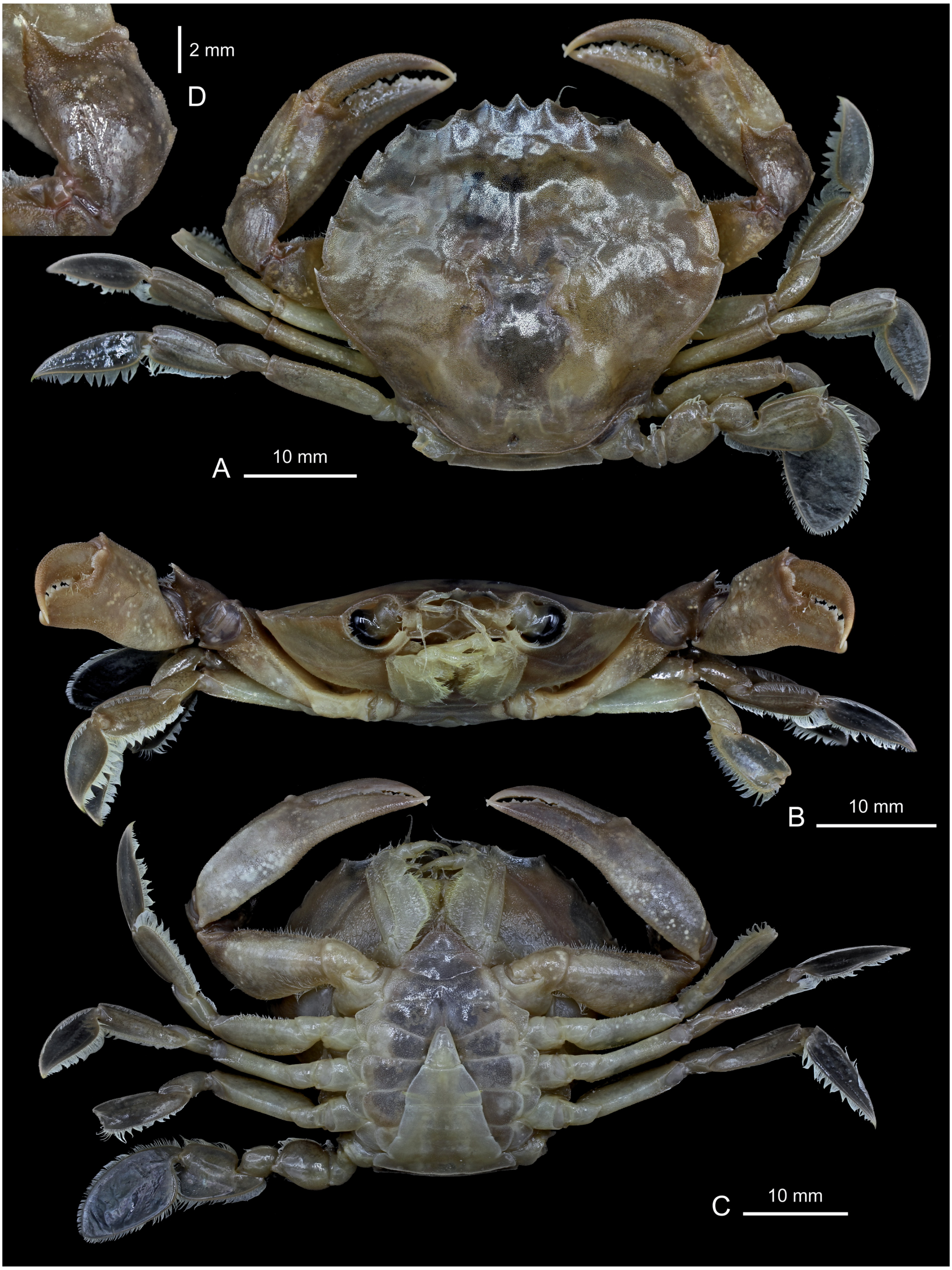

Fig. 15. *Polybius henslowii* Leach, 1820, ♂ from France, Bay of Biscay, cruise PELGAS 10, stn O.0627, chalut 68 (RBINS, INV. 187237). **A**. Dorsal habitus. **B**. Facial habitus. **C**. Ventral habitus. **D**. Carpus of right pereiopod.

species are Atlantic and Indo-Pacific in distribution (Ingle 1980; Poore 2004). Thus, the genus may have had a Tethyan distribution and dispersal route in the past (Schweitzer & Feldmann 2010).

The molecular data of the species show a high genetic similarity between some species of the former genus *Liocarcinus*. Schubart & Reuschel (2009) mentioned that *L. holsatus* is "genetically almost identical" to *P. henslowii* in the mitochondrial large ribosomal subunit 16S rRNA and the nuclear encoded histone 3 (H3) gene, and this was ratified by Plagge *et al.* (2016), as well as in the present study (Figs 1–2). This was an argument to synonymize some species of *Liocarcinus* with *Polybius*, but others may belong to different and separate genera (Spiridonov *et al.* 2014). Plagge *et al.* (2016) proposed the using the name *Liocarcinus*, due to its more frequent use in the literature (probably because it includes many species), but previously d'Udekem d'Acoz (1999) had selected the genus *Polybius*. Both names are commonly used, but *Polybius* is the senior name, and the valid name of a taxon is the oldest available name applied to it (ICZN 1999, art. 23.1). Some species of the genus *Liocarcinus* were previously included in other genera, such as *Macropipus* Prestandrea, 1833 (Prestandrea 1833; Zariquiey Álvarez 1968) and *Portunus* Weber, 1795 (Fabricius 1798; Bouvier 1940), while *Polybius henslowii* has always been placed in its original genus since its initial description in 1820. In this paper, and from this moment on, we follow the Principle of Priority (ICZN 1999, Art. 23) as d'Udekem d'Acoz (1999) previously considered. On the other hand, although *P. henslowii* and *P. holsatus* are genetically indistinguishable, we consider (as suggested by Schubart & Reuschel (2009) and Plagge *et al.* (2016)) that they are different and valid species, with *P. henslowii* being the result of a very recent speciation from a common ancestor with *L. holsatus*. In fact, the Pliocene fossil attributed to *P. holsatus* by van Bakel *et al.* (2003) and illustrated by them does not correspond to this species and perhaps it could belongs to the postulated common ancestor mentioned above. Also, Hyžný *et al* (2021) cites fossils of *Liocarcinus* sp. from the Pliocene of the Azores.

A new species of this genus is described, *Polybius dioscurus* sp. nov., morphologically and genetically related to the group formed by *P. holsatus*, *P. vernalis* and *P. marmoreus* (see remarks above). These four species, as well as *P. bolivari*, *P. depurator* and *P. zariquieyi*, should be included (Figs 1–2) in the genus *Polybius*, together with the type species of the genus, *Polybius henslowii*. The other species included within *Liocarcinus* were being studied by Christoph D. Schubart, who considered that their status positions needed to be analyzed and justified in more detail (Schubart pers. com. to other co-authors before his sudden death).

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Supplementary file

Supp. file 1. List of 16S and COI sequences (fasta format) of the specimens of *Polybius* Leach, 1820 that were in Christoph Schubart´s laboratory when he passed away and could not be deposited in Museums (specimen not available), and for this reason these sequences cannot be upload to GenBank. The codes XX (in bold in this list) are included after the species names in the Figures 1 and 2, and other data of the specimens are in Table 1. https://doi.org/10.5852/ejt.2024.930.2501.11187