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Redescription of the hermit crab *Diogenes pugilator* (Decapoda: Anomura) reveals the existence of a species complex in the Atlanto-Mediterranean transition zone, resulting in the resurrection of *D. curvimanus* and the description of a new species

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Examination of material from the coasts of the Iberian Peninsula and nearby areas has revealed that more than one species is mixed under the name for the common diogenid hermit crab, *Diogenes pugilator*. In this study, three species are recognized, primarily on the basis of a combination of morphological characters and live colour patterns. *Diogenes pugilator* is redescribed on the basis of a neotype selected from near the supposed type locality, as well as specimens from other localities. *Diogenes curvimanus* is resurrected and the name attributed to a second species, whereas a third morphotype is described as a new species, ***Diogenes armatus* sp. nov.**. The last two species are also fully described and differentiating characters among the three species are discussed. Newly generated sequences from two mitochondrial genes and one nuclear gene, and comparative analyses with other available DNA sequences for the genus, are also included. The corresponding molecular phylogenies support the recognition of the three species and suggest the presence of additional unknown species in the *D. pugilator* species complex. All previous records of *D. pugilator* should be revised in the light of these new findings. Finally, a comprehensive identification key to the eastern Atlantic and western Mediterranean species of *Diogenes* is also provided.

ADDITIONAL KEYWORDS: biodiversity – biogeography – comparative sequence analysis – ribosomal – identification key – mitochondrial and ribosomal DNA – molecular systematics – morphological comparison – speciation – species delineation – taxonomy.

INTRODUCTION

The genus *Diogenes* Dana, 1851 is one of the most diverse genera of the hermit crab family Diogenidae, with 72 species recognized worldwide according to the most recent updates (Komai *et al.*, 2018; Asakura, 2020; Komai & Yoshida, 2020; Lemaitre & McLaughlin, 2020; WoRMS, 2021). Species of *Diogenes* are easily recognizable and diagnosed by a much larger left cheliped compared to the right one, and the presence of an intercalary rostriform process between the ocular acicles. Although this is true for most species in the genus, the group known as the '*Troglopagurus* group' presents a markedly reduced, vestigial or obsolete intercalary rostriform process (McLaughlin, 2005).

Although representatives of this genus can be found in almost any coastal area worldwide, with the exception of the West Atlantic, most of the known species (88%) have an Indo-West Pacific distribution

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(N = 64), with a considerable number of species having been described from there in the last decade (Asakura & Tachikawa, 2010; Komai *et al.*, 2012, 2013, 2018; Rahayu, 2012, 2015; Xiao *et al.*, 2015; Trivedi *et al.*, 2016; Igawa & Kato, 2017; Landschoff & Rahayu, 2018; Asakura, 2020; Komai & Yoshida, 2020). Contrary to evident efforts to improve the knowledge and clarify taxonomic ambiguities in the Indo-Pacific area, the situation in the eastern Atlantic seems more stagnant. Eight species have been recorded so far from the latter region: *D. brevirostris* Stimpson, 1858, *D. costatus* Henderson, 1893, *D. denticulatus* Chevreux & Bouvier, 1892, *D. extricatus* Stebbing, 1910, *D. mercatoris* Forest, 1952, *D. ortholepis* Forest, 1961, *D. ovatus* Miers, 1881 and *D. pugilator* (Roux, 1829) (see: Chevreux & Bouvier, 1892; Barnard, 1950, 1955; Forest, 1952, 1961; Kensley, 1981). In the case of *D. costatus*, only a few records have been published from the Atlantic part of South Africa, its typical distribution being otherwise the western Indian Ocean (Barnard, 1950; Reay & Haig, 1990, El-Wakeil *et al.*, 2009). The actual status of the species is problematic and the real identity of *D. costatus* needs to be re-examined (T. Komai, pers. comm.).

Two other species of the genus occur in South African waters, although entirely on the Indian Ocean side: *D. albimanus* Landschoff & Rahayu, 2018 and *D. custos* (Fabricius, 1798) (see: McLaughlin & Holthuis, 2001). Forest (1956) briefly mentioned a single male specimen from Accra in the former Côte de l'Or (today Ghana) and referred to it as *Diogenes* sp.. It shows clear differences to *D. pugilator*, although we wonder whether it could be a different species or simply an extreme morphological variant.

It is interesting to note that among the eastern Atlantic and South African species listed above, only *D. albimanus* has been described as new to science within the last five decades (Landschoff & Rahayu, 2018), suggesting that after the landmark studies conducted from the mid-19th to 20th centuries, taxonomic studies on the East Atlantic *Diogenes* are scarce and must be considered as outdated.

Since a complete revision of the genus from the whole Atlantic and its marginal seas is beyond the scope of this study, we restrict the revision to *Diogenes pugilator* and the representatives from Western European Atlanto-Mediterranean waters, with a special focus on the Iberian Peninsula.

Diogenes pugilator was was described in 1829, possibly based on specimens from the Gulf of Marseille, and is now considered a western Palaearctic species, with a wide distribution and large bathymetric range (Nöel, 2016). Several authors have described *D. pugilator* as extremely variable in morphology, in some cases leading to the description of new species (e.g. *Pagurus varians* Costa, 1838; *Pagurus dillwynii* Spence Bate, 1851; *Pagurus bocagii* de Brito Capello, 1875), subspecies (e.g. *Diogenes pugilator subcristata* Balss, 1921, *Diogenes pugilator orientalis* Codreanu & Balcesco, 1968) or varieties (e.g. var. *ovata* Miers, 1881, var. *intermedius* Bouvier, 1891, vars. *subcristata*, *cristata* and *gracilima* Balss, 1921) within this complex. These were later synonymized by other authors, referring to the inherent variability of the nominal species (Forest, 1955; McLaughlin *et al.*, 2010). The consequent uncertainty is in part caused by the complex morphological delimitation of this group and the fact that the original description by Roux (1829) is short, general and accompanied by an illustration that lacks detail. The taxonomic clarification is made further difficult by the fact that the original type material apparently was lost long ago, thus preventing earlier authors to compare their material with the types.

Species delimitations have traditionally been based on morphological characters, but sometimes it is challenging to obtain an accurate identification exclusively based on this approach, especially after the discovery of the occurrence of cryptic and pseudocryptic species. To try to solve these difficulties, the combination of morphological characters with molecular markers has been demonstrated to be a powerful tool in providing accurate identifications in marine organisms in general, and in hermit crabs in particular (Mantelatto *et al.*, 2006; Matzen da Silva *et al.*, 2011; Negri *et al.*, 2014; Raupach *et al.*, 2015; Landschoff & Gouws, 2018). In the present study, we used partial DNA sequences from the mitochondrial genes 16S ribosomal RNA (16S rRNA) and cytochrome *c* oxidase subunit I (*COI*), as well as from the nuclear gene 28S ribosomal RNA (28S rRNA), to investigate the relationships between and within species. The 16S and *COI* markers have been extensively used and have proved to be an effective tool in studies of decapod crustaceans (Schubart *et al.*, 2000; Morrison *et al.*, 2002; Porter *et al.*, 2005; Ahyong *et al.*, 2007). Also, 28S is becoming a popular marker in crustacean studies (Matzen da Silva *et al.*, 2011; Bracken-Grissom *et al.*, 2013). The information of the three markers (individually or in combination) can help to support the morphological results, not only for the identification of new species, but also to elucidate the taxonomic validity of closely related species (Thiercelin & Schubart, 2014; Shih *et al.*, 2016).

The current revision of *Diogenes* specimens from the Atlanto-Mediterranean coasts of the Iberian Peninsula and surrounding areas has revealed the existence of at least three distinct morphotypes formally assigned to *Diogenes pugilator*. This was initially explained by the reported variability of Roux's species and its wide distribution which includes the present study area.

However, a closer look, and first molecular results obtained by both involved study groups, strengthened the hypothesis that possibly more than one species is present. The aim of this work is thus to test this hypothesis and to clarify whether the recorded variation can in fact be attributed to different morphotypes within *D. pugilator*, or to well-definable, distinct species. Molecular information and comparative analyses based on available DNA sequences of the genus are included to support the species delimitation and to facilitate genetic assignments in future studies.

MATERIAL AND METHODS

Specimens included in this revision come from different sources. Most of them were obtained by the authors during numerous sampling trips conducted from 2017 to 2020, using different sampling gear, scuba-diving and direct inspection of intertidal and subtidal areas, attempting to cover most regions of the Iberian coastline. Additional samples were recovered from previous projects to complete or to support the information about the distribution of the identified morphotypes and to investigate an alternative hypothesis of a possible recent arrival of the species. The final set of samples thus covers the period from 1982 to 2020.

When possible, specimens were photographed *in situ* to gather information about the unique colour patterns of each species. Specimens were kept alive in sea water and transported to the laboratory for further studies and detailed photography, if necessary. The specimens were frozen in seawater before shell extraction and preservation in absolute ethanol. All specimens were studied under the stereomicroscope and classified to the lowest taxonomic level possible.

Colour descriptions, based on Werner's nomenclature of colours, is now accessible online for consultation at https://www.c82.net/werner/.

For preventing damage of key structures for morphological identification, a piece of one antenna or single ambulatory leg was used as tissue sample for DNA extraction in males and non-ovigerous females, while eggs were employed from berried females. These extractions were carried out in the Instituto de Ciencias Marinas de Andalucía (ICMAN-CSIC) and the University of Regensburg (UR) following the protocols from Estoup *et al.* (1996) and Reuschel *et al.* (2010), respectively. The lengths of the obtained sequences and the primers used for each gene are listed in Table 1. Polymerase chain reaction (PCR) amplicons were sent for purification and sequencing to external laboratories (viz. Stab Vida or Macrogen Europe).

Consensus sequences were generated from different gene fragments or the complementary strands with BioEdit v.7.0.5 (Hall, 1999). Comparative searches were performed with the National Center for Biotechnology Information (NCBI) and Barcode of Life Data System (BOLD) databases to roughly confirm the identification.

For the phylogenetic analyses, available sequences of 16S (9) and *COI* (49) assigned to *Diogenes* were downloaded from the NCBI and BOLD databases and used together with the 152 new sequences generated in this study (Table 2). NCBI/BOLD sequences with less than 200 bp or

Table 1. List of sequenced genes including: primers used for each gene, pair combined, length of the sequences obtained (bp), and references

Gen	Primer	Sequence	Pair	bp	References
16S	16L2	5′-TGC CTG TTT ATC AAA AAC AT-3′	1472	570	Schubart *et al.* (2002)
	16L12	5′-TGA CCG TGC AAA GGT AGG ATA A-3′	1472	450	Schubart *et al.* (1998)
	1472	5′-AGA TAG AAA CCA ACC TGG-3′		570	Crandall & Fitzpatrick (1996)
COI	COL6b	5′-ACA AAT CAT AAA GAT ATY GG-3′	COH6	640	Schubart & Huber (2006)
	COH6	5′-TAD ACT TCD GGR TGD CCA AARAAY CA-3′		640	Schubart & Huber (2006) (modification of HCO2198)
	LoboF1	5′-KBT CHA CAA AYC AYA ARG AYA THG G-3′	COH6	670	Lobo *et al.* (2013)
	LoboR1	5′-TAA ACY TCW GGR TGW CCR AARAAY CA-3′	LoboF1	670	Lobo *et al.* (2013)
	LCO1490	5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′	HCO2198	640	Folmer *et al.* (1994)
	HCO2198	5′-TAA ACT TCA GGG TGA CCA AAAATC A-3′		640	Folmer *et al.* (1994)
28S	28L1	5′-CGG AGG AAA AGA AAC CAA CAG-3′		750	Mock & Schubart (2021)
	28D2H	5′-TGA CTC GCA CAC ATG TTA GA-3′		750	Mock & Schubart (2021)

with duplicated information were discarded, finally reducing the number of downloaded sequences to 6 of the 16S and 22 of *COI*. The final datasets were then aligned by MUltiple Sequence Comparison by Log-Expectation (MUSCLE) (Edgar, 2004), implemented in MEGA7 (Kumar *et al.*, 2016).

Blocks of ambiguous data in the non-protein-coding gene alignments were identified and excluded using GBlocks with relaxed settings (Talavera & Castresana, 2007). Gene concatenation of the 16S + *COI* (1185 bp) was performed in MESQUITE 3.31 (Maddison & Maddison, 2019), and the best-fitting nucleotide substitution models for each gene separately, and for the concatenate alignment, were assessed with jModelTest 2.1.10 (Darriba *et al.*, 2012), using the Akaike information criterion, as recommended by Posada & Buckley (2004). According to the results of this method, the Tamura 3-parameter model of nucleotide substitution using discrete gamma-distributed rates for the variable sites and with invariant sites (T92+G+I) was selected in all cases.

Maximum likelihood (ML) analyses were conducted for the concatenated dataset, as well as for the individual genes (16S, *COI* and 28S). Concatenated analyses were partitioned based on gene identity (i.e. 16S and *COI*). Two other species of the family Diogenidae, viz. *Dardanus arrosor* (Herbst, 1796) and *Paguristes eremita* (Linnaeus, 1767), were selected as outgroups. ML analyses were performed using the MEGA 7.0.26 software under the T92+G+I model. A random starting tree was generated using the Neighbour-Joining method, selecting the partial deletion option (75% site coverage cut-off). A ML tree was generated using the Nearest-Neighbour interchange option. Topological robustness was investigated using 1000 nonparametric bootstrap replicates. In the resulting trees, only bootstrap values of > 70% nodal support are shown. To test the distinct species hypothesis, the online version of the Automatic Barcode Gap Discovery (ABGD) method (Puillandre *et al.*, 2012) was used for the *COI* gene, with default parameters (Jukes–Cantor). This method for species delimitation detects the gap in the pairwise distribution of the genetic distances calculated between all pairs of specimens. The barcode gap corresponds to a threshold between intra- and interspecific distances and is used to propose species-level boundaries.

RESULTS

SYSTEMATIC ACCOUNT

Synonymies with enough information to be reasonably assigned to the species addressed here are included when appropriate.

FAMILY DIOGENIDAE ORTMANN, 1892

GENUS *DIOGENES* DANA, 1851

DIOGENES PUGILATOR (ROUX, 1829) *S.S.*

(FIGS 1A–F, 2A–F, 7A, D, G, J)

Pagurus pugilator P. Roux, 1829 (in Roux, 1828–30): part 3, pl. XIV, figs 3, 4.
Pagurus varians O.G. Costa, 1838 (in Costa & Costa, 1838–71).

Type material: Neotype: ♂ 3.0 mm (MNHN-IU-2019-3215), **France, Mediterranean Sea**: Frontignan, near Sète, 43°27′11.5″N, 3°48′49″E, sand, shallow subtidal, 29 August 2019.

Topotypes: 2♂, same data as neotype, (ZSMA20190 400-0401), 1 ♂ (IEOCD-BR/2664); 1 ♂ (IEOCD-BR/2676), 09 June 2018; 6 ♂ (IEOCD-BR/2665-2669), 29 August 2019.

Other revised material: **Spain**: off Ebro Delta, 2 ♂ (ICMD 143/1998), 40°35′N, 0°43′E, 3–6 m, 4 May 1982; La Carihuela, Torremolinos, Málaga, 13 ♂ and 4 ♀ (IEOCD-BR/2660-2663), 36°36′28.2″N, 4°30′13.6″W, sand, 2–4 m, 11 December 2019; Fuengirola, Málaga, 1 ♂ and 1 ♀ (IEOCD-BR/2670), 36°32′57.92″N, 4°36′30.89″W, sand, 4 m, 4 March 2014; Pozuelo, Granada, 5 ♂ (IEOCD-BR/2677-2678-2679), 36°44′37.95″N, 3°39′30.47″W, sand, subtidal, 10 January 2020; Guadarranque, Algeciras, 1 ♀ (IEOCD-BR/2675), 36°10′49.7″N, 5°24′42.1″W, sand, 4 m depth, 11 December 2019; San García, Algeciras, 1 ♂ (IEOCD-BR/2674), 36°06′17.5″N, 5°25′56.7″W, sand, 4 m depth, 25 July 1996; **Tunisia:** La Goulette, Tunis, 1 ♂ (IEOCD-BR/2659), 4 ♀(IEOCD-BR/2671-2673), 36°49′10.80″N, 10°18′45.11″E, sand, 3–4 m, 24 November 2009.

Redescription: **Shield** (Figs 1A, 7D) subquadrate, nearly as long as broad; rostral lobe broadly rounded, exceeded by lateral projections that are triangular, acutely pointed, with single spine at apex; anterior margins of shield between rostral lobe and lateral projections slightly concave; anterolateral margins sloping, smooth; anterolateral angles rounded, usually with two to three small spines (two left and three smaller right in holotype); lateral margins slightly convex; posterior margin truncate; dorsal surface slightly vaulted, with lateral margins each usually cut by few transverse spinulose ridges extending on to lateral surface of shield; dorsal surface with additional faint short, transverse rows of small tubercles and tufts of short, stiff setae. Branchiostegites with dorsal margin bearing a row of eight to nine strong spines. Posterolateral plates not well calcified, unarmed.

Table 2. Voucher numbers for the specimens of *Diogenes* sequenced for this study, with collection area and accession numbers for 16S, *COI* and 28S genes, along with the selected sequences downloaded from NCBI/BOLD databases; type specimens are indicated by an asterisk and sequences generated in this study are shown in bold

			Gene		
Species	Collection location	Voucher	16S	*COI*	28S
Diogenes curvimanus	Spain	MNHN-IU-2019-3214*	**MW791779**	**MW776663**	**MW802642**
Diogenes curvimanus	Spain	IEOCD-BR/2581	**MW791781**	**MW776675**	-
Diogenes curvimanus	Spain	IEOCD-BR/2582	**MW791782**	**MW776662**	**MW802643**
Diogenes curvimanus	Spain	ZSMA2019 0398	**MW791784**	**MW776672**	-
Diogenes curvimanus	Spain	IEOCD-BR/2596	**MW791785**	**MW776674**	-
Diogenes curvimanus	Spain	IEOCD-BR/2597	**MW791786**	**MW776673**	-
Diogenes curvimanus	Spain	IEOCD-BR/2598	**MW791792**	**MW776669**	-
Diogenes curvimanus	Spain	IEOCD-BR/2599	**MW791788**	**MW776668**	**MW802644**
Diogenes curvimanus	Spain	IEOCD-BR/2600	**MW791789**	**MW776667**	-
Diogenes curvimanus	Spain	IEOCD-BR/2601	**MW791787**	**MW776676**	-
Diogenes curvimanus	Spain	IEOCD-BR/2604	**MW791783**	-	-
Diogenes curvimanus	Spain	IEOCD-BR/2605	**MW791790**	**MW776671**	**MW802645**
Diogenes curvimanus	Spain	IEOCD-BR/2606	**MW791791**	**MW776670**	**MW802646**
Diogenes curvimanus	Spain	IEOCD-BR/2607	**MW791777**	**MW776666**	**MW802639**
Diogenes curvimanus	Spain	IEOCD-BR/2608	**MW791778**	**MW776665**	**MW802640**
Diogenes curvimanus	Spain	IEOCD-BR/2609	**MW791780**	**MW776664**	**MW802641**
Diogenes curvimanus	Belgium	IEOCD-BR/2612	-	**MW776659**	-
Diogenes curvimanus	Belgium	IEOCD-BR/2618	-	**MW776658**	**MW802648**
Diogenes curvimanus	Belgium	IEOCD-BR/2619	-	**MW776660**	-
Diogenes curvimanus	France	IEOCD-BR/2621	**MW791793**	**MW776661**	**MW802647**
Diogenes curvimanus	Spain	IEOCD-BR/2622	**MW791776**	-	-
Diogenes armatus	Spain	MNHN-IU-2014-5736*	**MW791814**	**MW776705**	**MW802658**
Diogenes armatus	Spain	MNHN-IU-2019-3213*	**MW791815**	**MW776704**	**MW802659**
Diogenes armatus	Spain	IEOCD-BR/2645	**MW791813**	**MW776701**	**MW802657**
Diogenes armatus	Spain	ZSMA2019 0402	**MW791806**	**MW776709**	**MW802653**
Diogenes armatus	Spain	IEOCD-BR/2623	**MW791818**	**MW776700**	-
Diogenes armatus	Spain	IEOCD-BR/2624	**MW791820**	**MW776695**	-
Diogenes armatus	Spain	IEOCD-BR/2625	**MW791810**	**MW776696**	-
Diogenes armatus	France	IEOCD-BR/2627	-	**MW776697**	**MW802661**
Diogenes armatus	Corsica	IEOCD-BR/2628	**MW791816**	**MW776699**	-
Diogenes armatus	Spain	IEOCD-BR/2631	-	**MW776698**	-
Diogenes armatus	Spain	IEOCD-BR/2639	-	-	**MW802660**
Diogenes armatus	Tunisia	IEOCD-BR/2640	**MW791817**	-	-
Diogenes armatus	Tunisia	IEOCD-BR/2641	**MW791819**	-	-
Diogenes armatus	Spain	IEOCD-BR/2642	**MW791807**	**MW776708**	**MW802654**
Diogenes armatus	Spain	IEOCD-BR/2643	**MW791811**	**MW776703**	**MW802656**
Diogenes armatus	Spain	IEOCD-BR/2644	**MW791812**	**MW776702**	-
Diogenes armatus	Portugal	IEOCD-BR/2647	**MW791808**	**MW776707**	**MW802655**
Diogenes armatus	Portugal	IEOCD-BR/2648	**MW791809**	**MW776706**	-
Diogenes pugilator	France	MNHN-IU-2019-3215*	-	**MW776683**	-
Diogenes pugilator	Tunisia	IEOCD-BR/2659	**MW791795**	-	-
Diogenes pugilator	Spain	IEOCD-BR/2660	**MW791796**	**MW776692**	-
Diogenes pugilator	Spain	IEOCD-BR/2661	**MW791797**	**MW776688**	-
Diogenes pugilator	France	ZSMA2019 0400	-	**MW776678**	-
Diogenes pugilator	France	ZSMA2019 0401	-	**MW776681**	-
Diogenes pugilator	Spain	ICMD 143/1998	**MW791805**	**MW776686**	-
Diogenes pugilator	Spain	ICMD 143/1998	-	**MW776687**	-
Diogenes pugilator	Spain	IEOCD-BR/2662	**MW791801**	**MW776694**	-
Diogenes pugilator	France	IEOCD-BR/2664	**MW791804**	**MW776677**	-

Table 2. Continued

Species	Collection location	Voucher	Gene		
			16S	*COI*	28S
Diogenes pugilator	France	IEOCD-BR/2665	-	**MW776684**	-
Diogenes pugilator	France	IEOCD-BR/2666	-	**MW776682**	-
Diogenes pugilator	France	IEOCD-BR/2667	-	**MW776685**	-
Diogenes pugilator	France	IEOCD-BR/2668	-	**MW776680**	-
Diogenes pugilator	France	IEOCD-BR/2669	-	**MW776679**	-
Diogenes pugilator	Spain	IEOCD-BR/2670	**MW791802**	-	-
Diogenes pugilator	Spain	IEOCD-BR/2670	**MW791802**	-	-
Diogenes pugilator	Tunisia	IEOCD-BR/2673	**MW802638**	-	-
Diogenes pugilator	Spain	IEOCD-BR/2674	**MW791799**	**MW776690**	-
Diogenes pugilator	Spain	IEOCD-BR/2675	**MW791800**	**MW776689**	-
Diogenes pugilator	France	IEOCD-BR/2676	-	-	**MW802652**
Diogenes pugilator	Spain	IEOCD-BR/2677	**MW791798**	**MW776691**	-
Diogenes pugilator	Spain	IEOCD-BR/2678	**MW791803**	**MW776693**	-
Diogenes ovatus	Mauritania	IEO-CD-CCLME11/1572	**MW791794**	-	-
Diogenes ovatus	Guinea Conakry	IEO-CD-CCLME11/1667	-	-	**MW802650**
Diogenes ovatus	Guinea-Bissau	IEO-CD-CCLME12/2569	-	**MW776721**	**MW802649**
Diogenes ovatus	Guinea-Bissau	IEO-CD-CCLME12/2571	-	**MW776720**	**MW802651**
Diogenes sp.2	Spain	IEOCD-BR/2682	**MW791826**	**MW776713**	-
Diogenes sp.2	Spain	IEOCD-BR/2683	**MW791825**	**MW776712**	-
Diogenes sp.2	Spain	IEOCD-BR/2684	**MW791827**	**MW776718**	-
Diogenes sp.2	Spain	IEOCD-BR/2686	**MW791828**	-	-
Diogenes sp.2	Senegal	IEO-CD-CCLME12/2572	**MW791830**	**MW776715**	-
Diogenes sp.2	Mauritania	IEO-CD-CCLME12/2573	**MW791824**	-	-
Diogenes sp.2	Mauritania	IEO-CD-CCLME12/2575	**MW791831**	**MW776714**	-
Diogenes sp.2	Morocco	IEO-CD-CCLME12/2576	**MW791823**	**MW776719**	**MW802664**
Diogenes sp.2	Morocco	IEO-CD-CCLME12/2577	**MW791829**	**MW776716**	-
Diogenes sp.1	Spain	IEOCD-BR/2680	**MW791821**	**MW776710**	**MW802662**
Diogenes sp.1	Morocco	IEO-CD-CCLME12/2578	**MW791822**	**MW776711**	**MW802663**
Dardanus arrosor	Morocco	IEO-CD-CCLME11/1575	**MW791834**	**MW776656**	-
Paguristes eremita	Morocco	IEO-CD-CCLME11/690	**MW791833**	**MW776657**	-
Diogenes pugilator	North Sea	-	-	BNSC192-11	-
Diogenes pugilator	North Sea, German Bight	-	-	BNSDE084-11	-
Diogenes pugilator	North Sea, German Bight	-	-	BNSDE086-11	-
Diogenes miles	India	-	-	GBCMA6701-14	-
Diogenes alias	India	-	-	GBCMA6707-14	-
Diogenes canaliculatus	India	-	-	GBCMA6708-14	-
Diogenes dubius	India	-	-	GBCMA6709-14	-
Diogenes manaarensis	India	-	-	GBCMA6710-14	-
Diogenes merguiensis	India	-	-	GBCMA6711-14	-
Diogenes planimanus	India	-	-	GBCMA6717-14	-
Diogenes violaceus	India	-	-	GBCMA6718-14	-
Diogenes brevirostris	South Africa, Western Cape	-	-	HONS017-19	-
Diogenes brevirostris	South Africa	HVDBC-53	-	HVDBC053-11	-
Diogenes viridis	Vanuatu	MNHN-IU-2008-16281	-	MDECA648-10	-
Diogenes viridis	Vanuatu	MNHN-IU-2008-16282	-	MDECA649-10	-
Diogenes pallescens	Vanuatu	MNHN-IU-2008-16294	-	MDECA658-10	-
Diogenes pallescens	Vanuatu	MNHN-IU-2008-16297	-	MDECA660-10	-
Diogenes pugilator	Portugal, Alentejo	LMBSWB1-001	-	MLALE067-14	-

Table 2. Continued

Species	Collection location	Voucher	Gene		
			16S	*COI*	28S
Diogenes pugilator	Portugal, Alentejo	LMBSWB1-002	-	MLALE068-14	-
Diogenes pugilator	Portugal, Alentejo	LMBSWB1-003	-	MLALE069-14	-
Diogenes costatus	South Africa, KwaZulu-Natal	MB-A066693	-	MH481985	-
Diogenes costatus	South Africa, Western Cape	MB-A066759	-	MH481993	-
Diogenes spinicarpus	Vanuatu	MNHN-IU-2008-16275	-	MDECA642-10	-
Diogenes spinicarpus	Vanuatu	MNHN-IU-2008-16276	-	MDECA643-10	-
Diogenes goniochirus	China	-	MK610031	-	-
Diogenes edwardsii	China	-	MK610030	-	-
Diogenes nitidimanus	China	-	MK610029	-	-
Diogenes rectimanus	China	-	MK610028	-	-
Diogenes deflectomanus	China	-	MK610027	-	-
Diogenes avarus	China	-	MK610026	-	-

Ocular peduncles (including corneas) about 0.6 times as long as shield, moderately stout, slightly narrowed in middle; corneas not dilated, corneal diameter about 0.3–0.4 peduncular length; row of short, plumose setae on mesial margin of peduncles. **Ocular acicles** (Fig. 1A, B) subtriangular, with sinuous mesial margin; anterior margin slightly convex, bearing three to four (sometimes a small fifth) distal spines decreasing in size towards outer margin, innermost distal spine distinctly larger and often slightly curved; rest of anterolateral outer margin with 11–12 small tubercles of about the same size, occupying at least half of anterior margin. **Intercalary rostriform process** simple, slightly shorter than ocular acicles (including spines), tapering acutely.

Antennular peduncles (Fig. 1A, C) overreaching distal corneal margin by about 0.8–0.9 length of ultimate segment, reaching distal margin of antennal peduncle; third segment unarmed, not broadened distally, about 3.5 times longer than distal width, subequal in length to penultimate segment, with three simple setae on dorsal margin and a distal tuft near distodorsal margin; second segment unarmed, with row of short setae on dorsodistal margin; basal segment unarmed, except for the spinulose rounded ventrodistal border.

Antennal peduncles (Fig. 1A) overreaching distal corneal margin by 0.6–0.7 length of fifth segment; fifth segment with row of moderately long stiff setae on ventral surface and short setae dorsodistally, unarmed; fourth segment unarmed, with tufts of long setae on dorsodistal and ventrodistal border; third segment unarmed; second segment with distolateral outer process stout and acute, with subdistal smaller spine; smaller but strong spine on distomesial angle; plumose setae near both spines and ventral surfaces; ventrodistal border spinose; first segment with spinules of different sizes on distal border; plumose, short setae present on lateral and ventral surfaces. **Antennal acicle** short, subtriangular, reaching slightly below distal margin of fourth peduncular segment, bearing a simple strong terminal spine plus usually five spines along mesial margin, and tufts of setae on both mesial and lateral margins. **Antennal flagellum** short and robust, noticeably setose; articles with paired long ventrolateral setae and shorter setae on dorsal and ventral surfaces.

Third maxilliped (Fig 1D) basis unarmed; ischium with *crista dentata* bearing two prominent and two small distal spines, with two additional variably sized spines on proximal half; ischium and merus with rows of scarce setae on lateral margins; carpus, propodus and dactylus with dense tufts of thick, long setae in dorsodistal and dorsomedian margin, concealing part of segments; exopod peduncle reaching one-third of endopod carpal length.

Male left cheliped (Figs 2A, B, F, 7A, G) much larger than right (Fig. 1E). **Dactylus** about 0.8 times as long as palm measured along upper margin, slightly arched, ending in large calcareous claw, crossing tip of fixed finger; upper, inner margin well defined by a row of spinose tubercles, upper, outer margin by small spines; two more incomplete rows of small subacute tubercles running parallel to upper, outer margin; conspicuous one to two strong spinose tubercles at beginning of these additional rows, near joint of the dactyl with the palm; outer surface not flattened, covered with small subacute tubercles; lower margin with two rows of tufts of setae; some sparse setae covering outer surface and between dorsal rows; cutting edge sinuous, with row of calcareous teeth of various size,

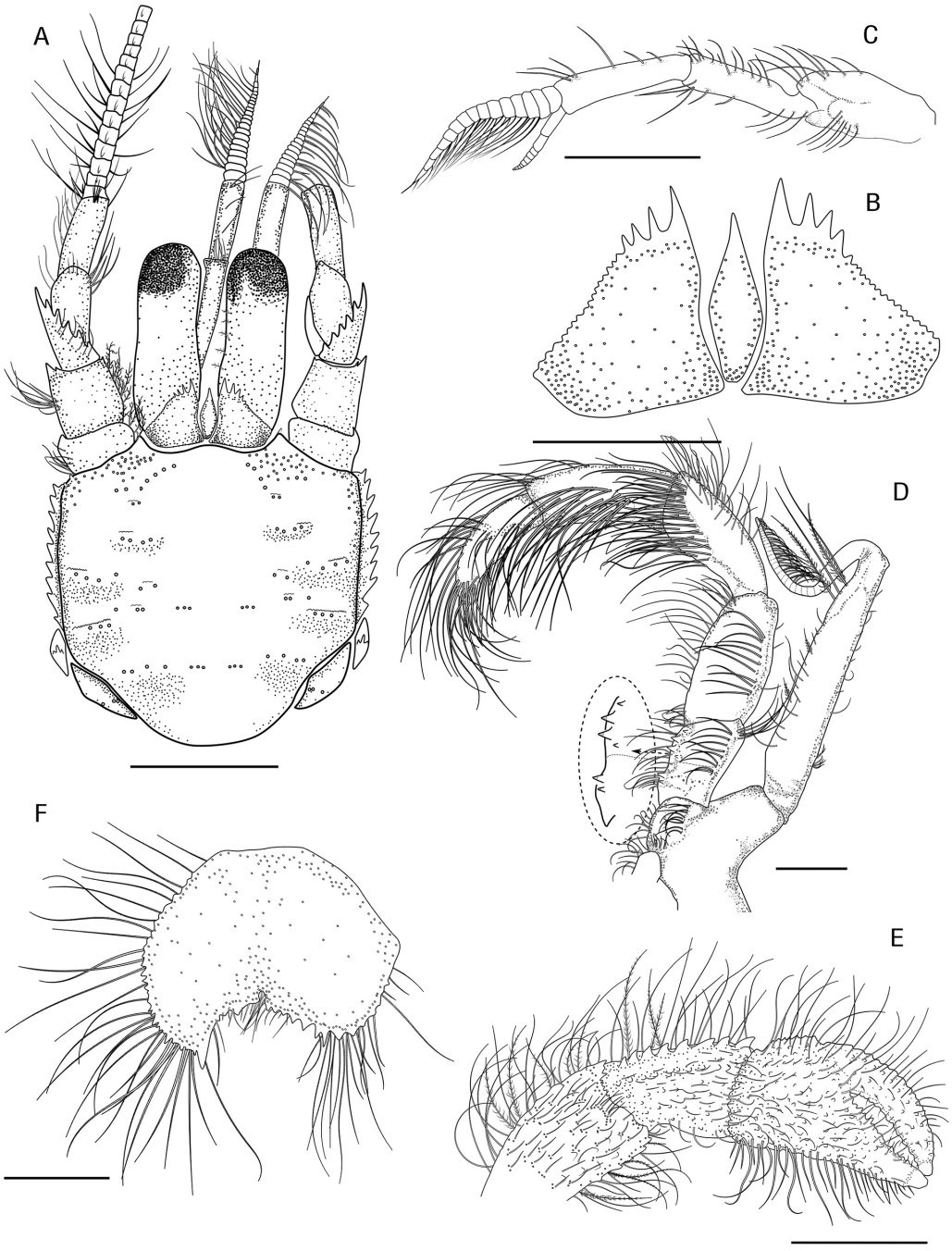

Figure 1. *Diogenes pugilator s.s.* ♂ 3.0 mm, Frontignan, France, neotype, (MNHN-IU-2019-3215): A, anterior part of body; B, ophtalmic scales; E, right cheliped, outer aspect; F, telson, dorsal aspect. *Diogenes pugilator s.s.* ♂ 2.7 mm, Frontignan, France, topotype (ZSMA2019 0400): C, right antennular, inner view; D, left maxiliped 3, (inset: detail of the spines, ventral aspect). (Scales: A, C, E = 1 mm, B, D, F = 0.5 mm).

largest at distal half of dactyl; inner surface with irregular rows of tubercles in upper half running parallel to upper margin, reaching distal part of dactylus, defining a shallow concave area between the two rows; two irregular rows of tufts of dense plumose setae just above the cutting edge.

Fixed finger delimited proximoventrally by a shallow concavity separating the slightly convex outer surface of fixed finger from markedly inflated palm surface; lower margin with two to three rows of small, rounded tubercles extending on to palm;

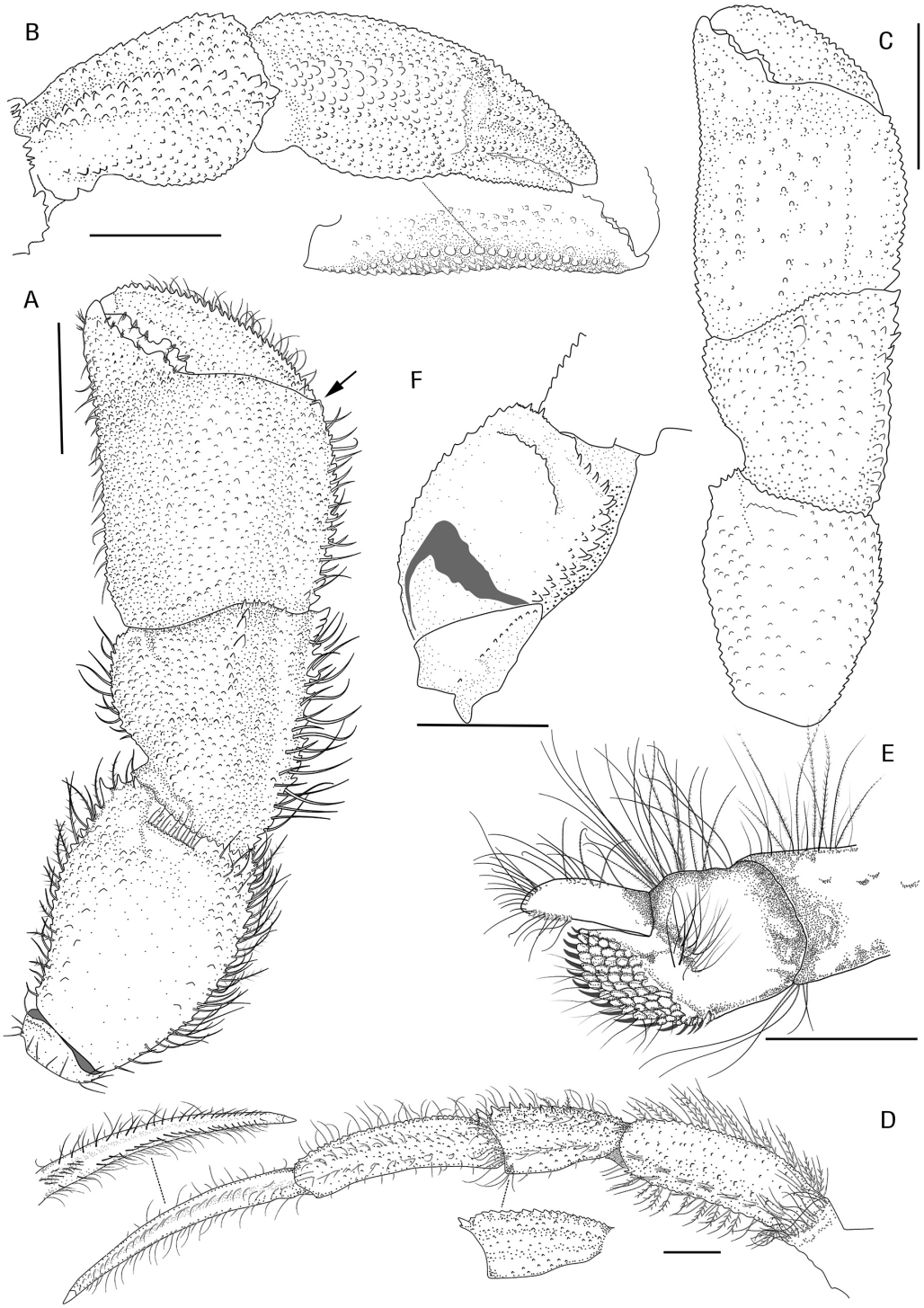

Figure 2. *Diogenes pugilator s.s.* ♂ 3.0 mm, Frontignan, France, neotype, (MNHN-IU-2019-3215): A, left cheliped, outer aspect (arrow indicating bispinose protuberance); B, left cheliped, dorsal aspect (inset: detail of the row of tubercles on the lower, inner surface). *Diogenes pugilator s.s.* ♀ 2.5 mm, La Carihuela, Málaga, Spain, topotype, (IEOCD-BR/2660-2661): C, left cheliped, outer aspect. *Diogenes pugilator s.s.* ♂ 2.7 mm Frontignan, France, topotype, (ZSMA2019 0400): D, left pereiopod 2 (insets: variations in P3 carpus; dactylus inner aspect); E, pereiopod 4; F, merus, mesial view (setae omitted). (Scales: A–C, F = 2 mm, D = 1 mm, E = 0.5 mm).

outer surface covered with small subacute tubercles; cutting edge sinuous, with single row of various sized teeth, largest in proximal area, with a row of spaced tufts of setae below it; inner surface almost smooth with some tubercles on proximal surfaces and three rows (upper, medial and lower) of tufts of short, stout setae.

Palm robust, about as long as high (max. medial length – maximum height); upper margin shorter than carpus; dorsal surface with irregular rows of spines, more produced on upper, outer margin, decreasing in size towards inner margin; space between rows widening distally and with less produced tubercles; outer surface strongly inflated in upper half, decreasing gently to lower region; distal lower part depressed near fixed finger; upper, outer part (below spinose row on upper margin) slightly concave, covered with small acute tubercles; distinct bispinose protuberance present at upper disto-outer angle; lower margin almost straight, defined by row of obtuse tubercles, with distal lower margin slightly concave; rest of palm outer surface with small spinose tubercles and some slightly larger subacute tubercles forming diffuse and not always well-defined rows; ventral margin of palm with blunt tubercles that continue along lower, inner face, defining a more or less flattened tuberculate area, delimited by sinuous crest-like row of large, rounded tubercles (Fig. 2B inset; see also Fig. 7G), defining an inflection change; rest of inner surface slightly flattened, covered with rounded, flat tubercles of different sizes and scarce simple setae associated with some of them; sometimes two rows of longitudinal slightly bigger tubercles outlined on upper half, and on medial zone, similar in extension reaching distal margin.

Carpus longer than high (Figs 2A, B, 7A); upper margin with two to three irregular rows of strong spines; outer surface convex, covered with small spines; row of stronger spines present on middle outer surface, largest near distomedial margin; area just below upper, outer and inner margins slightly concave, becoming deeper and widening proximally, innermost shallower; lower margin denticulate, convex in distal two-thirds, forming a marked sinus proximally; disto-outer margin spinulose submarginally; pilosity on outer surfaces abundant but not dense; inner surface covered with closely spaced thick tubercles and tufts of stiff, plumose setae.

Merus longer than high (Fig. 2A, F), subtriangular in dorsal view; distal margin with spines of different sizes, largest on dorsal area, without setae; dorsal surface with rows of low acute tubercles, turning to obtuse spines distally, and tufts of long, plumose setae; lateral surface with small spines adjacent to dorsolateral and ventrolateral margins and spinose transversal furrow subdistally with sparse long setae, rest of lateral surface smooth and glabrous; ventrolateral margin denticulate, slightly concave in proximal half, accompanied by long, plumose setae and strong subdistal spines; mesial face with weakly calcified, u-shaped patch, distally divided by shallow transversal furrow dorsally bearing denticulate protuberances (Fig. 2F) and tufts of long thick setae; dorsodistal margin with spines of different sizes; ventrodistal margin defined by large acute tubercles with associated long, plumose setae. **Ischium** with short transverse row of small spines on distolateral surface (Fig. 2A) and longitudinal row of spines on ventromesial surface (Fig. 2F), with tufts of setae associated with spines and tubercles.

Female left cheliped (Fig. 2C) similar to males; larger tubercles on outer surface of palm more numerous than in males, but arranged in similar way; lower margin of palm slightly more sinuous, faintly concave distally; lower margin of carpus only slightly convex, forming a less prominent sinus proximally; spines on dorsolateral and ventrolateral merus margins smaller than in males, rest of lateral surface with low, rounded tubercles.

Right cheliped (Fig. 1E) appreciably shorter than left, robust, not reaching proximal margin of palm (usually midlength of carpus) of left cheliped; dactylus and fixed finger with relatively narrow hiatus, both terminating in small calcareous claws. **Dactylus** slightly more than 2.0 times longer than palm (measured along mesial margin), gently arched; upper, inner and outer margins defined by rows of small tubercles with long setae; outer surface convex, covered with small spines arranged in rows; cutting edge with row of small calcareous teeth, regular in size, terminating in small calcareous claw and tufts of setae parallel to cutting edge; inner surface smooth except for tufts of setae parallel to cutting edge. **Palm** with upper, outer margin defined by a row of small spinose tubercles; outer surface broad, strongly convex, with irregular rows of small spinose tubercles, obscured by tufts of long setae; lower margin defined by small, obtuse tubercles; fixed finger broadened proximally; cutting edge with row of small, subacute calcareous teeth and two rows of tufts of long, stout setae parallel to the cutting edge; inner surface covered with evenly distributed low tubercles and associated long, plumose setae.

Carpus widened distally, with row of strong spines on upper, outer margin increasing in size distally, and an additional row of rounded tubercles below it, delimiting a broad depression between them; outer surface with low tubercles and numerous tufts of long setae; lower surface nearly smooth, with some scattered low, rounded tubercles; inner surface with distal margin dentate, rest of inner surface covered with low, rounded tubercles and sparse tufts of short, plumose setae.

Merus distal margin with spines of different size, largest on dorsal area, with long, simple setae; dorsal margin weakly delimited by a row of small, blunt tubercles, becoming obtuse small spines distally and tufts of long, plumose setae; lateral surface with small spines adjacent to dorsolateral margin and crenulate transversal furrow subdistally, with sparse, long setae, rest of lateral surface with small, rounded tubercles and sparse setae; ventrolateral margin delimited by a row of low, acute tubercles increasing in size distally, and tufts of long, plumose setae; mesial face with weakly calcified, u-shaped patch proximally, smooth, with ventromesial margin defined by row of acute tubercles of similar size. **Ischium** with short, transverse row of small spines on distolateral surface and longitudinal row of acute tubercles on ventromesial margin, with tufts of setae associated with spines and tubercles.

Second and third pereiopods (Figs 2D, 7J) moderately stout, subequal in length. **Dactylus** about 1.2 times as long as propodus, weakly curved; terminating in moderately small corneous claw; upper and lower outer surfaces unarmed, with rows of long, simple setae more numerous in lower outer surface; outer surface with shallow, longitudinal sulcus medially, with row of setae along lower margin of sulcus in one-fifth proximal border, then continuing along upper border; inner surface with longitudinal rows of long, stout setae adjacent to upper and lower margins and a short row of plumose setae occupying proximal one-fifth of inner sulcus.

Propodus about same length as merus (second) or shorter (third), with upper margin defined by row of spinules (second) or tiny blunt tubercles (third), and with row of setae; lateral surfaces each with longitudinal row of setae arising from tiny, low protuberances near upper margin and second inconspicuous row below midline; lower margins smooth with scarce short setae.

Carpus upper margin with row of strong spines, increasing in size distally and with row of sparse, plumose setae dorsally (second), or with small spines on upper margin, with only one dorsodistal spine (third); lateral surfaces with low tubercles arranged in two rows, and setae associated with them; ventral surfaces with sparse, short setae.

Merus upper margin with small spines increasing in size distally (second), almost smooth (third); lower margin dentate, with well-developed distal spine (second), or almost smooth, without distal spine (third); tufts of long, plumose setae on upper and lower surfaces. **Ischium** unarmed, with long setae on distal margin.

Fourth pereiopods (Fig. 2E). **Dactyl** with row of nine to ten minute spiniform setae on distal part of ventral margin. **Propodus** suboval, with numerous setae on unarmed dorsal margin; propodal rasp consisting of five to six rows of corneous scales, covering distoventral part, including fixed finger; rest of segments unarmed, with clumps of long, plumose setae.

Fifth pereiopods. Propodus almost as long as merus and two times longer than carpus; group of subacute corneous scales in distodorsal surface of propodus and smaller ones in dactylus and fixed finger; long clumps of strong simple setae.

Male unpaired left pleopods 2–5 uniramous, marginally setose. **Female gonopores** paired; two to four unpaired **pleopods** well-developed, biramous; fifth pleopods without exopod, as in male.

Telson (Fig. 1F) with small, median cleft, markedly asymmetrical; left posterior lobe with a strong terminal spine and with row of spinules on lateral margin, becoming blunt anteriorly; oblique terminal margin with few small spines; right posterior lobe with row of small spines on less oblique terminal margin, extending on to posterior half of lateral margin.

Coloration (Fig. 7A, D, G, J). Whitish ocular peduncles with orange stain at base, projecting towards apex in diffuse narrow line. Antennules with the central dorsal area covered by a brownish orange line; honey yellow flagellum. Antennal scales with a vermilion red stain at the base; antennal flagellum with vermilion red rings evenly spaced. Characteristic vermillion red paired stains on branchial zone of cephalothorax. Left cheliped with snow white background colour; merus and carpus with the upper half orange with greenish tints, and a narrow scarlet red stripe in the middle zone, complete in the merus, partial in the carpus. Hand with broad wood brown well defined spots in: upper half of the base of the dactylus, lower distal area of the palm, and proximal central area of the palm; faint oil green areas on the distal area of the propodus, and pale orange on the upper, proximal area. Right cheliped snow white background colour; arterial blood red spot on the upper, proximal carpal area; orange zones on the superior distal zone of the carpus and proximal of the propodus; buff orange ring near the proximal area of the dactylus. Second and third pereiopods of buff orange colour at the dorsal part (with the proximal and distal parts darker), whiter at the ventral half; arterial blood red dorsal lateral stripes at the mid merus, carpus (incomplete), propodus and base of the dactylus.

Habitat: Sandy beaches of tidal lagoons along intertidal or shallow subtidal areas, up to 25 m, although more frequent around 5 m depth.

Distribution: Known with certainty from the French Mediterranean (Frontignan, neotype locality), north-eastern (Barcelona), and south-eastern Iberian

Peninsula (Málaga, Granada, Algeciras) and Tunisian coasts (La Goulette). By the figure and coloration of the large cheliped in Costa (1839, T2, f2), its presence in Italy (Gulf of Naples and Taranto), seems also probable.

Remarks: A number of subspecies or varieties of *D. pugilator* have been established based on morphological differences, e.g. *Diogenes pugilator orientalis* for the Black Sea and Adriatic populations (Codreanu & Balcesco, 1968). Currently, none of the European varieties have been accepted so far, because of the consideration of *D. pugilator* as a highly variable species (Ingle, 1993). The application of molecular techniques has shown that, even if this consideration is true to a certain extent, there is in fact a number of different well-defined species, previously lumped under *D. pugilator* and that in future studies, some of these synonymized taxa could be revalidated in the light of new and updated information.

Since the type specimen is missing, and based on what is assumed to be the type locality area for Roux's *Diogenes pugilator*, as well as morphological similarities, *Diogenes pugilator sensu* Roux (1829) is herewith re-described, and a neotype is proposed (based on recent material collected from the presumed type locality area), in order to establish a reference for future studies, helping to elucidate the real identity of *D. pugilator s.s.* and to distinguish it from other potential species of the complex. This is further achieved by replacing Roux's missing samples with topotypes that may facilitate future comparisons.

DIOGENES ARMATUS ALMÓN *ET AL.* SP. NOV.

(FIGS 3A–G, 4A–G, 7B, E, H, K)

The description of the new species in this paper has been carried out by four of the authors, B. Almón, J. Cuesta, C. Schubart and J.E. García Raso.

Zoobank registration: lsid:zoobank.org:act:10CBBC54-4576-463A-AFE5-E7BE0D3A179A

Type material: Holotype: ♂ 3.4 mm, Spain: Torregorda, Cádiz, (MNHN-IU-2019-3213), 36°26′51.7″N 6°14′49.4″W, sandy beach, intertidal shallow pools, 16/03/2015; *Allotype:* ♀ 3.8 mm, Isla Canela, Huelva, (MNHN-IU-2014-5736), 37°10′51.8″N 7°20′15.3″W, sand intertidal, 25 July 2014.

Paratypes: Spain: Torregorda, Cádiz, 1 ♀ (IEOCD-BR/2645), 36°26′51.7″N 6°14′49.4″W, intertidal sandy beach, 27 July 2014; 1 ♂ (ZSMA2019 0402), 30 May 2018; 1 ♀ (IEOCD-BR/2643), 23 October 2014; 1 ♂ (IEOCD-BR/2644), 27 July 2014; 1 ♂ (IEOCD-BR/2642), 30/05/2018; 1 ♂ (IEOCD-BR/2646), 16/03/2015.

Other material: **Spain:** Bajo la Cabezuela, Cádiz, 5 ♂ and 1 ♀ (IEOCD-BR/2623-2626), 36°31′43.6″N 6°15′01.0″W, intertidal, 30 August 2019; Es Torrent, Ibiza, 8 ♀ and 4 ♂ (IEOCD-BR/2629-2638), 38°58′02.2″N, 1°16′07.2″E, shallow subtidal, 26 May 2018; Port D'Es Torrent, 1 ♂ (IEOCD-BR/2639), 38°58.036′N, 1°16.12′E, shallow subtidal, 22 May 2018; **Portugal**: Lagoa da Albufeira, 2 ♂ (IEOCD-BR/2647-2648), 38°30′34.9″N, 9°10′28.6″W, sand, intertidal, 12 June 2018; **French Mediterranean:** Corsica, 1 ♂ (IEOCD-BR/2628), 42°42′49.8″N, 9°18′0.06″E, sand, shallow subtidal, 12 June 2003; **French Atlantic**: Arcachon, 1 ♂ (IEOCD-BR/2627), 44°40′0.04″N, 1°10′34.5″E, sand, intertidal, 02 October 2018; **Tunisia**: La Goulette, Tunis, 7 ♂ (IEOCD-BR/2640-2641), 36°49′10.80″N, 10°18′45.11″E, sand, 3–4 m, 24 November 2009.

Etymology: The specific name *armatus*, masculine Latin adjective for armed, is given to highlight the spiny appearance of the chelipeds of this species compared to other Atlantic congeners, with more developed ornamentation composed mainly of spines and spiny tubercles instead of more rounded ones.

Description: **Shield** (Figs 3A, 7E) slightly longer than broad; rostral lobe acutely rounded, exceeded by lateral projections that are triangular, acutely pointed, with single spine at apex; anterior margins between rostral lobe and lateral projections markedly concave and thickened; anterolateral margins sloping, slightly concave, mostly smooth, sometimes with some isolated minute spine; anterolateral angles rounded, with one spine on each side and another smaller submarginal spine sometimes inconspicuous; lateral margins slightly convex; posterior margin roundly truncate; dorsal surface slightly vaulted, with lateral margins usually cut by few transverse tuberculate ridges, extending on to lateral surface of shield; dorsal surface with additional short, transverse rows of small tubercles and tufts of short, stiff setae. Branchiostegites with dorsal margin bearing row of 10–11 strong spines, proximal two to three smaller. Posterolateral plates not well calcified, unarmed.

Ocular peduncles (including corneas) about 0.6 times as long as shield, moderately stout, slightly inflated in upper half; corneas not dilated, corneal diameter about 0.25 peduncular length; row of short, plumose setae over inner surface of peduncles. **Ocular acicles** (Fig. 3A, C) subtriangular, with slightly concave mesial margin; anterior margin slightly convex, bearing 11–12 acute spines, decreasing in size towards outer margin, covering entire length of

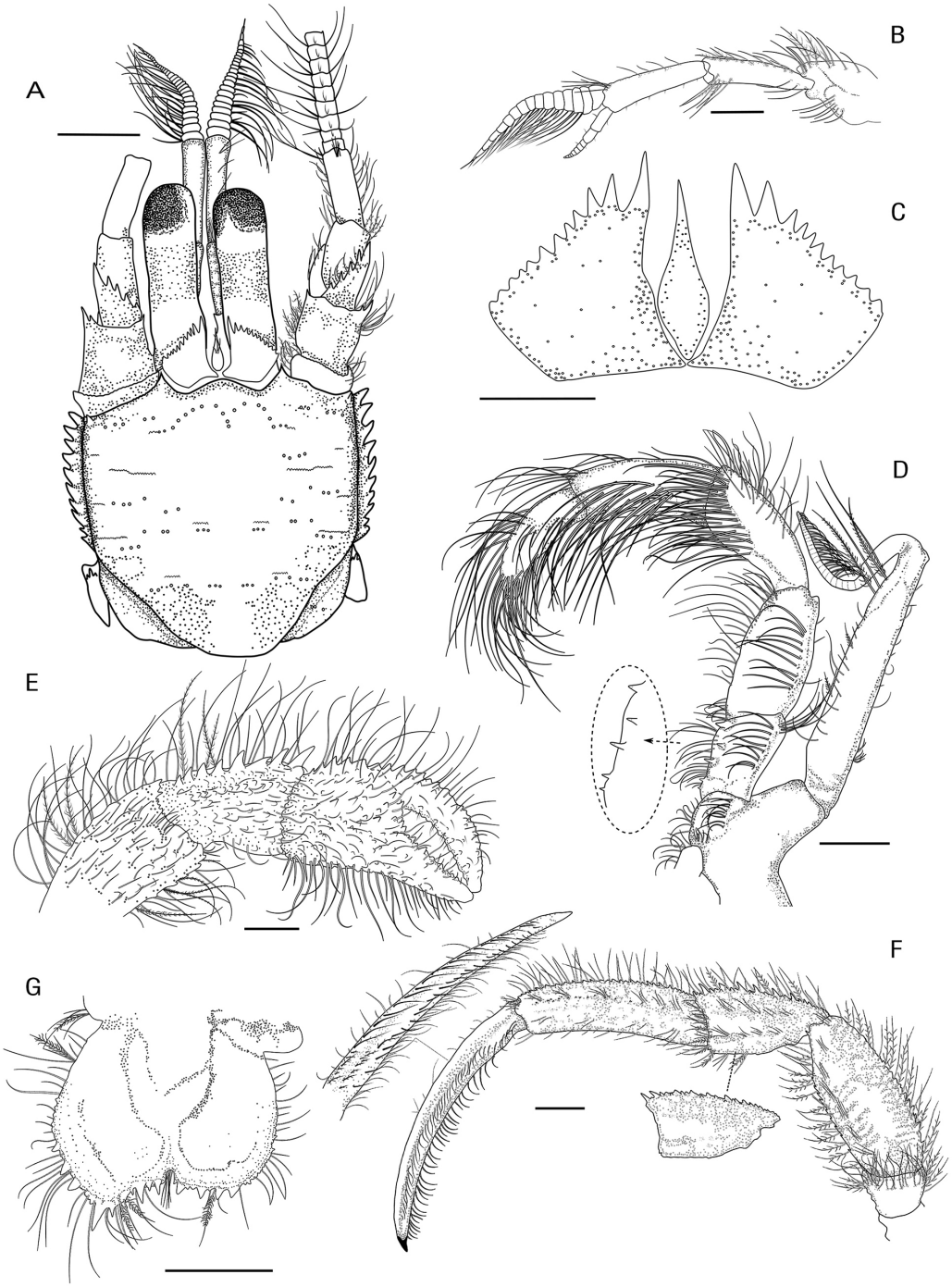

Figure 3. *Diogenes armatus* sp. nov. ♂ 3.4 mm, Torregorda, Cádiz, Spain, holotype, (MNHN-IU-2019-3213): A, anterior part of body; B, right antennule, inner aspect; C, ophtalmic scales; D, left maxiliped 3 (inset: detail of the spines, ventral aspect); E, right cheliped, dorsal aspect; F, left pereiopod 2 (insets: variations in P3 carpus; dactylus inner aspect); G, telson, dorsal view. (Scales: A, E–G = 1 mm, B–D = 0.5 mm).

anterior margin; innermost spine distinctly larger and often slightly curved laterally. **Intercalary rostriform process** simple, shorter than ocular acicles, tapering acutely.

Antennular peduncles (Fig. 3A, B) overreaching distal corneal margin by about 0.4 length of ultimate segment, extending slightly beyond distal margin of antennal peduncle; third segment unarmed, not broadened

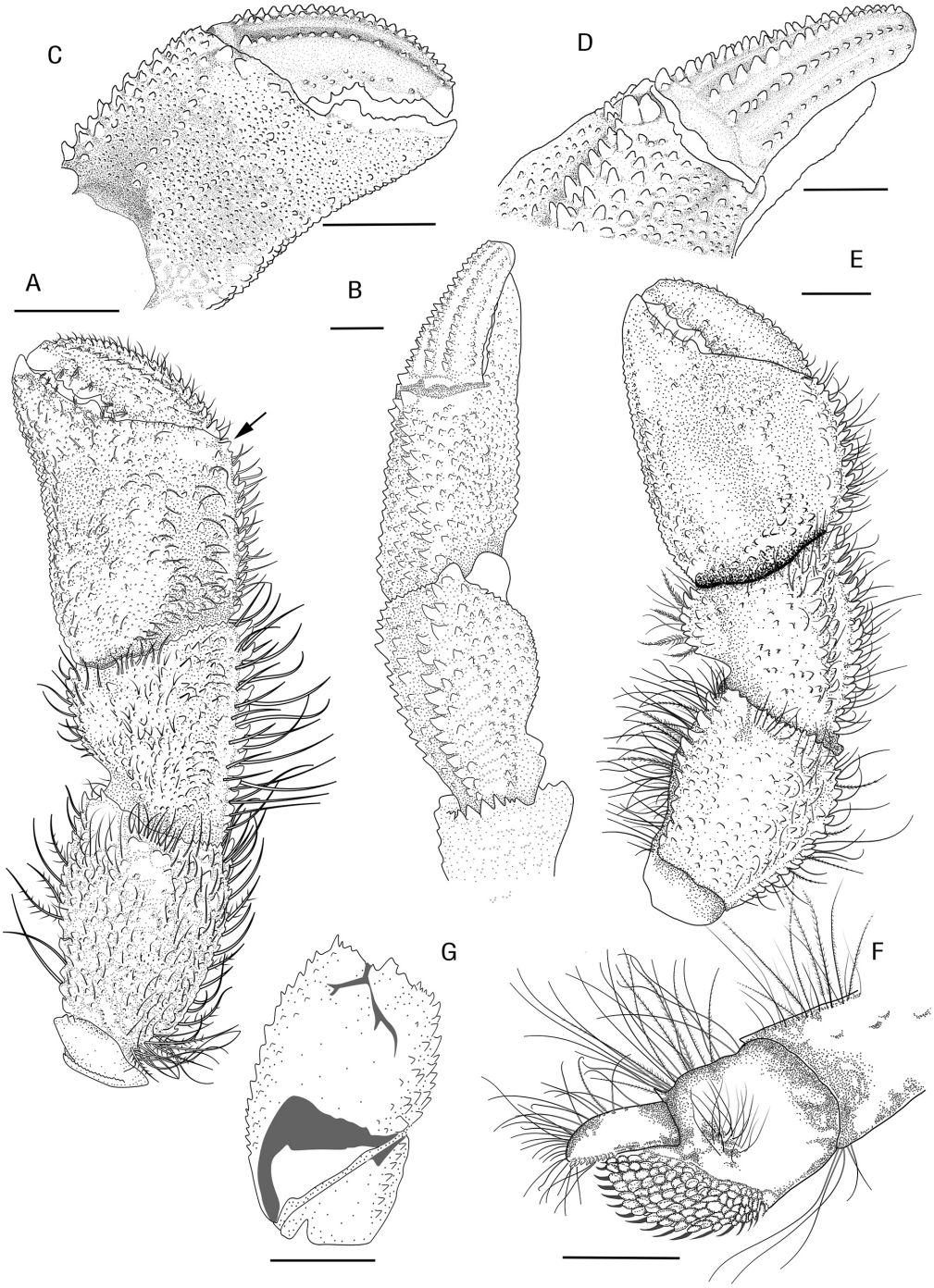

Figure 4. *Diogenes armatus* sp. nov. ♂ 3.4 mm, Torregorda, Cádiz, Spain, holotype, (MNHN-IU-2019-3213): A, male left cheliped, outer aspect (arrow indicating bispinose protuberance); B, left cheliped, dorsal aspect; C, left cheliped inner surface; D, left cheliped dactylus, dorsal aspect; F, left pereiopod 4, outer aspect; G, left cheliped merus, mesial view (setae omitted). *Diogenes armatus* sp. nov. ♀ 3.8 mm, Isla Canela, Huelva, Spain, allotype, (MNHN-IU-2014-5736): E, female left cheliped, outer aspect. (Scales: A, C, G = 2 mm; B, D, E = 1 mm; F = 0.5 mm).

distally, slightly less than five times longer than distal width, subequal in length to penultimate segment, with some isolated setae on dorsal surface and distal tuft; second segment unarmed, with tuft of plumose, short setae on dorsodistal margin; basal segment unarmed, except for the spinose, rounded, ventrodistal border.

Antennal peduncles (Fig. 3A) overreaching distal corneal margin by 0.5 length of fifth segment; fifth segment unarmed, with row of moderately long, stiff setae on ventrolateral surfaces, and tuft of short setae on distodorsal margin; fourth segment unarmed, with tufts of plumose setae on disto-inner and some scarce simple setae on disto-outer margins; additional tuft of plumose setae on ventrolateral inner margin; third segment unarmed; second segment distolateral outer process stout and acute, with subdistal smaller spine; smaller but strong spine on distomesial angle; plumose setae near both spines and ventral surfaces; first segment with distal margin crenulated; plumose, short setae present in lateral and ventral surfaces. **Antennal acicle** short, subtriangular, reaching slightly below distal margin of fourth peduncular segment, bearing a simple strong terminal spine plus three to four strong spines on mesial margin and tufts of plumose setae on both mesial and lateral margins. **Antennal flagellum** short and robust, noticeably setose; articles with paired, long, ventrolateral and shorter ventral paired setae; short paired ones also on dorsal and outer articles surface.

Third maxilliped (Fig. 3D) basis unarmed; ischium with *crista dentata* bearing three prominent (distal) and two smaller (proximal) spines; ischium and merus with rows of scarce setae on lateral margins; carpus, propodus and dactylus with dense tufts of thick, long setae in dorsodistal and dorsomedian margin, concealing part of the segments; exopod peduncle reaching one-third of endopod carpal length.

Male left cheliped (Figs 4A–D, G, 7B, H) much larger than right (Fig. 3E). **Dactylus** about 1.2 times as long as upper margin of palm, gently arched, ending in large calcareous claw, crossing tip of fixed finger; upper, outer margin defined by rows of well-developed spines, inner margin by row of acute tubercles; two additional rows of subacute tubercles below upper, outer margin, first one incomplete; conspicuous strong spine at beginning of first row, near joint of dactyl with palm; dorsal surface between rows concave; rest of outer surface flattened, covered of small subacute tubercles; cutting edge sinuous, with row of calcareous teeth of various size, largest at distal half of dactyl; lower margin with irregular row of blunt sunken tubercles and tufts of setae associated with most of tubercles; inner surface with an additional complete row of rounded tubercles, separated by a depression from tubercles of upper, inner margin; inner, lower surface with two irregular rows of smaller sunken tubercles parallel to cutting edge, with tufts of dense setae associated with each tubercle.

Fixed finger delimited proximoventrally by a shallow concavity separating the slightly convex outer surface of fixed finger and beginning of inflated palm surface; lower margin with two to three rows of small, rounded tubercles extending on to palm; a row of larger blunt sunken tubercles above this, another row parallel to cutting edge and a third medially, each with tufts of short, stout setae; rest of outer surface with small, blunt or subacute tubercles; cutting edge sinuous, with single row of various sized teeth, largest on proximal one-third; inner surface almost smooth except for three to four irregular rows of sunken tubercles, each with tufts of short dense setae.

Palm robust, about 1.2 as long as high (max. medial length – maximum height); upper margin shorter than carpus; dorsal surface with four to six irregular rows of spines, space between rows widening distally with less produced spines; spines on upper, outer margin stronger and more produced, decreasing in size towards upper, inner margin; outer surface strongly inflated in proximal half, with proximal border defined by a crest of subacute tubercles; distal, lower surface depressed, near fixed finger; upper, outer part (below upper, outer row of spines), markedly concave; distinct bispinose protuberance present at distal angle just below upper margin; lower margin sinuous, convex proximally and slightly concave at distal half, defined by closely spaced rows of obtuse, spinose tubercles; rest of palm outer surface covered with spines of different sizes, biggest forming four longitudinal rows, usually evident especially when some colour remains; marginal series of subacute tubercles on upper, proximal half, as extension of proximal crest; transverse row of small spines at distal part of palm; inner surface covered with scattered rounded tubercles, with several rows of bigger tubercles below upper, inner margin; two additional well-defined rows, first on upper half, running from proximal medial margin to upper, distal margin, ending in a blunt protuberance, and second on midline zone, extending to half length of palm; sometimes a third faint row on lower half, composed by scattered tubercles; lower, inner surface, with irregular rows of low tubercles; most of largest tubercles with tufts of short thick setae.

Carpus longer than high (Fig. 4A, B); dorsal margin with two to three irregular rows of spines; outermost row strongest; outer surface convex, covered with small spines becoming rounded tubercles near lower proximal area; row of stronger spines present on middle outer surface, largest near distal margin; broad almost smooth, concave area just below upper, outer and inner margins, becoming deeper and widening proximally; lower margin denticulate, gently protruded, forming a sinus proximally; disto-outer border dentate; pilosity abundant, with simple setae, except in lower, outer margin, where they are less abundant and plumose; inner surface covered with closely spaced, thick tubercles, and dense tufts of stiff, plumose setae; distal inner margin crenulated.

Merus longer than high (Fig. 4A, G), subtriangular in dorsal view; distal margin with spines of different

sizes, largest on dorsal area, with row of short setae; dorsal surface with rows of acute tubercles decreasing in size proximally and associated tufts of long, plumose setae; lateral surface with acute tubercles adjacent to dorsolateral margin and small spines near ventrolateral margin, with sparse setae associated with tubercles and spines; spinose transversal furrow subdistally, with short setae; rest of lateral surface smooth; ventrolateral margin denticulate, slightly concave in proximal half, with a row of strong acute tubercles increasing in size distally, accompanied by rows of plumose, long setae; mesial face with weakly calcified u-shaped patch, distally divided by shallow, transverse, unarmed furrow, with tufts of long setae; distal mesial part divided into dorsal and ventral lobes by median cleft; dorsal lobe with distal margin bearing spines of different sizes and tufts of medium-sized setae; ventral lobe with distoventral margin defined by large, acute tubercles, and dense tufts of long, plumose setae. **Ischium** with transversal row of small spines on distolateral margin and row of minute tubercles on proximal margin; mesial surface with longitudinal row of strong spines on ventral margin (Fig. 4G).

Female left cheliped (Fig. 4E) differs from male in the following features. **Palm** oval, globose, almost as long as high, with lower margin convex throughout, without sinuous, concave area of males. **Carpus** lower margin with pronounced smooth sinus at proximal half; distal half protruding in a rounded projection defined by large spines of similar sizes. **Merus** dorsal and ventrolateral margins defined by well-developed spines.

Right cheliped (Fig. 3E) appreciably shorter than left, robust, usually reaching proximal one-third of palm of left cheliped; dactylus and fixed finger with prominent hiatus, both terminating in small but strong calcareous claws. **Dactylus** (measured along mesial margin) slightly more than 2.0 times longer than palm, noticeably arched; upper, inner and outer margins defined by rows of small spines decreasing in size distally, with tufts of long setae arising from tubercles; outer surface with additional row of spines parallel to upper, outer margin with tufts of long setae; inner surface with two rows of tufts of long, stout setae, first on upper half and second near lower margin. **Palm** with outer surface not broadened, slightly flattened, with irregular rows of strong spines obscured by tufts of long setae, especially evident at midline and distal margin of propodus and fixed finger; upper, outer margin defined by row of strong spinose tubercles, inner margin not well defined; lower margin defined by row of small low acute tubercles; fixed finger not broadened proximally, cutting edge with row of small subacute calcareous teeth decreasing in size distally, and two rows of tufts of setae parallel to cutting edge.

Carpus with row of large spines on upper, outer margin, increasing in size distally, and an additional row of small acute tubercles below it defining a concave area between them; rest of outer surface with low tubercles arranged regularly and numerous long, simple and plumose setae; lower surface unarmed; disto-outer margin spinose; inner surface smooth and glabrous.

Merus distal margin with spines of different size, largest on dorsal area, with long, simple setae; dorsal margin with row of small, obtuse spines of similar size and tufts of long, plumose setae; lateral surface covered with low, rounded tubercles, with long setae; shallow furrow subdistally, with sparse setae; ventrolateral margin delimited by row of subacute tubercles, with subdistal spine and tufts of long, plumose setae; mesial face with small, weakly calcified, u-shaped patch proximally, smooth, with ventromesial margin defined by row of acute tubercles increasing in size proximally. **Ischium** with row of spinules on distolateral and ventromesial margins.

Second and third pereiopods stout (Figs 3F, 7K) subequal in length. **Dactylus** 1.4 times as long as propodus, weakly curved; terminating in small corneous claws; upper, outer surfaces unarmed, with sparse simple setae of different length; lower with row of more numerous, long setae; outer surface with shallow, longitudinal sulcus medially, with row of setae below sulcus in proximal one-fifth, then continuing along upper border of sulcus; inner surface with two rows of long, stout setae running along upper and lower margins, and a short row occupying proximal one-fifth of inner sulcus.

Propodus about same length as merus (second) or shorter (third), each with upper margin defined by rows of small spines (second), or faintly dentate (third), and with row of short to long stiff, simple setae combined with some plumose; lateral surfaces each with longitudinal row of setae arising from tiny, low, spinose tubercles near upper margin; lower margins smooth, with two rows of short setae; inner surface smooth and almost glabrous, with few sparse, plumose setae.

Carpus upper margin defined by rows of strong spines (second) or smaller spines (third) increasing in size distally, with rows of simple and plumose setae; lateral surfaces with two rows of low tubercles in the upper half, with moderately long setae; lower surface smooth except for three to four tufts of stout, plumose setae on distal half; inner surface smooth and almost glabrous.

Merus upper margin of second and third pereiopods defined by row of low, small, spinose tubercles decreasing in size distally, with tufts of long, plumose setae; lower margin of both pereiopods with row of low, spinose, small tubercles and long, simple and plumose setae; lower distal margin with a single spine (second) or without spines (third); rest of outer and inner surfaces smooth and glabrous. **Ischium** with

upper and lower distal margin serrated, with long, plumose setae.

Fourth pereiopods (Fig. 4F). **Dactyl** with row of 11 outer subacute submarginal spiniform setae. **Propodus** suboval, with a conspicuous spine dorsodistally and abundant plumose setae; propodal rasp consisting of seven to eight rows of corneous scales increasing in size distally, covering one-third of propodus distoventral surface. **Carpus** with a row of small tubercles dorsally, ending in a broad spine; with clumps of long, simple and plumose setae.

Fifth pereiopods. **Propodus** slightly shorter than merus, carpus 1.5 times shorter than propodus; groups of subacute corneous scales in distodorsal surface of propodus and smaller ones in dactylus and fixed finger; long clumps of strong simple setae.

Male unpaired left pleopods 2–5 uniramous, marginally setose. **Female gonopores** paired; two to four unpaired **pleopods**, well-developed, biramous; fifth pleopods without exopod, as in male.

Telson (Fig. 3G). Asymmetrical, with small, median cleft; left posterior lobe distinctly larger than right, with strong terminal spine and row of smaller spines on lateral margin, becoming blunt anteriorly; oblique terminal margin with strong spines mixed with some small ones; right posterior lobe with row of strong spines mixed with small ones on less oblique terminal margin, becoming blunt anteriorly and extending on to posterior half of lateral margin.

Coloration (Fig. 7B, E, H, K). Ocular peduncles reddish white, with brownish red, triangular stain covering around two-thirds of peduncle; eyeballs velvet black with honey yellow stippling. Ocular acicles orange proximally, turning greenish medially and white apically. Antennular background bluish; third segment and flagellum with diffuse orange patch mingled with background; second segment with dark brown dorsal stripe. Antennas translucent blue, going greenish at basal segments level; characteristic brown spot on antennal scale proximally. Merus and carpus of left cheliped greenish in background, with some diffuse tile red areas; brown transversal stripes on medial zone of merus, and base, medial and disto-inner areas of carpus. Palm greenish white, lighter than merus and carpus, with orange path in upper, proximal surface of dactylus, and some narrow ones following main spinose ridges; base of largest tubercles with orange taints; small, deep reddish-brown taints at mid-dorsal and apical area of palm. Right cheliped overall colour oil green, with white ventral area; brown spots on mid-dorsal area of the merus, mid-dorsal and basal area of carpus and more blurred one at apex of carpus, base of palm and basal area of fingers. Second and third pereiopods with general green colour in dorsal part, yellowish white ventrally; brown dorsolateral stripes in middle and apical areas of merus, basal and middle areas of carpus and propodus, and base of dactylus.

Habitat: Sandy beaches, intertidal, tide pools and shallow subtidal up to 25 m depth.

Distribution: Known, so far, from Mediterranean islands (Ibiza and Corsica), Tunisian coasts (La Goulette), Andalusian Mediterranean and Atlantic coasts (Cádiz, Huelva, Algeciras), South Portugal (Lagoa da Albufeira) and French Atlantic (Arcachon).

Remarks: Within the East Atlantic, only *Diogenes pugilator s.s.* shares some characters with the new species. However, there are several characters that can be used to separate them. The new species has a slightly longer than broader shield, the rostrum rounded but elevate and thickened, while in *D. pugilator* the shield is subquadrate and the rostrum is lower and broader, not thickened. Branchiostegites with 10–11 spines in *D. armatus*, while *D. pugilator* usually has eight to nine. The ocular acicles carry 11–12 spines in *D. armatus*, decreasing in size from the inner margin, while *D. pugilator* has three to four (sometimes five) large spines decreasing in size from inner margin, with the rest of anterior margin with 11–12 small blunt tubercles. The ocular peduncles are proportionally shorter in *D. pugilator* in relation to the antennae and antennulae, and the antennal acicle has one terminal spine and an additional five in *D. pugilator*, while only three to four in *D. armatus*; the acicle is also shorter in the new species, reaching well below distal margin of the fourth antennal segment. Shape and proportions of the left cheliped are also different, although the spination can be similar in many cases. In *D. pugilator*, spination is always less developed for the same shield length; palm is as long as high in *D. pugilator*, while in *D. armatus* it is longer than high and with a conspicuous concavity at distal half of lower margin; outer surface strongly and regularly inflated throughout in *D. pugilator*, while in *D. armatus* only the proximal half is elevated, more abruptly in the middle; inner surfaces of the palm and carpus are also inflated in *D. pugilator* when observed in dorsal view, while in *D. armatus*, those surfaces are flat, depressed. The right cheliped also differs between species, with the fixed finger proximally broadened in *D. pugilator* and small spines in upper margin of the carpus and palm outer surface, while *D. armatus* has several rows of strong spines, combined with smaller ones on the palm surface.

DIOGENES CURVIMANUS (CLÉMENT, 1874)

(FIGS 5A–E, 6A–G, 7C, F, I, L)

Pagurus curvimanus Clément, 1874: pl. III, fig. 1.
Diogenes pugilator - Forest & Guinot, 1956: 32, fig. 3.

Type material: *Neotype*: 1 ♂ 3.4 mm, **Spain:** Guadalquivir, Doñana National Park, Huelva, (MNHN-IU-2019-3214), 36°47′59.5″N, 6°23′27.3″W, sand, shallow sublitoral, 17 July 2018.

Topotypes: 1 ♂, 1 ♀, same data as neotype, (IEOCD-BR/2581-2582); 5 ♂ (IEOCD-BR/2585).

Other studied material: **Belgium**: Nieuwpoort-bad, 5 ♂ and 5♀ (IEOCD-BR/2611-2620), 51°09′08″N, 2°43′00″E, sand, intertidal, 29 September 2018; **French Atlantic**: Arcachon, 1 ♂ (IEOCD-BR/2621), 44°40′0.04″N, 1°10′34.5″E, sand, shallow sublitoral, 02 October 2018; **Spain**: Ribeira, Galicia, 1 ♂, 1 ♀ (ZSMA2019 0398-0399); 1 ♀ (IEOCD-BR/2603), 42°33′46.36″N, 8°59′15.07″W, sand, 4–5 m depth, 07 October 2017; Doñana N.P., Huelva, 2 ♂ (IEOCD-BR/2586), 36°48′13.6″N, 6°23′46.2″W, sand, intertidal, 09 September 2018; 2 ♂ (IEOCD-BR/2589,2595), 37°12′06.5″N, 7°01′37.0″W, sand, intertidal, 01 October 2020; 1 ♂, 1 ♀ (IEOCD-BR/2593-2594), 37°10′44.6″N, 7°20′37.3″W, sand, intertidal, 13 January 2020; 1 ♂ (IEOCD-BR/2592), 36°58′02.6″N, 6°30′32.2″W, sand, intertidal, 14 January 2020; 4 ♂ (IEOCD-BR/2587-88, 2591-91), 36°48′11.6″N, 6°23′39.3″W, sand, intertidal, 11 February 2020; Isla Canela, Huelva, 2 ♂, 1 ♀ (IEOCD-BR/2598-2600), 37°10′51.8″N, 7°20′15.3″W, sand, intertidal, 25 July 2014; Santibáñez, Cádiz, 3 ♂ (IEOCD-BR/2609-2610), 36°27′52.3″N, 6°15′21.4″W, sand, intertidal, 5 October 2015; 2 ♂ (IEOCD-BR/2605-2606), 15 October 2015; 2 ♂ (IEOCD-BR/2607-2608), 30 May 2018; Fuengirola, Málaga, 15 ♂, 7 ♀ (IEOCD-BR/2583-2584), 36°32′57.92″N, 4°36′30.89″W, sand, 4 m, 04 March 2014; La Carihuela beach, Torremolinos, Málaga, 3 ♂ (IEOCD-BR/2601-2602), 36°36′28.2″N, 4°30′13.6″W, sand, 2–4 m, 11 December 2019; Guadarranque, Algeciras, 1 ♂, 1 ♀ (IEOCD-BR/2696-2597), 36°10′49.7″N, 5°24′42.1″W, sand, 4m depth, 27 October 1995; San García, Algeciras, 1 ♂ (IEOCD-BR/2604), 36°06′17.5″N, 5°25′56.7″W, sand, 4m depth, 25 July 1996; Cabo Pino, Marbella, 1 ♂ (IEOCD-BR/2622), 36°29′05.6″N 4°45′00.4″W, intertidal, 28/04/2005.

Redescription: **Shield** (Figs 5A, 7F) slightly broader than long; rostral lobe broadly rounded, exceeded by lateral projections that are triangular, acutely pointed, with single spine at apex; anterior margins of shield between rostral lobe and lateral projections slightly concave; anterolateral margins sloping, slightly concave, smooth; anterolateral angles rounded, with a small spine and usually another smaller below; lateral margin straight or slightly convex; posterior margin truncate; dorsal surface not vaulted, smooth, with groups of paired setae, and lateral margins with few faint transverse tuberculate ridges extending on to lateral surface of shield. Branchiostegites with dorsal margin bearing row of small spines (up to 12). Posterolateral plates not well calcified, unarmed.

Ocular peduncles (including corneas) about 0.6 times as long as shield, moderately stout, slightly inflated in distal half; corneas not dilated, corneal diameter about 0.3 peduncular length; row of short, plumose setae over inner surface of the peduncles. **Ocular acicles** (Figs 5A, C) broad, subtriangular, concealing basal part of ocular peduncles, with slightly concave mesial margin; anterior margin sloping outwards, bearing 14–16 acute spines, decreasing in size towards outer margin, covering the entire length of the anterior margin; innermost distal spine distinctly larger. **Intercalary rostriform process** simple, shorter than ocular acicles (including spines), tapering acutely.

Antennular peduncles (Figs 5A, B) overreaching distal corneal margin by about 0.4–0.6 length of ultimate segment, not reaching distal margin of antennal peduncle; third segment short, unarmed, broadened distally, maximum length slightly more than three times distal width, subequal in length to penultimate segment, with a tuft of setae on distodorsal margin; second segment unarmed, with tufts of plumose setae on dorsodistal and ventrodistal margins; basal segment moderately broadened distally, unarmed, except for tiny spinules on rounded ventrodistal border.

Antennal peduncles (Fig. 5A) overreaching distal corneal margin by almost the entire fifth segment length (0.8–0.9); fifth segment with row of moderately short, stiff setae on ventral surface, and tuft of short setae dorsodistally, unarmed; fourth segment unarmed, with tuft of long setae on distomesial margin; third segment unarmed; second segment with distolateral outer process stout and acute, with subdistal smaller spine and sparse, short setae on lateral outer margin; distomesial spine usually small and obtuse but evident with associated tuft of long setae; mesial margin bearing some sparse, short setae; first segment unarmed. **Antennal acicle** short and broad, subtriangular, slightly overreaching the proximal half of fourth peduncular segment, not reaching distal margin, bearing a simple strong terminal spine plus usually six to seven spines almost equal in size along mesial margin, and tufts of setae on both mesial and lateral margins. **Antennal flagellum** short and robust, noticeably setose, with rows of paired setae in dorsolateral (short), ventral (medium) and ventrolateral (long) surfaces.

Third maxilliped (Fig. 5D) basis unarmed; ischium with *crista dentata* bearing one prominent distal spine and two smaller on distal half, with additional one to two spinules on proximal half; ischium and merus with rows of scarce setae on lateral margins;

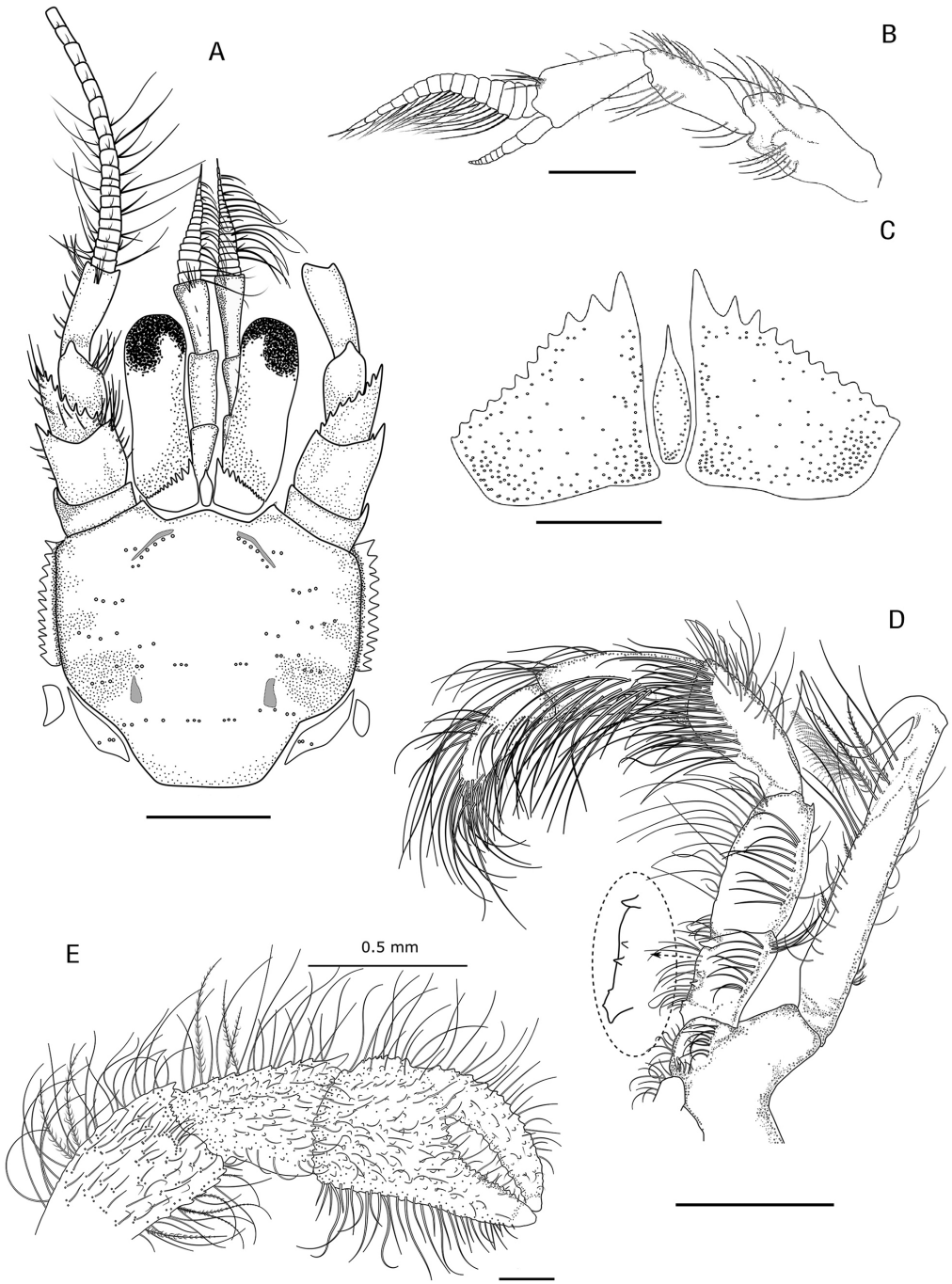

Figure 5. *Diogenes curvimanus.* ♂ 2.6 mm, Guadalquivir N.P., Huelva, Spain, neotype, (MNHN-IU-2019-3214): A, anterior part of body; B, right antennular, inner aspect; C, ophtalmic scales; D, maxiliped 3 (inset: detail of the spines, ventral aspect); E, right cheliped, outer aspect. (Scales: A = 1 mm, B = 0.2 mm, C–E = 0.5 mm).

carpus, propodus and dactylus with dense tufts of thick, long, simple and plumose setae at distolateral and distoventral margins, with less numerous long setae at distodorsal margin, concealing part of the segments; exopod peduncle reaching half carpal length of endopod.

Male left cheliped (Figs 6A, B, 7C, F, I) much larger than right (Fig. 5E); length and shape variable in males. **Dactylus** shorter than palm dorsal surface, slightly arched, ending in small but strong calcareous claw, crossing tip of fixed finger; upper, inner margins defined rows of small, obtuse tubercles, upper, outer

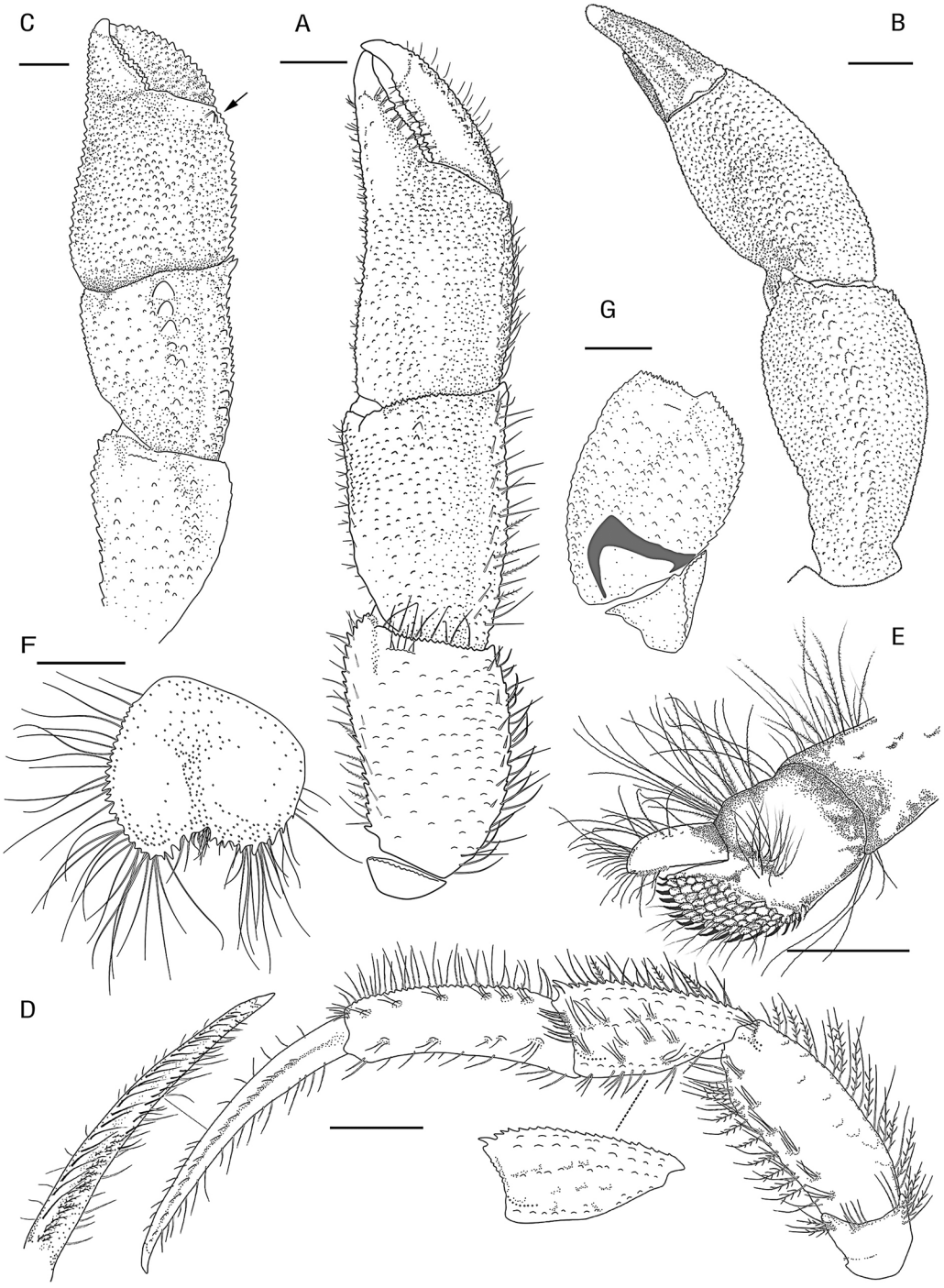

Figure 6. *Diogenes curvimanus*. ♂ 2.6 mm, Guadalquivir N.P., Huelva, Spain, neotype, (MNHN-IU-2019-3214): A, left cheliped, outer aspect; B, left cheliped, dorsal aspect; D, left pereiopod 2 (insets: variations in P3 carpus; dactylus inner aspect); E, left pereiopod 4, outer aspect; F, telson, dorsal aspect; G, merus, mesial view (setae omitted). *Diogenes curvimanus*. ♀ 2.9 mm, Ría de Arousa, Galicia, Spain (ZSMA2019 0399): C, Left cheliped, outer aspect (arrow indicating bispinose protuberance). (Scales: A–B, G = 1 mm; C, E–F = 0.5 mm; D = 2.0 mm).

by larger acute tubercles with associated sparse setae; dorsal surface between upper, outer and inner rows slightly concave; outer surface convex, not flattened, smooth; lower margin with tufts of stout, short setae; cutting edge almost straight, with row of teeth of similar sizes; inner surface with two rows of tubercles

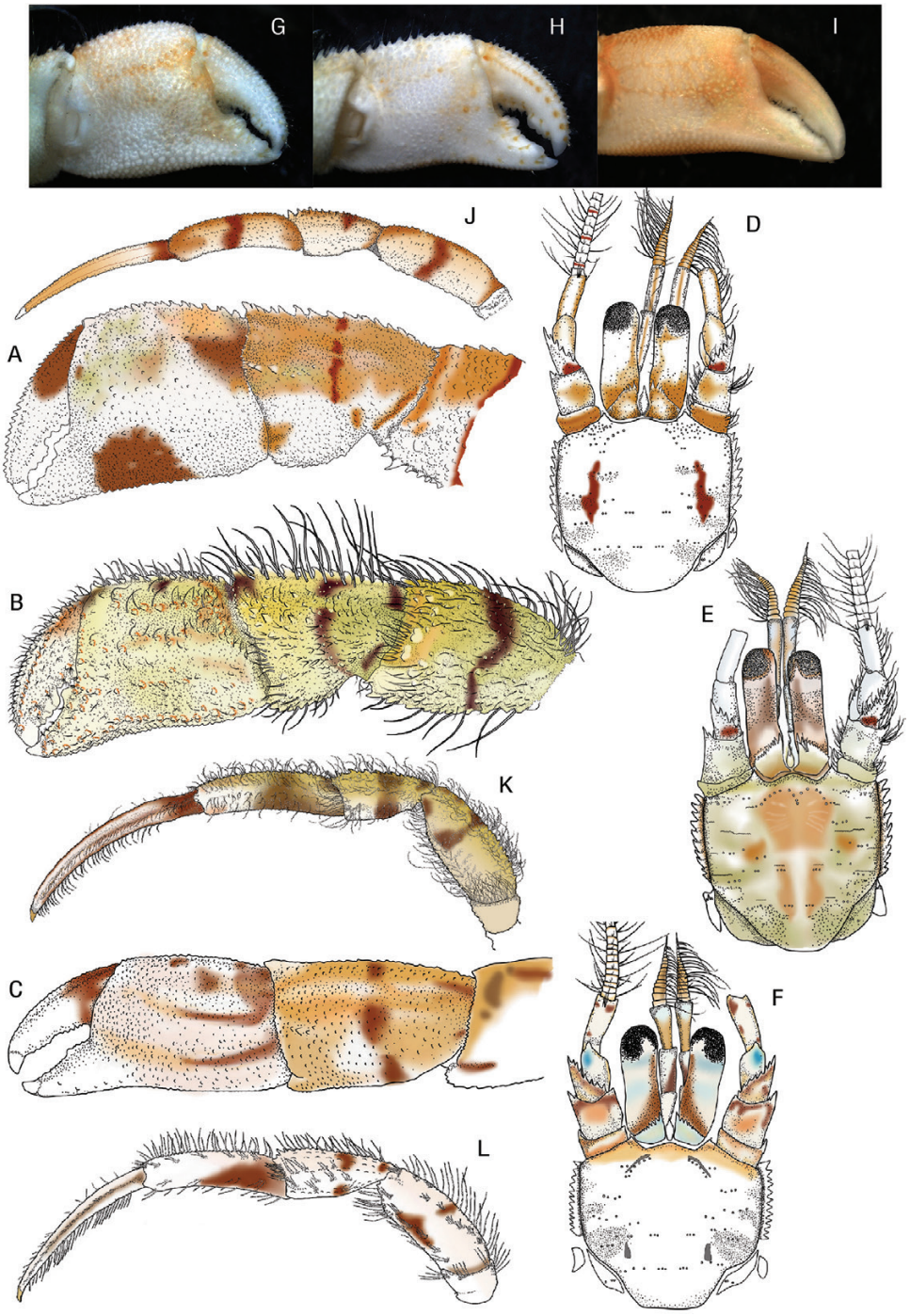

Figure 7. Live coloration of the three species of *Diogenes*: A–C, left cheliped, outer aspect; D–F, cephalothorax and cephalic appendages; G–I, detailed photographs of the inner face of palms, showing the shape of the row of tubercles; J–L, left pereiopod 2. A, D, G, J, *Diogenes pugilator*; B, E, H, K, *Diogenes armatus* sp. nov. C, F, I, L, *Diogenes curvimanus*.

running parallel to upper margin on upper half, reaching distal part of dactylus; proximal surface with small subacute to obtuse tubercles.

Fixed finger triangular, not proximally broadened and almost smooth, except for some sparse, small tubercles on outer surface and irregular row of low tubercles on lower margin; tufts of stout, short setae on upper margin; inner surface smooth, with tufts of short setae near cutting edge and lower, inner margin. **Palm** narrow, about 1.5 times as long as high (max. medial

length – max. height); upper margin shorter than carpus; dorsal surface of palm slightly convex, covered with evenly spaced obtuse tubercles and rows of short setae; upper, inner margin not well defined; upper, outer delineated by obtuse tubercles; outer surface glabrous, with upper part slightly concave, medially strongly and evenly convex, with numerous small, obtuse tubercles arranged as discernible longitudinal rows; lower palmar margin slightly concave in distal half, defined by row of large obtuse tubercles, and tufts of short setae; inner surface covered with low, rounded tubercles and sparse, short setae.

Carpus of males long, about as long as merus and twice as long as high (Fig. 6A, B); usually longer and higher than palm; dorsal surface broadened, with upper, inner margin indistinctly delineated by row of tubercles; upper, outer well defined by curved row of subacute to obtuse tubercles, increasing in size distally, with associated medium-sized setae; outer surface with upper part slightly concave, medially strongly and evenly convex with small, obtuse evenly distributed tubercles, largest near distomesial margin; distal margin serrated; lower margin defined by row of small, obtuse tubercles; lower margin straight in distal part, short and slightly concave proximally, with tufts of short setae; inner surface covered with low, rounded tubercles and tufts of short simple setae.

Merus longer than high (Fig. 6A, B, G); subovate in dorsal view; distal margin spinose throughout, with short setae; dorsal surface with small subacute tubercles of similar sizes and tufts of long, simple and plumose setae; lateral surface with evenly distributed rows of rounded tubercles, except on distal lower area; small and shallow transversal furrow subdistally on lower half, with sparse, short setae; ventrolateral margin denticulate accompanied by sparse medium-sized simple and plumose setae, slightly concave in proximal half, with larger subacute tubercle on proximal margin; mesial face with weakly calcified, u-shaped patch; subdistal transversal furrow short and faint, with small tubercles and short setae (Fig. 6G); dorsodistal margin with spines of similar size; ventrodistal margin defined by slightly larger spines with associated plumose setae. **Ischium** with row of small tubercles on distal margin (Fig. 6A) and row of slightly bigger tubercles on ventromesial margin (Fig. 6G).

Variability. Propodus of male varies from form described to one where lower margin is strongly concave, giving a sinuous appearance. **Carpus** can also show on occasion a row of well-developed rounded tubercles at distomedial part. This is especially common in females and young males with short chelipeds (the reduction in size of the tubercles seems to be quicker because of the faster grow rate of male cheliped).

Female left cheliped differs from male in the following features (Fig. 6C). **Dactyl** higher and shorter in proportion, with upper margin delineated by row of acute to subacute tubercles. **Palm** short and broad, slightly longer than high; outer surface covered in small, acute tubercles, with two prominent, acute tubercles distodorsally. **Carpus** relatively much shorter; upper, outer margin with two to three strong spines distally; outer medial surface with large, rounded tubercles increasing in size distally. **Merus** dorsal margin with larger, acute tubercles; lower margin defined by row of acute tubercles; lateral surface with subdistal transversal furrow more evident; mesial face with acute tubercles on ventral area and subdistal transversal furrow well defined.

Right cheliped (Fig. 5E). Much shorter than left, robust (reaching one-third of carpus in neotype); dactylus and fixed finger with prominent hiatus, both terminating in small but strong calcareous claws. **Dactylus** (measured along mesial margins) about 2.5 times as long as palm upper margin, noticeably arched; upper, inner and outer margins defined by row of subacute tubercles with associated long setae; dorsal surface convex, broad and tuberculate; outer surface strongly convex with row of subacute tubercles parallel to the upper, outer margin; rest of outer surface with sparse, small tubercles and short, simple setae; inner surface with row of tubercles below upper, inner margin, and associated long, plumose setae; lower, inner margin with sparse setae.

Palm with dorsal surface broad, short and convex; upper, outer and inner margins defined by row of subacute tubercles; outer surface broad, convex medially, with evenly spaced, subacute tubercles grading distally to acute tubercles; lower palmar margin defined by flat, setosed tubercles with long setae; fixed finger proximally broadened, outer surface slightly concave, with flat, setosed tubercles grading to acute near cutting edge; lower margin defined by flat, setosed tubercles; inner surface with low, rounded tubercles and long setae especially dense on fixed finger inner surface.

Carpus dorsal surface narrow throughout; upper, outer margin defined by longitudinal row of spines and short setae; upper, inner margin defined by row of subacute tubercles with long, simple and plumose setae; additional row of small tubercles below the upper, outer margin, delimiting a shallow concave area; rest of outer surface slightly convex with low tubercles and numerous tufts of long setae; lower surface nearly smooth with sparse, short setae; inner surface weakly tuberculated, with sparse, long, plumose setae.

Merus distodorsal margin with spinules and long setae; dorsal margin defined by row of small, obtuse spines and tufts of long, plumose setae; lateral surface covered

with low, rounded tubercles and sparse, short setae, giving an almost smooth appearance; shallow tuberculate furrow subdistally, bearing short setae; ventrolateral margin delimited by row of small spines decreasing in size proximally, and tufts of long, plumose setae; mesial face with small, weakly calcified, u-shaped patch proximally, smooth, with ventromesial margin defined by row of minute spines and long, plumose setae. **Ischium** crenulated on distolateral and ventromesial margins.

Second and third pereiopods slender (Figs 6D, 7L) subequal in length. **Dactyl** about 1.3 times as long as propodus, weakly curved; terminating in small corneous claw; upper and lower, outer margins unarmed, with rows of long thin setae, more numerous and longer on lower margin; outer surface with shallow, longitudinal sulcus medially, without setae in the proximal one-fifth, then continuing with sparse, short setae associated with sulcus; inner surface with two longitudinal rows of thin-spaced, long, stout setae adjacent to upper and lower margin, the proximal one-third with additional irregular rows of short, plumose setae placed over the sulcus.

Propodus slightly longer than merus in second and third pereiopods, with upper margin defined by row of small acute tubercles (second), or faintly dentate (third), covered with long, simple setae; two rows of small tubercles running parallel to upper and lower margins, with tufts of short setae associated with tubercles; lower margin smooth, with sparse, short setae.

Carpus upper margins defined by row of obtuse spines (second) or spinules (third), with dense, medium-sized, simple and plumose setae, ending in two (second) or one (third) conspicuous distal spines; rows of small, obtuse tubercles near outer upper, medial and lower surfaces with tufts of short setae in outer medial and lower surfaces; lower margin smooth with scarce short setae.

Meral length about three times the maximum width; upper margin defined by small tubercles (second and third), with sparse, long, plumose setae; lower margin defined by row of low, small, subacute tubercles (second and third), with poorly developed spinules on lower distal margin (second) or without distal spines (third), and dense rows of long, plumose setae. **Ischium** unarmed, with long, plumose setae on distal margin.

Fourth pereiopod (Fig. 6E). **Dactyl** with row of eight minute, spiniform setae on distal part of ventral margin. **Propodus** suboval, much longer than broad, with plumose, long setae along unarmed dorsal margin; propodal rasp consisting of five to six rows of corneous scales, covering distoventral part including fixed finger; rest of segments unarmed, with clumps of long, plumose setae.

Fifth pereiopods. **Propodus** slightly shorter than merus, and about 1.7 times longer than carpus; group of subacute corneous scales in distodorsal surface of propodus and smaller ones in dactylus and fixed finger; long clumps of strong simple setae.

Male unpaired left pleopods 2–5, uniramous, marginally setose. **Female gonopores**, paired; two to four unpaired **pleopods** well-developed, biramous; fifth pleopods without exopod, as in male.

Telson (Fig. 6F) with shallow, median cleft, slightly asymmetrical; left posterior lobe slightly larger than right, with small spines on lateral margin, becoming blunt tubercles anteriorly; oblique terminal margin with larger spines; right posterior lobe with row of spines on less oblique terminal margin, extending on to posterior half of lateral margin.

Coloration (Fig. 7C, F, I, L). Greyish white eye peduncles, with two diffuse bluish rings and a broader proximal brown triangular stain, projecting towards apex as a narrow line. Bluish ophthalmic scales. Whitish antennules, with triangular brown patch on second segment, orange in proximal two-thirds of third segment and flagellum. Antenna with greenish white or reddish peduncle, with scattered reddish brown streaks and conspicuous greenish blue spot on dorsal face of fourth segment. Carpus of the left cheliped with deep reddish orange background and an incomplete medial reddish brown ring. Orange coloured white hand with chestnut brown spot proximally, extending in two narrow lines towards middle outer surface; additional, more apparent, stain in proximal part of dactylus. Right cheliped with white background on merus and carpus, with some brown spots, and orange proximal carpal area; white palm with some brown spots in proximal upper area, which extends following central rows of tubercles. Second and third pereiopods with reddish white background colour; merus with reddish brown rings on middle (incomplete) and proximal areas. Carpus with an incomplete brown ring on medial area and small spot in the upper, proximal area. Propodus with large stain covering almost the entire proximal half, shorter in dorsal surface. Dactylus with a brown base that extends along the sulcus, sometimes faint and almost imperceptible.

Habitat: Sandy beaches, in tide pools and subtidal areas up to 15 m depth, with maximum abundances in the shallow subtidal, between 4–6 m.

Distribution: Described from French Mediterranean, although according to the samples examined in this work, it is the dominant species in Atlantic European waters. Despite the limited geographic range of the samples studied (covering the Atlantic coast of the Iberian Peninsula, France and Belgium), the abundance of images posted online suggest that its distribution could be wider, probably including most part of the southern North Sea. Its presence in the

Mediterranean, where there are at least two more species sharing part of its distribution, seems to be more reduced, currently with records in areas close to the strait of Gibraltar with strong influence of Atlantic waters (Málaga, Marbella, Algeciras) and Tunisia (see: Forest & Guinot, 1956: fig. 3; García Raso, pers. comm.).

Remarks: The specific name *D. curvimanus* is resurrected from Clément (1874), based on the striking consistency of his drawing with the here described species, including the characteristic shape of the left chela. Clément (1874) mentioned that this species occurs in the Gulf of Aigues-Mortes (French Mediterranean). However, all investigations carried out to locate the type of this species have been unsuccessful so far, bringing us to the conclusion that the type is most likely lost. Even if the mentioned locality raises some questions concerning the distribution range of the here described species, Clément's short description, and especially the specimen shown on the accompanying plate, leave no doubt about the identity of his specimen with the above described morphotype. Following a series of synonymizations affecting most of the European species of *Diogenes*, in consequence of their presumed morphological variability and wide distributions (Nöel, 2016), *D. curvimanus* became a junior synonym of *Diogenes pugilator* (Roux, 1829). Despite the doubts of Clément (1876), the identity of his drawing and our morphotype brought us to the decision to restore the validity of this species within the genus *Diogenes* and to propose a neotype to replace the missing type.

Diogenes curvimanus (Clément, 1874) can be easily differentiated from any other eastern Atlantic and western Mediterranean species of *Diogenes* by means of male left cheliped shape and size, which is slender and long, almost without pilosity and less spinose. The third antennular segment of the former is short and markedly broadened distally (shorter or equal than antennal peduncle), ocular scales serrated throughout and telson only slightly asymmetrical.

Female left chelipeds share some similarities with *D. pugilator s.s.*, but are less globose in *D. curvimanus*, with the distal part narrowing towards the tip and the palm not inflated; spination is also less developed in the latter, usually with mesial evenly distributed tubercles increasing in size distally.

Taxonomic remarks

Seven other species of *Diogenes* occur in the East Atlantic Ocean. All of them can be easily differentiated from the three species described above by the following characters.

Diogenes mercatoris Forest, 1952 has a short and reduced intercalary rostriform process, long ocular peduncles and a shield bearing strong spines on the laterodorsal surfaces. *Diogenes ortholepis* Forest, 1961 and *D. denticulatus* Chevreux & Bouvier, 1981 have a well-developed intercalary rostriform process bearing denticles, while this piece is always smooth in the three species described above. *Diogenes ovatus* Miers, 1881 is characterized by a large depression on the upper face of the chelar carpus, which is not present in any of the three species of the *D. pugilator* complex. *Diogenes brevirostris* Stimpson, 1858 and *D. extricatus* Stebbing, 1910 have only two to three spines on the posterior branchiostegite, while our three species have continuously serrate branchiostegites. The left cheliped of *D. costatus* Henderson, 1893 has an obliquely longitudinal ridge on the outer surface and the carpi of the pereiopods bear some scarce spines, never being continuously serrated. A confusion is furthermore unlikely, as *D. brevirostris*, *D. extricatus* and *D. costatus* have been exclusively recorded from Atlantic South African waters.

The form described by Forest (1956) from Accra in Ghana as *Diogenes* sp., although still not officially described (nor properly), is here included also for comparative purposes. This form has reduced corneas and ocular peduncles reaching behind the distal margin of antennal segment 4. There is also a conspicuous tooth on the disto-exterior upper margin of the left cheliped palm, which is not present in any of the three species described above.

Among the species recorded from the Indian Ocean coasts of South Africa, and that could possibly cross to the nearby Atlantic waters, only *D. albimanus* and *D. custos* seem to have currently valid records, while the presence of *D. senex* Heller, 1865 from Mozambican waters appears doubtful and still unconfirmed (McLaughlin & Dworschak, 2001).

Diogenes albimanus has short antennal acicles, not reaching to mid-length of the fourth antennal peduncular segment; it also shows a different armature of the left cheliped, lack of spines on propodus and merus of pereiopods, and even different coloration (Landschoff & Rahayu, 2018).

Diogenes custos has a spinose intercalary rostriform process (McLaughlin & Holthuis, 2001), and the ocular peduncles are in *D. senex* are longer than the antennal peduncles; also, the shape and ornamentation of the left cheliped is different.

The species considered here as new share some characters with a group of Indo-Pacific species included in the informal '*edwardsii*' group, defined by Asakura & Tachicawa (2010) by 'having simple intercalary rostral process, antennal peduncles longer than ocular peduncles and antennal flagellum with paired long setae in each article'. Two of these species (*D. pallescens* Whitelegge, 1897 and *D. avarus* Heller, 1865) have been recorded outside their original distribution area, reaching the Red Sea (McLaughlin, 2002; Siddiqui

et al., 2004; El-Wakeil *et al.*, 2009), which opens the possibility for further expansion to the Mediterranean Sea. The species *D. avarus* is characterized by the presence of six (five to eight) minute spinules on the margins of the branchiostegites, a male left cheliped carpus 1.6–1.7 longer than palm (dorsally), the dorsal margin of the P3 carpus often with a single row of smaller spinules (occasionally only a dorsodistal spine), a P2 carpus with one or two rows of small spines (occasionally only a cluster of small spines distally) and a left cheliped without a longitudinal ridge on the outer surface. Moreover, *D. pallescens* has long ocular peduncles, equal in length to the antennular peduncle, a dorsal surface of left P2 carpus without a row of spines, but only with two spines (dorsodistal and dorsoproximal).

Diogenes tirmiziae Siddiqui & McLaughlin, 2003, is currently known only from the Sindh coast of Pakistan and is easily recognizable by the short antennal peduncles, not reaching or slightly overreaching distal corneal margins and the subquadrate antennal acicles, reaching only to mid-length of fourth antennal segment, while in the species described above, acicles always overreach this length.

Like all other species of *Diogenes*, the three species included in this work show some morphological variation, especially of the left cheliped. This feature is more accentuated in *D. curvimanus*, where both the length and width of the male left cheliped can be markedly variable, probably produced by a markedly ontogenic allometry, although always conserving the unique morphological characters of the species, thus distinguishing it from the rest of the congeners.

Phylogenetic analyses

We analysed the phylogenetic relationships among five species of *Diogenes* in order to test whether they constitute genetically separate evolutionary units. Maximum likelihood analyses of the combined (Fig. 8A) and individual genes datasets (Supporting Information, Figs S1–S3) all yielded similar results, recovering the three putative species as monophyletic units, with relatively long branches and strong nodal supports (Fig. 8A). These three species are clustered together as a species complex, here referred to as the *D. pugilator* species complex, with strong support. Therefore, the DNA evidence agrees with separations based on morphological characters and live colour patterns and confirms the taxonomic delimitation of the species.

The partitions defined by the ABGD method (Puillandre *et al.*, 2012) are also congruent with the species delimitation obtained from the other methods. The groups recovered by the ABGD method (*COI*) were equivalent to those obtained from the concatenated dataset and have been included in the concatenated tree for illustrative purposes (Fig. 8A). For this species complex, the barcode gap seems to be between 0.05 and 0.12% divergence (Fig. 8B).

Results from individual gene analyses allowed us to obtain a general overview of the taxonomic status of the species complex, based on the sequences obtained from NCBI/BOLD databases (Supporting Information, Figs S1–S3). For the 16S gene, only nine sequences were available and none of them corresponds to species within the study area, while for the nuclear 28S gene, no sequence was available for species of this genus. However, the greater number and representatives of species among the sequences of the *COI* gene allowed us to draw some conclusions that agree with the preliminary geographical distribution of the different species arising from the examination of the samples included in this work. The specimens sequenced by Lobo *et al.* (2013) originating from the Portuguese coast, correspond without doubt to *D. armatus*, while the rest of the species collected from Atlantic European waters and labelled as *D. pugilator* correspond to the species described here as *D. curvimanus*, and should, therefore, be reviewed and renamed in the light of new information. None of the available sequences on the online databases matched those of *Diogenes pugilator s.s.*.

Key to the presently known Atlantic species of *Diogenes* Dana, 1851

Most studies of taxonomic significance dealing with the genus *Diogenes* in eastern Atlantic waters were published in the late-19th and mid-20th centuries, being frequently devoted to limited areas, as a result of surveys or specific collecting campaigns (Roux, 1829; Rossignol, 1962; Clément, 1874; Chevreux & Bouvier, 1892; Forest, 1955, 1956, 1961). Despite the fact that identification keys were included in some of these monographs (Barnard, 1950; Forest, 1956; Ingle, 1993), an effort to summarize current information, including the maximum number of species in the genus, appears useful in order to compare all the species and account for the changes implemented in the last decades. Hence, we present below an updated identification key, including all the species recorded so far from the eastern Atlantic.

CONCLUSIONS

Throughout the past two centuries, few researchers dealt with the delimitation of species included in the hermit crab genus *Diogenes* from Atlanto-Mediterranean waters. Their conclusions already

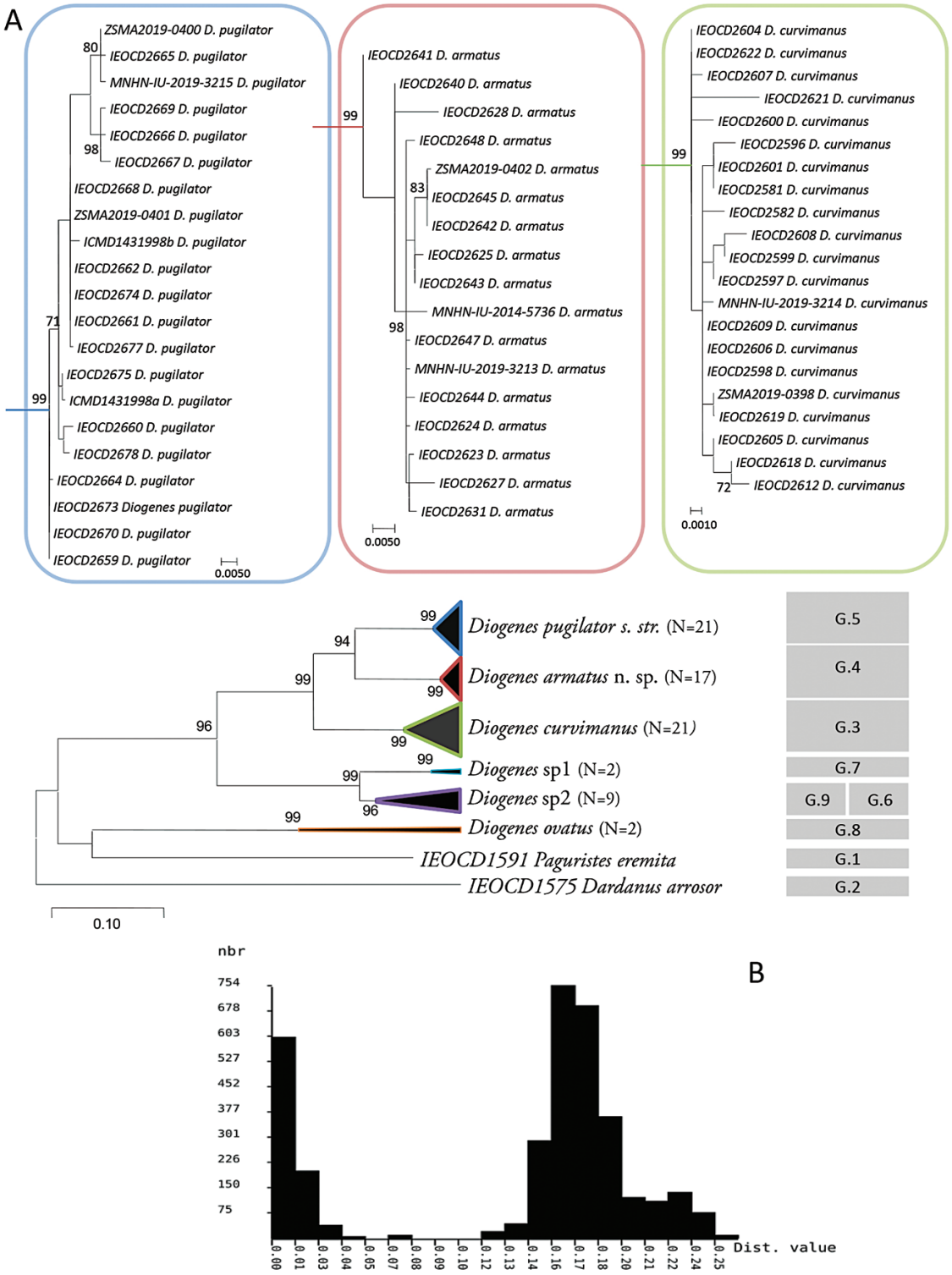

Figure 8. A, maximum likelihood phylogenetic tree based on the concatenated mitochondrial data (*COI* + 16S) using 1000 nonparametric bootstrap replicates. Numbers on the branches represent ML bootstrap values; only bootstrap values > 70 (ML) are included. The species *Dardanus arrosor* and *Paguristes eremita* are included as outgroups. Groups recovered from the ABGD analysis (G.1–G.9) are also included. B, histogram of genetic distances (JC69 Jukes–Cantor) showing the barcoding gap for the *COI* gene.

IDENTIFICATION KEY FOR THE SPECIES OF *DIOGENES* FROM THE EAST ATLANTIC OCEAN

1. Intercalary rostriform process between ocular acicles reduced. Shield with oblique rows of strong spines (see Forest, 1952: figs 1–5; Forest, 1955: fig. 14, pl. II, 8)..... *Diogenes mercatoris* Forest, 1952
1' Intercalary rostriform process between ocular acicles not reduced. Spines on shield not as above.....2
2. Intercalary rostriform between ocular acicles process spinose.....3
2' Intercalary rostriform process between ocular acicles smooth.....4
3. Ocular peduncles not overreaching base of fifth segment of antennal peduncles. Inner border of antennal acicle concave (see Forest, 1955: fig. 13, pl. II, fig. 7)..... *Diogenes denticulatus* Chevreux & Bouvier, 1892
3' Ocular peduncles long, overreaching base of fifth segment of antennal peduncle. Inner border of antennal acicle straight (see Forest, 1961: figs 1–4)..... *Diogenes ortholepis* Forest, 1961
4. Branchiostegites partially serrated.....5
4' Branchiostegites serrated throughout.....6
5. Upper surface of carpus of left chela convex, with irregularly arranged conical tubercles; no red spot on left chela. Wide ocular acicles (see Barnard 1950: figs 81a, c, d)..... *Diogenes brevirostris* Stimpson, 1858*
5' Upper surface of carpus of left chela flat, with two conspicuous rows of tubercles; one red spot on outer surface at propodus base of left chela. Narrow ocular acicles (see Barnard, 1950: fig. 81h)..... *Diogenes extricatus* Stebbing, 1910*
6. Palm of left cheliped oval, depressed; outer surface with depression at lower region. Carpus short, with deep depression on upper face (see Forest 1955: figs 15, 16; pl. II, 9)..... *Diogenes ovatus* Miers, 1881
6' Palm of left cheliped not oval. Carpus without depression on upper face.....7
7. Palm of male left cheliped clearly longer than wide, carpus frequently higher than palm; outer surface of palm finely granulate or smooth. Lower margin of carpus of left cheliped long and straight distally, slightly concave proximally. Antennular peduncle shorter than antennal peduncle, widened distally (Forest & Guinot, 1956: fig. 3; Figs 5, 6, 7C)..... *Diogenes curvimanus* Clément, 1874
7' Palm of male left cheliped not clearly longer than wide, carpus about the same height as palm; outer surface of palm with tubercles or spines, not smooth. Lower margin of carpus of left cheliped convex at distal half, forming a prominent sinus proximally. Antennular peduncle subequal or longer than antennal, not markedly widened distally.....8
8. Antennular and antennal peduncles subequal in length. Ocular acicles subtriangular, with three to five distal spines (innermost larger), rest of anterolateral outer margin with small tubercles of similar size. Outer surface of left cheliped palm medially inflated, covered with small spinose tubercles; lower, inner surface of palm defined by a sinuous crest-like row of large, rounded tubercles (Figs 1, 2, 7A, D)..... *Diogenes pugilator* Roux, 1829
8' Antennular peduncles longer than antennal ones. Ocular acicles with spines on the whole length of anterolateral margin, or few spines on distal half, without tubercles. Outer surface of left cheliped palm not medially inflated, with at least some larger tubercles or spines defining ridges; lower, inner surface of palm not defined by a sinuous crest-like row of large, rounded tubercles.....9
9. Ocular acicles subtriangular with 11–12 acute spines decreasing in size, innermost larger, covering entire length of anterolateral margin. Outer surface of male left cheliped palm spinose, with largest spines forming longitudinal rows. Left cheliped hirsute (Figs 3, 4, 7B, E)..... *Diogenes armatus* sp. nov.
9' Ocular acicles with minor dentition restricted to distal half of anterolateral margin. Outer surface of left cheliped palm almost smooth, with short, but prominent oblique granulated proximal ridge. Left cheliped glabrous (see Barnard, 1950: fig. 81e, f; Henderson 1893: pl. 39: 7, 8; Lewinsohn 1969: fig. 6)..... *Diogenes costatus* Henderson, 1893*

*Species with Atlantic records restricted to South African waters only.

The form *Diogenes* sp. mentioned in Forest (1956) is not included here, as it has not yet been formally described as a new species. Nevertheless, this form can be easily separated from the rest of the Atlantic species by the reduced corneas and ocular peduncles reaching behind distal margin of antennal segment 4. Forest also points out the presence of a conspicuous tooth on the disto-outer upper margin of the left cheliped palm.

pointed to the possibility of the existence of more than one species included under the name *Diogenes pugilator* (see: Costa, 1838; Bate, 1851; Capello, 1875; Miers, 1881; Bouvier, 1891; Balss, 1921; Codreanu & Balcesco, 1968). The general opinion was that they were dealing with an extremely variable species, given the difficulties for a single researcher to gather enough specimens from different localities for their study in order to account for and classify intraspecific variability and, furthermore, the absence of modern tools such as genetic analyses, which nowadays are invaluable to delimit relationships among individuals (Forest, 1955; McLaughlin *et al.*, 2010).

The present review agrees in part with early works and revalidates a previously synonymized species. The realization that at least three different species were until now included under the name *Diogenes pugilator* should be the starting point to undertake a more comprehensive review of these variations that were already described decades ago, which will surely result in more revalidations or description of several new species in the future.

In this study, the application of molecular tools, combined with traditional morphological analyses and the study of live colour patterns, has revealed the existence of three different species along the coasts of the Iberian Peninsula, previously hidden within the species *Diogenes pugilator*. As these findings are based on samples collected between 1982 and 2020, it reduces the possibility of a recent arrival from other areas, confirming that their distinctness had been masked by the alleged variability of the species.

In this study, we have established the basis for a better differentiation of the evolutionary independent units within the *Diogenes pugilator* species complex. In addition to re-describing *Diogenes pugilator* and the revalidated *D. curvimanus*, an additional species is here described as new. While reviewing specimens for this study, additional morphotypes were detected and identified in the phylogenetic trees as *Diogenes* sp. 1 and sp. 2, but these still need to be carefully studied and will be targeted in the near future; it is expected and predicted to lead to the description/revalidation of additional species, previously included in the *Diogenes pugilator* complex. Future studies including samples from a wider geographic area will thus allow a better delineation of the distribution limits of each of the species here described.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY

The data underlying this article are available in GenBank Nucleotide Database at [www.ncbi.nlm.nih.gov] and can be accessed with accession number.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. Maximum likelihood phylogenetic tree based on the 16S gene using 1000 nonparametric bootstrap replicates. Numbers on the branches represent ML bootstrap values; only bootstrap values > 70 (ML) are included. Type specimens indicated by an asterisk and *Dardanus arrosor* and *Paguristes eremita* are included as outgroups.
Figure S2. Maximum likelihood phylogenetic tree based on the *COI* gene using 1000 nonparametric bootstrap replicates. Numbers on the branches represent ML bootstrap values; only bootstrap values > 70 (ML) are included. Type specimens indicated by an asterisk and *Dardanus arrosor* and *Paguristes eremita* are included as outgroups.
Figure S3. Maximum likelihood phylogenetic tree based on the 28S gene using 1000 nonparametric bootstrap replicates. Numbers on the branches represent ML bootstrap values; only bootstrap values > 70 (ML) are included. Type specimens indicated by an asterisk and *Dardanus arrosor* is included as an outgroup.