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A new cryptic species of *Inachus* Weber, 1795 (Decapoda: Brachyura: Inachidae) from European waters and an updated identification key to the species of *Inachus* with two protogastric tubercles

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ABSTRACT

Integrative taxonomy studies have allowed us to clarify some taxonomic problems in cryptic species within species of *Inachus* Weber, 1795 with two protogastric tubercles found in European waters. Several morphotypes of *Inachus phalangium* (Fabricius, 1775) are recognized, and a new species is described from the Atlantic coast of the Iberian Peninsula, for which distribution data are provided. Furthermore, two *Inachus* cf. *thoracicus* specimens with a unique sternal morphology were collected from Málaga Spain, but their preservation in formaldehyde prevented molecular analyses. Specimens of *I. guentheri* (Miers, 1879) have been re-examined and the validity of previous reports from tropical and subtropical Atlantic waters is discussed. These results allow us to separate and clarify the status of species within this group. An identification key for *Inachus* species with two protogastric tubercles is also provided.

KEY WORDS: Crustacea, DNA barcoding, Mediterranean region, morphotypes, new species, species delimitation, taxonomy, Western Atlantic region

INTRODUCTION

The genus *Inachus* was described by Weber (1795), with the type species being *Cancer scorpio* Fabricius 1779, a subjective junior synonym of *Cancer dorsettensis* Pennant, 1777 by subsequent designation by H. Milne Edwards, 1834 (Guinot *et al.*, 2022). It is mainly distributed along eastern Atlantic waters and the Mediterranean Sea, with 10 out of the 13 known species (Ng *et al.*, 2008; WoRMS, 2022a) inhabit this region (Monod, 1956; Zariquiey Álvarez, 1968; Manning & Holthuis, 1981; D'Udekem d'Acoz, 1999). Species of *Inachus* can be grouped according to the number of protogastric tubercles on the carapace, with the following taxa showing only two: *I. aguiarii* Brito Capello, 1876 (Atlantic: Portugal, Madeira, Morocco, Sahara, Canary Islands, Mauritania, and Guinea; Mediterranean Sea), *I. biceps* Manning & Holthuis, 1981 (Atlantic: Senegal to Nigeria), *I. guentheri* (Miers, 1879) (Atlantic: Azores, Mauritania, Senegal to South Africa), *I. leptochirus* Leach, 1817 (Leach, 1815–1875) (Atlantic: Faroe Island, Norway, Denmark, UK, France, Spain, Morocco, Mauritania; Mediterranean Sea), *I. phalangium* (Fabricius, 1775) (Atlantic: Scandinavia, UK, North Sea, France, Spain, Portugal, Morocco, Sahara, Mauritania, Savage Islands, Canary Islands, Cabo Verde; Mediterranean Sea), and *I. thoracicus* Roux, 1830 (Roux, 1828–1830) (Atlantic: Portugal, Morocco, Sahara, Canary Islands to "Congo"; Mediterranean Sea).

The close similarity between the different species of *Inachus*, together with their relatively high morphological intraspecific variability, has caused significant taxonomic confusion, from synonymisation to the recognition of new taxa (see Monod, 1956; Manning & Holthuis, 1981). The present study aims to apply an integrative taxonomy approach to clarify the status of some morphotypes, particularly those belonging to the *I. phalangium* species group and those with flat rostral spines. A total

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of 35 specimens collected from Atlantic and Mediterranean waters are compared with type material, descriptions, and figures of all known species (Fabricius, 1775; Leach, 1814; Roux, 1828–1830; Brito Capello, 1876; Miers, 1879; Barnard, 1950; Monod, 1956; Zariquiey Álvarez, 1968; Griffin, 1974; Ingle, 1980; Kensley, 1981; Manning & Holthuis, 1981). Finally, an updated identification key is provided for all known *Inachus* with two protogastric tubercles from European waters.

MATERIAL AND METHODS

Morphological study

A general review of *Inachus* crabs with two protogastric tubercles has been undertaken, with special consideration to *I. phalangium*. We reviewed in detail the original description of *I. phalangium* by Fabricius (1775), type material currently deposited in the Zoological Museum of Kiel (ZMK), as well as a photograph of dry specimen NHMD-82400 (https://collections.snm.ku.dk/en/object/NHMD-82400), kept at the Natural History Museum of Denmark, University of Copenhagen (ZHMD). The type material of the Atlantic species *Inachus Dorynchus* Leach, 1814, deposited in the Natural History Museum of London (NHMUK), and descriptions of the Mediterranean *Cancer satuak* Herbst, 1782 (Herbst, 1782–1790) and *Macropus aracnides* Risso, 1816 (Herbst, 1782–1790; Risso, 1816), all three considered synonyms of *I. phalangium* (see WoRMS, 2022b), were carefully re-examined.

Thirty-five specimens of *Inachus* with two protogastric tubercles from Atlantic and Mediterranean waters were examined and used for molecular analyses (see below and Supplementary material Table S1), 23 belonging to *I. Phalangium*-like specimens. Specimens were collected from Anglesey (Wales, UK; coll. E. González-Ortegón), Normandy and Brittany (France; coll. C. d'Udekem d'Acoz), Galicia (Spain; coll. V. Urgorri and B. Almón), Gulf of Cadiz (Spain; collected by different members of the Instituto de Ciencias Marinas de Andalucía (ICMAN-CSIC) and deposited in the Crustacean Decapod Collection in the Cadiz Oceanographic Centre (IEO-CD), and Alboran Sea (Spain; colls. J.E. García-Raso and J.E. García Muñoz). We also examined specimens sent from the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium; Museo de Historia Natural, Universidade de Santiago de Compostela (MHN USC), Santiago de Compostela, Spain; Museu Municipal do Funchal (MMF), Madeira, Portugal; and National Museum of Natural History (USNM), NOAA/NMFS Systematics Laboratory Smithsonian Institution, Washington, DC, USA.

Photography and a *camera lucida* attached to a stereomicroscope Leika MZ12 (Leica Biosystems, Wetzlar, Germany) were used to illustrate the specimens. Measurements (in mm) were obtained for carapace length (including rostrum; CL) and maximum width (CW), using a *camera lucida* or calliper.

Molecular analyses

Total genomic DNA was extracted from muscle tissue following a modified Chelex 10% protocol by Estoup *et al.* (1996). Partial sequences of the mitochondrial large ribosomal subunit (16S rDNA) and cytochrome oxidase subunit I (COX1) genes were amplified through polymerase chain reaction (PCR) using the same primers as in Pérez-Miguel *et al.* (2019) and Genis-Armero *et al.* (2019). PCR products were sent to Stab-Vida laboratories to be purified and then bidirectionally sequenced. Sequences were edited using the software Chromas Lite version 2.6.4 (http://technelysium.com.au/wp/chromas/). Alignments for the new data and sequences available in BOLD (http://v3.boldsystems.org/) and GenBank (http://www.ncbi.nlm.nih.gov) (Supplementary material Table S1) were built using MAFFT (Katoh & Standley, 2013) with default parameters and concatenated using a custom PERL script. Before running phylogenetic analyses, the most suitable DNA substitution model was selected following the Bayesian information criterion (BIC) as implemented in MEGA X (Kumar *et al.*, 2018). The alignment and evolutionary model were then used to estimate the ML phylogenetic tree in RAxML (Stamatakis, 2014). Node support was evaluated with 1,000 bootstrap replicates. Matzen da Silva *et al.* (2011) obtained the frequency distribution of COX1 Kimura 2-Parameter (K2P) genetic distances at the intra-species (S), intra-genus (G), and intra-family (F) levels using 302 species, 154 genera, and 58 families of decapod crustaceans. To allow for comparison with these previous estimates, K2P genetic distances were also estimated from our COX1 dataset using MEGA X (Kumar *et al.*, 2018).

RESULTS

Molecular analyses

After sequence alignment and trimming, the final datasets included a total of 551bp (16S rDNA) and 603bp (COX1) respectively. The best model considered to describe the nucleotide substitution pattern of the concatenated alignment was the Hasegawa-Kishino-Yano model according to both the corrected Akaike information criterion (AICc) value (6446.13) and BIC score (7064.11). Nonuniformity of evolutionary rates among sites was modelled by using a discrete Gamma distribution (G = 0.10) with five rate categories. The tree with the highest log-likelihood is shown in Figure 1. The phylogenetic analyses of the new sequence data, combined with sequences obtained from GenBank, support our morphological observations. ML analyses show *Inachus gaditanus* **sp. nov.** to be sister clade to *I. phalangium*, but clearly distinct as reciprocally monophyletic clades. Samples of *I. aguiarii* from Atlantic waters and *I. thoracicus* from the Mediterranean also clustered together with high bootstrap support. Genetic distances (K2P) between *I. gaditanus* **sp. nov.** and *I. phalangium* (0.035 + 0.007) were twice as large as those between *I. thoracicus* and *I. aguiarii* (0.015 + 0.005). Furthermore, nucleotide differences in both 16S and COX1 genes resulted in reciprocally monophyletic clades with significant bootstrap support (> 70; Fig. 1) corresponding to specimens of *I. phalangium* from the English Channel (La Manche, France), Madeira and Alboran Sea.

Morphological analysis

Comparative morphological analyses of material from European Atlantic, Mediterranean Sea, and Madeira, together with the revision of type material (including synonyms) and

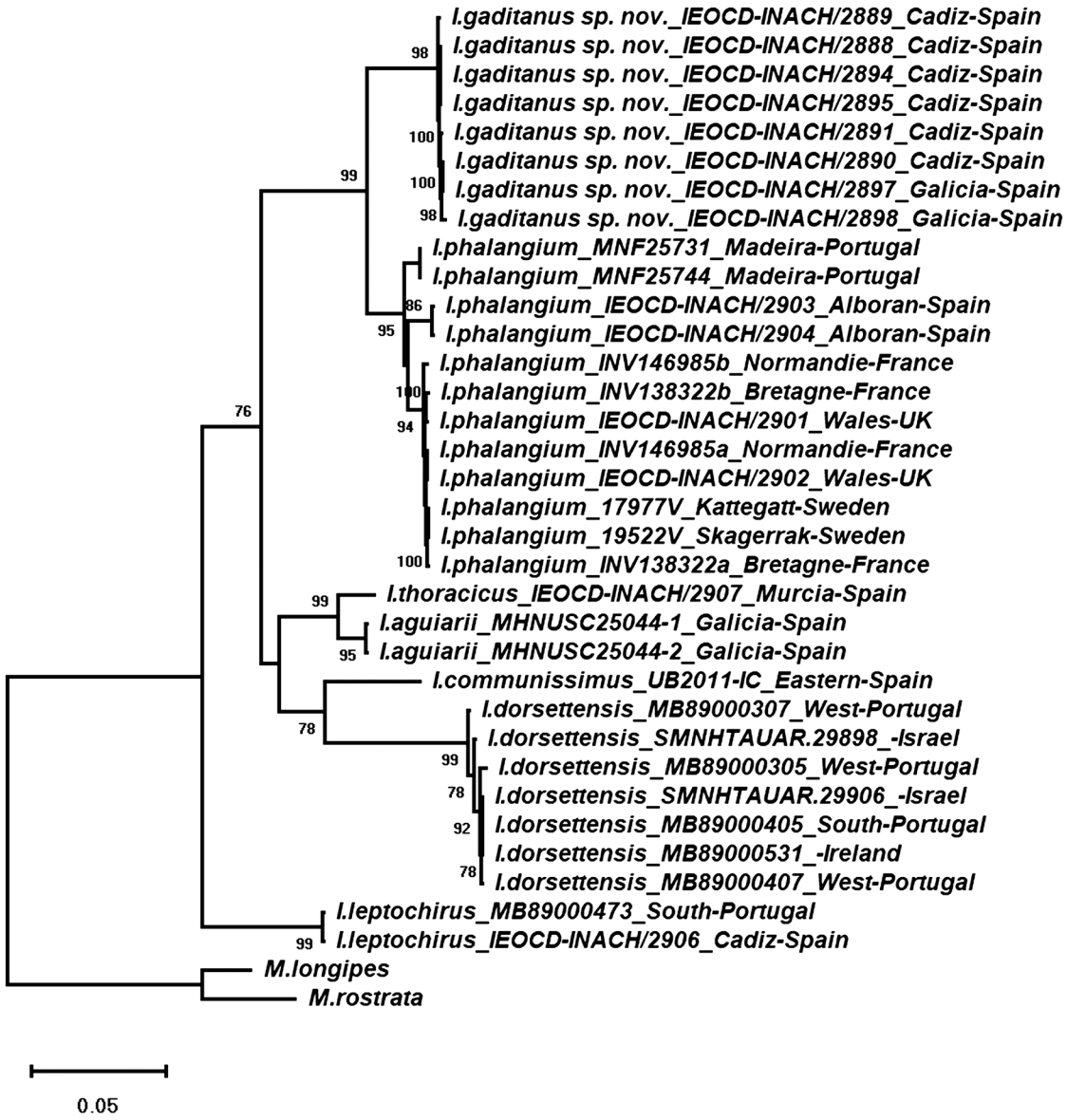

Figure 1. Inferred phylogenetic relationships of representatives of the genus *Inachus,* (with *Macropodia rostrata* and *M. longipes* as outgroups) obtained from the concatenated alignment of 16S and COX1 genes. Numbers close to nodes indicate bootstrap support (only values > 70% are shown). Details of samples in Supplementary material Table S1.

bibliography, allowed us to discriminate four morphogroups within the *Inachus Phalangium*-like specimens: Atlantic specimens from UK and France (group 1), Mediterranean specimens from Alboran (group 2), Atlantic specimens from Madeira (group 3), and Atlantic specimens from Galicia and Gulf of Cádiz (group 4). Molecular analyses (Fig. 1) and some morphological features show the fourth group (specimens from Galicia and Gulf of Cádiz) to be distinct from the others, corresponding to a cryptic species described in this study for the first time (*Inachus gaditanus* **sp. nov.**). Furthermore, two *Inachus thoracicus*-like females with a previously undescribed sternal morphology were collected from Malaga (Spain). Given that formaldehyde preservation prevented molecular analyses, only morphological evidence could be obtained for those specimens, and they are not described as a new species, pending the finding of fresh material.

Taxonomy

Infraorder Brachyura Latreille, 1802

Family Inachidae MacLeay, 1838.

Subfamily Inachinae MacLeay, 1838

Genus *Inachus* Weber, 1795

Inachus phalangium (Fabricius, 1775)

(Figs. 2–5)

Cancer Phalangium J.C. Fabricius, 1775: 408.

Cancer tribulus Linnaeus, 1767 (suppressed, ICZN Opinion 708; ICZN, 1964).

Inachus dorhynchus Leach, 1814 (incorrect spelling).

Inachus Dorynchus Leach, 1814 (junior synonym): 431.

Macropus aracnides Risso, 1816: 40?

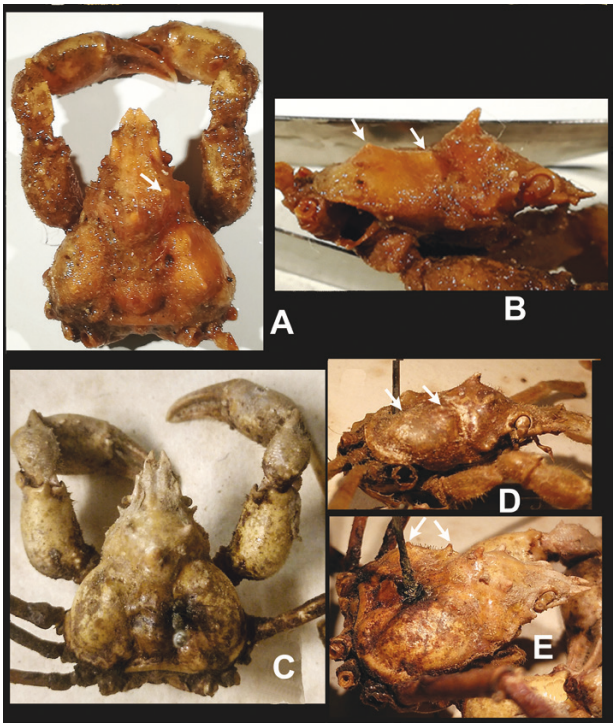

Figure 2. *Inachus phalangium* (Fabricius, 1775). Holotype NHMD-82400: dorsal view (arrow points a protogastric tubercle) (**A**); lateral view (arrows point the epibranchial and mesobranchial tubercles) (**B**). Specimens from the type series of *Inachus Dorynchus* in dorsal (**C**) and lateral (**D, E**) views (arrows point the epibranchial and mesobranchial tubercles).

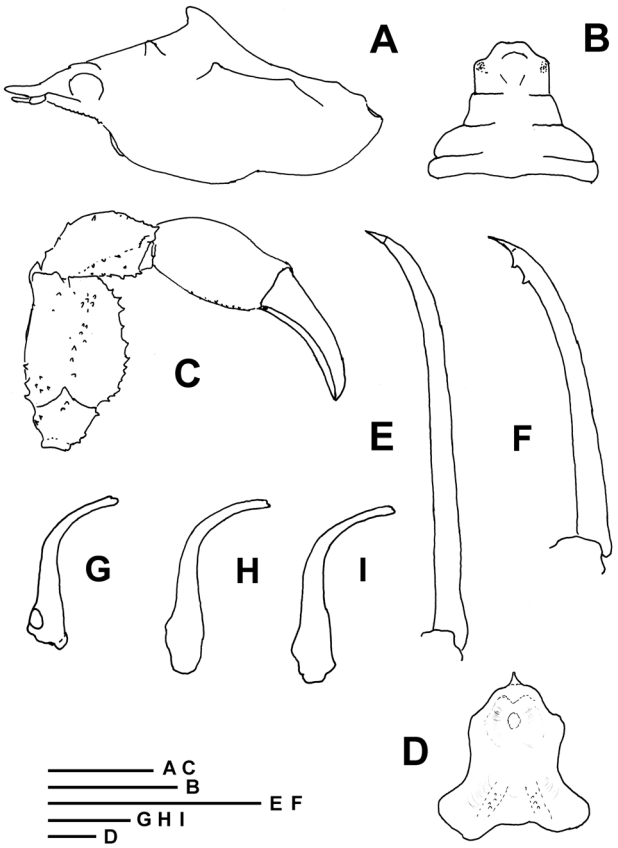

Figure 3. *Inachus phalangium* (Fabricius, 1775). Carapace in lateral view (**A**); male pleon (**B**); male left cheliped, upper view (**C**); sternum (**D**); dactyl of the second right pereiopod (**E**); dactyl of the fifth left pereiopod (**F**); first male gonopods (**G, H–I**). Male from North Wales (UK) (IEOCD-INACH/2901, 19.5 mm CL) (A, B, D–F); Male from North Wales (UK) (IEOCD-INACH/2902, 16.6 mm CL) (C); Males from the English Channel (La Manche, France) (G: INV146985a, 17.5 mm CL; H: INV13822b, 21.8 mm CL) (G, H); Male from Alboran Sea (IEOCD-INACH/2903, 18.6 CL) (I). Scale = 0.5 mm (A–C, E, F), 2 mm (D, G–I).

Material examined: Type material (Fig. 2): holotype of *Inachus phalangium* (Fabricius, 1775), no locality, 1 male, dry specimen, NHMD-82400, in alcohol at the ZMK. Type series of *Inachus Dorynchus* Leach, 1814, 5 dry specimens kept at the NHMUK and collected from Jersey, Devon, and Salcombe/Devon (United Kingdom).

Other material examined (Figs. 3–5): **United Kingdom**: 2 males (CL ×CW = 19.5 × 16.0 mm, 16.6 × 14.9 mm) (IEOCD-INACH/2901, IEOCD-INACH/2902), North Wales, Isle of Anglesey, 53°25'03.3"N 4°19'01.8"W, 12 m depth, November 2011, caught by traps for shrimp fishery, Genbank MZ401130-MZ401131 (16S); MZ400776 (COX1, second specimen); **France**: 2 males (19.8 × 16.9 mm, 21.9 × 18.6 mm) (RBINS IG33362-INV138322a, RBINS IG33362-INV138322b), Brittany, Île Callot, east side, 48°41'24.0"N 3°55'12.0"W, 22 March 2015, coll. C. d'Udekem d'Acoz, Genbank MZ707250-MZ707251 (16S), MZ707357-MZ707358 (COX1); 1 male and 1 ovigerous female (17.5 × 14.8 mm, 17.1 × 15.0 mm) (RBINS INV146985a, RBINS INV146985b), Normandy, St Vaast-la-Hougue, intertidal, 4 October 1994, coll. C. d'Udekem d'Acoz, Genbank MZ707252-MZ707253 (16S), MZ707359-MZ707360 (COX1); **Spain**: 2 males (18.6 × 16.6 mm, 14.9 × 12.0 mm) (IEOCD-INACH/2903, IEOCD-INACH/2904), Alboran Sea, Torrequebrada, Málaga, 6 m depth, August 1980, coll. J.E. García-Raso, Genbank MZ401132-MZ401133 (16S), MZ400777 (COX1, second specimen). Others specimens from Alboran Sea (coll. J.E. García-Raso): 2 males, Calahonda, Mijas, Málaga, 36°29'24.0"N 4°41'00.0"W, August 2006, 1 m depth; 1 ovigerous female, Los Escullos, Cabo de Gata, Almería, 25 June 1989, intertidal; 1 male and 1 female, Alboran Island, July 1983, 2–20 m depth; **Madeira (Portugal)**: 1 ovigerous female (12.5 × 11.0 mm) (MMF25731), P. Gorda, 17 December 1993, Genbank MZ707254 (16S), MZ707361 (COX1); 1 female (6.4 × 5.7 mm) (MMF 25744), Bahia do Funchal, Genbank MZ707255 (16S), MZ707362 (COX1).

Amended diagnosis: Species belongs to *Inachus* group with 2 protogastric tubercles; rostral spines flattened, wider at base; with epibranchial and mesobranchial tubercles (not spines); with an erect robust gastric spine (*I. phalangium, I. leptochirus, I. guentheri,* and *I. gaditanus* **sp. nov.**) It differs from all congeners by the development of epibranchial spine, which could be similar or little higher and protruding than mesobranchial ones (Atlantic) or slightly less protruding (Mediterranean); gastric spine leaning forward, with blunt apex (Atlantic) or straight and pointed (Mediterranean); rostrum flattened, wider at base, with outer distal margins convergent anteriorly, parallel inner edges with U-shaped, narrow central open region, sometimes in V-shape or with inner edges touching.

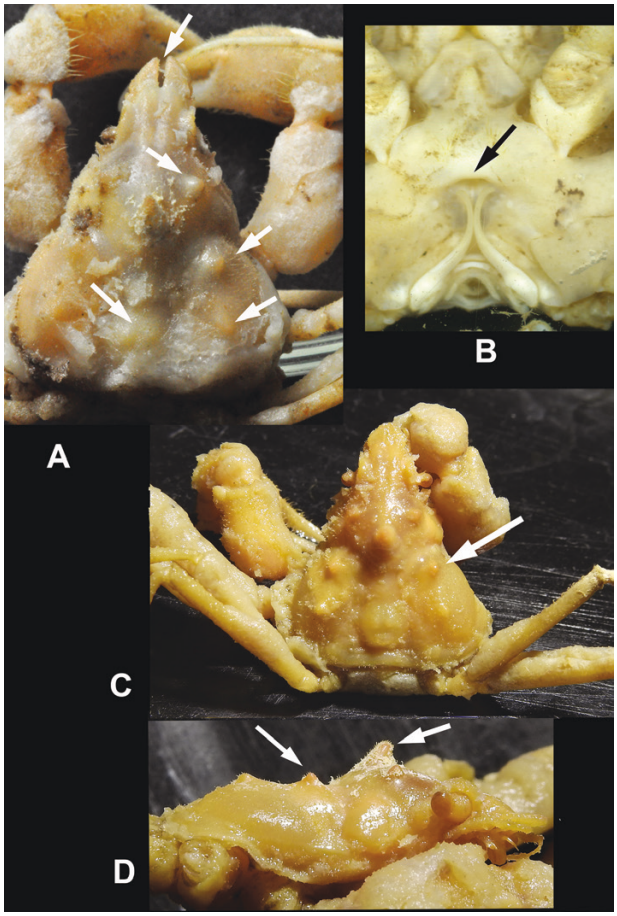

Figure 4. *Inachus phalangium* (Fabricius, 1775). Male from North Wales (UK) (IEOCD-INACH/2901, 19.5 mm CL): carapace in dorsal view (arrows show the rostral spines, the protogastric, epibranchial, mesobranchial, and the cardiac bilobed tubercles) (**A**); sternal region and first male pleopods (**B**). Male from St. Vaast-la-Hougue, Normandy, France (INV 146985a, 17.5 mm CL) in dorsal (**C**) and lateral (**D**) views (arrows point the epibranchial (C, D) and the gastric spine (D)).

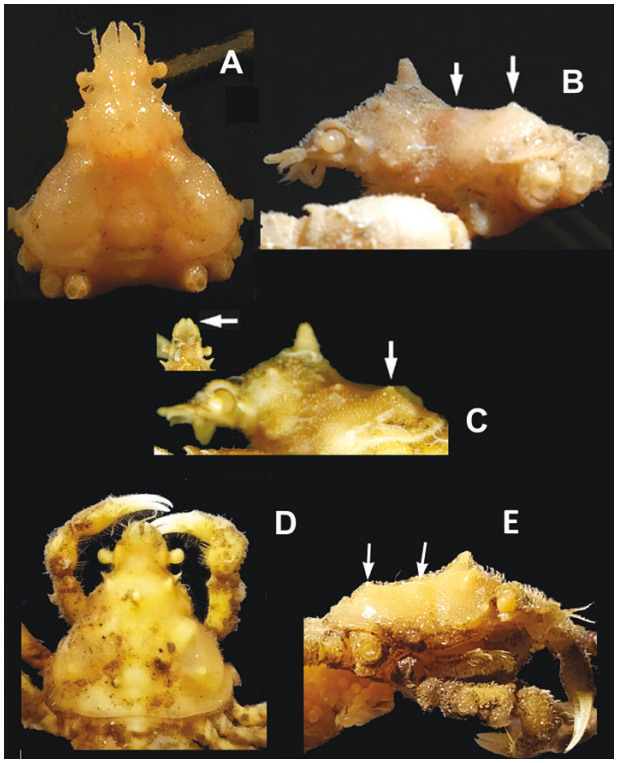

Figure 5. *Inachus phalangium* (Fabricius, 1775). Males from Alboran Sea (Málaga, Spain), dorsal and lateral views (**A, B**); rostrum (upper left corner) and carapace in lateral view (**C**). Female from Madeira (Portugal) (MNF25731, 12.5 mm CL), dorsal and lateral views (**D, E**). Arrows in B and E indicate the epibranchial and mesobranchial tubercles, C the rostrum and mesobranchial tubercle.

Redescription: Carapace (Figs. 2A–E, 3A, 4A, C, D, 5A–E) distinctly longer than broad, length/width: 1.1–1.2. Gastric region with 2 protogastric tubercles well developed, and gastric robust spine, inclined forwards. Each branchial region with well-developed epibranchial and mesobranchial tubercles (not spines), epibranchial could be similar or little higher and protruding than mesobranchial ones (Figs. 2D, E, 3A, 4A, C, D; UK and French specimens) or less protruding (Figs. 5B, C; Mediterranean specimens); without metabranchial tubercle (only slight protrusion). Cardiac region with low tubercle, bilobed in transversal view (Figs. 4A, C) followed by another smaller (simple or bilobed) tubercle. This region is more protruding than the mesobranchial tubercles in females. Hepatic regions slightly swollen, each with some small lateral tubercles. Rostrum flattened, wider at base, with outer distal margins convergent anteriorly, parallel inner edges, with U-shaped, narrow central open region (Figs. 4A, 5A), sometimes V-shaped (Figs. 2A, C, 5D) or with the inner edges touching (Fig. 5C). Inter-antennular triangular lobe not projected anteriorly, not visible in dorsal view between rostral teeth. Basal antennal segment with double row of tubercles and spines (lateral and mesial) exceeding half, or all, the segment length; lateral basal tubercles are largest. Eyes large, not extending laterally beyond prominent postorbital spine, with intracorneal setose tubercle. Orbital border without spines, smooth, with short erect setae. Posterolateral border of carapace continuous with free epimeral margin. Epistome with 2, 3 large tubercles anterolateral to urinary pore. Chelipeds subequal with propodus enlarged in males, ~0.74–0.79× CL (Figs. 2A, C, 3C). Merus and propodus markedly inflated, former longer than propodus. Inner side of merus and carpus with spines mainly arranged in rows on upper and lower margins, with other small spines scattered on upper side. Fingers curved, as long as palm. Dactylus of chela with dentate cutting edge (as in fixed finger), with 2 proximal rounded teeth. Second pereiopod (right) robust and longest (P2 > P3 > P4 > P5), 2.4–2.8× longer than CL. Merus and propodus with similar length (m/p = 1.0–1.1), both shorter than CL (0.7–0.8×respectively). Dactylus straight but curved distally (Fig. 3E), longer than others (d2 > d3 > d4 ≈ d5), without subdistal spines, slightly shorter than propodus (0.8-0.9). Third pereiopod 1.9–2.2× longer than CL. Merus subequal to that of P2, but longer than those of P4 and P5, slightly longer than propodus P3 (1.0–1.3×). Dactylus with subdistal spine. Fourth pereiopod 2.2× longer than CL. Merus shorter than carapace (0.6–0.7). Dactylus straight, with similar length to that of P5, shorter than propodus (0.66–0.7), with 2 subdistal ventral spines (sometimes one). Fifth pereiopod shortest, 1.6–1.8× longer than CL. Merus shorter than carapace (0.5–0.6). Dactylus straight, curved distally, shorter than propodus (0.5–0.76) and with 2 subdistal ventral spines (Fig.

3F). P5 dactylus reaches or overreaching half the length of P4 dactyl. Male sternum (Fig. 3D) with well-developed anterior tubercle and 2 divergent lateral-posterior tuberculate elevations. Male pleon with telson truncated distally (Fig. 3B). First male pleopod curved as Figs. 3G–I, 4B.

Habitat: Collected on rocky intertidal bottoms at up to 12 m in depth; some specimens were covered with sponges. Association with sponges, which can cover the entire carapace, is frequent and well known in the northern Atlantic (e.g. in French specimens from the English Channel (La Manche); C. d'Udeken d'Acoz, personal communication). It appears that North Atlantic and Madeira specimens are mainly living in association with sponges (Wirtz, 1997), whereas this association is rare or less frequent in the Mediterranean (Martinelli *et al.*, 2006 in the Adriatic). *Inachus phalangium* is found associated with anemones, *Anemonia sulcata* (Pennant, 1777) or *A. viridis* (Forskål, 1775) in shallow Alboran Sea waters and no specimens with significant sponge coverage on the carapace have been found. This association with anemones was also mentioned in Banyuls-sur-Mer, southern France (also occasionally on *Aiptasia mutabilis* (Gravenhorst, 1831)) with or without sponges on the carapace (Wirtz & Diesel, 1983)), Adriatic Sea, Croatia (Weinbauer *et al.*, 1982; Landmann *et al.*, 2016), Turkey (Ďuriš *et al.*, 2013), and under the anemone *Telmatactis cricoides* (Duchassaing, 1850) in Madeira (Wirtz, 1997). Sometimes crabs could be caught free, with the movement mentioned by Wirtz & Diesel (1983).

Distribution: Previously cited from Norway to Cape Verde Islands, and Mediterranean Sea (Christiansen, 1969; Manning & Holthuis, 1981; Fransen & Wirtz, 1997, Ďuriš *et al.*, 2013; González, 2018). Additional localities based on new specimens and those from Genbank used for molecular analyses include Sweden (according to COX1 sequences MG934962 and MG935059), United Kingdom (Wales), France (English Channel (La Manche), Roscoff), Madeira, and Alboran Sea (Málaga and Almería, Spain).

Remarks: Specimens from the English Channel (La Manche, France), Madeira and Alboran Sea show significant molecular variation but weak morphological differences. The specimens from the English Channel (typically identified as *I. dorynchus*) present well-developed epibranchial tubercles, similar or more protruding than the mesobranchial ones (Figs. 2D, E, 3A, 4A, C, D). This is in contrast to what may be observed in *I. phalangium* specimens from the Alboran Sea and Madeira (even in the type of *I. phalangium*), which are, in general, less developed, and less protruding (Figs. 5B, C). The two Madeira specimens examined (Fig. 5D, E), which resemble those from Alboran by the development of epibranchial and mesobranchial tubercles, are differentiated by their more developed and pointed (spine) protogastric tubercles. C. d'Udekem d'Acoz stated (in Araújo & Wirtz, 2015: 213) that "it is not ruled out that the Madeiran (and Azorean) populations belong to a separate species." Other morphological structures, which are sometimes variable, include: 1) the gastric spine, which is robust and leans forward in the type specimen (Fig. 2B), specimens from UK and the English Channel (La Manche), France (Figs. 2D, E, 3A, 4D), and Madeira (Fig. 5E). Alboran Sea specimens have a gastric spine generally straighter (front view) and pointed upwards (Figs. 5B, C); 2) the rostral spines are, apparently, more separated (open central region more divergent) in the type, in some UK (English Channel) and France specimens and in the Madeira ones (Figs. 2A, C, 5D) compared with specimens from the Alboran Sea (Figs. 5A, C); 3) the first male gonopods are, in our specimens, curved distally (Figs. 3G–I, 4B) like those of *I. thoracicus* (Monod, 1956: fig. 735), but different to those of *I. guentheri* (Barnard, 1950: fig. 5c) and *I. gaditanus* **sp. nov.** (Fig. 7E). Morphological differences among the North Atlantic, Alboran, and Madeira specimens show variability and overlap, and molecular divergences are not large enough to be considered different species (Fig. 1; see below).

Inachus gaditanus sp. nov.

(Figs. 6, 7)

Type material: Holotype: **Spain**: 1 male (13.7 × 11.9 mm) (IEOCD-INACH/2888), La Caleta, Cádiz, 10 February 2016, intertidal, associated with *Anemonia viridis*, coll. M. Rodríguez, Genbank MZ401122 (16S), MZ400770 (COX1). Paratypes: **Spain**: 1 ovigerous female (14.7 × 13.5 mm) (IEOCD-INACH/2889), La Garita (off Cortadura Beach), Cádiz, 31 August 2019, 8 m depth, captured by diving, coll. A. Moreno, Genbank MZ401123 (16S); 1 ovigerous female (14.0 × 12.9 mm) (IEOCD-INACH/2890), 20 February 2015, Genbank MZ401124 (16S), MZ400771 (COX1), 1 female (11.5 × 11.0 mm) (IEOCD-INACH/2891), 23 February 2014, Genbank MZ401125 (16S), MZ400772 (COX1),1 female with *Sacculina* sp. (15.8 × 14.0 mm) (IEOCD-INACH/2892), 9 February 2016, and 1 ovigerous female (15.7 × 13.9 mm) (IEOCD-INACH/2893), 9 February 2016, Castillo de Santa Catalina, La Caleta, Cádiz), intertidal, associated with *Anemonia viridis,* coll. M. Rodríguez; 1 female (8.6 × 7.9 mm) (IEOCD-INACH/2894), Sancti Petri, Cádiz, 18 July 1997, intertidal, associated with *Anemonia viridis,* Genbank MZ401126 (16S) and MZ400773 (COX1); 1 female (7.5 × 7.8 mm) (IEOCD-INACH/2895), 29 August 1995, Genbank MZ401127 (16S), and 1 ovigerous female (14.4 × 13.9 mm) (IEOCD-INACH/2896), 24 April 1996, inner Cádiz Bay.

Other material: **Spain**: 2 males (23 × 21, 16 × 14 mm) (IEOCD-INACH/2897-2898), Ria de Arousa, Riveira, Galicia, 23 May 2019, coll. B. Almón, Genbank MZ401128-MZ401129 (16S), MZ400774-MZ400775 (COX1); 2 males (19.5 × 17.6, 22.8 × 20.9 mm) (MHN USC) Ría de Arousa, Galicia, 7 January 1984, coll. V. Urgorri.

Diagnosis: Inachus species with two protogastric tubercles, rostrum or rostral spines flattened, wider at base, with epibranchial and mesobranchial tubercles (not spines), erect robust gastric spine (as in *I. phalangium*, *I. leptochirus* and *I. guentheri*). *Inachus gaditanus* **sp. nov.** can be distinguished by the poorly developed protogastric and epibranchial tubercles (both less protruding than those of *I. phalangium*); gastric spine leaning forward and with blunt apex (as in some Atlantic specimens of *I. phalangium*). Rostrum like *I. phalangium* in large specimens, but with parallel outer basal side edges and rounded distal margins touching in the midline, leaving rounded central space in small specimens.

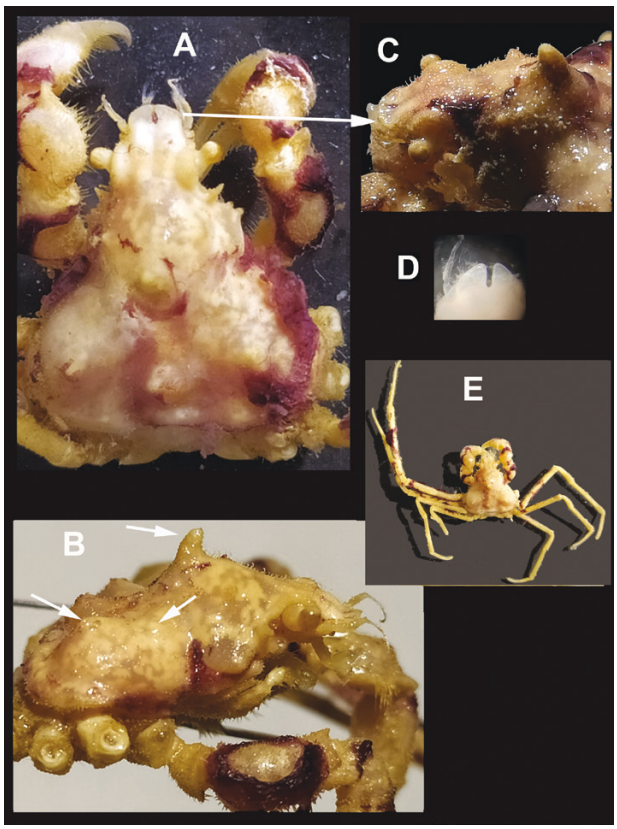

Figure 6. *Inachus gaditanus* **sp. nov.** Holotype male (IEOCD-INACH/2888, 13.7 mm CL): dorsal view of carapace (**A**); lateral view of carapace (**B**); detail of anterolateral view of carapace (**C**), and general view (**E**). Female (IEOCD-INACH/2889, 14.7 mm CL), detail of the rostrum (**D**), both from La Caleta, Cádiz, Spain. Arrows in B point the gastric spine and the epibranchial and mesobranchial tubercles.

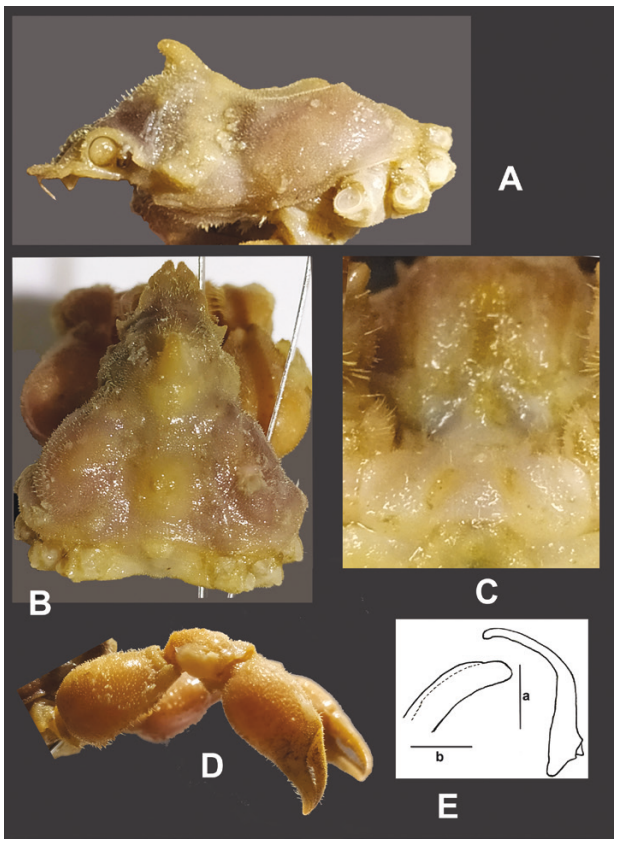

Figure 7. *Inachus gaditanus* **sp. nov.** Large male specimen from Galicia, Spain (IEOCD-INACH/2897, 20.3 mm CL): carapace in lateral view (**A**); carapace in dorsal view (**B**); sternal region (**C**); first pereiopods (**D**); first pleopod (**E**) (a, ventral view, scale = 5 mm; b, detail of distal part, scale = 2 mm).

Description: Carapace (Figs. 6, 7) longer than broad, length/width: 1.05–1.15. Gastric region with 2 protogastric tubercles anterior to robust gastric spine leaning forward and with blunt apex (Figs. 6B, C) particularly evident in large specimens from Galicia (Fig. 7A). Epibranchial tubercles (not spines) poorly developed (slightly more marked in large specimens from Galicia), mesobranchial tubercles well developed (Figs. 6A, B, 7A). Small metabranchial tubercles present. Cardiac region well developed, with bilobed tubercle (in transverse view) followed by smaller tubercle, more protruding than the mesobranchial tubercles (in females) or practically similar (in males). Hepatic regions slightly swollen with 2 lateral tubercles each. Rostral spines flattened, short, with parallel outer basal side edges and rounded distal margins touching in midline, leaving rounded central space (Figs. 6A, C); or the distal parts projecting, with outer distal margins converging anteriorly leaving an open U-shaped (Fig. 6D) or V-shaped (Fig. 7B) central region. Rostrum reaches or just exceeds the distal part of the antennal peduncle. Inter-antennular triangular lobe not projected anteriorly, not visible between rostral teeth in dorsal view. Basal antennal segment with double row of tubercles and spines (lateral and mesial) exceeding half the segment, lateral basal ones largest. Eyes large, not extending laterally beyond prominent postorbital spine, with intracorneal setose tubercle. Orbital border without spines, smooth, with short erect setae. Posterolateral border of carapace continuous with free epimeral margin. Epistome with 2–4 large tubercles anterolateral to urinary pore. Chelipeds subequal (Figs. 6A, E, 7D) with propodus enlarged in males, ~0.68–0.8× CL. Merus longer than propodus, both markedly inflated in larger males. Inner side of merus and carpus slightly concave and flat respectively, with spines mainly arranged in rows on upper and lower margins, with other spines on upper side. Fingers curved, practically as long as palm. Dactylus of chela with dentate cutting edge (as in fixed finger), with 2 proximal, more developed rounded teeth. Chelipeds 1.49–1.63× longer than CL. Second pereiopod longest (P2 > P3 > P4 > P5) and robust, 3.1–3.3× longer than CL. Merus and propodus subequal, both shorter than CL (~0.95×). Dactylus straight but curved distally, longer than others (d2 > d3 > d4 ≈ d5), without subdistal spines, slightly shorter than propodus (~ 0.98). Third pereiopod 2.6× longer than CL. Merus slightly shorter than P2 merus (but longer than P4, P5 meri), subequal to P3 propodus (1.1–1.2×). Dactylus with subdistal spine. Fourth pereiopod 2.3–2.4× longer than CL. Merus shorter than carapace (0.7–0.8×). Dactylus straight, similar in length to P5 dactylus, shorter than propodus (~ 0.7×), with 2 subdistal ventral spines. Fifth pereiopods shortest, 2× longer than CL. Merus shorter than carapace (0.7–0.9×). Dactylus straight, curved distally, shorter than propodus (~0.79×), with 2 subdistal ventral spines. Sternal region of male (Fig. 7C) with well-developed anterior tubercle, 2 lateral-posterior tuberculate elevations, converging forward, defining 2 lateral concave areas with the lateral edges. Male pleon with telson truncated distally.

First male gonopods curved distally in our specimens (Fig. 7E), like that of *I. guentheri* figured by Monod (1956: fig. 730), but not by Barnard (1950: fig. 5c).

Etymology: The specific epithet refers to *Gadir*, the Phoenician name of the topotypical locality, Cádiz.

Habitat: Specimens were collected from intertidal rocky bottoms up to 8 m depth, associated to *Anemonia viridis*. Specimens show different degrees of sponge coverture, and those from Galicia also having barnacles (probably as consequence of their age or size).

Distribution: The new species is only known from the Spanish Atlantic coast: Gulf of Cádiz and Galicia. Figures of the carapace and first male pleopod of *I. guentheri* from Dakar shown by Monod (1956: figs. 723–730) are like those of our new species, although not as those described by Barnard (1950) for the same species. Monod (1956) also mentioned the presence of barnacles (*Balanus* sp.) on their carapace.

Remarks: *Inachus gaditanus* **sp. nov.** is a cryptic species within the *Inachus phalangium* group. Rostrum and gastric spines are similar to those in some *I. phalangium* specimens, in particular when considering the variability existing in both species. Differs from *I. phalangium* by less developed protogastric and epibranchial tubercles (even less than in the *I. phalangium* from the Alboran Sea), the latter are sometimes almost absent. Likewise, the morphology of the first male pleopod shows a greater curvature (although it is close to that of some Alboran specimens). *Inachus gaditanus* **sp. nov.** differs from *I. leptochirus* by the presence of a rounded sternal callus in males (Supplementary material Figs. S2C, D); shorter rostral spines, which are pointed, and more or less V-shaped (Supplementary material Fig. S2A); a more acute and vertical gastric spine (Supplementary material Fig. S2B); a cardiac region with an erect spine, and slightly spiny or pointed mesobranchial tubercles.

Inachus guentheri (Miers, 1879)

(Fig. 8)

Achaeopsis Güntheri Miers, 1879: 2, pl. IV, fig. 1.

Inachus antarcticus Doflein, 1904 (junior synonym): 74, pl. XXVIII, fig. 2.

Inachus guentheri – Barnard 1950: 27, fig. 5a–c – Kensley 1969: 177; 1981: 60 – Monod 1956: 529 (in part?).

Material examined: **South Africa:** 4 specimens (NOAA/NMFS): lot 1: 1 male (19.4 × 18.8 mm), (USNM 221773), 15 August 1980, lot 2: 1 female (15.6 × 15.5 mm) (USNM 2527121), 2 males (19.1 × 17, 15.5 × 14.2 mm) (USNM 346612), 8 Feb. 1980, Mossel Bay to Algoa Bay (South Africa, topotypical region), 40–46 m depth, R/V *Thomas B Davie*, coll. B. Kensley.

Amended diagnosis: *Inachus* species with 2 protogastric tubercles, rostral spines flattened wider at base, with epibranchial and mesobranchial tubercles (not spines), erect robust gastric spine (as in *I. phalangium*, *I. gaditanus* **sp. nov.**, and *I. leptochirus*). Differs from all congeners by very poorly developed, almost non-existent protogastric tubercles; mesobranchial region with pointed distal tubercles more developed than the epibranchial tubercles, which are very small or practically non-existent (as in *I. gaditanus* **sp. nov.**), central gastric spine very well developed, high, pointed, curved forward. Rostral spines flattened, clearly separated with wide, central V-shaped region and small distal spine (non-existent in other species of the group). With a supraocular spine (also non-existent in other species). Male sternum with a well-developed anterior-median tubercle and pair of small posterior tubercles, with slightly swollen, polished, rounded region between them (as in *I. leptochirus*).

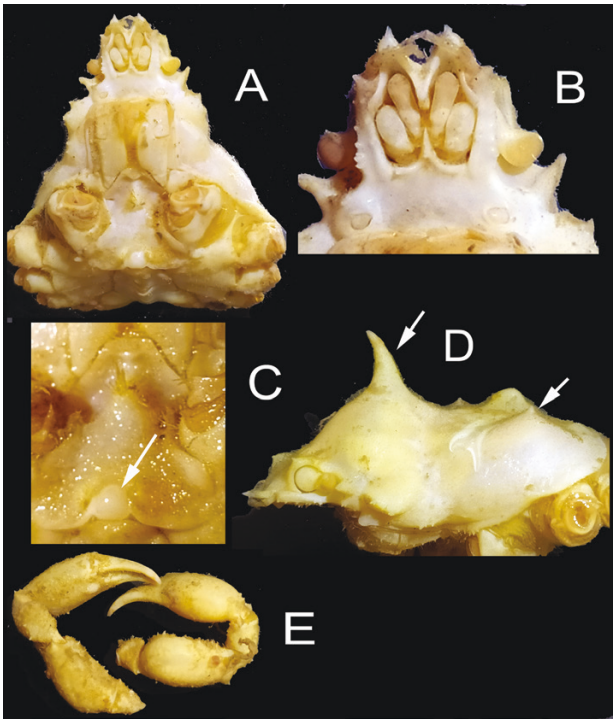

Figure 8. *Inachus guentheri* (Miers, 1879). Male from South Africa (USNM 221773, 19.4 mm CL). Ventral view of cephalothorax (**A**); detail of the anteroventral region (**B**); sternal region (**C**); lateral view (**D**); chelipeds (**E**). Arrows point the rounded sternal callus in males (C), the gastric spine and mesobranchial pointed tubercle (D).

Remarks: Another species related to the *I. phalangium* group regarding its morphology is *I. guentheri* (described from Cape of Good Hope, South Africa, as *Achaeopsis Güntheri* Miers, 1879), whose northernmost records (doubtful, specimens lost) are from the Canary Islands and Azores (Anadón, 1981; Paula *et al.*, 1992; Borges *et al.*, 2010). The morphology and figures of the material from the topotypic locality are in accordance with those described by Barnard (1950) and Miers (1879) from South Africa, but not with those by Monod (1956) from Senegal. Both *I. guentheri* and *I. phalangium* have two protogastric tubercles (but see below) and a robust central gastric spine (curved forward, as in *I. phalangium* from the English Channel (La Manche), France). The latter is pointed and higher in *I. guentheri* (Fig. 8D; Miers, 1879: fig. 1a; Barnard, 1950: fig. 5a) but not in Monod (1956), whose specimens, at least in part, probably belong to a different species; branchial region swollen and spineless; mesobranchial region with pointed distal tubercles (a small spine is figured in Barnard, 1950: fig. 5a), more developed than the epibranchial tubercles, which are very small or practically non-existent (as in *I. gaditanus* **sp. nov.**). Cardiac region is also swollen, but Barnard's figures and

descriptions (1950: fig. 5a) and the topotypic material from South Africa that was studied (Fig. 8D) disagree with Monod (1956) specimens from Senegal. The cardiac region shows a small anterior spine (not in our specimens) and a single or double tubercle behind in Barnard (1950), but Monod (1956) found an anterior double cardiac tubercle followed by another simple spine, without a spine in Senegal specimens (as in *I. phalangium* and *I. gaditanus* **sp. nov.**). Other useful morphological differences include the rostral spines being flattened and clearly divergent and with a small distal spine in South African specimens (Fig. 8A, B; Barnard, 1950: fig. 5a; Doflein, 1904 (pl. 28, figs. 2, 3, as *I. antarcticus*), whereas they are flat, less divergent (shaped as a U or more closed V) or joined by its inner face, and without a distal spine in specimens referred to as *I guentheri* (Monod, 1956: figs. 723, 724, 726, 727), and in *I. gaditanus* **sp. nov.** and *I. phalangium*. Protogastric tubercles are more conspicuous in Senegal specimens figured by Monod (1956) and in *I. phalangium* (Figs. 2, 3A, 4, 5), but they are very poorly developed or insignificant in *I. guentheri* (Fig. 8D; Barnard, 1950: fig. 5a). The protogastric region (between the rostrum and gastric spine) of *I. guentheri* has a steeper slope as seen in a lateral view (Fig. 8D; Miers, 1879: fig. 1a) compared to the other species we studied. Specimens of South African *I. guentheri* have a supraocular spine (Fig. 8D; Miers, 1879: fig. 1a; Doflein, 1904, pl. 28, fig. 2, as *I. antarcticus*; Barnard, 1950: fig. 5a) that is absent in the Senegalese specimens (Monod, 1956: figs. 723, 725, 726, 728), as well as in *I. gaditanus* **sp. nov.** or *I. phalangium*. The male sternum in South African specimens of *I. guentheri* shows a well-developed anterior-median tubercle and a pair of small posterior ones (not two divergent lateral-posterior tuberculate elevations, as observed in *I. gaditanus* **sp. nov.** and *I. phalangium*). There is a swollen and polished rounded region between the tuberculate elevations (Fig 8A, C; Barnard, 1950: fig. 5b), which resembles that of *I. leptochirus* (Supplementary material Fig. S2C, D) and *I. biceps* (Manning & Holthuis, 1981; as *I. leptochirus* in Monod, 1956). The sternum in the Dakar specimen drawn by Monod (1956: fig. 729) shows a rounded posterior central region. The specimens and figures of *I. guentheri* of Barnard (1950: fig. 5a–c) and Monod (1956: 723-730, not 729) show clear differences in the carapace, the rostrum, supraocular spine, gastric region (slope of protogastric region in lateral view, central gastric spine), branchial tubercles, male sternal region, and first gonopod, all of which suggests that South African and Senegal specimens might belong to different species. Molecular analyses should be undertaken to verify the validity of these species, their distributions, and their relationship with congeners. Unfortunately, Monod's specimens have not been found, and the molecular study failed (failed PCRs) in the South Africans ones that were examined, because they were probably originally fixed in formalin, although they are now preserved in ethanol.

Inachus sp.

(Figs. 9, 10)

Material examined: **Spain:** 2 ovigerous females (18.5 × 19.8, 17.6 × 17.1 mm) (IEOCD-INACH/2899-2900), Fuengirola-Mijas coast, Málaga; January 1981, caught with trammel nets, probably from rocky outcrops (~15 m depth), off the Mijas coast, Málaga, 36°28′36.0″N 4°42′30.0″W, colls. J.E. García-Raso and J.E. García-Muñoz.

Description: Carapace (Figs. 9C, D, 10A, C) about as long as wide, length/width: 0.93 – 1.03. Gastric region with 2 pointed protogastric tubercles anterior to long, erect gastric central spine. Each branchial region with pointed epibranchial tubercle, mesobranchial and metabranchial spines erect, the mesobranchial one highest. Cardiac region with erect spine, practically as long as gastric one. Hepatic regions with robust lateral spine. Rostrum (Figs. 9A, C, 10A–C) with 2 divergent rostral spines, with open central region, wide, U-shaped. Inter-antennular spine triangular well developed, slightly projected anteriorly, inconspicuous, just visible in dorsal view between rostral teeth. Basal antennal segment with basal tubercle (simple or double) or with 2 tubercles. Eyes large, not extending laterally beyond prominent postorbital spine when retracted. Posterolateral border of carapace continuous with free epimeral margin. Epistome with 4 tubercles: 2 anterior, between bases of basal antennal segments, 2 anterolateral to urinary pores. Chelipeds of females (Figs. 9A, C–D, 10D) subequal, ~ 1.17× as long as CL. Fingers curved, practically as long as palm. Dactylus of chela and fixed finger with dentate cutting edge. Carpus with spines on upper inner side. Merus with strong antero-dorsal spine, with rows of medium-small spines on lateral and inner ventral sides. Length of walking legs: P2 > P3 > P4 > P5. Second pereiopod robust, 3.05× longer than CL. Merus and propodus

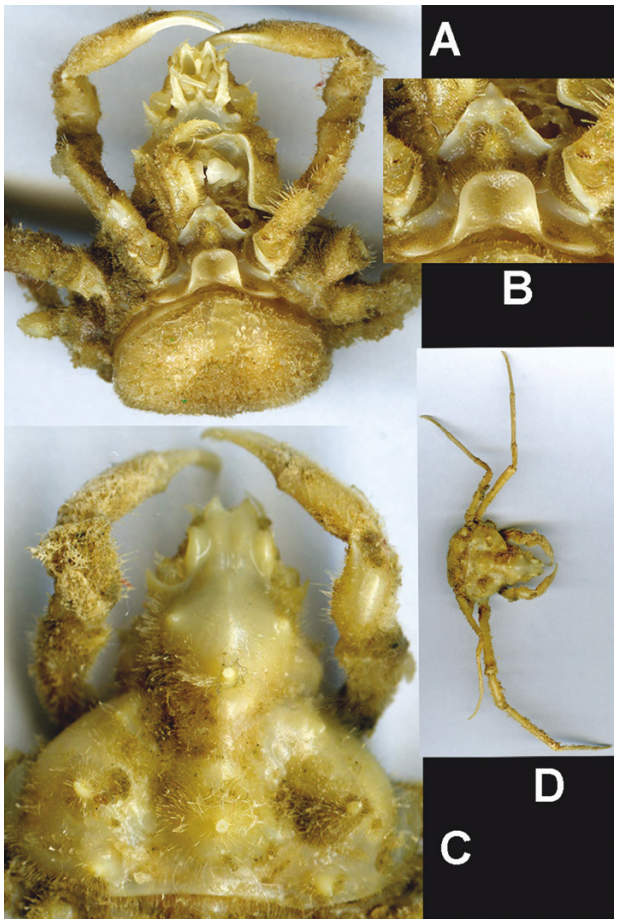

Figure 9. *Inachus* sp. Female from Málaga, Spain 18.5 mm CL (IEOCD-INACH/2899): ventral view (**A**); detail of sternal thoracic region (**B**); dorsal view of carapace (**C**); general view (**D**).

practically similar in length; merus shorter than CL (0.86–0.94×). Dactylus straight (Fig. 10E), longer than P3 dactylus (1.62×), P4 (2.34×), P5 (2.54×), without ventral distal spines, slightly longer than propodus (1.06×). P3 2.28× as long as CL. Merus shorter than CL (0.75–0.76×) and longer than propodus (1.13-1.26×) and dactylus (1.31×). Dactylus with subdistal spine. P4 1.80× as long as CL. Merus shorter than carapace (0.63–0.65×). Dactylus almost straight (Fig. 10F), slightly longer than in P5 (1.09×), shorter than propodus (0.83×), with 1 or 2 subdistal ventral spine. P5 shortest, tip of dactylus reaches basal third of P2 propodus. Merus shorter than carapace (0.54–0.59×). Dactylus slightly curved (Fig. 10G), shorter than propodus (0.73–0.86×), with 2 subdistal spines ventrally. In both female specimens, sternal region with an anterior tubercle and posterior edge projecting anteriorly as large concave tongue, without sternal callosity (Figs. 9A, B, 10H).

Remarks: These specimens belong morphologically to the species group that includes *I. thoracicus* and *I. aguiarii*. Males belonging to this complex of sibling species present identical morphology; but females of *I. thoracicus* and *I. aguiarii* can be easily distinguished through morphology (e.g., existence of sternal callosity). The two female specimens from Málaga, without sternal callosity, show an anterior tubercle and the posterior edge is projecting anteriorly as a large concave tongue (Figs. 9A, B,10H). This structure is very different from those present in *I. thoracicus* and *I. aguiarii* (Supplementary material Fig. S3A, B), which are present regardless of size. Unfortunately, these specimens were preserved at room temperature in formaldehyde for many years before being transferred to ethanol, so no DNA sequences could be obtained from them. The location where these specimens were collected is a rocky outcrop at about 15–20 m depth with strong currents and located within a Special Protection Area (García-Raso *et al.*, 2010). It was been visited several times in the past years, but no additional specimens were found. The morphological criteria applied to separate *I. thoracicus* and *I. aguiarii* could support the status of these specimens as a new species, but intraspecific variation within *I. thoracicus* should not be ruled until molecular results are available.

DISCUSSION

The original description of *Inachus phalangium* by Fabricius (1775: 408, as *Cancer Phalangium*) was brief and incomplete, making it inadequate to differentiate between close taxa, particularly with the presence of cryptic species. Fabricius (1775) unfortunately did not provide the topotypic locality. Leach (1814) subsequently described *I. Dorynchus* from the Kingsbridge estuary (English Channel, UK), but his brief and incomplete description prevent us from determining whether both are different species. Unfortunately, the type specimens of *I. phalangium* and *I. Dorynchus* were preserved dry at room temperature and molecular techniques could not be applied. We follow Rathbun (1897) consideration that *I. Dorynchus* should be known as a synonym of *I. phalangium*.

Two other names are still considered synonyms of *I. phalangium* (WoRMS, 2022b): *Cancer satuak* Herbst, 1782 (Herbst, 1782–1790) and *Macropus aracnides* Risso, 1816 (Herbst, 1782–1790; Risso, 1816). The *C. satuak* specimen

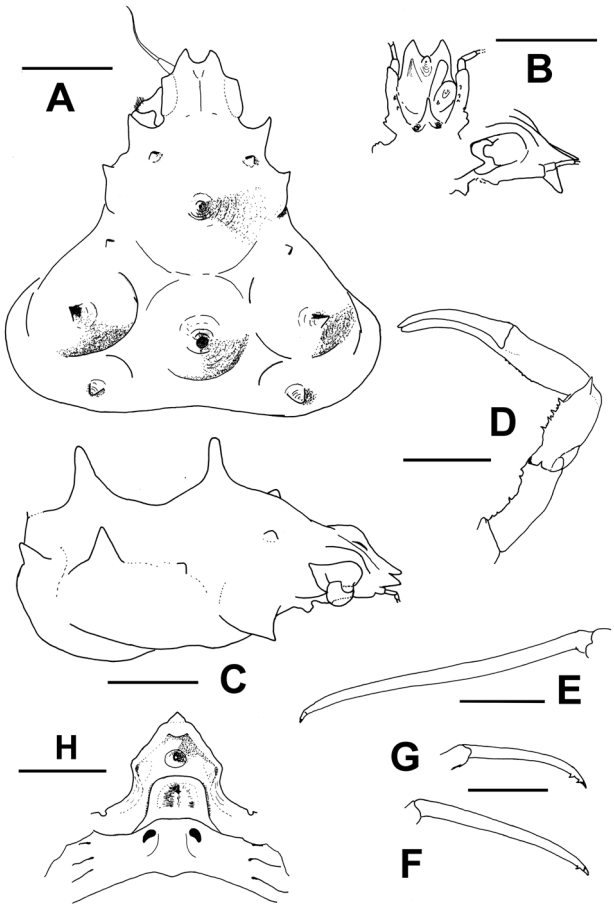

Figure 10. *Inachus* sp. Female from Málaga, Spain 18.5 mm CL (IEOCD-INACH/2899): carapace, dorsal view (**A**); rostrum in ventral and lateral views (**B**); carapace in lateral view (**C**); right cheliped in upper view (**D**); dactylus of right second pereiopod (**E**); dactylus of left four pereiopod (**F**); dactylus of right fifth pereiopod (**G**); female sternal region (**H**). Scales = 5 mm.

does not belong to *I. phalangium*, but rather to *Chionectes opilio* (Fabricius, 1788: 182), so this synonymy is incorrect. The description of *Macropus aracnides* Risso, 1816 is poor and confusing, and type material could not be found, although the topotypic locality is Nice (France, Mediterranean Sea). Risso (1816: 40) mentioned "*M. de Lamark a, dans la collection du Muséum d'histoire naturel, donné le nom d'arachnide à cette espèce de macrope que je n'avais considérée que comme une variété*" (of *Macropus Parvirostris* (= *I. dorsettensis*)). According to the description "*son rostre est peu avancé, presque arrondi*" so it could belong to *I. phalangium* (as suggested by Holthuis, 1997) or *I. gaditanus* **sp. nov.**, although our new species has not yet been found in the Mediterranean. For as long as the type of *Macropus arachnides* remains lost, the species should be considered *nomen dubium*.

The morphological analysis of specimens of *I. guentheri* show that this species is, as far as we know, restricted to southern Africa (South Africa) (Miers 1879; Doflein 1904; Barnard 1950) since the references from Senegal (Monod, 1956) are doubtful (at least in part). *Inachus gaditanus* **sp. nov.** is only known from the Atlantic coast of Spain (Galicia and Cadiz), but references to *I. guentheri* from the Canary Islands, Azores (lost specimens of Anadón,

1981; Paula *et al.*, 1992; Borges *et al.*, 2010) and some specimens from Senegal (Monod, 1956) could belong to this new species. This distribution is interspersed between that of *I. phalangium*, which has verified populations in Atlantic waters of the UK and France, Alboran Sea (western Mediterranean), and Madeira. It would be necessary to study additional populations from Portugal, the Eastern Mediterranean, and Africa, from Morocco to Senegal, to determine the actual distribution of these cryptic species.

Our results show that specimens from Walles and the English Channel (France), Madeira, and Alboran Sea present morphological and molecular differences, but the later are below the intraspecific threshold provided by Matzen da Silva *et al.* (2011) and the specimens should not be considered as belonging to different species. Genetic differentiation suggests a certain degree of isolation and restricted gene flow, maybe due to the comparatively small number of larval stages (two zoeas and one megalopa) of majoid crabs. Weber *et al.* (2000) found a similar situation for *I. dorsettensis*, with different genetic structure among populations separated by only 40 km, which suggests geographic isolation and limited dispersal. Nevertheless, molecular analyses using highly polymorphic nuclear markers, such as microsatellites, should be performed to confirm this hypothesis.

We include *I. thoracicus, I. aguiarii*, and two specimens from Málaga with a unique sternal morphology within the *Inachus* group with two protogastric tubercles and spines on branchial (epi-, meso-, and metabranchial) and cardiac regions. Rizza (1839) described *I. cocco* and *I. affinis*, and both are now accepted as synonyms of *I. thoracicus* and *I. leptochirus* respectively (WoRMS, 2022c, d). The description of *I. cocco* males and the comment about their females "large and velvety abdomen" and the absence of comments on the sternal structures or callosities (which are mentioned for the males) agree with the morphology of *I. thoracicus*. In the case of *I. affinis*, Rizza (1839) only found males (females unknown), and its description agrees with that of *I. leptochirus*. Although morphological evidence (using the same criterion applied to separate *I. thoracicus* and *I. aguiarii*) suggests the two specimens caught in Málaga with a unique sternal morphology might be a new species, preservation in formaldehyde has prevented molecular analyses, with negative DNA extraction and PCR results even after using well-protected tissues such as those located within eye stalks. The key we present aims to facilitate the identification of specimens to be collected in the future and help confirming or rejecting their validity as different species.

Key to *Inachus* species with two protogastric tubercles and an erect gastric spine

1) Branchial regions with erect spines: epibranchial (smaller), mesobranchial (largest) and metabranchial. Cardiac region with erect spine 2
   – Branchial regions with tubercles or blunt low spines but no strong acute spines..... 4
2) Sternal callosity present in both sexes, with a central region and two lateral projections..... ***Inachus aguiarii*** Brito Capello, 1876
   – Sternal callosity absent in females..... 3
3) Females with posterior edge of sternal region rounded. Males with sternal callosity, central region, and two lateral projections..... ***Inachus thoracicus*** Roux, 1830 (males of *I. thoracicus* and *I. aguiarii* are morphologically identical)
   – Females with posterior edge of sternal region projecting anteriorly, as central large concave tongue, without lateral projections. Males unknown ..... ***Inachus*** sp.
4) Cardiac region with simple spine. Males with rounded sternal callosity (absent in females). Rostral spines short, some flattened 5
   – Cardiac region swollen, without spines. Males with or without rounded sternal callosity. Rostral spines flattened, with parallel inner margins (U-shaped) or convergent (V-shaped) 6
5) Rostral spines short, pointed (not rounded) with inner margins convergent (V-shape). Low, blunt epibranchial tubercles ..... ***Inachus leptochirus*** Leach, 1817 (Leach, 1815–1875)
   – Rostral spines as rounded lobes, usually with an apical spinule. Without epibranchial tubercle..... ***Inachus biceps*** Manning & Holthuis 1981
6) With supraocular spine. Gastric spine robust, pointed, and directed upwards. Protogastric and epibranchial tubercles small and low (even practically absent). Males sternum rounded, with prominent tubercle (absent in females)..... ***Inachus guentheri*** (Miers, 1879)[1]
   - Without supraocular spine. Gastric spine robust, directed upwards, with pointed or blunt tip. Males and females without rounded prominent tubercle..... 7
7) Epibranchial tubercles well developed, higher (English Channel) or lower (Alboran) than mesobranchial tubercles. Protogastric tubercles well developed ..... ***Inachus phalangium*** (Fabricius, 1775)[2]
   - Epibranchial tubercles poorly developed (even less than in *I. phalangium* from Alboran) and sometimes almost non-existent (as in *I. guentheri*). Protogastric tubercles poorly developed. Rostrum shorter in small and medium specimens (up to 15 mm CL) ..... ***Inachus gaditanus* sp. nov.**

[1]A small mesobranchial spine is figured in Barnard 1950 (South African specimens), but it was not observed in the studied material.

[2]There are three different morphologies within *I. phalangium* (northeastern Atlantic, Alboran-Mediterranean, and Madeira; see remarks under *I. phalangium*).

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. List of specimens examined.

S2 Figure. Males of *I. leptochirus* from the Gulf of Cádiz and Mediterranean Sea.

S3 Figure. Sternal female region of *I. thoracicus* and *I. aguiarii*.

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