

Article

First Record of the Amphi-Atlantic Rafting Crab *Plagusia depressa* (Fabricius, 1775) (Crustacea, Decapoda, Brachyura) in the European Continental Waters: Southern Spain as a Gateway for Non-Native Species

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Abstract

The amphi-atlantic rafting crab *Plagusia depressa* (Brachyura: Plagusiidae) has been recorded for the first time in European continental waters. Three specimens were captured manually in a rocky shore intertidal/subtidal of a beach located in the Gulf of Cádiz (Spain). These specimens were identified using morphological and molecular techniques (DNA barcoding of the 16S and COI genes). The 16S sequence suggests that these specimens are more closely related to African specimens than to those from the Caribbean. However, given the rafting behavior of this species, the specimens recorded in the Gulf of Cádiz may have originated from more distant regions within its distribution range for which molecular data are not available. We present a detailed morphological identification of these specimens and compare them with *Plagusia squamosa*, which occurs in the nearby Mediterranean Sea. This comparison contributes to clarifying the morphological traits that distinguish the two species. This finding highlights the role of southern Iberian waters in facilitating the introduction and establishment of non-native species.

Keywords: Plagusiidae; DNA barcoding; 16S; COI; Gulf of Cádiz; allochthonous species



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1. Introduction

Biological invasion is a global problem as a result of the hyperconnectivity promoted by globalization [1]. Southern Iberian waters are very vulnerable to the arrival of non-native species because of the elevated maritime traffic through the Strait of Gibraltar and due to the port of Algeciras being the first in Spain in container traffic volume and second among all Mediterranean ports [2]. In this area, mainly in the Gulf of Cádiz, quite a few non-native decapod species have been recorded, some introduced by human activities from distant areas and others being subtropical African Atlantic species that are expanding their biogeographical range, naturally (tropicalization process) or not, toward more northern areas [3]. Many of these are recent additions of African species favored by climate change, which benefits this warm-water biota, and by anthropogenic alterations that modify the original structure of habitats, facilitating their settlement [4].

The genus *Plagusia* Latreille, 1804, is represented by five species [5]: *Plagusia depressa* (Fabricius, 1775), *Plagusia immaculata* Lamarck, 1818, *Plagusia integripes* Garth, 1973, *Plagusia speciosa* Dana, 1851 and *Plagusia squamosa* (Herbst, 1790). Other species previously placed in this genus are considered not valid, synonyms, and/or included in recent different genera [5,6].

Plagusia species present a tropical and subtropical distribution in the Atlantic and the Indo-Pacific Oceans, with presence in the Mediterranean Sea [7,8]. These crabs, as well as those of the genus *Planes* Bowdich, 1825, are commonly called rafting crabs because they are observed living on drifting debris, buoys, ship hulls, and even marine turtles [9]. This behavior allows them to disperse over great distances and have wide distributions. Concretely, *Plagusia immaculata* is present in the Tropical Indo-West Pacific: Indian Ocean, Indonesia, China Sea, Japan, Hawaii; Tropical East Pacific: Baja California, Costa Rica to Panama, Galapagos Islands to Ecuador (?) and Chile (Punta Arenas) (?) [7]. *Plagusia integripes* presents a restricted distribution since it is only known from the topotypical locality: Tropical East Pacific: Easter Island [7]. The distribution of *Plagusia speciosa* includes Tropical East and West Pacific: Tuamotu Island, Tahiti, Funafuti, Rotuma, Guam, Marshall Islands, Clipperton and Washington Islands and East Australia [7]. *Plagusia squamosa* partially shares distribution with *P. immaculata* and *P. speciosa*, and it has been recorded from the Indo-West-Pacific Ocean to the Eastern Pacific [7] (Figure 1a–f, as *P. depressa tuberculata*) [10–12], and it is invasive in the Mediterranean Sea (lessepsian species), found in Lebanon, Libya and Tunisia [8,13,14]. *Plagusia depressa* is distributed by the West Atlantic, from North Carolina to Brazil, including the Gulf of Mexico and the West Indies; and the East Atlantic from the Azores, Madeira and Canary Islands to Angola, including Congo, Ghana, Ivory Coast, Liberia, Senegal, St. Helena Island, Cape Verde Islands and Morocco [5,15].

Now, this work records for the first time the presence of *P. depressa* in the Atlantic waters of the Gulf of Cádiz, southwestern Spain, the first record in European continental waters. The specimens were identified by morphological characteristics and DNA barcoding of 16S and COI genes. We provide a detailed morphological identification of this species, comparing it with *P. squamosa*, which is present in the nearby Mediterranean Sea. This helps to clarify the morphological characteristics that differentiate the two species, which were not clearly defined until now due to morphological variability.

2. Materials and Methods

2.1. Study Area

The sampling area is an intertidal/subtidal rocky shore located at the Cape Punta Gracia on Los Alemanes beach in Zahara de los Atunes (Cádiz), in the Gulf of Cádiz, southwestern Spain (ca. 36.090358 N, 5.811856 W) (Figure 1). Three specimens (one in July 2025 and two in March 2026) were captured manually by the third author.

2.2. Morphological Identification

The works of Ng et al. [16] and Davie et al. [17] were followed for systematic taxonomy, and the updated DecaNet [5] was used to verify the validity of species' scientific names. The papers of Rathbun [18], Dawson [7], and Schubart and Ng [19], among others, were mainly used for identification. References to species descriptions and synonyms can be found and downloaded from the corresponding taxon fact sheets on DecaNet [5]. The measurements of the specimens are given in millimeters (mm) and refer to the maximum width of the carapace (cw) × maximum length (cl) along the dorsal midline, from the middle of the frontal region to the posterior margin.

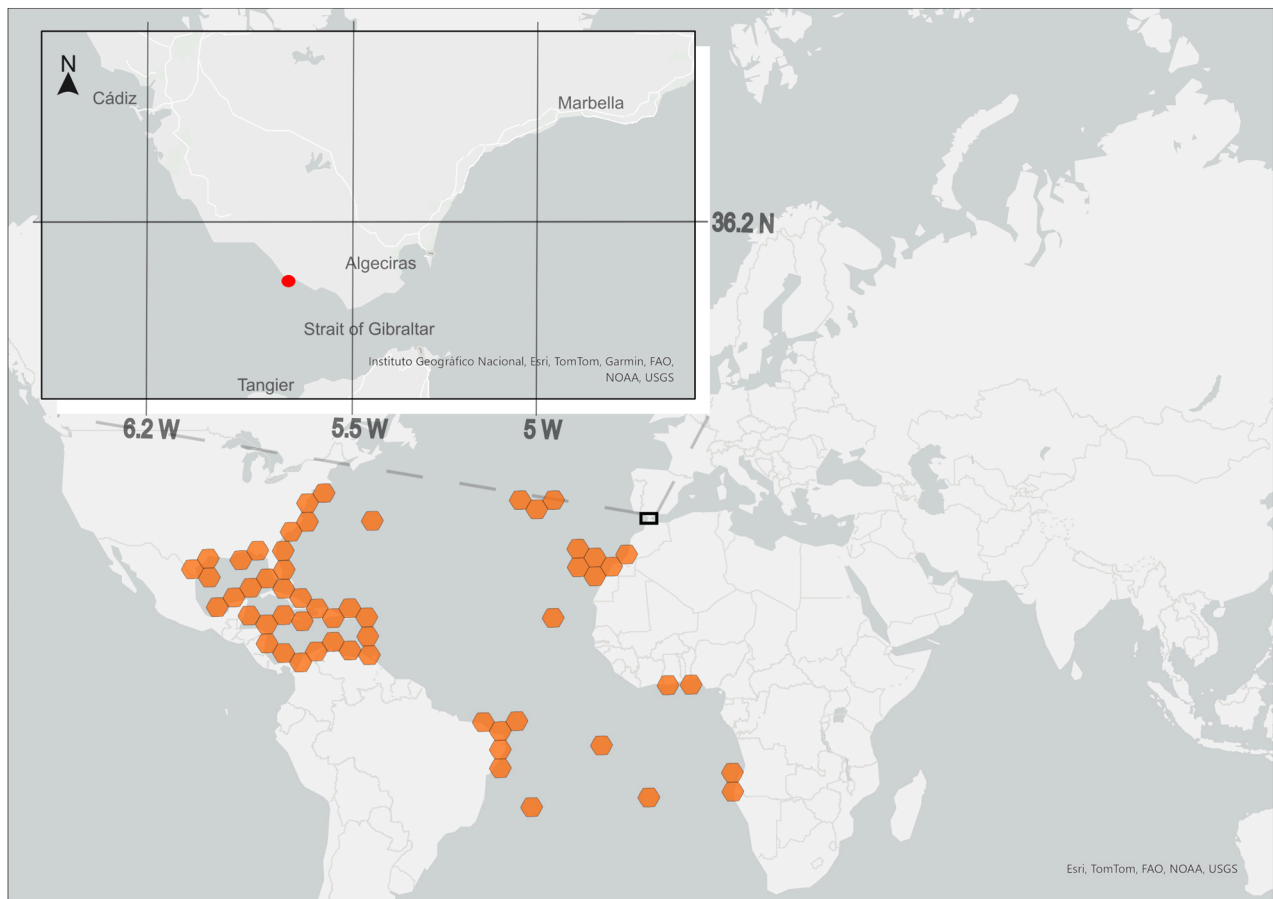


Figure 1. Geographic distribution of *Plagusia depressa* (Fabricius, 1775) pointed out as orange hexagons, including the new location recorded in this work (red point in the magnified area). Map generated in ArcgisPro 3.6.

2.3. Molecular Identification

DNA was extracted from a pereopod (left P5) muscle tissue of the three specimens using the Qiagen DNeasy Blood & Tissue Kit following the manufacturer's protocol. The mitochondrial genes, 16S rRNA and Cytochrome c Oxidase subunit I (COI), were amplified via Polymerase Chain Reaction (PCR). Cycling conditions of PCR were: 15 min at 95 °C, 35 cycles of 30 s at 95 °C, 30 s at 45 °C (16S)/35 s at 43 °C (COI), and 30 s at 72 °C, and finally 5 min at 72 °C. Primers 1472 (5'-AGA TAG AAA CCA ACC TGG-3') [20] and 16L2 (5'-TGC CTG TTT ATC AAA AAC AT-3') [21] were used to amplify a maximum of 551 bp of 16S, while primers COL6b (5'-ACA AAT CAT AAA GAT ATY GG-3') and COH6 (5'-TAD ACT TCD GGR TGD CCA AAR AAY CA-3') [22] allowed amplification of a maximum of 658 bp of COI. PCR products were purified and bidirectionally sequenced by Stab-Vida Laboratories and edited using Chromas version 2.6.6. Final sequences were validated via BLAST searches on the NCBI website (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>, accessed on 12 May 2026) and deposited in the GenBank database under the accession numbers PZ092430, PZ419818, and PZ429819 (16S) and PZ092434, PZ419855, and PZ419856 (COI). References to other Plagusiidae sequences used in identification and comparisons can be found using the number codes on GenBank and BOLD.

To visualize the species identification based on DNA barcoding, two Neighbor-Joining trees were constructed independently using the 16S and COI genes obtained in the current work, as well as a selection of 16S and all COI sequences of the *Plagusia* spp. available in GenBank and BOLD (COI sequences). Sequences of the Plagusidae genera *Guinusia*

Schubart & Cuesta, 2010, *Euchirograpsus* H. Milne Edwards, 1853 and *Miersiograpsus* Türkay, 1978 were included as outgroups.

The sequences for each gene were aligned using MEGA X [23] and trimmed manually. In the case of the 16S gene, Gblocks was not used, as all sequences are closely related and no ambiguities were observed. MEGA X was used to construct the NJ trees, and distances were calculated using the p-distance method [24].

3. Results

3.1. Molecular Data

The specimen identification was confirmed by DNA barcoding. The 16S sequences obtained (PZ092430, PZ419818, and PZ429819) present two haplotypes differing in just one mutation. Both haplotypes match at 99.28–99.09% (four–five mutations divergence, including two gaps) with the sequences of specimens of *P. depressa* from São Tome and Principe (FN539000), Ivory Coast (AJ311793) [6], and Ghana (FN538999) [25]. However, they also match at 99.26–98.90% (five to seven mutations divergence, including one or two gaps) with the sequences of specimens of *P. depressa* from Barbados, Jamaica, Panama and Puerto Rico. The distances are longer with respect to the 16S sequences of the sister species *P. squamosa* and *P. immaculata* with 94.71–93.85% similarity (29–32 mutations divergence, including seven gaps) and *P. speciosa* (90.25–90.07% similarity, 54–55 mutations divergence, including six gaps) (Figure 2).

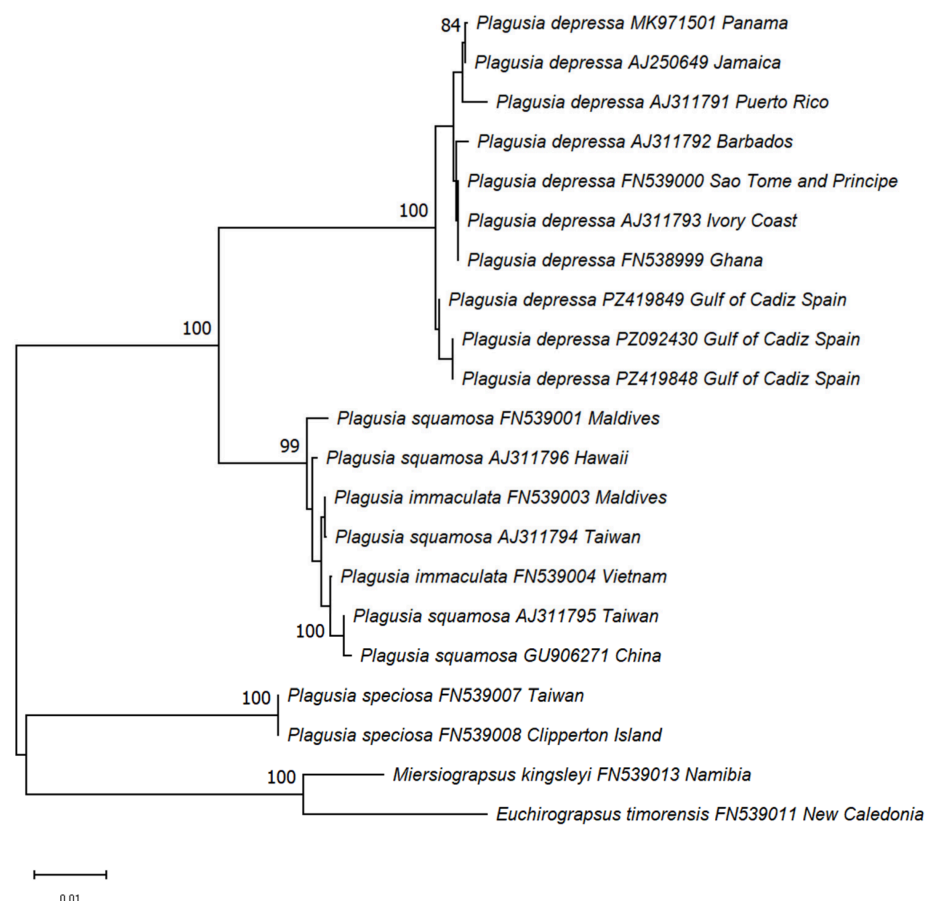


Figure 2. Topology of Neighbor-Joining tree based on 16S sequences, showing computed distances within a selected group of *Plagusia* spp., with *Miersiograpsus kingsleyi* (Miers in Tizard, Moseley, Buchanan & Murray, 1885) and *Euchirograpsus timorensis* Türkay, 1975 as outgroups. Numbers close to nodes indicate bootstrap support (after 2000 replicates, only values above 70% shown). After the name of each specimen, the accession number of sequences in GenBank and the locality are included.

The COI sequences obtained are different haplotypes for each specimen (PZ092434, PZ419855, and PZ419856), differing in two, four and six mutations. These haplotypes match at 97.87% and 97.57% (14 and 16 mutations divergence) with the unique COI sequence of *P. depressa* deposited in GenBank (MN184063) of the specimen ULLZ13403 from Panama, but are clearly distant from the sequences of *P. squamosa* from Hawaii, South Africa and China, and *P. immaculata* from Quintana Roo, China and Singapore, with 87–86.54% similarity (75–88 mutations divergence) (Figure 3).

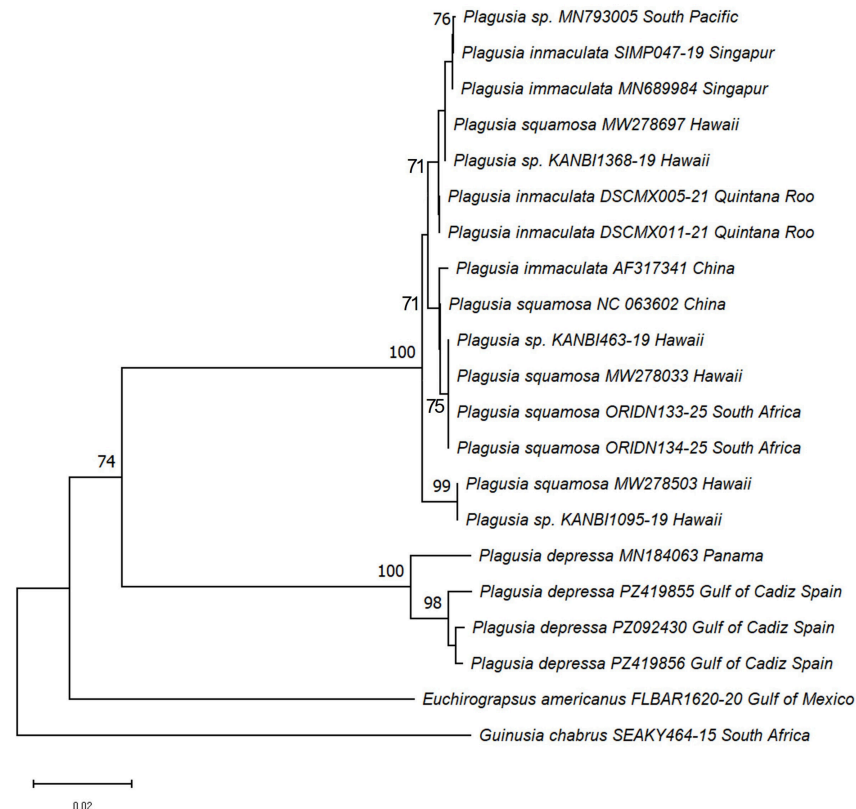


Figure 3. Topology of Neighbor-Joining tree based on COI sequences, showing computed distances within all available sequences of *Plagusia* spp., with *Guinusia chabrus* (Linnaeus, 1758) and *Euchirograpsus americanus* A. Milne-Edwards, 1880 as outgroups. Numbers close to nodes indicate bootstrap support (after 2000 replicates, only values above 70% shown). After the name of each specimen, the accession number of sequences in GenBank/BOLD and locality are included.

3.2. Morphological–Taxonomical Data

Plagusia depressa (Fabricius, 1775) (Figures 4–6).

Synonyms. *Cancer depressus* Fabricius, 1775; *Plagusia gracilis* de Saussure, 1858, and *Plagusia sayi* De Kay, 1844. Figures in Herbst [26] (pp. 117–118, figs PL III 35ab), Rathbun [18] (pp. 332–336, Figure 154a), Bouvier [27] (pp. 299–300, Pl XI, Figure 8), Barnard [28] (p. 134, Figure 26g–h), Monod [29] (pp. 455–457, Figures 614–617), Williams [30] (pp. 463–464, Figure 372), Schubart and Ng [19] (p. 330, Figure 1A–D), Cruz Da Rosa et al. [31] (p. 2, Figure 1).

Material examined. Three specimens: 1 ♂ (58.2 cL × 63.1 cw) CRUST_COMA/809 (16S: PZ092430, COI: PZ092434) from intertidal/subtidal rocky bottom at Cape Punta Gracia, Los Alemanes beach, Zahara de los Atunes, Cádiz, Spain, 31 July 2025; and 1 ♂ (57.55 cL × 63.38 cw) (CRUST_COMA/4354) (16S: PZ419818, COI: PZ419855) and 1 ♀ (44.23 cL × 47.44 cw) (CRUST_COMA/4355) (16S: PZ419819, COI: PZ419856) from the same locality on 28 March 2026. These specimens were deposited in the Marine Crustacean Collection of the Cádiz Oceanographic Center (CRUST_IEOCD) [32].

The morphology of these specimens (Figures 4–6) agrees with the description and observations made in previous works [7,18,19]. Although only three specimens were captured in two different years, a large group of individuals (at least ten) of various sizes and both sexes were observed in the area in each year, suggesting the existence of an established population.

Distribution. Amphi-atlantic (previously detailed in the introduction section). Now also in Spain (Gulf of Cádiz).

Habitat. It inhabits rocky intertidal/subtidal zones, commonly hiding in crevices, hollows, fissures, and tide pools; its body shape allows it to conceal itself in narrow cracks. It is also found on human-made structures such as breakwaters, platforms, and ship hulls. It prefers rocky to sandy bottoms, and it is not uncommon to find it on drifting debris [9].

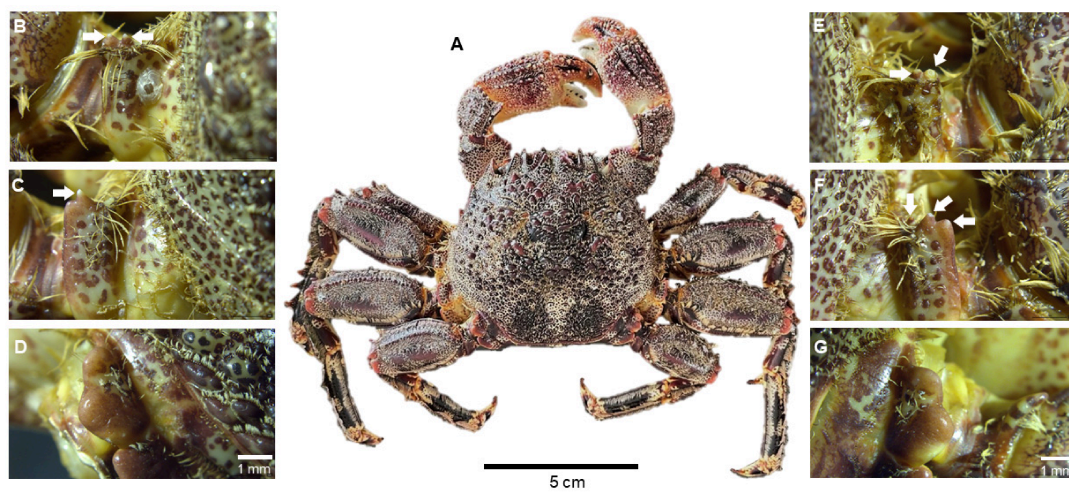


Figure 4. (A) Dorsal view of the male (CRUST_COMA/809) of *Plagussia depressa* (Fabricius, 1775) from Cape Punta Gracia, 31 July 2025. (B–D) Left ambulatory coxal superior lobes of P3–P5, respectively. (E–G) Right ambulatory coxal superior lobes of P3–P5, respectively. The white arrows indicate the teeth of each lobe.

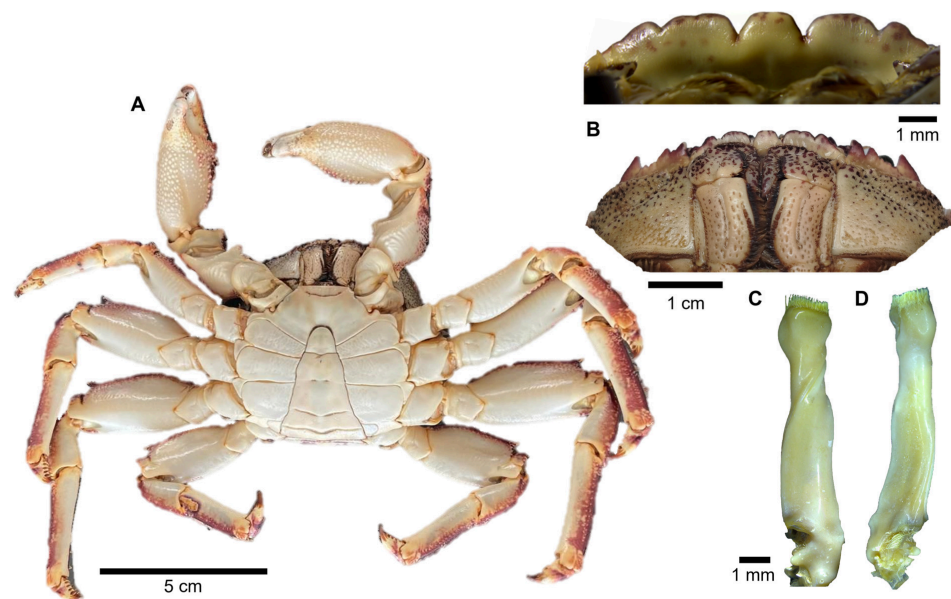


Figure 5. (A) Ventral view of the male (CRUST_COMA/809) of *Plagussia depressa* (Fabricius, 1775) from Cape Punta Gracia, 31 July 2025. (B) Ventral view of the margin of the epistome showing part of the buccal frame (below) and a close-up of the epistome (above). (C,D) Dorsal (right) and ventral (left) view of the left first gonopod, respectively.

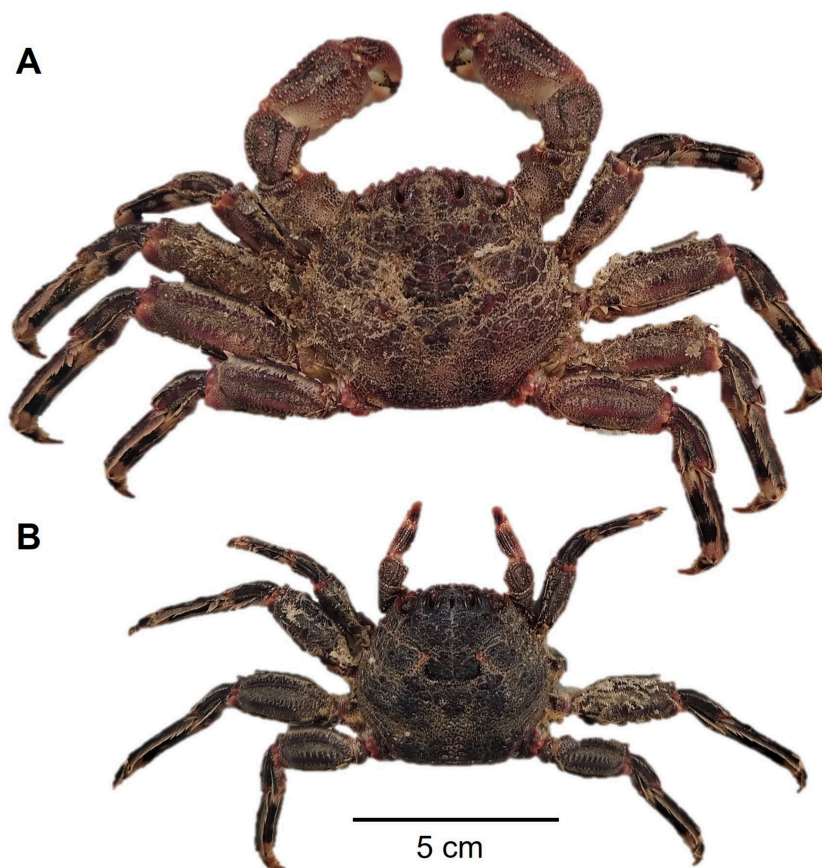


Figure 6. Dorsal view of (A) the male (CRUST_COMA/4354) and (B) female (CRUST_COMA/4355) of *Plagusia depressa* (Fabricius, 1775) from Cape Punta Gracia, 28 March 2026.

4. Discussion

4.1. Remarks on Morphology and Taxonomy

In Eastern Atlantic and Mediterranean waters, only two species of *Plagusia* have been recorded: *P. depressa* and *P. squamosa*.

A summary of the current information about *P. squamosa* also includes that mentioned under the following synonyms: *Cancer squamosus* Herbst, 1790; *Plagusia tuberculata* Lamarck, 1818; *Plagusia depressa tuberculata* Shiber, 1981 and *Plagusia orientalis* Stimpson, 1858. Figures in: Herbst [26] (pp. 260–261, Tab. XX, Figure 113), Rathbun [18] (pp. 332–336, Figure 154b and Pl.102, Figures 1–2), Crosnier [10] (pp. 80–81, Pl VII, Figure 3), Dai and Yan [11] (pp. 562–563, Figure 293–2, as *P. tuberculata*), Galil et al. [8] (p. 146), Schubart and Ng [19] (p. 331, Figure 2A–C as *P. orientalis*, p. 332, Figure 3 as *Cancer squamosus* and *Plagusia tuberculata*), Zaouali et al. [14] (p. 3, Figure 2), Naderloo [12] (pp. 366–367, Figure 33.2), and Muñoz et al. [33] (p. 20, Figure 16).

Updated information about *P. depressa* is already mentioned above.

Both species are very similar morphologically, which has led to discrepancies and confusion, partly due to disparities between the materials preserved in old collections and the dating, figures, etc. [18,19,34–38]. Finally, Schubart et al. [25] analyzed the morphology of larval stages (zoea I and megalopa) and the 16S rRNA sequences and found clear differences between both species, identifying *P. squamosa* as a fully valid species, formerly known as *P. depressa tuberculata* Lamarck, 1818 (see also [19]). The differences between both species have also been confirmed by the recent COI sequences of *P. depressa*, MN184063 and PZ092434, PZ419855, and PZ419856 (current study), with a long distance with respect to the sequences of *P. squamosa* (Figure 3).

The main morphological differences mentioned between both species are:

(1) Carapace: generally, with sparse, naked, dorsal tubercles, squamiform and bordered by a fringe of short, stiff setae in *P. depressa*, while *P. squamosa* shows more prominent, squamiform tubercles with a dense row of longer setae surrounding the anterior margins of the flattened granules. In the closely related species *P. immaculata*, the setae surrounding the granules are distinctly sparser and/or shorter, or absent [10]. In the key for the worldwide *Plagusia* species, Dawson [7] wrote: for *P. depressa*: tubercles well-marked, flat, pearly or squamiform, gastric region with series of about six prominent acute tubercles in front arranged in an arc curving forward, while for *P. squamosa*: tubercles of carapace conical or squamiform, variable, either prominent or depressed, or almost obsolete on the convex portion of the carapace [18] (p. 334), “usually with no series of prominent tubercles on the gastric region”. However, these differences do not appear to be valid or consistent. Laurie [39] mentioned that the tubercles are similar in both. Fringes of bristles are also variable in extent, and sometimes absent. In this regard, we have not observed clear differences in the tubercles of the carapace (including those in the gastric region) (Figures 4A, 6) of *P. depressa* specimens from Brazil [29] (Figure 1, with serrated coxal lobes) or from Senegal (Gorée) [29] (Figure 614) and those of *P. squamosa* cited by Schubart and Ng [19] (Figure 2 as leptotype *P. orientalis*) and the one from Mauritius [33] (Figure 16, with non-serrated coxal lobes). Moreover, variability is observed between specimens belonging to the same species, e.g., between the mentioned specimens of *P. depressa* from Brazil (or the one represented by Monod [29] and our specimen confirmed by DNA) (with apparently less developed tubercles, Figure 4A); likewise, between specimens of *P. squamosa*, such as those mentioned from Iran [12] (Figure 33.2) and Mauritius [33] (Figure 16). This could reflect variability related to size or sex, or even erroneous identifications. In fact, the two sympatric Indo-Pacific species *P. squamosa* and *P. immaculata* cannot be genetically distinguished based on 16S (Figure 2), H3 [6] and now, COI (Figure 3). Although the two taxa are morphologically very similar, they differ slightly in the setation surrounding the tubercles of the carapace and in the sulcae of the pereopods—present in *P. squamosa* but absent in *P. immaculata* [19]—although some specimens show only faintly developed setation. For this reason, the possible synonym between both species has been suggested previously [6,19]. Although now, considering the evidence from COI data, there is more molecular evidence that supports the synonymization, resolving this question is not the objective of the current work.

(2) The ambulatory coxal superior lobes, mainly in P4 and P3 (Figure 4B,C,E,F), are dentate in *P. depressa* (in accordance with the male lectotype of *Cancer depressus* Fabricius, 1775, ZMUC Cru 10-3, from the Copenhagen Museum material of Fabricius [19]), while *P. squamosa* shows a non-dentate superior lobe in the ambulatory legs [18] (Figure 154), [34] (p. 231), [39] (p. 429). This is a consistent morphological difference between both species (such as was mentioned by Rathbun [18]). However, there are variations in the intensity-degree of that dentition; in our specimens (Figure 4B–G), these lobes show 1, 2 or 3 spines as in [18] (Figure 154), but the Brazilian specimens [31] are more strongly dentated.

Others cited morphological differences: Stimpson [34] (p. 231) mentioned that *P. squamosa* (as *P. orientalis*) is distinguished from the Atlantic species (*P. depressa*) (in addition to having a non-dentate coxal superior lobe in the ambulatory legs) by the septem-dentate margin of the epistome. Dawson [7] wrote “epistome usually cut into five lobes” in *P. depressa*, while in *P. squamosa* “it has a tendency to be more divided, into seven lobes, but this is not a constant character”. In our specimens of *P. depressa*, the epistoma margin shows five lobes, although in some specimens an outer lobe may show a slight subdivision (Figure 5B) or be partially fused.

Chace [40] compared male first gonopods of the species of *Plagusia* and indicated that *P. depressa*, *P. immaculata*, and *P. squamosa* (as *P. tuberculata*) are most closely related to each other (although they are probably specifically distinct) than they are to the other two species. Unfortunately, he did not draw any pictures or comment on the differences. Dawson [7] wrote for *P. depressa*: first male pleopod with rounded apical lobes fringed with hair, spiral seminal groove (sperm duct); and for *P. squamosa*: first male pleopod subcylindrical with spiral seminal groove (sperm duct) as in the previous species. Comparing the figure of *P. squamosa* from China [11] (Figure 293-2 as *P. tuberculata*) with those of *P. depressa* from Dakar [29] (figs 615–617), differences can be seen, but the apical tip of *P. squamosa* is more rounded than that of *P. depressa*. The first male gonopod of our specimen (Figure 5C,D) is similar to that figured by Monod [29] from Dakar, with a dense crown of apical setae.

In conclusion, the main differential morphological characters between *P. depressa* and the closely related species *P. squamosa* are: (1) ambulatory coxal superior lobes (P4 and P3), with 1 to 3 spines in *P. depressa* and non-dentate in *P. squamosa*; (2) epistome, with five (although with certain variability) and seven lobes in *P. depressa* and *P. squamosa*, respectively; and (3) male first gonopods, with an apical tip that is more rounded in *P. squamosa* than in *P. depressa* and topped by a thick crown of setae in the last species.

The 16S and COI sequences obtained in the present work for *P. depressa* confirm morphological identification (Figures 2 and 3), with distances that fall in the intraspecific range, in the case of this genus, although close to the limit generally considered [21,41]. However, we are unable to identify the origin of the specimens since there is no full match with any of the available sequences of *P. depressa*. Initially, the 16S sequence is slightly closer to those of African specimens than Caribbean ones, but considering the rafting character of this species, the specimens found in the Gulf of Cádiz could come from more distant locations within the distribution of this species for which molecular data are currently unavailable, and this could explain the genetic distances shown in these two markers. Remarkably, the presence of three different COI haplotypes among the three analyzed specimens is unexpected for a recent punctual introduction event with low propagule pressure. Therefore, this could suggest that: (1) this is a population present in the area for a long time (not likely); (2) a large and diverse sample of the original population was introduced into the Gulf of Cádiz, which likely depends on the vector; or (3) this population is supplied by successive introductions from the population or populations of origin (high propagule pressure). Unfortunately, there are no COI sequences from different *P. depressa* populations, just one from Panama; therefore, it is difficult to determine the origin based on this type of data.

There could be several reasons to explain how *P. depressa* has reached the continental waters of the Gulf of Cádiz, including, like for other species already present in the area, the ships' ballast water or hull fouling, larval dispersal or accidental escape from cultures or transports. However, considering the rafting behavior of this species, introduction via heavy maritime traffic (ships and platforms) in the area could be the most reasonable possibility [2,9]. There are three major ports (Cádiz, Sevilla and Algeciras) with a high frequency of connections with the Canary Islands and other African ports, which could explain why DNA shows fewer similarities with African populations than Caribbean ones.

4.2. On Non-Native Littoral Species Present in the Area

The Gulf of Cádiz could be considered a gateway for non-native species due to its location in the waters off the southern coast of the Iberian Peninsula, near the Strait of Gibraltar and the African waters, as well as the intense maritime traffic in the area. There are numerous species that are not native to the area or are African species whose northernmost distribution limit is found here (regardless of whether they have reached it recently or not).

There are, therefore, introduced exotic species such as African species that have naturally expanded their biogeographical distribution area, the most recent ones partly thanks to the process known as tropicalization [42].

Invasive species with African or amphi-atlantic origin are: the amphi-atlantic shrimp *Penaeus* (*Farfanpenaeus*) *notialis* Pérez Farfante, 1967 [43]; the Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 [44]; the African crab *Callinectes pallidus* (de Rochebrune, 1883) [45] (as *C. exasperatus*); the mud crab *Rhithropanopeus harrisi* (Gould, 1841) [46] and the African crab *Grapsus adscensionis* (Osbeck, 1765) [47]. In addition, the invasive crab *Percnon gibbesi*, amphi-atlantic but widely spread, has been reported in the Alborán Sea [48].

Some African littoral species are present in the south of the Iberian Peninsula, especially in the Gulf of Cádiz, which in most cases are well established and represent their northern limit. Some of these species have arrived on their own in the Gulf of Cádiz, such as the cleaner shrimp *Lysmata unicoloris* Holthuis & Maurin, 1952 [49]; *Ogyrides rarispina* Holthuis, 1951 [50]; *Brachynotus atlanticus* Forest, 1957 [51]; *Panopeus africanus* A. Milne-Edwards, 1867 [52]; *Xaiva mcleayi* (Barnard, 1947) [53] (as *Liocarcinus mcleayi*)—for this latter species, although the northernmost location in African waters cited is Mauritania, we are convinced of its presence in Morocco; *Cryptosoma cristatum* Brullé, 1837, with only occasional captures [54]; and the hermit crab *Pagurus mbizi* (Forest, 1955) [55], as mentioned for *X. mcleayi*; although we have no record of it in Morocco, it must surely be there. This species was detected near the Strait of Gibraltar in 2006 and gradually moved towards the Mediterranean, reaching the eastern Alboran Sea in 2010–2013 [55]. Finally, a recent record of other African species in the Gulf of Cádiz is that of *Ilia spinosa* Miers, 1881 [56]. The reference of *Xantho sexdentatus* (Miers, 1881) [57] is doubtful.

In several of the mentioned cases, they could be species already present in the area before the separation of Europe and Africa; therefore, now their presence in the Gulf of Cádiz and West Portugal area would be the result of this separation and not recent colonization events, as it has been shown for *Afruca tangeri* (Eydoux, 1835) thanks to the finding of fossil samples in southern Europe [58].

Non-native introduced species found in the area (Gulf of Cádiz or Alboran Sea) but with Asian origin, and whose presence is undoubtedly due to human activity, are: the Asiatic shrimp *Penaeus* (*Marsupenaeus*) *pulchricaudatus* Stebbing, 1914 (or *P. japonicus*?) [58–60] (only recorded one time, and not more confirmed records); the Indo-West Pacific giant tiger prawn *Penaeus monodon* Fabricius, 1798 [4]; the Indo-Pacific snapping shrimp *Alpheus* cf. *lobidens* De Haan, 1849 [61,62]; the oriental shrimp *Palaemon macrodactylus* Rathbun, 1902 in 1999 [63]; the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853, detected in the Guadalquivir estuary in 1987 [64]; the portunid crab *Portunus segnis* (Forskål, 1775) from the Indian Ocean, Red Sea and Eastern Mediterranean [65]; and the Indo-West Pacific crab *Sphaerozium nitidus* Stimpson, 1858 [66].

It is highly probable that the increase in the establishment in these non-native species in this area will continue due to the constant rise in water temperature. This will further increase the specific richness of this biogeographical sector, which is a non-native species hotspot for decapod crustaceans in the Iberian Peninsula [4]. Many of these species can have economic value (shrimps, prawns and large crabs), and the fisheries activities could help to control them, but some will compete for resources with native species and could cause their displacement or population decline. This justifies the need for monitoring and control in order to take actions that allow us to positively manage marine resources and maintain sustainability, both in environmental and habitat quality, to recognize potential impacts on the ecosystem and the economy (including fishing and tourism) [67–69].

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References

- Hulme, P.E.; Bacher, S.; Kenis, M.; Kühn, I.; Pergl, J.; Pyšek, P.; Roques, A.; Vilà, M. Blurring alien introduction pathways risks losing the focus on invasive species policy. *Conserv. Lett.* **2017**, *10*, 265–266. [CrossRef]
- Acosta, M.; Coronado, D.; Cerban, M.M. Port competitiveness in container traffic from an internal point of view: The experience of the Port of Algeciras Bay. *Mar. Policy Manag.* **2007**, *34*, 501–520. [CrossRef]
- Galil, B.S.; Clark, P.F.; Carlton, J.T. (Eds.) *In the Wrong Place—Alien Marine Crustaceans: Distribution, Biology and Impacts*; Springer: Dordrecht, The Netherlands, 2011. [CrossRef]
- González-Ortegón, E.; Jenkins, S.; Galil, B.S.; Drake, P.; Cuesta, J.A. Accelerated invasion of decapod crustaceans in the southernmost point of the Atlantic coast of Europe: A non-natives’ hot spot? *Biol. Invasions* **2020**, *22*, 3487–3492. [CrossRef]
- DecaNet. *Plagusia* Latreille, 1804. World Register of Marine Species. Available online: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=106967> (accessed on 19 February 2026).
- Schubart, C.D.; Cuesta, J.A. Phylogenetic relationships of the Plagusiidae Dana, 1851 (Brachyura). *Crustac. Monogr.* **2010**, *11*, 279–299. [CrossRef]
- Dawson, E.W. A key to the world species of *Plagusia* (Crustacea: Brachyura), with a new record of *P. depressa tuberculata* Lamarck from New Zealand. *Natl. Mus. N. Z. Rec.* **1987**, *3*, 37–45.
- Galil, B.S.; Frogia, C.; Noël, P.Y. CIESM Atlas of Exotic Crustaceans in the Mediterranean Sea. 2002. Available online: <https://www.ciesm.org/atlas/appendix2.html> (accessed on 15 December 2008).
- Frick, M.G.; Kopitsky, K.; Bolten, A.B.; Bjørndal, K.A.; Martins, H.R. Sympatry in grapsoid crabs (genera *Planes* and *Plagusia*) from olive ridley sea turtles (*Lepidochelys olivacea*), with descriptions of crab diets and masticatory structures. *Mar. Biol.* **2011**, *158*, 1699–1708. [CrossRef]
- Crosnier, A. Crustacés décapodes, Grapsidae et Ocypodidae. *Faune Madag.* **1965**, *18*, 1–143.
- Dai, A.-Y.; Yang, S.-L. *Crabs of the China Seas*; China Ocean Press: Beijing, China; Springer: Berlin, Germany, 1991; pp. 1–608.
- Naderloo, R. *Atlas of Crabs of the Persian Gulf*; Springer: Cham, Switzerland, 2017; pp. 1–444.
- Shiber, J.G. Brachyurans from Lebanese waters. *Bull. Mar. Sci.* **1981**, *31*, 864–875.
- Zaouali, J.; Ben Souissi, J.; Galil, B.S.; d’Udekem d’Acoz, C.; Ben Abdallah, A. Grapsoid crabs new to the Sirte Basin. *Mar. Biodivers. Rec.* **2008**, *1*, e73. [CrossRef]
- Sasaki, K. The Species List of Decapoda, Euphausiacea, and Stomatopoda of the World. 2023. Available online: https://www.researchgate.net/publication/376519923_The_Species_List_of_Decapoda_Euphausiacea_and_Stomatopoda_all_of_the_World_Version_07-812-Worldwide_species_list_of_Decapoda_Euphausiacea_and_Stomatopoda-?channel=doi&linkId=657bcf906610947889ccc159&showFulltext=true (accessed on 6 April 2026). [CrossRef]
- Ng, P.K.L.; Guinot, D.; Davie, P.J.F. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bull. Zool.* **2008**, *17*, 1–296.
- Davie, P.J.F.; Guinot, D.; Ng, P.K.L. Systematics and classification of Brachyura. In *Treatise on Zoology—Anatomy, Taxonomy, Biology—The Crustacea*; Castro, P., Davie, P.J.F., Guinot, D., Schram, F.R., von Vaupel Klein, J.C., Eds.; Brill: Leiden, The Netherlands, 2015; pp. 1049–1130.

18. Rathbun, M.J. *The Grapsoidea Crabs of America*; U.S. National Museum Bulletin; Smithsonian Institution: Washington, DC, USA, 1918; Volume 97, pp. 1–461.
19. Schubart, C.D.; Ng, P.K.L. On the identities of rafting crabs *Plagusia* spp. *Raffles Bull. Zool.* **2000**, *48*, 327–336.
20. Crandall, K.; Fitzpatrick, J. Crayfish molecular systematics: Using a combination of procedures to estimate phylogeny. *Syst. Biol.* **1996**, *45*, 1–26. [[CrossRef](#)]
21. Schubart, C.D.; Cuesta, J.A.; Felder, D.L. Glyptograpsidae, a new brachyuran family from Central America: Larval and adult morphology and a molecular phylogeny of the Grapsoidea. *J. Crustac. Biol.* **2002**, *22*, 28–44. [[CrossRef](#)]
22. Schubart, C.D.; Huber, M.G.J. Genetic comparisons of German populations of the stone crayfish, *Austropotamobius torrentium*. *Bull. Français Pêche Piscic.* **2006**, *380–381*, 1019–1028. [[CrossRef](#)]
23. Kumar, S.; Stecher, G.; Li, M.; Knyaz, C.; Tamura, K. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Mol. Biol. Evol.* **2018**, *35*, 1547–1549. [[CrossRef](#)]
24. Nei, M.; Kumar, S. *Molecular Evolution and Phylogenetics*; Oxford University Press: New York, NY, USA, 2000.
25. Schubart, C.D.; González-Gordillo, J.I.; Reyns, N.B.; Liu, H.-C.; Cuesta, J.A. Are Atlantic and Indo-Pacific populations of the rafting crab *Plagusia depressa* distinct? *Raffles Bull. Zool.* **2001**, *49*, 301–310.
26. Herbst, J.F.W. *Versuch Einer Naturgeschichte der Krabben und Krebse*; Bei Gottlieb August Lange: Berlin, Germany, 1782; Volume 1, pp. 1–274.
27. Bouvier, E.-L. *Décapodes Marcheurs*; Faune de France; Lechevalier: Paris, France, 1940; Volume 37, pp. 1–404.
28. Barnard, K.H. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). *Ann. S. Afr. Mus.* **1950**, *38*, 1–837.
29. Monod, T. *Hippidea et Brachyura Ouest-Africains*; IFAN: Dakar, Senegal, 1956; pp. 1–674.
30. Williams, A.B. *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States*; Smithsonian Institution Press: Washington, DC, USA, 1984; pp. 1–550.
31. Cruz da Rosa, L.; Barbosa dos Santos, R.; Freire, K.M.F. First record of the cliff crab *Plagusia depressa* (Fabricius, 1775) (Decapoda: Plagusiidae) from the coast of Sergipe, Brazil. *Nauplius* **2018**, *26*, e2018030. [[CrossRef](#)]
32. Muñoz, I.; Serrano, M. *Colección de Crustáceos Marinos (CRUST-IEOCD)*; Instituto Español de Oceanografía (IEO-CSIC): Cádiz, Spain, 2025. Available online: <https://www.gbif.org/dataset/317fd0a9-1bcf-4e94-bc3c-a685c4693c10> (accessed on 6 April 2026).
33. Muñoz, I.; García-Raso, J.E.; Sánchez, B.; Cuesta, J.A. Marine crabs from African waters housed in the Museo Nacional de Ciencias Naturales (MNCN-CSIC). Part II: Thoracotremata. *Diversity* **2025**, *17*, 689. [[CrossRef](#)]
34. Stimpson, W. Notes on North American Crustacea. *Ann. Lyceum Nat. Hist. N. Y.* **1860**, *7*, 177–246.
35. Miers, E.J. Revision of the Plagusiinae. *Ann. Mag. Nat. Hist.* **1878**, *1*, 147–154. [[CrossRef](#)]
36. Hilgendorf, F. Einige carcinologische Mittheilungen. In *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*; Gesellschaft Naturforschender Freunde: Berlin, Germany, 1882; pp. 22–25.
37. De Man, J.G. Carcinological studies in the Leyden Museum. No. 3. *Notes Leyden Mus.* **1883**, *5*, 150–169.
38. Alcock, A. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa, or Grapsoidea. Part II. *J. Asiat. Soc. Bengal* **1900**, *69*, 279–456.
39. Laurie, R.D. Report on the Brachyura collected by Professor Herdman at Ceylon in 1902. In *Report on the Pearl Oyster Fisheries of the Gulf of Manaar*; Government of Ceylon: Ceylon, Sri Lanka, 1906; Volume 5, pp. 249–432.
40. Chace, F.A., Jr. Decapod crustaceans from St Helena Island, South Atlantic. *Proc. United States Natl. Mus.* **1966**, *118*, 623–661. [[CrossRef](#)]
41. Matzen da Silva, J.; Creer, S.; dos Santos, A.; Costa, A.C.; Cunha, M.R.; Costa, F.O.; Carvalho, G.R. Systematic and evolutionary insights derived from mtDNA COI barcode diversity in the Decapoda (Crustacea: Malacostraca). *PLoS ONE* **2011**, *6*, e19449. [[CrossRef](#)]
42. Azzola, A.; Bianchi, C.N.; Morri, C.; Montefalcone, M.; Enrichetti, F. The tropicalisation of the Mediterranean Sea: A return to the past or an unprecedented future? *Adv. Mar. Biol.* **2026**, *103*, 1–45. [[CrossRef](#)]
43. González-Ortegón, E.; de Carvalho-Souza, G.F.; Muñoz, I.; Gómez, C.L.; Arana, D.; Cuesta, J.A. Atlantic expansion of the pink shrimp *Penaeus notialis* Pérez Farfante, 1967. *Mar. Biodivers.* **2024**, *54*, 30. [[CrossRef](#)]
44. González-Ortegón, E.; Berger, S.; Encarnação, J.; Chairi, H.; Morais, P.; Teodósio, M.A.; Oliva-Paterna, F.J.; Schubart, C.D.; Cuesta, J.A. Free pass through the Pillars of Hercules? *Front. Mar. Sci.* **2022**, *9*, 918026. [[CrossRef](#)]
45. Cuesta, J.A.; Drake, P.; Arias, A.M. First record of the blue crab *Callinectes exasperatus* for European waters. *Mar. Biodivers. Rec.* **2015**, *8*, e36. [[CrossRef](#)]
46. Cuesta Mariscal, J.A.; García-Raso, J.E.; González-Gordillo, J.I. Primera cita de *Rhithropanopeus harrisi* en la Península Ibérica. *Bol. Inst. Esp. Oceanogr.* **1991**, *7*, 149–153.
47. GBIF Secretariat. *Grapsus adscensionis* (Osbeck, 1765). In *GBIF Backbone Taxonomy*; Checklist Dataset; Global Biodiversity Information Facility (GBIF) Secretariat: Copenhagen, Denmark, 2023. [[CrossRef](#)]
48. Moreno Lampreave, D. Flora y fauna alóctona del medio marino andaluz. In *Especies Exóticas Invasoras en Andalucía*; Junta de Andalucía: Sevilla, Spain, 2010; pp. 214–229.

49. González-Ortegón, E.; García-Raso, J.E.; Calado, R.; López de la Rosa, I.; Guerrero, M.; Cuesta, J.A. Atlantic expansion of *Lysmata unicornis*. *Mar. Biodivers.* **2020**, *50*, 26. [\[CrossRef\]](#)
50. Holthuis, L.B. First record of the family Ogyrididae from European waters (Decapoda, Caridea). *Crustaceana* **1977**, *33*, 108–111. [\[CrossRef\]](#)
51. García-Raso, J.E. Presencia de una población de *Brachynotus atlanticus* en el sur de la Península Ibérica. *Bol. Soc. Port. Entomol.* **1985**, 19–26.
52. Zariquiey Álvarez, R. Crustáceos Decápodos Ibéricos. *Investig. Pesq.* **1968**, *32*, xv + 510 pp.
53. García-Raso, J.E.; Manjón-Cabeza, M.E. New record of *Liocarcinus mcleayi* from South Europe. *Crustaceana* **1996**, *69*, 84–93. [\[CrossRef\]](#)
54. García-Raso, J.E. New record of *Cycloes cristata* from European waters. *Bios* **1993**, *1*, 215–221.
55. García-Raso, J.E.; Salmerón, F.; Baro, J.; Marina, P.; Abelló, P. The tropical African hermit crab *Pagurus mbizi* in the Western Mediterranean Sea. *Mediterr. Mar. Sci.* **2014**, *15*, 172–178. [\[CrossRef\]](#)
56. Muñoz, I.; Coján, M.; Silva, L.; García-Raso, J.E.; Cuesta, J.A. First record of *Ilia spinosa* in European continental waters. *Thalassas* **2026**, *42*, 95. [\[CrossRef\]](#)
57. Marco-Herrero, E.; Abelló, P.; Drake, P.; García-Raso, J.E.; González-Gordillo, J.I.; Guerao, G.; Palero, F.; Cuesta, J.A. Annotated checklist of Iberian brachyuran crabs. *Sci. Mar.* **2015**, *79*, 243–256. [\[CrossRef\]](#)
58. Gilbert, J.M.; Muñoz, F.; Belaústegui, Z.; Hyžný, M. Fossil and modern fiddler crabs (*Uca tangeri*) and their burrows from SW Spain. *J. Crustac. Biol.* **2013**, *33*, 537–551. [\[CrossRef\]](#)
59. Rodríguez, A. Presencia de *Penaeus japonicus* en el Golfo de Cádiz. In *Acuicultura Intermareal*; Yúfera, M., Ed.; 1989; pp. 321–332.
60. García-Raso, J.E.; Cuesta, J.A.; Abelló, P.; Macpherson, E. Updating Iberian decapod fauna after 50 years. *Sci. Mar.* **2018**, *82*, 207–222. [\[CrossRef\]](#)
61. Cuesta, J.A.; Acosta-Morillas, V.; González, G.; de Carvalho-Souza, G.F.; González-Ortegón, E. First record of *Alpheus cf. lobidens* in the Gulf of Cádiz. *Crustaceana* **2024**, *97*, 429–451. [\[CrossRef\]](#)
62. de Carvalho-Souza, G.F.; Cuesta, J.A.; Acosta-Morillas, V.; Sánchez-Guerrero-Hernández, M.J.; Laiz, I.; González-Ortegón, E. Population structure of *Alpheus cf. lobidens* in southwestern Europe. *J. Shellfish Res.* **2024**, *43*, 59–68. [\[CrossRef\]](#)
63. Cuesta, J.A.; González-Ortegón, E.; Drake, P.; Rodríguez, A. First record of *Palaemon macrodactylus* in Europe. *Crustaceana* **2004**, *77*, 377–380. [\[CrossRef\]](#)
64. García-de-Lomas, J.; Dana, E.; López-Santiago, J.; González, R.; Ceballos, G.; Ortega, F. Management of *Eriocheir sinensis* in southern Spain. *Aquat. Invasions* **2010**, *5*, 323–330. [\[CrossRef\]](#)
65. de Carvalho-Souza, G.F.; Cuesta, J.A.; Arana, D.; Lobato, C.; González-Ortegón, E. Expansion of *Portunus segnis* into European waters. *BioInvasions Rec.* **2023**, *12*, 1033–1044. [\[CrossRef\]](#)
66. Relini, G.; Vallarino, G. Species richness of Crustacea Decapoda in MEDITS surveys. *Biol. Mar. Mediterr.* **2016**, *23*, 277–278.
67. Triay-Portella, R.; Martín, J.A.; Luque, L.; Pajuelo, J.G. Feeding ecology in invasive crabs. *Estuar. Coast. Shelf Sci.* **2022**, *274*, 107949. [\[CrossRef\]](#)
68. de Carvalho-Souza, G.F.; Kourantidou, M.; Laiz, I.; Núñez, A.; González-Ortegón, E. How to deal with invasive species that have high economic value? *Biol. Conserv.* **2024**, *292*, 110548. [\[CrossRef\]](#)
69. Ceca, E.D.; Corsetti, S.; Sagratini, G.; Vittori, S.; Borsetta, G. Socio-economic pathways for blue crab management. *Sci* **2026**, *8*, 48. [\[CrossRef\]](#)

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