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NOTES ON GEOGRAPHIC DISTRIBUTION

Deep protected habitats in the Gulf of Cádiz reveal an overlooked Iberian distribution of *Pagurus chevreuxi* (Bouvier, 1896) (Decapoda, Paguridae)

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Abstract. We report *Pagurus chevreuxi* (Bouvier, 1896) for the first time from Spanish waters of the Gulf of Cádiz, filling a gap in this species' documented distribution along the Iberian Atlantic margin. The specimen was collected at 418 m depth on Gazul mud volcano during the CIRCASUR2025 survey and identified using diagnostic morphological characters and mitochondrial 16S rRNA sequence data. This find represents the deepest confirmed record of the species, which was previously regarded as predominantly inhabiting shallow water. The new record also provides new evidence that the geographic and bathymetric distribution of *P. chevreuxi* may be broader and more continuous than currently documented across its known range.

Keywords. 16S, Anomura, hermit crab, Northeast Atlantic, new record, range extension

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Introduction

The family Paguridae Latreille, 1802 comprises more than 610 species worldwide (DecaNet 2026), with *Pagurus* Fabricius, 1775 representing its most species-rich genus. Its taxonomy is complicated by high morphological variability and interspecific similarity, which have led to the recognition of several species complexes (McLaughlin 1974; Ingle 1985; Olguín and Mantelatto 2013). *Pagurus* is well represented in the Northeastern Atlantic and Mediterranean Sea, although the distribution of several species remains incompletely known, particularly in the Gulf of Cádiz (d'Udekem d'Acoz 1999; García-Raso et al. 2014; Almón et al. 2022).

Pagurus chevreuxi (Bouvier, 1896) has been reported from the Eastern Atlantic and the Mediterranean Sea, where it is associated with soft- and rocky-bottom habitats and has been recorded predominantly between 3 and 50 m depth (Ledoyer 1968; Zariquiey Álvarez 1968; López de la Rosa and García Raso 1992; Grippa 1993; d'Udekem d'Acoz 1999; González and Telle 2024). This hermit crab has been infrequently reported in Spanish waters, and its distribution remains poorly documented. The first record of *P. chevreuxi* from the Iberian Peninsula was provided by Zariquiey Álvarez (1950), based on specimens collected in Cadaqués (Cap de Creus, northeastern Spain). Later, García-Raso (1984) reported the species from Alborán Island. More recently, new records from Galicia, northwestern Spain (Almón et al. 2023) and the Canary Islands (González and Telle 2024) have considerably expanded its known Atlantic distribution along the Spanish coasts. The Spanish waters of the Gulf of Cádiz remain the only region where the species has not yet been recorded, representing a persistent gap in its known distribution.

The Gulf of Cádiz (GoC) represents one of the most relevant regions in the southwestern Iberian Peninsula for marine conservation within the framework of the Natura 2000 network. This region constitutes an important biogeographic transition zone between the Atlantic Ocean and the Mediterranean Sea and is characterized by high habitat heterogeneity resulting from the interaction between

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Atlantic and Mediterranean water masses and the geomorphological complexity of the continental margin (Hernández-Molina et al. 2003; Díaz del Río et al. 2014; Sánchez-Leal et al. 2017). Consequently, the area supports diverse assemblages of benthic invertebrates and includes several protected Sites of Community Importance (Rueda et al. 2012; Díaz del Río et al. 2014; Sitjà et al. 2018; González-García et al. 2020), which play a crucial role not only in the conservation of vulnerable habitats and species (Rueda et al. 2016), but also as key reference areas for biodiversity assessment.

These protected areas include diverse benthic habitats, from deep soft bottoms and rocky outcrops to sponge- and coral-dominated biogenic structures that provide important microhabitats for associated fauna (Díaz del Río et al. 2014; Urra et al. 2021). At Gazul mud volcano, fluid seepage and methane-derived authigenic carbonates (MDAC) create heterogeneous hard-substrate habitats and distinct geochemical conditions that support specialized deep-sea communities and enhance local biodiversity (Rueda et al. 2012; Palomino et al. 2016; Fernández-Salas et al. 2021). Despite the ecological importance and protected status of the Gulf of Cádiz, its deep and sublittoral benthic fauna remains insufficiently explored, particularly small and cryptic invertebrates associated with structurally complex substrates.

In deep-marine protected areas, sampling is highly restricted, with no routine specimen collection and only limited trawling in accessible zones, resulting in persistent undersampling. This highlights the need for complementary approaches such as Remotely Operated Vehicles (ROVs), which enable largely non-invasive exploration while allowing occasional targeted sampling.

This study reports the first confirmed record of *P. chevreuxi* in the Spanish waters of the GoC, based on both morphological and molecular evidence. Besides extending the known geographic distribution of the species in the Northeastern Atlantic, this record also extends the known bathymetric range of the species, which has previously been regarded as predominantly inhabiting shallow water to depths exceeding 400 m. The record contributes new baseline data for future biogeographical and ecological research on regional decapod fauna. Considering the restricted sampling possibilities in deep marine protected areas, the study also emphasizes the value of complementary, minimally invasive technologies such as ROVs for documenting poorly known benthic biodiversity.

Methods

The specimen was collected during the CIRCASUR2025 survey aboard the R/V *Ángeles Alvariño*. Sampling operations were conducted during May–June 2025 using the ROV *Liropus 2000* across a bathymetric range of 75–500 m in the GoC (35°–37°N, 006.0°–007.3°W; southwestern Iberian Peninsula). The ROV *Liropus* is equipped with a high-definition Kongsberg video camera, a Kongsberg tooling camera, and three frontal LED matrix lighting units. In addition, the ROV has two precision hydraulic manipulator arms and a suction system for collecting samples. The specimen, once collected, was morphologically identified using specific literature (preliminary identification), photographed, and preserved in 70% ethanol for further examination in the laboratory. A tissue sample was taken for molecular confirmation. Molecular analyses were conducted at the ICMAN-CSIC Molecular Laboratory. The voucher specimen was deposited in the Marine Crustacean Collection of the Cádiz Oceanographic Center (CRUST-IEOCD) (Muñoz and Serrano 2026), where it is available for future reference and comparative studies.

The maps shown in Figure 1 were generated from DEMs derived from the ISUNEPCA 0616 survey, with a spatial resolution of 3 m, using CARIS Easy View for 3D visualization and CARIS HIPS & SIPS for bathymetric data processing. Geographic coordinates are expressed in degrees, minutes, and seconds.

The specimen, an ovigerous female, was examined under a stereomicroscope (Leica S9 i) and was identified following the original description by Bouvier (1896) and subsequent taxonomic keys and redescriptions of *Pagurus* species from the Northeastern Atlantic and Mediterranean regions (Ingle 1993). The colour of the specimen matched the predominant colour pattern described by Almón et al. (2023).

Measurements were taken with digital calipers (Absolute AOS Mitutoyo 500-181-30) and are given in millimetres (mm). Cephalothorax length (CL) was measured from the tip of the rostrum to the posterior border of the carapace at the midline including the membranous part, and shield length (ShL) was measured along the dorsal midline from the tip of the rostrum to the posterior margin of the shield.

For molecular confirmation, DNA was extracted from five eggs of the specimen using the Qiagen

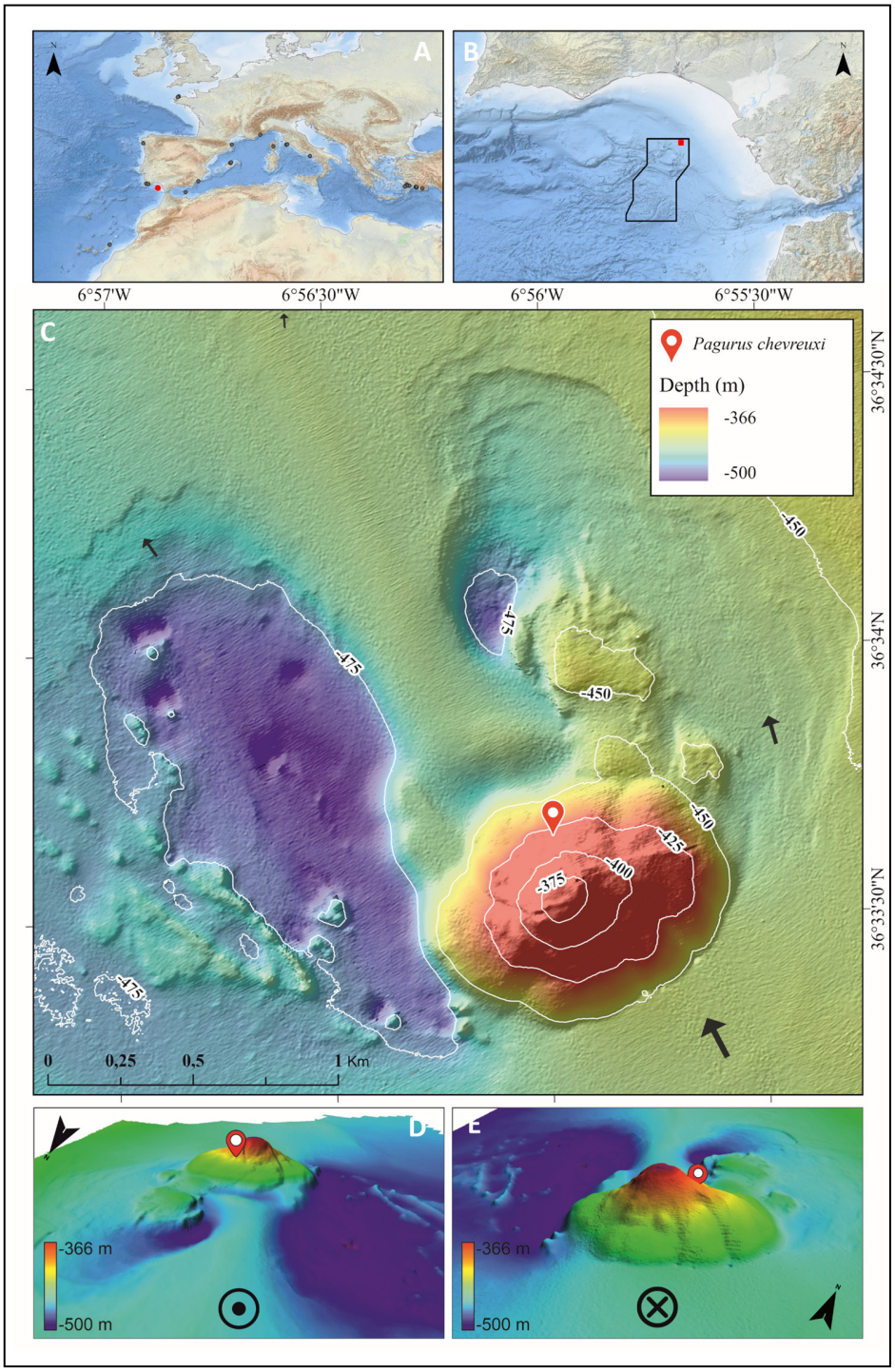

Figure 1. Geographic distribution and location of the new record of *Pagurus chevreuxi* in the Gulf of Cádiz. **A.** Previously published records of *P. chevreuxi* in the Northeastern Atlantic and Mediterranean region (black circles) and the new record from Gazul mud volcano (red circle). **B.** Detail of the Gulf of Cádiz showing the "Volcanes de fango del Golfo de Cádiz" Site of Community Importance (SCI ESZZ12002); the black rectangle indicates the area shown in C. **C**. High-resolution bathymetric model of the Gazul mud volcano; the red marker indicates the exact position of the *P. chevreuxi* record, and black arrows show the direction and velocity of near-bottom currents (0.19–0.43 m · s^{-1}). **D, E.** Three-dimensional views of the Gazul mud volcano from the leeward (**D**) and stossward (**E**) sides, showing the record location (red marker). Current direction is indicated using out-of-plane symbols (dot: current towards the observer; cross: current away from the observer).

DNeasy Blood and Tissue Kit following the manufacturer's protocol. The target mitochondrial gene, the large subunit ribosomal RNA (16S rRNA), was amplified by Polymerase Chain Reaction (PCR). Primers 1472 (5'-AGA TAG AAA CCA ACC TGG-3') (Crandall and Fitzpatrick 1996) and 16L2 (5'-TGC CTG TTT ATC AAA AAC AT-3') (Schubart et al. 2002) were used to amplify a maximum of 545 bp. PCR products were purified and bidirectionally sequenced by Stab-Vida Laboratories. Forward and reverse chromatograms were inspected, trimmed, and assembled into a consensus sequence at ICMAN-CSIC using Chromas version 2.6.6. The final sequence was validated through the Basic Local Alignment Search Tool (BLAST; Morgulis et al. 2008) on the NCBI nucleotide database.

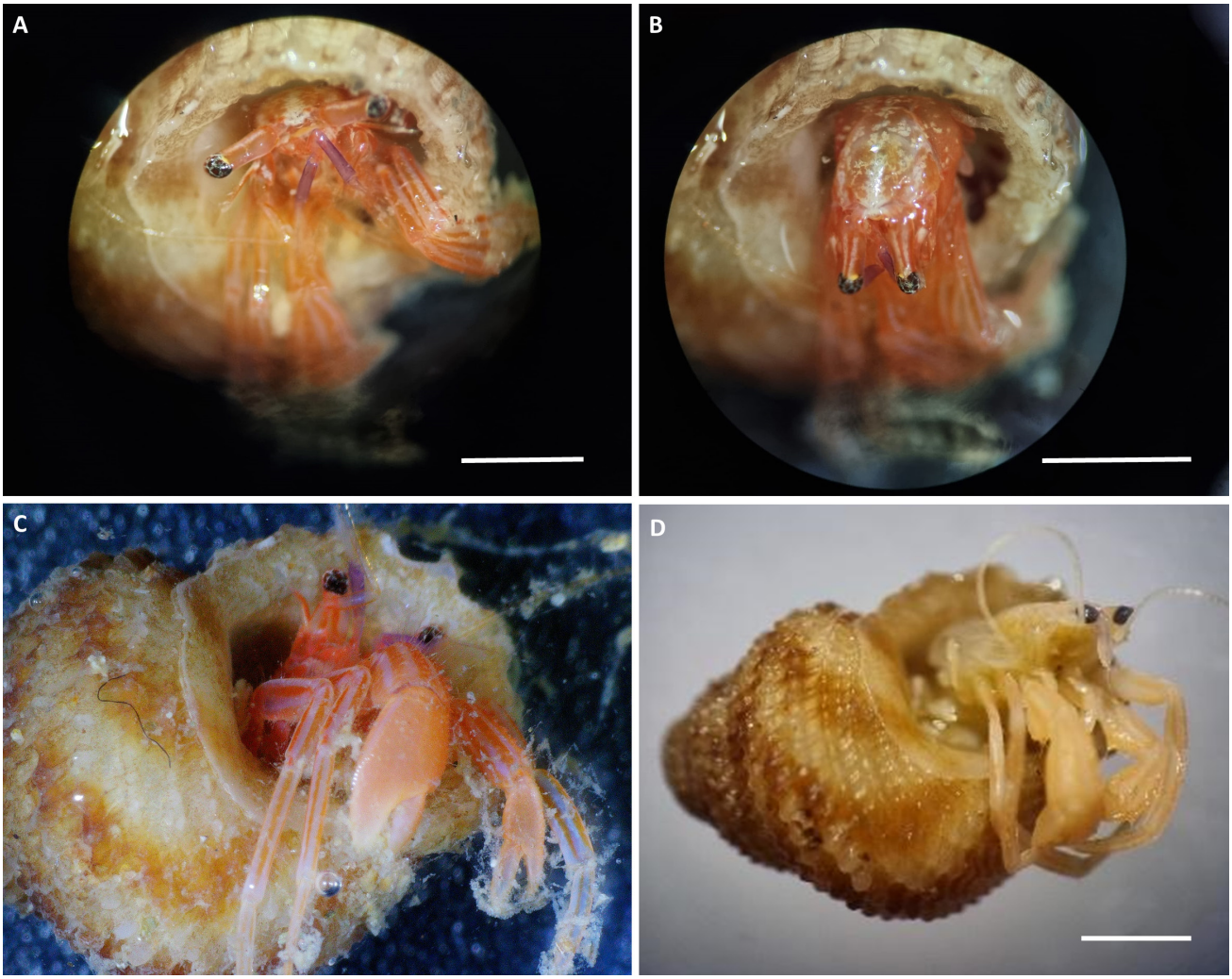

Figure 2. *Pagurus chevreuxi* from the Gulf of Cádiz. Live specimen occupying a shell of the gastropod *Danilia tinei* (Calcara, 1839), illustrating in situ colouration and general morphology. **A, B.** Frontal view. **C.** Slightly lateral view. **D.** Preserved specimen in ethanol. Scale bars: 0.5 cm.

Results

Superfamily Paguroidea Latreille, 1802
Family Paguridae Latreille, 1802

***Pagurus chevreuxi* (Bouvier, 1896)**
Figure 2

Basionym. *Eupagurus chevreuxi* Bouvier, 1896

New record. SPAIN — Cádiz • Gulf of Cádiz, Gazul mud volcano; 36°33′39″N, 006°55′59″W; 418 m depth; 30.V.2025; CIRCASUR2025 team leg.; CIRCASUR2025 survey, Station 15, ROV *Liropus 2000*; GenBank PZ443604; CRUST-IEOCD, CRUST-CS25/4455, 1 ovigerous ♀, preserved in 70% ethanol, CL 5.5 mm, ShL 4.2 mm.

Identification. The specimen agrees with the morphological description and diagnostic characters of *P. chevreuxi* provided by Bouvier (1896) and Ingle (1993). The live colouration also matches the predominant colour pattern in the Atlantic, as described by Almón et al. (2023), particularly the whitish corneas spotted with red and the orange ocular peduncles with pale longitudinal stripes (Figure 2). The morphological identification was further supported by the 16S rRNA sequence obtained from the specimen (see DNA identification below).

Distribution. The type locality of *P. chevreuxi* is Corsica in the Mediterranean Sea, at a depth of 11 m. The species is distributed in the Northeastern Atlantic from Brittany and the Bay of Biscay Southwards to the Canary Islands and widely throughout the Mediterranean Sea (Western, Central, and Eastern

basins) (Figure 1A). This species is herein recorded for the first time from the Spanish waters of the Gulf of Cádiz. Generally, this species is found in shallow waters down to approximately 50 m depth (Bouvier 1896; Bourdon 1965; Zariquiey Álvarez 1968; García-Raso 1984; Ingle 1993; d'Udekem d'Acoz 1999; Sampaio et al. 2016; Almón et al. 2023). However, the present study extends the known depth range of *P. chevreuxi* to a depth of 418 m along the continental slope.

Size. The reported size of *P. chevreuxi* ranges from a minimum of 0.6 mm shield length (ShL) (González and Telle 2024) to a maximum of approximately 4.5 mm in cephalothorax length (CL) in the original description (Bouvier 1896). The specimen examined in the present study measured 4.2 mm in ShL and 5.5 mm in CL and may represent one of the largest individuals reported for *P. chevreuxi*, although direct comparison with previous records is limited by differences in measurement criteria.

Habitat. *Pagurus chevreuxi* has traditionally been regarded as a shallower species, occurring mainly at depths between 3 and 50 m. It has been reported from coralligenous rocky substrates with bryozoans and sponges, calcareous bottoms associated with *Posidonia* seagrass, particularly among rhizomes and leaf layers, and occupying gastropod shells such as those of *Monophorus perversus* (Linnaeus, 1758) (Ledoyer 1968; Zariquiey Álvarez 1968; López de la Rosa and García Raso 1992; Grippa 1993; d'Udekem d'Acoz 1999; Almeida 2008; Sampaio et al. 2016; González and Telle 2024). In the present study, *P. chevreuxi* was found at 418 m depth on Gazul mud volcano, occupying a shell of *Danilia tinei* (Calcara, 1839), a gastropod relatively frequent on this mud volcano (Utrilla et al. 2020). The specimen occurred on hard bottoms comprising methane-derived authigenic carbonates (MDACs) and coral rubble, within assemblages dominated by *Madrepora oculata* Linnaeus, 1758 and *Desmophyllum pertusum* (Linnaeus, 1758). The associated benthic assemblage was characterized by colonial scleractinians, mainly *M. oculata*, together with the antipatharian black coral *Antipathella subpinnata* (Ellis & Solander, 1786), highly branched hydrozoans, small gorgonians such as *Callistephanus dubia* (Thomson, 1929), poriferans such as *Haliclona* spp. and *Poecillastra compressa* (Bowerbank, 1866), bryozoans, and echinoids such as *Cidaris cidaris* (Linnaeus, 1758) (Figure 3).

The specimen was collected on the leeward side of the Gazul mud volcano relative to the near-bottom current direction, in an area influenced by estimated current velocities of 0.19–0.43 $m \cdot s^{-1}$ (Sánchez-Leal et al. 2017) and characterized by hard substrates, coral rubble, and suspension-feeder assemblages (Figure 1C–E).

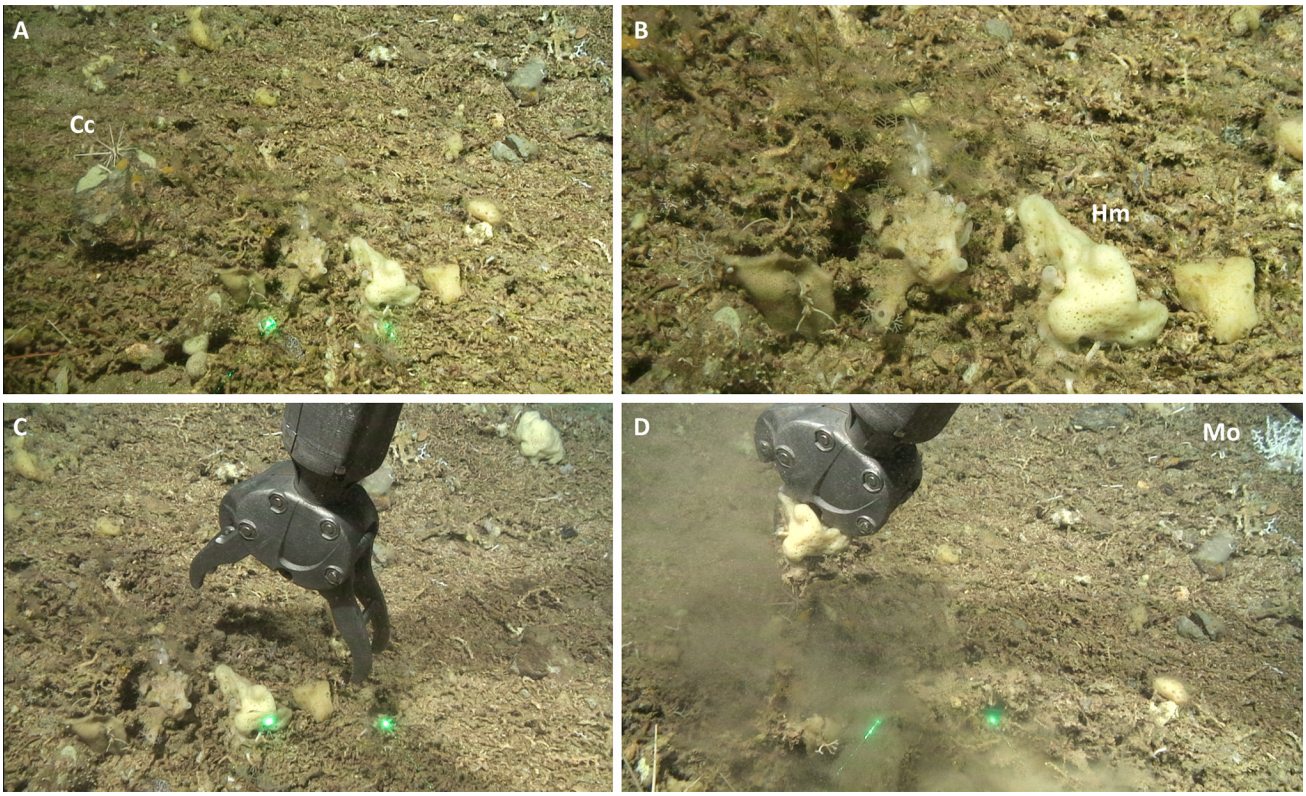

Figure 3. Sequence showing the habitat and collection of *Pagurus chevreuxi*. **A.** Habitat context. **B.** Associated fauna. **C.** ROV manipulator approach. **D.** Specimen recovery. *Cidaris cidaris* (Cc), *Haliclona mucosa* (Hm), *Madrepora oculata* (Mo).

DNA identification. The 16S sequence obtained (PZ443604) matches 100% with the sequences PQ590531 (527 bp, 97% coverage) and PQ579266 (522 bp, 96% coverage), and 99.82% with the sequence PQ579267 (differing in only one position, 545 bp, 100% coverage) of specimens IEOCD-BR/287, IEOCD-BR/297, and IEOCD-BR/3160, respectively. All these specimens were collected in Galicia (northwestern Spain) (Almón et al. 2023). The difference between specimen IEOCD-BR/3160 and the remaining specimens, including the specimen reported in the present study, is a C/T transition at position 349, therefore, this difference is not attributable to sequence length.

Discussion

The present work represents the first confirmed record of *Pagurus chevreuxi* from the Spanish waters of the Gulf of Cádiz, filling a distributional gap between known Atlantic and Mediterranean populations (Zariquiey Álvarez 1968; García-Raso 1984; Almón et al. 2023; González and Telle 2024; Figure 1). Although the present record does not represent the first occurrence of *P. chevreuxi* in the southwestern Iberian Peninsula, previous evidence from the region is limited to an M.Sc. thesis reporting the species from the Portuguese sector, specifically in the Algarve region (Portimão, two specimens, and Albufeira, one specimen, 10–30 m depth; Almeida 2008). Subsequently, Sampaio et al. (2016) reported eight specimens from seven Portuguese localities, but these records lack precise locality data and refer to specimens collected in shallow waters (25–50 m depth). Moreover, neither the specimens reported by Almeida (2008) nor those reported by Sampaio et al. (2016) appear to have been deposited in a reference collection, which precludes their subsequent re-examination. In contrast, the present study provides the first confirmed and well-documented record from the Spanish waters of the GoC, supported by both morphological and molecular identification, and significantly extends the known bathymetric range of the species in the region. To our knowledge, this represents the first documented record of *P. chevreuxi* occupying a shell of *Danilia tinei*.

The occurrence of *P. chevreuxi* at depths exceeding 400 m represents a considerable extension of its previously reported bathymetric range, as the species has generally been associated with shallow-water habitats down to approximately 50 m. However, the ecological significance of this bathymetric difference remains uncertain. The presence of hard substrates, biogenic structures and suspension-feeder assemblages at the Gazul mud volcano may indicate that some habitat features potentially suitable for the species persist at greater depths. Therefore, the bathymetric distribution of *P. chevreuxi* could be broader than currently documented, although further records and habitat-specific comparisons are needed to support this interpretation.

The occurrence of *P. chevreuxi* in the hydrodynamically active Gazul mud volcano may be favoured by local conditions that support structurally complex suspension-feeder assemblages. The specimen was collected on the leeward side of the mud volcano, where reduced hydrodynamic exposure may provide suitable microhabitats while maintaining proximity to corals, sponges, hydrozoans, and bryozoans. Such habitats could offer refuge for small cryptic decapods, although additional records are needed to confirm this association.

This finding is consistent with the recognized role of the GoC as a biogeographic transition zone between the Atlantic Ocean and the Mediterranean Sea, influenced by water mass exchange through the Strait of Gibraltar and by its geomorphological characteristics (Bellanco and Sánchez-Leal 2016; Sánchez-Leal et al. 2017). This mosaic of habitats promotes faunal overlap and reinforces its role as a highly permeable transition zone, rather than a sharp biogeographic boundary (González-Duarte et al. 2013). Within this context, the specimen of *P. chevreuxi* was collected in the Gazul area, a marine protected zone within the Natura 2000 network, representative of the diverse benthic habitats characteristic of the region. This record also supports a broader ecological and biogeographic amplitude for *P. chevreuxi*, which is better regarded as a Northeastern Atlantic–Mediterranean species that may be more continuously distributed than currently documented. However, since the present record is based on a single specimen, no inference can yet be made regarding population establishment, habitat preference, frequency of occurrence, or reproductive population size at Gazul mud volcano.

The absence of previous records of *P. chevreuxi* from Spanish waters of the GoC is likely due to the small body size and cryptic nature of *Pagurus* species, limited and uneven sampling effort in deep and protected areas, the scarcity of taxonomic expertise focused on small pagurid taxa, and insufficient habitat-specific surveys in structurally complex benthic habitats. Rather than indicating a true biogeographic restriction, this apparent gap probably reflects sampling artefacts, as suggested by the increasing number of recent records from previously undersampled sectors of the Iberian Peninsula.

ROVs are valuable tools for surveying deep and protected environments where conventional sampling is limited, as they combine targeted specimen collection with in situ observations of habitat structure and associated fauna. This approach improves the ecological interpretation of records such as that of *P. chevreuxi*.

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Additional information

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

No ethical statement is reported.

Use of artificial intelligence (AI)

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI. No AI tools were used in the preparation of this manuscript.

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Author contributions

Data curation: IM, SR, CC, JAC, CF, MS. Formal analysis: IM, JAC. Funding acquisition: JGH, YV, MD. Investigation: IM, SR, JAC, JGH, MD. Methodology: IM, SR, JAC. Visualization: MS, RJR, LMF. Software: JAC, MS, RJR, LMF. Validation: IM, MD. Writing – original draft: IM. Writing – review and editing: IM, SR, JAC, LMF, MS, JGH, MD.

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Data availability

Molecular data generated in this study are available in GenBank under accession number PZ443604. The voucher specimen is deposited in the Marine Crustacean Collection of the Cádiz Oceanographic Center (CRUST-IEOCD) under accession code CRUST-CS25/4455.

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