

Description of unique live colour patterns as a tool for discriminating hermit crab species in the Iberian Peninsula

Bruno Almón^{1,2}, Eva García-Isarch³, Jose A. Cuesta⁴, J. Enrique García-Raso⁵

¹ Instituto Español de Oceanografía, IEO-CSIC, Centro Oceanográfico de Vigo. Subida a Radio Faro, 50-52, 36390 Vigo, Spain.

(BA) (Corresponding author) E-mail: brunoalmon2@yahoo.es. ORCID iD: <https://orcid.org/0000-0001-7350-6035>

² Grupo de Estudio do Medio Mariño (GEMM), Puerto Deportivo s/n. 15960 Ribeira. A Coruña. Spain.

³ Instituto Español de Oceanografía, IEO-CSIC, Centro Oceanográfico de Cádiz. Muelle de Levante s/n, 11006 Cádiz, Spain.

(EG-I) E-mail: eva.garcia@ieo.csic.es. ORCID iD: <https://orcid.org/0000-0003-3027-382X>

⁴ Instituto de Ciencias Marinas de Andalucía, ICMAN-CSIC. Avenida República Saharaui, 2, 11519 Puerto Real, Cádiz, Spain

(JAC) E-mail: jose.cuesta@icman.csic.es. ORCID iD: <https://orcid.org/0000-0001-9482-2336>

⁵ Universidad de Málaga, Fac. de Ciencias, Dep. Biología Animal, Campus Teatinos, s/n, 29071, Málaga, Spain.

(JEG-R) E-mail: garciaraso@uma.es. ORCID iD: <https://orcid.org/0000-0003-3092-9518>

Summary: The unique colour patterns of the hermit crab species inhabiting the Iberian Peninsula and geographically close areas are studied based on colour patterns observed in live specimens either in the field or live in the laboratory. Live colour patterns are shown to be useful for differentiating species in the Paguroidea from Iberian waters. Colour information has not been frequently documented in previous studies, mainly because of difficulties in accessing live specimens. Up to 51 species are currently recorded within the study area, 45 of which are included in the present work, focusing on the distinctive colour traits for each species that can be observed in the field. A complete key for identifying the species within the study area based on colour patterns is included. This study is the first attempt to put in place this type of tool oriented to field work. Further studies will be required to complete and update this information, especially for species which are scarce or difficult to observe alive.

Keywords: taxonomy; Paguroidea; morphology; biogeography; biodiversity; adaptation; ecology; cryptic species.

Descripción de patrones únicos de coloración en vivo como herramienta para la discriminación de especies de cangrejos ermitaños en la península ibérica

Resumen: El estudio de los patrones de coloración en ejemplares vivos observados tanto en el campo como en laboratorio, han permitido investigar la existencia de patrones de coloración distintivos para las especies de cangrejos ermitaños que habitan en la península ibérica y zonas geográficamente cercanas. Estos patrones de coloración han demostrado ser de gran utilidad en los Paguroidea de aguas Ibéricas para la identificación de especies. La información relativa al color ha sido frecuentemente obviada en el pasado, principalmente debido a las dificultades para acceder a los ejemplares vivos. En la actualidad existen alrededor de 51 especies registradas en la zona de estudio, 45 de las cuales se incluyen en el presente trabajo, poniendo el foco en los rasgos de color distintivos de cada especie que pueden observarse en el campo. Se incluye una clave completa para la identificación de las especies dentro del área de estudio basada en los patrones de color. Este estudio es el primer intento de implementar este tipo de herramienta orientada al trabajo de campo. Serán necesarios más estudios para completar y actualizar esta información, especialmente para aquellas especies que son escasas o difíciles de observar en vivo.

Palabras clave: taxonomía; Paguroidea; morfología; biogeografía; biodiversidad; adaptación; ecología; especies crípticas.

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INTRODUCTION

The marine environment is a changing scenario in which species are frequently forced to adapt to ensure their survival. Among other adaptive capacities, many taxa are known to have the ability to develop different chromatic patterns (Duarte et al. 2017), evolving at different rates depending on the organism's life strategy and the relative importance of those changes for their survival. This behaviour is fostered by several factors and can serve various purposes, most commonly related to camouflage and predator avoidance but also to sexual selection and recognition between congeners (Irion and Nüsslein-Volhard 2019). The existence of popular examples of this behaviour is well-known within groups such as cephalopods and fish, but crustaceans are no exception, with many documented examples of chromatic changing behaviour in *Brachyura* (Abelló et al. 1997, Detto et al. 2008), *Caridea* (Gallardo-Escárate et al. 2007) and in hermit crabs (Pessani and Premoli 1992, Pessani and Tirelli 2006, Poupin and Lemaitre 2003). Some of these colour changes occur in a short period of time, usually associated with rapid changes in the environment, while others are the product of the evolutionary history of the species, thus being fixed and species-specific (McNamara and Milograna 2015).

Despite the attention that this biological trait has received in some crustaceans (e.g. Bauer 2004, Martin and Zimmerman 2007), the available literature addressing colour descriptions on hermit crabs has focused mainly on genera involving very striking species such as *Calcinus* (Pessani and Tirelli 2006, Malay and Paulay 2010, Mandai et al. 2018), *Ciliopagurus* (Poupin and Lemaitre 2003, Poupin and Malay 2009), *Clibanarius* (Negri et al. 2014), *Paguropsis* (Lemaitre et al. 2018) and *Cancellus* (Felder and Lemaitre 2020), all of them with a greater number of species in tropical latitudes.

In contrast, the taxonomy of the Paguroidea in temperate zones has traditionally been based on the morphological study of preserved specimens, in which colour had been lost or sometimes modified by interaction with preservative substances or procedures. Although colour descriptions have been included occasionally as complementary information when available (Forest 1955, Lemaitre 2004, 2014, García-Raso et al. 2014), this information remains absent or incomplete for many species. One important exception to this rule is the work conducted by Dr. Ricardo Zariquiey Álvarez, who devoted several articles to a detailed description of the colour patterns of some common hermit crab species of the Iberian Peninsula (Zariquiey Álvarez 1949, 1954), also including a summary version in his posthumous work dedicated to Iberian decapods (Zariquiey Álvarez 1968).

In line with this spirit, this study contains descriptive information about the colour patterns of hermit crab species from an area covering the whole Iberian Peninsula and neighbouring areas such as the Canary Islands, Madeira, the North African coast and the southern part of the North Sea, all of them with some connection with the Iberian coasts and therefore susceptible to species exchange. Of a total of 51 species recorded in the area, the present work provides descrip-

tions of 45 species distributed in 15 genera and belonging to three families. The descriptions included here attempt to focus especially on characters that are distinctive of the species and that can be observed in the field. It is clear that variations occur within species, and when known, the different patterns are also described. Colours in nature are not a discrete variable, but more often a gradual palette. For this reason, although the illustrations presented in this work are intended to represent the variations observed, special emphasis has been placed on colour patterns that are unique to the species, and secondary importance is given to backgrounds or patterns that are more variable.

Although colour patterns do not always reflect genetic differences (Mandai et al. 2018), they can reveal an ongoing evolutionary process through which two or more species diverged from a common ancestor, the colour sometimes being the only discernible difference between them (Udekem d'Acoz 1995, Poupin and Malay 2009). An example among the species found in our study area is the case of *Clibanarius aequabilis* (Dana, 1851), found in the Macaronesian islands and genetically different from *Clibanarius erythropus* (Latreille, 1818), which is present in waters off the Iberian Peninsula (Almón et al. *in prep.*). Because they occur more quickly than other morphological changes, colour patterns can reflect subtle changes at the moment they are occurring. For this reason, they could be a very useful tool, in combination with other available techniques, for studying changes occurring over time, leading to a more flexible monitoring of species differentiation and variations in faunal composition.

The aim of this study was to analyse and describe the unique colour patterns of the Paguroidea species recorded so far from the Iberian Peninsula and surrounding areas, thus providing a new tool for improving identification of species in the field.

MATERIALS AND METHODS

Specimens were obtained from different areas and by different methods that depended mainly on their depth occurrence. Individuals from littoral and sub-littoral shores were searched by direct visual observation and collected by hand on foot from the shore in intertidal areas or by scuba diving. The main sampling areas were located strategically around the Iberian coasts, mainly in waters off Galicia, the Gulf of Cádiz, the Canary Islands, the Mediterranean coasts of Andalusia and the eastern Iberian Peninsula. Deep-sea individuals were collected during series of bottom-trawl scientific surveys carried out by the Spanish Institute of Oceanography (*Instituto Español de Oceanografía* - IEO-CSIC) that covered the shelf and slope of most Iberian waters: ARSA (2017, 2018, 2020, 2021) in the Spanish Atlantic waters of the Gulf of Cádiz, DEMERSALES (2019, 2021) and CIRCAS (2021) on the north coast of the Iberian Peninsula, MEDITS (2017 and 2018) and CIRCA_LEBA (2021) covering the whole Mediterranean Iberian coasts. Other relevant areas were covered by PORCUPINE (2012, 2017 and 2018) in the North Sea and CIRCAN (2020) in the Canary archipelago. Several samples were

also obtained from the Canary seamounts (INCOECO and INFUECO 2010) and from the mud volcano complex near Cádiz (INDEMARES-CHICA 2011), both areas included in the LIFE+ Project INDEMARES (<https://www.indemares.es/>). All specimens are preserved in one of the following collections: the Marine Crustacean Collection (CRUST-IEOCD) belonging to Cádiz Oceanographic Centre (CSIC) (Muñoz et al. 2022), the Crustaceans Collection (IU) of the Muséum national d'Histoire naturelle (MNHN, Paris) (MNHN, Chagnoux 2022), the Biological Reference Collections (ICM-CSIC) (Guerero et al. 2021) and the Bavarian State Collection for Zoology (ZSM) (<https://doi.org/10.15468/hrzzrc>). A list with a selection of the most important samples and references used to study the colour patterns can be consulted in Appendix 1.

Each collected shallow water specimen was photographed alive, underwater when possible, or in a salt-water aquarium in the laboratory. The individuals collected during the scientific surveys were photographed in situ when possible, or otherwise they were frozen to prevent the loss of colouration and photographed later in the laboratory. Some of these images have been included for reference, as vouchers of the material used to study the coloration of the species. All specimens were then preserved in 70% ethanol to perform taxonomic revisions and molecular analyses as part of a work in progress to obtain DNA sequences of the Iberian hermit crabs in order to confirm the initial identification based on colour information. Colour patterns were represented through a series of figures devoted to illustrating the unique colorimetric signature of each species. All figures reflect primarily adult specimens, except for cases in which noteworthy differences were observed in juvenile stages, for which the juvenile colouration is also described. In addition, all drawings correspond to male specimens unless otherwise indicated. For some species, the coloration of certain body parts has not been described, either because of lack of information (it has been lost or is not clear) or because they are not considered relevant. Illustrations were drawn using a digital tablet combined with Inkscape software (www.inkscape.com) for vectorial artwork and processed later in Photoshop (www.adobe.com) to produce colour raster layers. The vector designs combine original drawings with others modified from previous works, as indicated in the figure captions.

Colour descriptions are based on Werner's nomenclature of colours, a classic taxonomic guide to the colours of the natural world recently reedited, whose catalogue is now also accessible online for consultation at <https://www.c82.net/werner/>.

RESULTS

Family DIOGENIDAE Ortmann, 1892
Genus *Calcinus* Dana, 1851
Calcinus tubularis (Linnaeus, 1767)

(Figs 1A, 16A)

Eyes (Fig. 1A.1). Ocular peduncles with proximal part bluish grey, turning to red lilac purple fading to

yellowish white in distal half; numerous thick rounded bright arterial blood red spots covering the entire surface of peduncles; velvet black corneas surrounded by a cream yellow ring. **Ocular acicles** (Fig. 1A.2) bright arterial blood red. **Antennular** (Fig. 1A.3) peduncles with segments 1-2 umber brown or smoking grey; proximal part of segment 3 same colour, going berlin blue in distal 2/3; reddish flagellum. **Antennal** (Fig. 1A.4-5) segments 1-4 and acicle clove brown tinged with arterial blood red; segment 5 sienna yellow; flagellum hyaline with alternating brownish red articles. **Shield** (Fig. 1A.6). Protogastric region with vermilion red shield-shaped patch. **Chelipeds** (Fig. 1A.7) both with a similar pattern; merus and carpus arterial blood red; propodus with numerous bright arterial blood red rounded spots over a red lilac purple background covering proximal half of palm; distal part and fingers, with white background and scattered bright arterial blood red spots. **Pereiopods 2-3** (Fig. 1A.8-9). Ischium, merus and propodus with red lilac purple background tinged with variable amount of bluish grey and longitudinal buff orange stripes; propodus with distal dorsolateral surface vermilion red; dactylus snow-white with bright arterial blood red spots arranged as transversal rings.

Genus *Clibanarius* Dana, 1852
Clibanarius erythropus (Latreille, 1818)
(Figs 1B, 16B)

General colouration in this species varies between individuals, with two main chromatic variations: one with oil green general background and orpiment orange tones (the one illustrated here) and one with hyacinth red background and scarlet red tones.

Eyes (Fig. 1B.1-2). Ocular peduncles deep reddish orange in proximal 1/4, turning to olive distally; corneas velvet black with snow-white spots. **Ocular acicles** brownish. **Antennules** (Fig. 1B.3) buff orange, with distal part of segment 3 turning to orpiment orange. **Antennae** (Fig. 1B.4) with basal articles oil green, changing to deep reddish orange in distal part of segment 4 and entire segment 5, as well as flagellum. **Chelipeds** (Fig. 1B.5) both with a similar pattern; oil green background; palm pale verditer blue; arterial blood red stripes in fingers outlined by ultramarine blue; tubercles ultramarine blue; black claws. **Pereiopods 2-3** (Fig. 1B.6-7) ranging from reddish orange background in merus to deep olive green in carpus and propodus; merus, carpus and propodus with cream yellow lines in dorsolateral surfaces; dactylus with scarlet red longitudinal stripes over white or berlin blue background. **Maxillipeds** (Fig. 1B.8). Exopods 1, 2 and 3 dark chocolate red, turning translucent distally; ultramarine blue stripes on tips and base of flagellum.

Clibanarius aequabilis (Dana, 1851)
(Figs 1C, 16C)

Eyes (Fig. 1C.1-2). Ocular peduncles with proximal 2/3 deep reddish orange, turning to oil green distal-

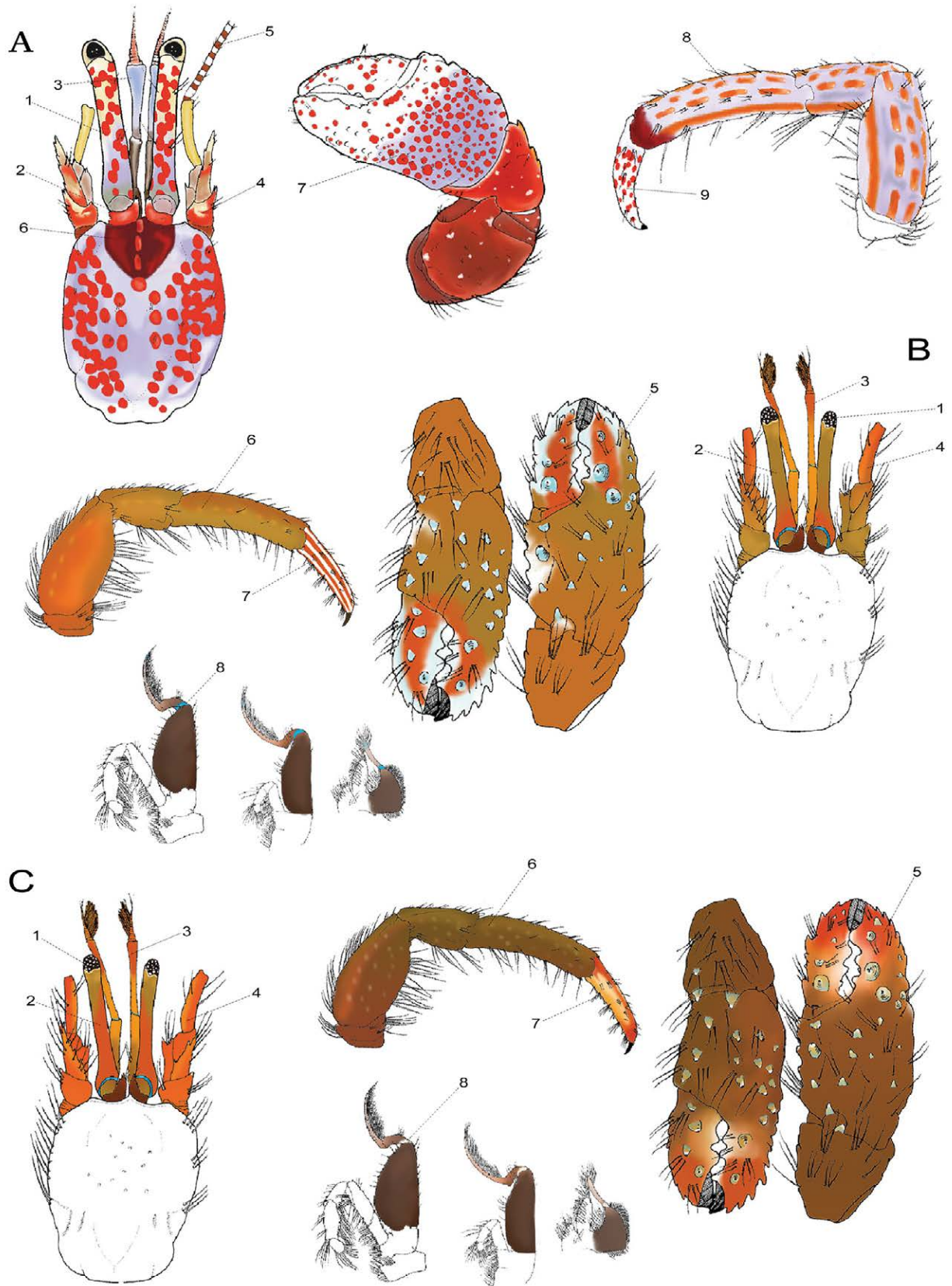


Fig. 1. – Colour patterns of the Diogenidae species: *Calcinus tubularis* (A, 1-9); *Clibanarius erythropus* (B, 1-8); *Clibanarius aequabilis* (C, 1-8). All vectorial drawings modified from Ingle (1993).

ly; black corneas with snow-white spots. **Antennules** (Fig. 1C.3) buff orange with distal part of segment 3 and flagellum deep reddish orange, almost red; lower half of segments 2-3 oil green. **Antennae** (Fig. 1C.4) deep reddish orange, with outer and inner margins as well as flagellum almost red. **Chelipeds** (Fig. 1C.5) both with a similar pattern; dark hyacinth red background and lighter areas at base of fingers; scarlet red path in distal margin of fingers; tubercles bluish green proximally, oil green medially and white at tip. **Pereiopods 2-3** (Fig. 1C.6-7) with yellowish dotted lines running along dorsal, medial and ventral surfaces of merus, carpus and propodus; dactylus saffron yellow with scarlet red proximal, distal and dorsal areas. **Maxillipeds** (Fig. 1C.8). Exopods 1-3 dark chocolate red, turning translucent distally; bright dirty white rings on tips and base of flagellum.

Genus *Diogenes* Dana, 1851

Diogenes curvimanus (Clément, 1874)
(Figs 2A, 17C, D)

Eyes (Fig. 2A.1). Greenish white ocular peduncles, with broad chestnut brown triangular dorsal patch, broadened proximally and running along inner surface reaching the base of corneas; velvet black corneas. **Ocular acicles** (Fig. 2A.2) dull verditer blue. **Antennules** (Fig. 2A.3) skimmed milk white, with pale wood brown patch on segment 2, buff orange in proximal 2/3 of segment 3 and flagellum. **Antennal** (Fig. 2A.4) peduncles greenish white or reddish tinged with pale buff orange and dull chestnut brown, with conspicuous verditer blue spot on dorsal face of segment 4. **Chelipeds. Left** (Fig. 2A.5-6) carpus with reddish orange background, and incomplete medial chestnut brown ring; orange-coloured white hand with chestnut brown spot at base of palm, extending in two narrow lines towards medial surface in males, and another more apparent at base of dactylus. **Right** (Fig. 2A.7) smaller, whitish; carpus with buff orange proximal area; all segments with scattered yellowish brown spots, especially associated with larger spines or tubercles. **Pereiopods 2-3** (Fig. 2A.8-11) with reddish white background colour; merus with yellowish brown medial (incomplete) and proximal (complete but duller) rings; carpus with incomplete chestnut brown ring medially, and a small spot dorso-proximally; propodus with large proximal stain extending latero-ventrally to half propodus length; dactylus with a yellowish brown base that extends along the sulcus; sometimes this line is very faint and almost imperceptible.

Diogenes armatus Almón, Cuesta, Schubart and García-Raso, 2021 in Almón et al. (2022a)
(Figs 2B, 17A, B)

Eyes (Fig. 2B.1). Ocular peduncles orange-coloured with tile red tones, with smoke grey triangular dorsal patch, broadened proximally and running along inner surface reaching the base of corneas; velvet black corneas outlined with reddish orange spots. **Ocular acicles** (Fig. 2B.2) buff orange proximally, grading

to snow-white distally. **Antennules** (Fig. 2B.3) background hyaline berlin blue; buff orange line (not always well-defined) running along dorsal margin; buff orange flagellum. **Antennae** (Fig. 2B.4) background berlin blue, going oil green at basal segment level; characteristic chestnut brown stain on antennal scale proximal surface. **Chelipeds. Left** (Fig. 2B.5-7) merus and carpus with oil green background and some diffuse tile red areas; umber brown transversal stripes on medial zone of merus, and proximal, medial and disto-inner areas of carpus; palm oil green, lighter than merus and carpus, with orpiment orange patch on upper proximal surface of dactylus, and some narrow ones following the main spinose ridges; base of the bigger tubercles with orpiment orange taints; small umber brown taints in mid-dorsal and apical areas. **Right** (Fig. 2B.8-9) overall colour oil green, with whiter ventral area; umber brown spots in middle upper area of merus, proximal and middle upper area of carpus and other more blurred in distal part of carpus, proximal upper palm and proximal area of fingers. **Pereiopods 2-3** (Fig. 2B.10-11) general oil green colour dorsally, fading to white ventrally; umber brown dorsolateral rings in medial and distal areas of merus, basal and medial areas of carpus, base and 2/4 of propodus; dactylus pale brownish red, with white ring distally; brownish red patch in proximal area extending in thin lines along dorsal, ventral and medial areas.

Diogenes pugilator (Roux, 1829)
(Figures 2C, 17E, F)

Eyes (Fig. 2C.1). Orange-coloured white ocular peduncles with uniform reddish orange triangular dorsal patch, broadened proximally and running along inner surface reaching the base of corneas. **Ocular acicles** (Fig. 2C.2) pale reddish orange. **Antennules** (Fig. 2C.3) translucent with dorsal buff orange line; honey yellow flagellum. **Antennal** (Fig. 2C.4) segment 1 uniform reddish orange; segments 2-5 white, tinged with reddish orange in dorsal surface of segment 2 and lateral margins of segments 4-5; antennal acicles with vermilion red stain in proximal inner area; flagellum with vermilion red rings evenly spaced. **Shield** (Fig. 2C.5) with paired brownish red longitudinal stains. **Chelipeds. Left** (Fig. 2C.6-7) with snow-white background colour; merus and carpus with upper half reddish orange tinged with green, with narrow vermilion red stripe medially, complete in merus, partial in carpus; hand with broad chestnut brown well-defined spots in upper proximal half of dactylus, lower distal area of palm, and proximal medial area of palm; very faint oil green areas in distal area of propodus, and pale buff orange in upper proximal area. Some new colour varieties have recently been found in the chelae of this species, which are mentioned in the discussion and illustrated in Figure 15. **Right** (Fig. 2C.8-9) snow-white background colour; vermilion red spot in upper proximal carpus area; reddish orange zones in dorso-distal margin of carpus and proximal area of propodus; reddish orange ring in proximal area of dactylus. **Pereiopods 2-3** (Fig. 2C.10) reddish orange, darker in dorsal

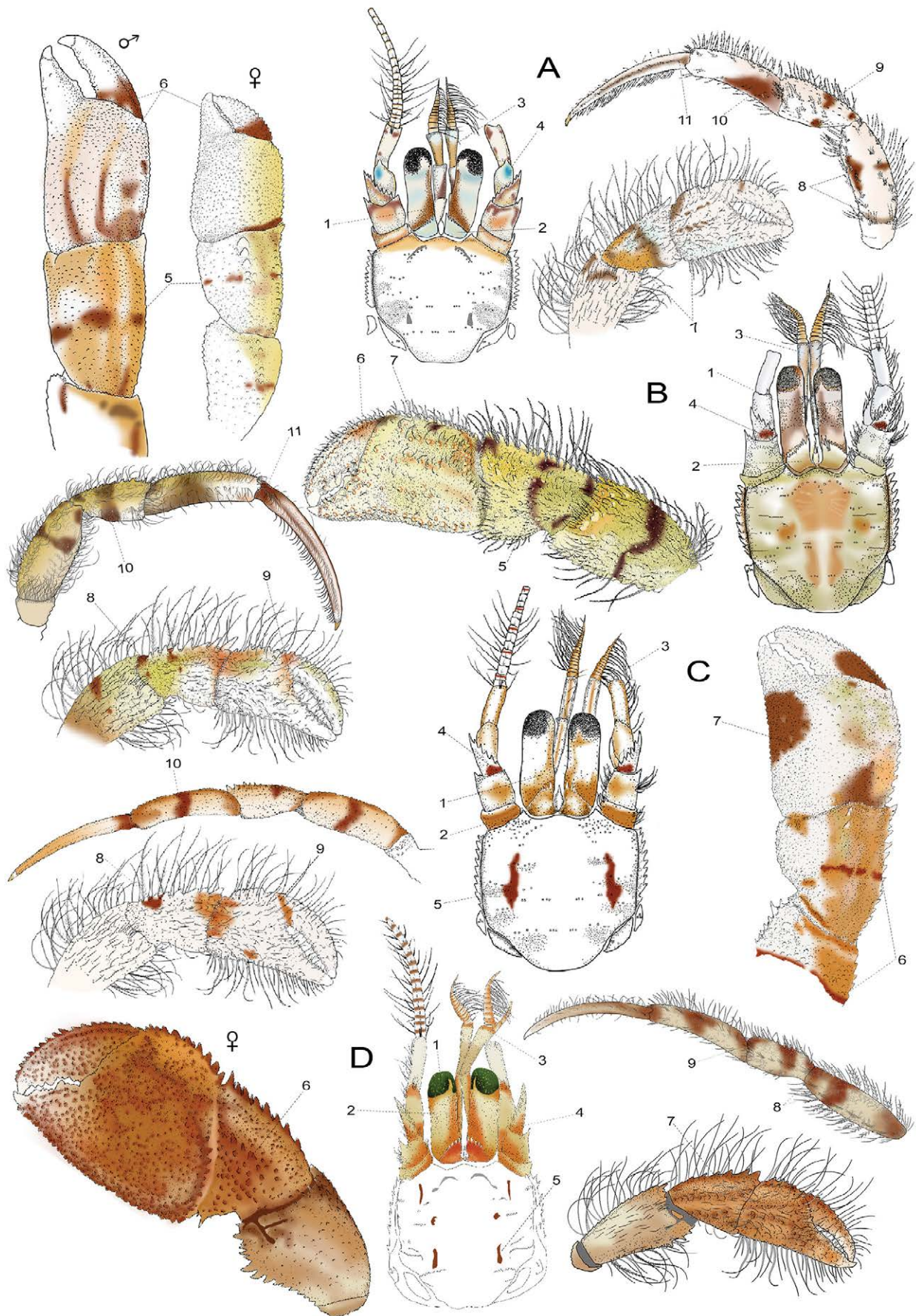


Fig. 2. – Colour patterns of the Diogenidae species: *Diogenes curvimanus* (A, 1-11); *Diogenes armatus* (B, 1-11); *Diogenes pugilator* (C, 1-10); *Diogenes erythromanus* (D, 1-9). Vectorial drawings are originals from: Almón et al. (2022a, 2022b).

and proximal margins of merus and carpus, and dorsal, proximal and distal margins of propodus; all with whiter ventral half; vermilion red dorsolateral rings in medial area of merus, carpus (only dorsal) and propodus; dactylus buff orange, paler proximally; brownish red proximal ring, extending through paired longitudinal lines reaching a white ring distally, behind the nail.

Diogenes erythromanus Almón, Cuesta and
García-Raso, 2022
(Figs 2D, 17G, H)

Eyes (Fig. 2D.1-2). Emerald green corneas spotted with saffron yellow; ocular peduncles pale buff orange with brownish orange triangular dorsal patch, broadened proximally and then running along inner surface reaching the base of the corneas; additional diffuse ring of the same colour outlining corneas. **Ocular acicles** hyacinth red. **Antennules** (Fig. 2D.3). Background pale buff orange; segment 1 reddish orange; segment 2 with reddish orange patch on inner surface; segment 3 with proximal half buff orange, and reddish orange distal ring; flagellum tinged with reddish orange. **Antennae** (Fig. 2D.4). Pale buff orange background; segments 1-3 and acicle tinged with reddish orange, with paler distal margins; segment 4 with distal reddish orange ring; segment 5 translucent, with faint reddish orange lateral margins; flagellum translucent with brownish orange rings at distal part of each segment. **Shield** (Fig. 2D.5). Usually with three paired brownish red stains on dorsal margin, at longitudinal sulci level. **Chelipeds. Left** (Fig. 2D.6) uniformly deep orange-coloured brown, with spines and tubercles brownish red. **Right** (Fig. 2D.7) similar to left, with whitish areas at distal part of dactylus and fixed finger, proximal part of palm and area of carpus between upper and medial row of spines. **Pereiopods 2-3** (Fig. 2D.8-9). Pale buff orange background; merus with one distal and second subdistal vermilion red rings and paler proximal stain; carpus with vermilion red stains at proximal and distal upper margins, and incomplete ring of the same colour medially; propodus with vermilion red stains proximally and distally, and irregular ring medially; dactylus with faint brownish orange proximal area.

Diogenes arguinensis Almón, Cuesta
and García-Raso, 2022

The description of this species was based solely on preserved specimens. Colour unknown.

Genus *Dardanus* Paulson, 1875
Dardanus arrosor (Herbst, 1796)
(Figs 3A, 16D)

Eyes (Fig. 3A.1-2). Corneas siskin green; ocular peduncles reddish white with scarlet red proximal ring, another twice as wide medially, somewhat lighter, and another of the same colour next to corneas. **Ocular acicles** (Fig. 3A.3) tile red with white tips. **Antennules** (Fig. 3A.4) with articles running from violet purple to scarlet red on lateral margins, fading distally; reddish orange flagellum. **Antennal** (Fig. 3A.5) segments 1-4 reddish

orange, with segment 5 cream yellow or violet purple; yellow-light pink flagellum. **Chelipeds** (Fig. 3A.6-8) both with a similar pattern; reddish orange merus, tile red proximally, with scarlet red transverse stripe distally, brighter towards the lower edge, more pink dorsally; transverse scales slightly red lilac purple; gamboge yellow hairiness covering its edges; carpus scarlet red, with gamboge yellow hairiness on scales; scarlet red hand, with the edge of the stripes and scales that cover its convex face violet purple; hairiness of the scales reddish orange; teeth on the dactylus snow-white; black claws. **Pereiopods 2-3** (Fig. 3A.9-10) with carmine red merus, carpus and propodus, with reddish orange hairy inserts; dactylus with deep reddish orange background, being somewhat lighter on upper half; marked buff orange hair inserts.

Dardanus calidus (Risso, 1827)
(Figs 3B, 16E)

Eyes (Fig. 3B.1-2). Corneas siskin green; ocular peduncles, yellowish white on their dorsal side, with four transverse scarlet red rings, evenly spaced, distal one surrounding the corneas. **Ocular acicles** (Fig. 3B.3) tile red with some cream yellow spots. **Antennules** (Fig. 3B.4) saffron yellow, reddish orange laterally. **Antennal** (Fig. 3B.5) segments 1-2 and acicle tile red; segments 3-5 saffron yellow flanked in reddish orange; flagellum saffron yellow. **Chelipeds** (Fig. 3B.6-7) both with a similar pattern; merus, carpus and hand aurora red; broad peach blossom red ring on the apical end of the merus, divided into two parts by scarlet red lines; tubercles covering the hand with peach blossom red base and black tips. **Pereiopods 2-3** (Fig. 3B.8-10) with scarlet red background; ischium and dactylus uniformly scarlet red; peach blossom red rings in medial part of merus, proximal area of carpus, and proximal and distal margins of propodus.

Genus *Paguristes* Dana, 1851
Paguristes eremita (Linnaeus, 1767)
(Figs 3C, 16F)

Eyes (Fig. 3C.1-2). Corneas greenish blue; ocular peduncles reddish orange, fading distally. **Ocular acicles** scarlet red. **Antennules** and **antennae** (Fig. 3C.3-4) uniform scarlet red. **Chelipeds** (Fig. 3C.5-6) both with a similar pattern; scarlet red background; merus with anterolateral dark vermilion red stain, with anterior borders surrounded by cream yellow line; inner distal face of merus with characteristic stain divided into two parts; apical half scarlet red outlined in snow-white; basal Prussian blue, outlined in white; fingers with white tips basally bordered by a bright scarlet red ring; black claws. **Pereiopods 2-3** (Fig. 3C.7) reddish orange; dactylus with apical snow-white and subapical scarlet red rings.

Paguristes rubropictus A. Milne-Edwards
and Bouvier, 1892
(Figs 3D, 16G)

Eyes (Fig. 3D.1-2). Corneas vivid azure blue; ocular peduncles reddish orange fading distally. **Ocular**

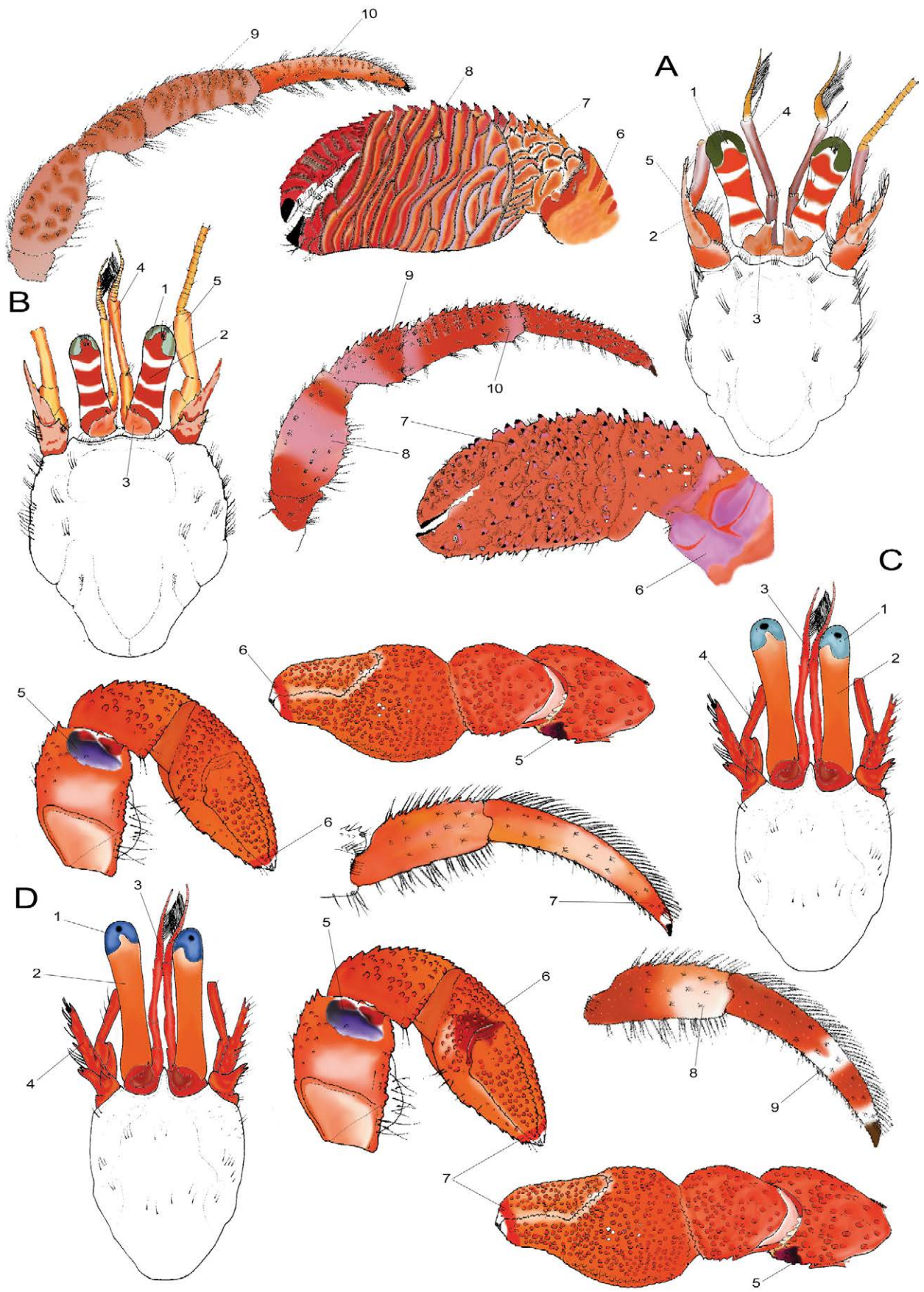


Fig. 3. – Colour patterns of the Diogenidae species: *Dardanus arrosor* (A, 1-10); *Dardanus calidus* (B, 1-10); *Paguristes eremita* (C, 1-7); *Paguristes rubropictus* (D, 1-9). All vectorial drawings modified from Ingle (1993).

acicles scarlet red. **Antennules** and **antennae** (Fig. 3D.3-4) scarlet red. **Chelipeds** (Fig. 3D.5-7) both with a similar pattern; scarlet red background; merus with vermilion red stain on apical outer face, with anterior margin surrounded by small cream yellow line; inner distal face of merus with very characteristic stain split in two, the apical half scarlet red surrounded by snow-white, basal part Prussian blue medially, outlined in white; vermilion red stain on the inner lateral surface of the hand, at base of dactylus; fingers with white tips basally bordered by bright scarlet red ring; black claws. **Pereiopods 2-3** (Fig. 3D.8-9). Propodus with proximal half scarlet red, clearing towards apex; dactylus scarlet red, with one distal and one subdistal white rings.

Family PAGURIDAE Latreille, 1802
Genus *Anapagurus* Henderson, 1886
Anapagurus adriaticus García-Gómez, 1994

Colour unknown.

Anapagurus alboranensis García-Gómez, 1994
(Figs 4A, 18A)

Eyes (Fig. 4A.1). Diffuse yellowish brown ring under corneas; orange-coloured white ocular peduncles with hyacinth red stripes scattered near basal area forming an almost complete ring, and sparse stripes on medial inner surface; ocular peduncles, corneas, antennules and antennae spotted in lemon yellow. **Ocular acicles** orange-coloured white tinged with buff orange. **Antennules** (Fig. 4A.2) with diffuse saffron yellow bands on segments 1 and 2; segment 3 with longitudinal dorsal reddish orange line widened distally. **Antennae** (Fig. 4A.3) translucent with buff orange tones and scattered tile red spots, especially on lateral margins. **Chelipeds. Right** (Fig. 4A.4) with buff orange background; merus tinged with apple green; carpus with chestnut brown spots on dorsal and lateral margins as well as at base of spines; palm uniformly buff orange, darker around fingers except for snow-white claws. **Left** (Fig. 4A.5) with yellowish fingers and chestnut brown spines on carpus. **Pereiopods 2-3** (Fig. 4A.6-9) translucent greyish white; ischium reddish orange; merus with four chestnut brown dorsal spots and two darker spots ventrally; carpus with an ovoid chestnut brown spot on dorso-proximal margin, and a more elongated one ventrally, covering more than 1/2 of its length; propodus with three longitudinal chestnut brown stripes laterally; dactylus, with two very pale reddish orange lines throughout their length, becoming discontinuous towards the tip.

Anapagurus bicorniger A. Milne-Edwards
and Bouvier, 1892
(Fig. 4B)

Eyes (Fig. 4B.1-2). Corneas with pistachio green background dotted with black; translucent white ocular peduncles with proximal and distal tile red rings. **Ocular acicles** tinged with tile red. **Antennules** (Fig. 4B.3) translucent white spotted with tile red and yellow,

especially on segment 3. **Antennae** (Fig. 4B.4) with translucent white background and scattered tile red areas; acicle with tile red horizontal bands. **Chelipeds. Right** (Fig. 4B.5) orange-coloured white, with two tile red bands on carpus, one on distal half and one paler proximally; orange-coloured white hand with very diffuse tile red mid-dorsal area. **Left** (Fig. 4B.6). Carpus orange-coloured white with transversal tile red bands on proximal (complete), medial and distal (discontinuous) areas; palm uniformly orange-coloured white, with tile red spines. **Pereiopods 2-3** (Fig. 4B.7-10) orange-coloured white background; merus with tile red stripe at the base and another of the same colour, wider on distal half; carpus with tile red proximal, dorsal and ventral margins; propodus with tile red dorsal and ventral margins; dactylus orange-coloured white throughout. Corneas, ocular peduncles, antennules, antennae and pereiopods 2-3 spotted with sulphur yellow.

Anapagurus breviaculeatus Fenizia, 1937
(Figs 4D, 18C)

Eyes (Fig. 4D.1). Ocular peduncles with orange-coloured white background, with proximal and distal hyacinth red rings. **Antennules** (Fig. 4D.2) with whitish background; segments 1-2 with mesial hyacinth red stripes; segment 3 with proximal and medial dorsal hyacinth red stains, and distal ring of the same colour. **Antennae** (Fig. 4D.3) whitish with some areas tinged with hyacinth red, especially proximal areas of all segments. **Chelipeds. Right** (Fig. 4D.4) with whitish carpus and spines hyacinth red; palm reddish orange, paler on lower half; dactylus with tuberculate medial crest darker; fingers with scarlet red subdistal ring. **Left** (Fig. 4D.5) similar to right, with carpus more reddish. **Pereiopods 2-3** (Fig. 4D.6-8). Merus whitish with numerous hyacinth red spots forming a reticulated pattern on dorsal half, and several thick longitudinal lines in the ventral half; carpus whitish, with dorsal, medial and ventral longitudinal hyacinth red stains; propodus with two hyacinth red rings, one proximal, one distal, both crossed by longitudinal lines of the same colour; dactylus with tile red background, and a hyacinth red line running medially to the apex; dorsal and ventral margins also hyacinth red.

Anapagurus chiroacanthus (Lilljeborg, 1856) (
Figs 4C, 18D9)

Eyes (Fig. 4C.1-2). Corneas with pistachio green background colour dotted with scarlet red; scarlet red ocular peduncles with more or less abundant snow-white spots dorsally, usually forming complete stripes. **Ocular acicles** tinged with scarlet red. **Antennules** (Fig. 4C.3) with segments 1-3 scarlet red, the third with purplish white apex, very striking auricula purple flagellum. **Antennae** (Fig. 4C.4) with scarlet red peduncles and acicle; acicle with interspersed horizontal snow-white stripes. **Chelipeds. Right** (Fig. 4C.5) reddish orange, darker dorsally; hand with distal half fading to white, with a thick scarlet red ring on fingers medially. **Left** (Fig. 4C.6) same pattern as right.

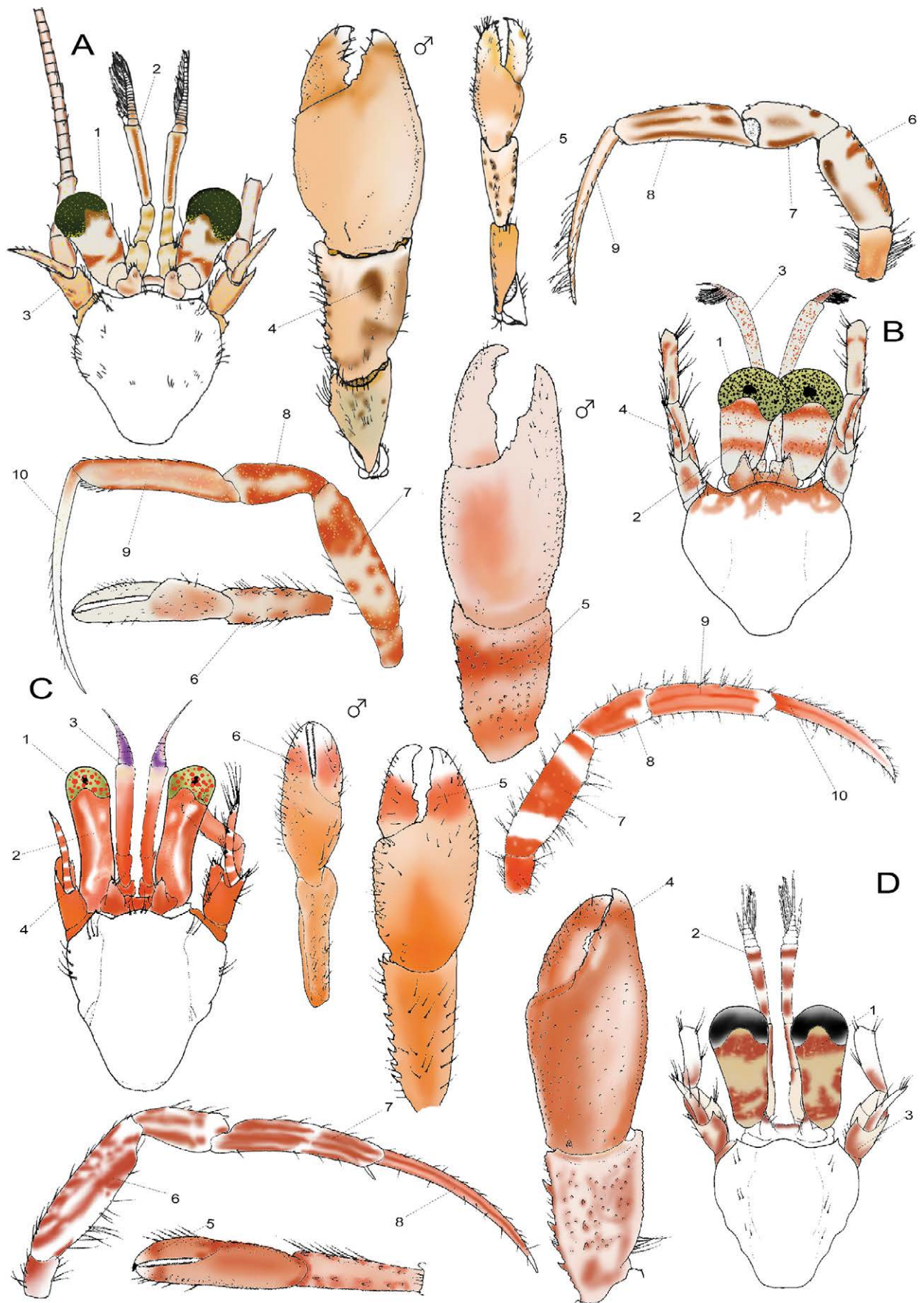


Fig. 4. – Colour patterns of *Anapagurus* species: *Anapagurus alboranensis* (A, 1-9); *A. bicorniger* (B, 1-10); *A. chiroacanthus* (C, 1-10); *A. breviaculeatus* (D, 1-8); Vectorial drawings modified from A, García-Gómez (1994); B-D, Ingle (1993).

Pereiopods 2-3 (Fig. 4C.7-10) scarlet red, with snow-white rings on proximal, subdistal and distal part of merus, and distal margin of carpus and propodus; hair inserts of propodus darker than the background, forming two lines; dactylus with scarlet red background colour fading towards the apex, darker proximally and medially, almost reaching the apex.

Anapagurus curvidactylus Chevreux
and Bouvier, 1892
(Figs 5A, 18H)

Eyes (Fig. 5A.1-2). Corneas with duck green background colour dotted with black; greyish white translucent ocular peduncles. **Ocular acicles** tinged with greyish white. **Antennules** (Fig. 5A.3) orange-coloured white with wood brown stripes covering proximal half of first segment and proximal 2/3 of second. **Antennae** (Fig. 5A.4). Whitish background tinged with wood brown spots in peduncles and proximal and distal part of acicles. **Chelipeds** (Fig. 5A.5-6) both with a similar pattern; background reddish white; merus with brownish red ring near distal margin; greyish white carpus; hand like carpus, with diffuse wood brown spot on proximal margin of dactylus. **Pereiopods 2-3** (Fig. 5A.7-10) whitish, fading to greyish blue on propodus and dactylus. Merus with brownish red dorsal spot extending slightly into the lateral surfaces; carpus with proximal 1/4 brownish red; propodus brownish red proximally, with brownish red hairy inserts forming 2 lines; dactylus with brownish red proximal margin and medial stripe extending almost to apex, fading distally.

Anapagurus hyndmanni (Bell, 1845)
(Figs 5B, 18B)

Eyes (Fig. 5B.1-2). Corneas with honey yellow background colour, dotted with red; greyish white translucent ocular peduncles, with chestnut brown ring surrounding corneas, extending backwards dorsally, reaching approximately mid-length of ocular peduncle length; another narrower and more diffuse ring proximally. **Antennules** (Fig. 5B.3) gallstone yellow with longitudinal wood brown or reddish orange line dorsally and another equal ventrally. **Antennae** (Fig. 5B.4) peduncles translucent, with chestnut brown lateral margins; flagellum with dull brownish red rings interspersed with pairs of regularly spaced white snow spots. **Chelipeds. Right** (Fig. 5B.5) white or buff orange, merus with 2-3 chocolate red rings on inner surface, usually complete; stain of same colour on palm ventro-mesial margin; carpus and palm dorsal surface with scattered pale chocolate red spots, slightly more defined on medial area of fingers. **Left** (Fig. 5B.6) whiter than right, with two chocolate red stripes on merus. **Pereiopods 2-3** (Fig. 5B.7-10) with yellowish white or slightly orange background; merus with two transversal chestnut brown stripes (sometimes incomplete); carpus with proximal half wood brown or berlin blue (variable extension), fading distally, sometimes with diffuse crimson red spots; propodus with chestnut

brown proximal and distal white rings; rest of propodus surface Berlin blue (sometimes chestnut brown); chestnut brown hairy inserts forming two parallel lines laterally; dactylus brownish red proximally, extending in medial line almost until apex, fading distally. **Maxillipeds** (Fig. 5B.11) with chestnut brown rings on all segments.

Anapagurus laevis (Bell, 1846)
(Figs 5C, 18G)

Eyes (Fig. 5C.1-2). Corneas apple green, tinged with reddish orange; ocular peduncles orange-coloured white, with buff orange ring near proximal region, and another reddish orange distally. **Antennules** (Fig. 5C.3) translucent bluish lilac purple with hyacinth red spots forming dorsal rings in distal segments 2-3. **Antennae** (Fig. 5C.4) translucent bluish lilac purple with hyacinth red spots especially in lateral margins of all segments and acicles; flagellum with brownish red rings alternating with snow-white ones. **Chelipeds. Right** (Fig. 5C.5-6) with reddish orange background and scattered orpiment orange spots in merus and carpus; palm dorsal surface with a distinctive Y-shaped reddish orange patch covering median surface of palm, inner part of fixed finger, and proximal part of dactylus; whitish claws; **Left** (Fig. 5C.7) similar to right, but palm almost white, without central Y-shaped patch. **Pereiopods 2-3** (Fig. 5C.8-11) translucent bluish lilac purple; ischium with carmine red spots almost completely covering proximal 3/4; merus with reddish orange transverse dotted proximal band (diffuse) and distal ring; carpus with pale reddish orange patch covering proximal 3/4; propodus with proximal and subdistal reddish orange rings; ventral margin also tinged with buff orange; whitish hairy inserts forming longitudinal lines; dactylus translucent with very pale buff orange medial line; all segments dotted in yellow.

Anapagurus longispina A. Milne-Edwards
and Bouvier, 1900
(Fig. 6A)

Eyes (Fig. 6A.1-2). Corneas with oil green background colour dotted with black; translucent yellowish white ocular peduncles with orpiment orange area distally fading backwards; **Ocular acicles** with deep brownish orange distal area, remaining even after long periods in alcohol. **Antennules** (Fig. 6A.3) translucent with orpiment orange inner line dorsally. **Antennae** (Fig. 6A.4) translucent with orpiment orange spots on lateral margins and throughout the acicle and basal segments. **Chelipeds. Right** (Fig. 6A.5) deep orpiment orange, darker at proximal area of carpus; hand with distal half gradually losing colour, turning to snow-white on fingers. **Left** (Fig. 6A.6) showing same pattern as right. **Pereiopods 2-3** (Fig. 6A.7-8) deep orpiment orange, with darker areas on disto-ventral part of carpus and forming diffuse rings on proximal and distal parts of merus and propodus; dactylus pale deep orpiment orange, with slightly darker medial line.

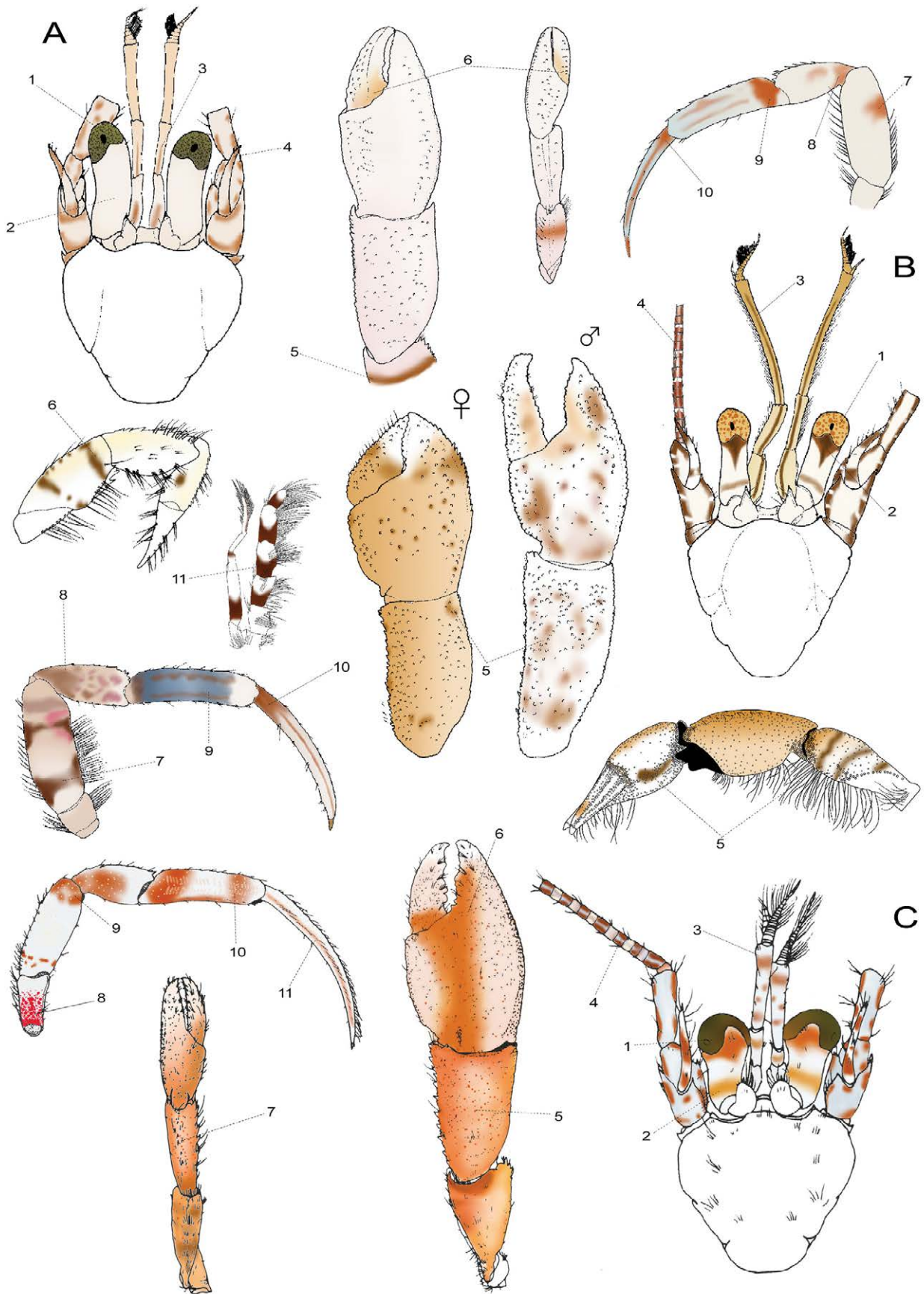


Fig. 5. – Colour patterns of *Anapagurus* species: *A. curvidactylus* (A, 1-10); *A. hyndmanni* (B, 1-11); *Anapagurus laevis* (C, 1-11). All vectorial drawings modified from Ingle (1993) except dorsal view of right cheliped in B (present work).

Anapagurus petiti Dechancé and Forest, 1962
(Figs 6B, 18E)

Eyes (Fig. 6B.1-2). Black corneas spotted and outlined at their base with gamboge yellow; yellowish white ocular peduncles tinged with very pale buff orange proximally. **Antennules** (Fig. 6B.3) orange-coloured white with brownish red and orange rings over proximal and distal half of segment 3, respectively, both fading towards the apex; buff orange patches at proximal half of segment 2. **Antennae** (Fig. 6B.4) orange-coloured white with oil green tones; acicle with buff orange spots. **Chelipeds. Right** (Fig. 6B.5-6) oil green merus and carpus; carpus with two snow-white spots almost occupying entire distal margin; dark spot on dorsal 2/4; snow-white hand, with broad chestnut brown patch at base of fingers, extending towards apex on fixed finger and fading backwards until near the base of the palm. **Left** (Fig. 6B.7) similar to right, with palmar medial patch brownish red. **Pereiopods 2-3** (Fig. 6B.8-10) oil green, with greenish white apical areas; merus with series of chestnut brown spots on dorsal margin; carpus with spot of same colour latero-proximally; propodus with dorsal chestnut brown spot dorso-proximally, a more blurred ring on apical 3/4 and distal white ring; oil green dactylus fading to white in distal half.

Anapagurus pusillus Henderson, 1888
(Figs 6C, 18F)

Eyes (Fig. 6C.1-2). Brownish orange corneas outlined basally in yellow; tile red ocular peduncles with proximal, medial and distal vermilion red rings. **Antennules** (Fig. 6C.3) translucent with brownish purple red dorsal stripe on segment 3 ending proximally in simple ring and apically in tridentate ring; segments 2 and 3 with stains of the same colour; buff orange flagellum, more reddish dorsally. **Antennae** (Fig. 6C.4) translucent yellowish white with dark vermilion red bands on segment 2 proximally, and lateral margins of 4 and 5; acicle with bands of the same colour; hyacinth red flagellum with some white spots every two segments. **Chelipeds. Right** (Fig. 6C.5) with light buff orange background colour; palm with brownish orange areas, especially marked on fingers, fading distally. **Left** (Fig. 6C.6) with a similar pattern and stains as right. **Pereiopods 2-3** (Fig. 6C.7-10) whitish; merus with vermilion red ring proximally, an incomplete one in distal 1/3, both with some darker areas, and reddish narrow band subdistally; carpus with deep reddish brown dorso-proximal and vermilion red ventro-distal stains; propodus with two vermilion red rings, one proximal and one on distal 1/3, with additional longitudinal lines of the same colour overlapping the rings; distal margins of merus, carpus and propodus with saffron yellow areas; dactylus with vermilion proximal area extending in medial line towards apex. **Maxillipeds** (Fig. 6C.11) with basal half scarlet red, fading into white distally.

Anapagurus smythi Ingle, 1993

Colour unknown.

Genus *Catapaguroides* A. Milne-Edwards
and Bouvier, 1892
Catapaguroides iris Bouvier, 1922

Colour unknown. In the original description of Bouvier (1922), only some iridescent areas, especially on the right cheliped, are mentioned.

Catapaguroides megalops A. Milne-Edwards
and Bouvier, 1892

Colour unknown. The only information available is the whitish colouration described by Milne-Edwards and Bouvier (1892, 1900).

Catapaguroides microps A. Milne-Edwards
and Bouvier, 1892
(Fig. 7A)

There is not much information about this species. Some photographs show individuals with more reddish general colouration.

Eyes (Fig. 7A.1-2). Scarlet red corneas; skimmed milk white ocular peduncles, very faint. **Antennules** (Fig. 7A.3) uniformly yellowish white; skimmed milk white flagellum. **Antennae** (Fig. 7A.4) yellowish white turning to rose red on basal segments. **Chelipeds. Right** (Fig. 7A.5) rose red, fading to snow-white towards distal part of hand. **Left** (Fig. 7A.6) same pattern as right. **Pereiopods 2-3** (Fig. 7A.7-9) with rose red background on merus, carpus and propodus (propodus slightly paler); carpus and propodus with a very faint wood brown distal area; dactylus white with a very pale wood brown line running along midline, reaching the tip.

Genus *Cestopagurus* Bouvier, 1897
Cestopagurus timidus (Roux, 1830)
(Figs 7B, 19A)

Eyes (Fig. 7B.1-2). Corneas very striking emerald green, with scarlet red dots; ocular peduncles with thick longitudinal cream yellow lines over scarlet red background. **Antennules** (Fig. 7B.3) cream yellow in segments 1, 2 and proximal part of 3, turning then to auricula purple, brighter distally; buff orange flagellum. **Antennae** (Fig. 7B.4) buff orange with diffuse yellowish white spots, especially evident at the base and apex of acicles. **Chelipeds. Right** (Fig. 7B.5) brownish orange background, with scarlet red tubercles and spines; brighter scarlet red stripes on both fingers. **Left** (Fig. 7B.6) similar pattern as right. **Pereiopods 2-3** (Fig. 7B.7-8) reddish orange, darker on dorsal margins, fading to reddish white at distal margin of each segment.

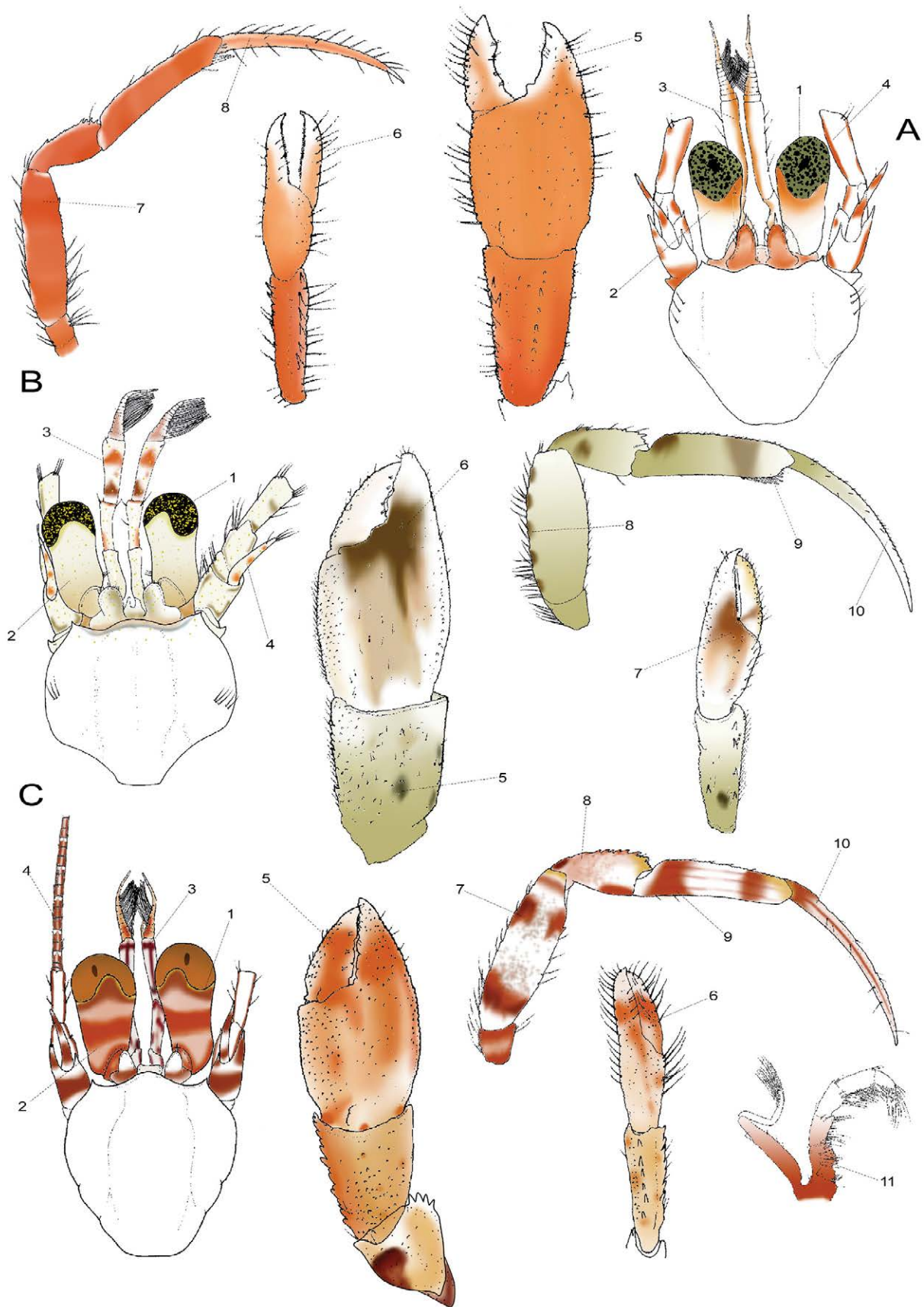


Fig. 6. – Colour patterns of *Anapagurus* species: *A. longispina* (A, 1-8); *A. petiti* (B, 1-10); *A. pusillus* (C, 1-11). All vectorial drawings modified from Ingle (1993).

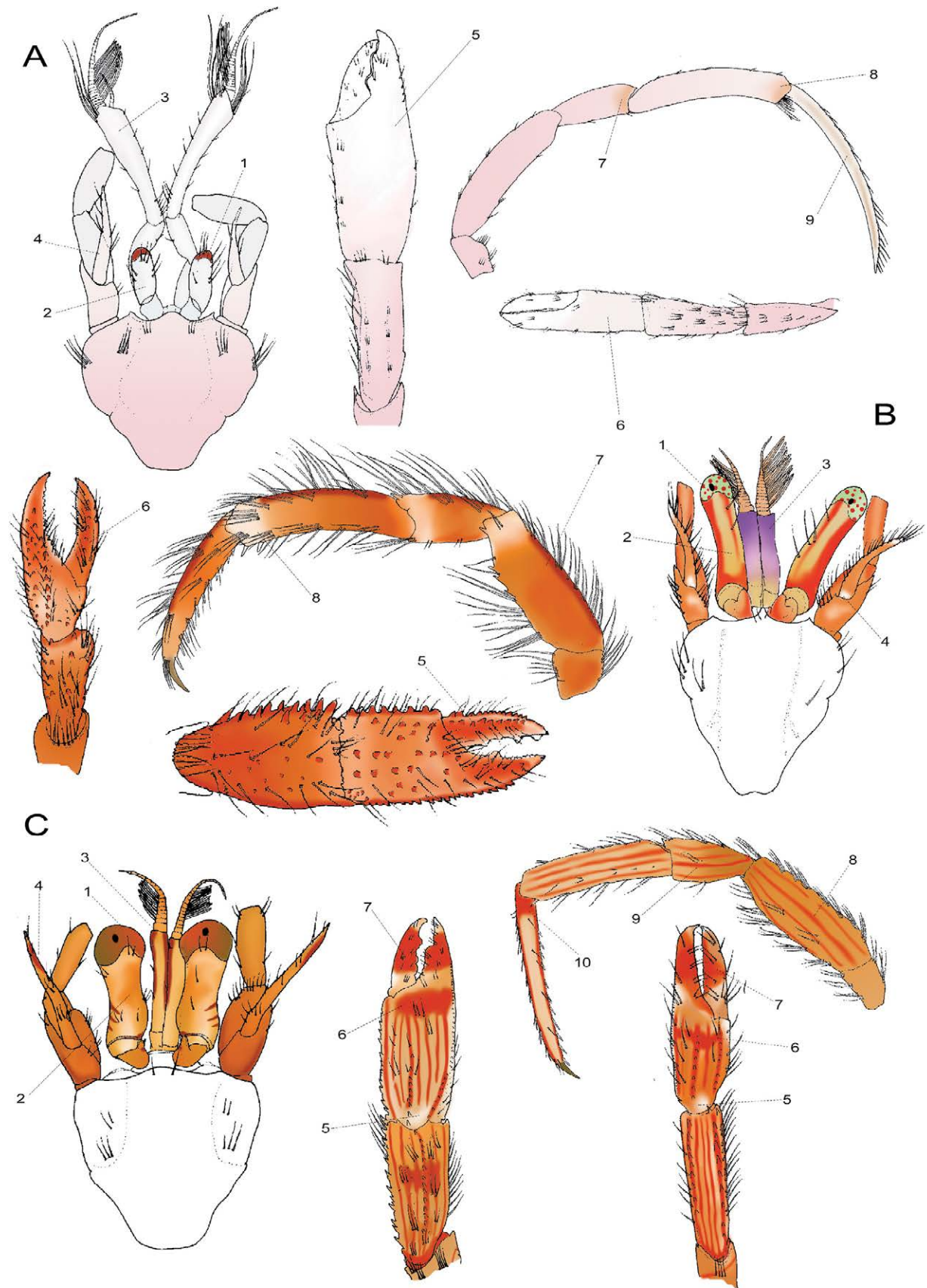


Fig. 7. – Colour patterns of Paguridae species: *Catapaguroides microps* (A, 1-9); *Cestopagurus timidus* (B, 1-8); *Nematopagurus longicornis* (C, 1-10). All vectorial drawings modified from Ingle (1993).

Genus *Nematopagurus* A. Milne-Edwards
and Bouvier, 1892

Nematopagurus longicornis A. Milne-Edwards
and Bouvier, 1892
(Figs 7C, 19B)

Eyes (Fig. 7C.1-2). Oil green corneas, with tile red areas; reddish orange ocular peduncles, with darker areas on inner medial surfaces, and three scarlet red stripes on outer side, visible in part in dorsal view. **Antennules** (Fig. 7C.3) buff orange, with scarlet red patches on lateral areas covering the distal 2/3 of segment 3. **Antennae** (Fig. 7C.4) reddish orange with scarlet red areas on outer margins of segment 2 and scarlet red patch at distal part of acicle; flagellum with scarlet red segments interspersed with white ones at a rate of approximately 7-2. **Chelipeds** (Fig. 7C.5-7) both with a similar pattern; reddish orange background, with whitish areas on proximal areas of palm and fingers; a series of scarlet red longitudinal lines running parallel along carpus and propodus, thickening in distal part of palm and central part of carpus; fingers with broad scarlet red stripe covering distal 2/3. **Pereiopods 2-3** (Fig. 7C.8-10) with reddish orange background and series of longitudinal scarlet red lines running along merus, carpus and propodus; dactylus with scarlet red path proximally, extending towards the tip along dorsal and ventral margins; abundant thick and long orange-coloured white hairs on all body appendages.

Genus *Pagurus* Fabricius, 1775
Pagurus anachoretus Risso, 1827
(Figs 8A, 19C)

Eyes (Fig. 8A.1-2). Verdigris green corneas; primrose yellow ocular peduncles, with chestnut brown ring near proximal margin and thinner one distally. **Ocular acicles** (Fig. 8A.3) cream yellow, tinged with yellowish brown. **Antennules** (Fig. 8A.4-5) primrose yellow; segment 2 with proximal and distal brownish red rings; segment 3 with subdistal brownish red ring; primrose yellow flagellum with tuft tinged with brownish red or buff orange. **Antennae** (Fig. 8A.6-7) segments 1-2 tile red with some vertical scarlet red stripes; in young specimens these stripes are larger; rest of segments primrose yellow, with brownish red lateral margins; flagellum dull brownish reddish with pale primrose yellow rings. **Shield** (Fig. 8A.8) yellowish brown with six bluish lilac purple longitudinal stripes, three on each side; medial lines are anastomosed twice with neighbouring ones; all these bluish lines are outlined by vermilion red stripes. **Chelipeds** (Fig. 8A.9) both with a similar pattern; chestnut brown background with bluish lilac purple longitudinal lines framed in vermilion red; cream yellow hairiness. **Pereiopods 2-3** (Fig. 8A.10-11) buff orange background with three ultramarine blue longitudinal lines on dorsal, medial and ventral surfaces, and scarlet red oval spots arranged in regular intervals over them; dactylus buff orange with oval scarlet red large spots arranged in a dashed line along dorsal and ventral margins.

Pagurus alatus Fabricius, 1775
(Figs 8B, 19D)

Two predominant colourations were observed. One with reddish orange background that seems to be more frequent in Atlantic waters (Fig. 8B right) and one rose red that is more frequent in the Mediterranean (Fig. 8B left).

Eyes (Fig. 8B.1-2). Oil green corneas with black dots, frequently outlined at their base in reddish orange; snow-white ocular peduncles with reddish orange ring near proximal margin (pale rose red in rose red variety). **Antennules** (Fig. 8B.3) reddish orange fading distally. **Antennae** (Fig. 8B.4) buff orange; segment 2 with reddish orange and white vertical bands. **Chelipeds** (Fig. 8B.5) both with a similar pattern; buff orange background, spines and tubercles with reddish orange tips; palm with central and lateral ridges reddish orange. **Pereiopods 2-3** (Fig. 8B.6-7) with a buff orange background; merus with reddish orange dorsal margin and some longitudinal lines medially; carpus, propodus and dactylus with reddish orange dorsal margins and proximal areas; additional reddish orange spots on hair inserts of carpus and propodus; rest of dactylus surface siskin green.

Pagurus carneus (Pocock, 1889)
(Figs 8C, 19E)

Eyes (Fig. 8C.1-2). Black corneas; tile to flesh red ocular peduncles, darker in proximal 3/4 and with rather defined lighter area distally. **Antennules** (Fig. 8C.3) uniformly tile to flesh red fading proximally. **Antennae** (Fig. 8C.4) tile to flesh red, similar to antennule, with basal segment and acicle paler. **Shield** (Fig. 8C.5) with general tile to flesh red colour, uniform without spots; only a reddish orange rim that surrounds the shield from epibranchial region to frontal margin. **Chelipeds** (Fig. 8C.6) both with a similar pattern; tile to flesh red background with orpiment orange spots scattered on distal margin of merus, carpus and propodus; mesial and lateral dentate borders tinged with ochre yellow. **Pereiopods 2-3** (Fig. 8C.7-8) tile to flesh red with orpiment orange bands on dorso-proximal parts of ischium, merus and carpus, dorso-distal margin of merus, and complete rings at distal margin of carpus and propodus; dactylus with a small band of the same colour at dorso-proximal margin.

Pagurus chevreuxi (Bouvier, 1896)
(Figs 9A, 19F)

Two predominant colourations were observed: one in specimens from Atlantic locations (described below) and one in specimens from Mediterranean locations, with darker tones closest to brown colours and sometimes retaining only the longitudinal pattern on ocular peduncles and frequently on the shield.

Eyes (Fig. 9A.1-3). Corneas snow-white spotted with scarlet red; ocular peduncles orpiment orange,

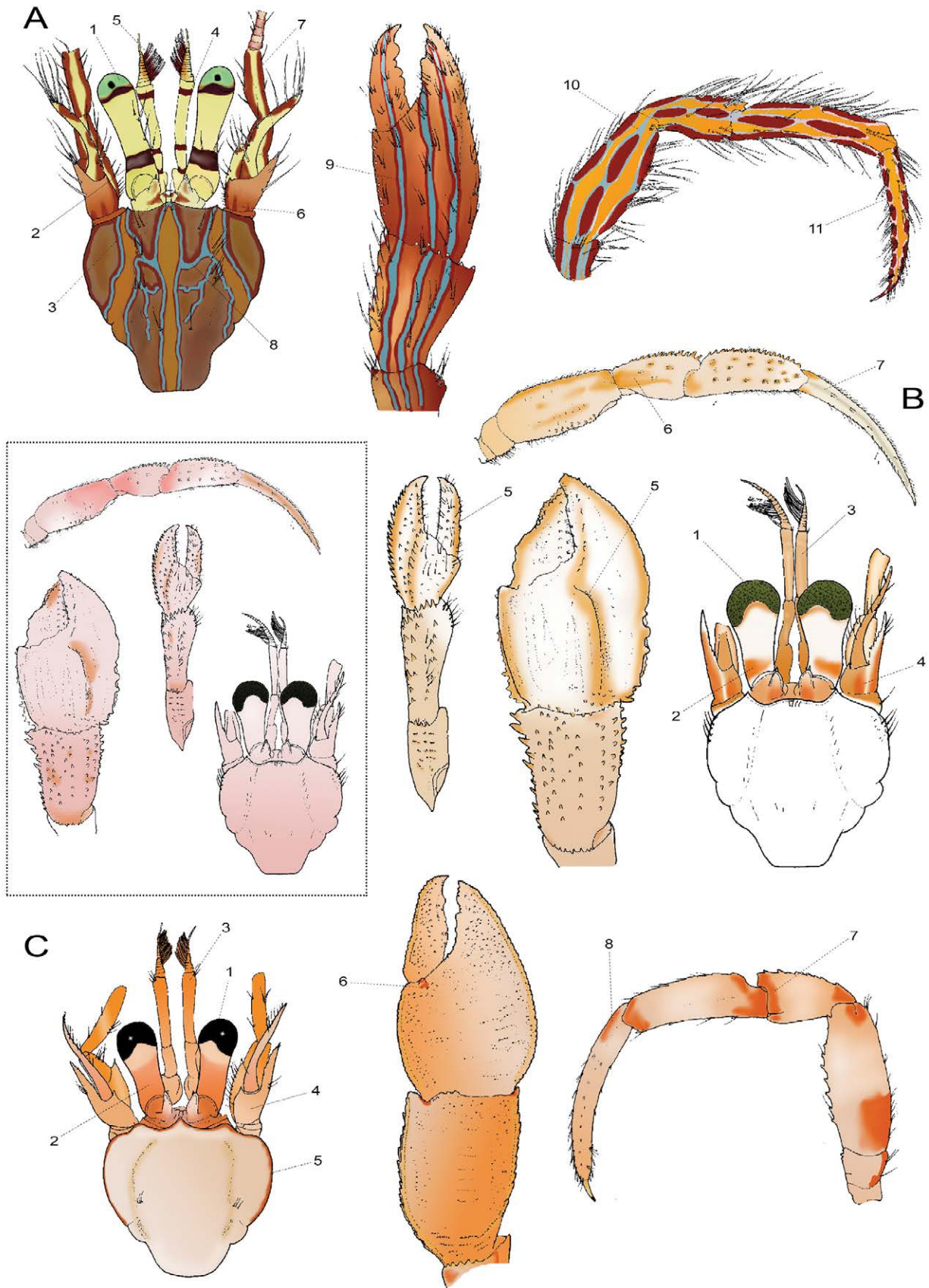


Fig. 8. – Colour patterns of *Pagurus* species: *P. anachoretus* (A, 1-11); *P. alatus* (B, 1-7; area in the square corresponds to the rose red Mediterranean colouration); *P. carneus* (C, 1-8). All vectorial drawings modified from Ingle (1993).

with longitudinal straw yellow stripes on dorsal margin, and imperial purple stripe on ventral margin. **Antennules** (Fig. 9A.4). Segment 1-2 orpiment orange, turning to imperial purple at distal margin of segment 2 and entire segment 3, which is whiter distally. **Antennae** (Fig. 9A.5) orpiment orange, with distal margin of segments 2-3 snow-white. **Shield** (Fig. 9A.6) with straw yellow background and reddish orange longitudinal stripes; the extension and shape of the stripes are somewhat variable. **Chelipeds** (Fig. 9A.7-8) both with a similar pattern; carpus with orpiment orange longitudinal stripes alternating with straw yellow ones; palm uniformly bright orpiment orange, going white around fingers on right cheliped; very small straw yellow tubercles scattered all over cheliped surface. **Pereiopods 2-3** (Fig. 9A.9) orpiment orange with dorsal, medial and ventral longitudinal straw yellow stripes in all segments; dactylus with corneous spines along lower margin.

Pagurus cuanensis Bell, 1845
(Figs 9B, 20A)

Eyes (Fig. 9B.1-2). Corneas greenish blue; ocular peduncles orange-coloured white with wood brown ring near proximal margin and another reddish orange distally; basal area of ocular peduncles is also tinged in reddish orange but often difficult to observe. **Antennules** (Fig. 9B.3) with distal half of segment 2 and entire segment 3 deep orange-coloured brown, fading distally; brownish red flagellum. In young specimens, antennular segments 1-2 are orange-coloured white, with chestnut brown stains on distal half of segment 2; segment 3 is chestnut brown on proximal half, turning to deep auricular purple, fading distally. Flagellum translucent (Fig. 9B.4). **Antennae** (Fig. 9B.5) orange-coloured white with buff orange stains in segment 2 and acicle, and scarlet red tints on segments 3-5; scarlet red flagellum with white rings. **Chelipeds** (Fig. 9B.6-7) both with a similar pattern; brownish orange, covered with abundant long hairiness; carpus with deep vermilion red stain on proximal region and some more diffuse ones on distal part; hand with some scattered diffuse vermilion stains and with whiter areas around the teeth; spines with white tips; corneous claws. **Pereiopods 2-3** (Fig. 9B.8-9) brownish orange, darker on merus, clearing towards dactylus; all segments with numerous snow-white stains of different size blending with each other; ventro-proximal vermilion red stains on carpus and propodus; dactylus with white stains arranged in two lines; all segments with abundant long hairiness.

Pagurus excavatus (Herbst, 1791)
(Fig. 9C)

Eyes (Fig. 9C.1-2). Corneas oil green; ocular peduncles pale wood brown, with tile red distal ring under corneas. **Antennules** (Fig. 9C.3) pale yellowish white. **Antennae** (Fig. 9C.4) pale yellowish white. **Chelipeds** (Fig. 9C.5-6) with a similar pattern. **Right** pale wood brown; merus with spines tinged with deep

reddish brown; palm with central and lateral ridges as well as part of the depressions between them yellowish brown. **Left**, similar to right but ridges and depressions less coloured. **Pereiopods 2-3** (Fig. 9C.7-8) light wood brown, with numerous scattered white spots; dactylus chestnut brown proximally, fading towards the tip.

Pagurus forbesii Bell, 1845
(Figs 10A, 20E)

Eyes (Fig. 10A.1-2). Emerald green corneas; pale buff orange ocular peduncles, with darker distal area. **Antennules** (Fig. 10A.3) pale buff orange, getting darker distally, including flagellum. **Antennae** (Fig. 10A.4) buff orange, darker in segments 1-4, proximal half and margins of segment 5; mottled with small whitish spots; acicle with alternating white stripes. **Chelipeds** with a similar pattern. **Right** (Fig. 10A.5-6) buff orange with some whitish areas; vermilion red stains in proximal and disto-lateral areas of carpus, proximo-lateral part of palm and base of dactylus; claws and bigger spines snow-white. **Left** (Fig. 10A.7) buff orange with vermilion ring near proximal margin of carpus; snow-white tips on fingers and claws. **Pereiopods 2-3** (Fig. 10A.8-11) buff orange with numerous scattered snow-white spots decreasing in number from merus to propodus; merus with two vermilion red rings proximally; carpus and propodus with vermilion red ring proximally; distal margin of propodus snow-white; dactylus with vermilion red ring near proximal margin and white spots forming 2 parallel lines that reach the tip; white small ring distally.

Pagurus mbizi (Forest, 1955)
(Figs 10B, 20C)

Eyes (Fig. 10B.1-2). Grass green corneas with black spots; ocular peduncles orange-coloured white with reddish orange ring near proximal margin and a diffuse peach blossom red band above it; hyacinth red ring distally. **Antennules** (Fig. 10B.3) cream yellow, with segments 1-2 and flagellum buff orange. **Antennae** (Fig. 10B.4) cream yellow with buff orange or wood brown patches, especially evident in proximal areas of segment 2 and acicle; cream yellow flagellum tinged with tile red. Young specimens with hyaline peach blossom red flagellum (Fig. 10B.5). **Chelipeds** (Fig. 10B.6-7) both with a similar pattern; pale buff orange with some peach blossom red areas, sometimes very diffuse and especially evident on distal half of carpus and proximal area of fixed finger; some tile red or buff orange patches on proximal half of carpus and base of dactylus. In young specimens the palm is lighter, almost white. **Pereiopods 2-3** (Fig. 10B.8-10) pale buff orange with peach blossom red patches on medial and distal parts of merus, distal part of carpus and proximal area of propodus; tile red or buff orange patches on distal part of merus, proximal half of carpus and near distal part of propodus, extending backwards in a longitudinal line medially; dactylus with buff orange stain proximally fading towards the tip.

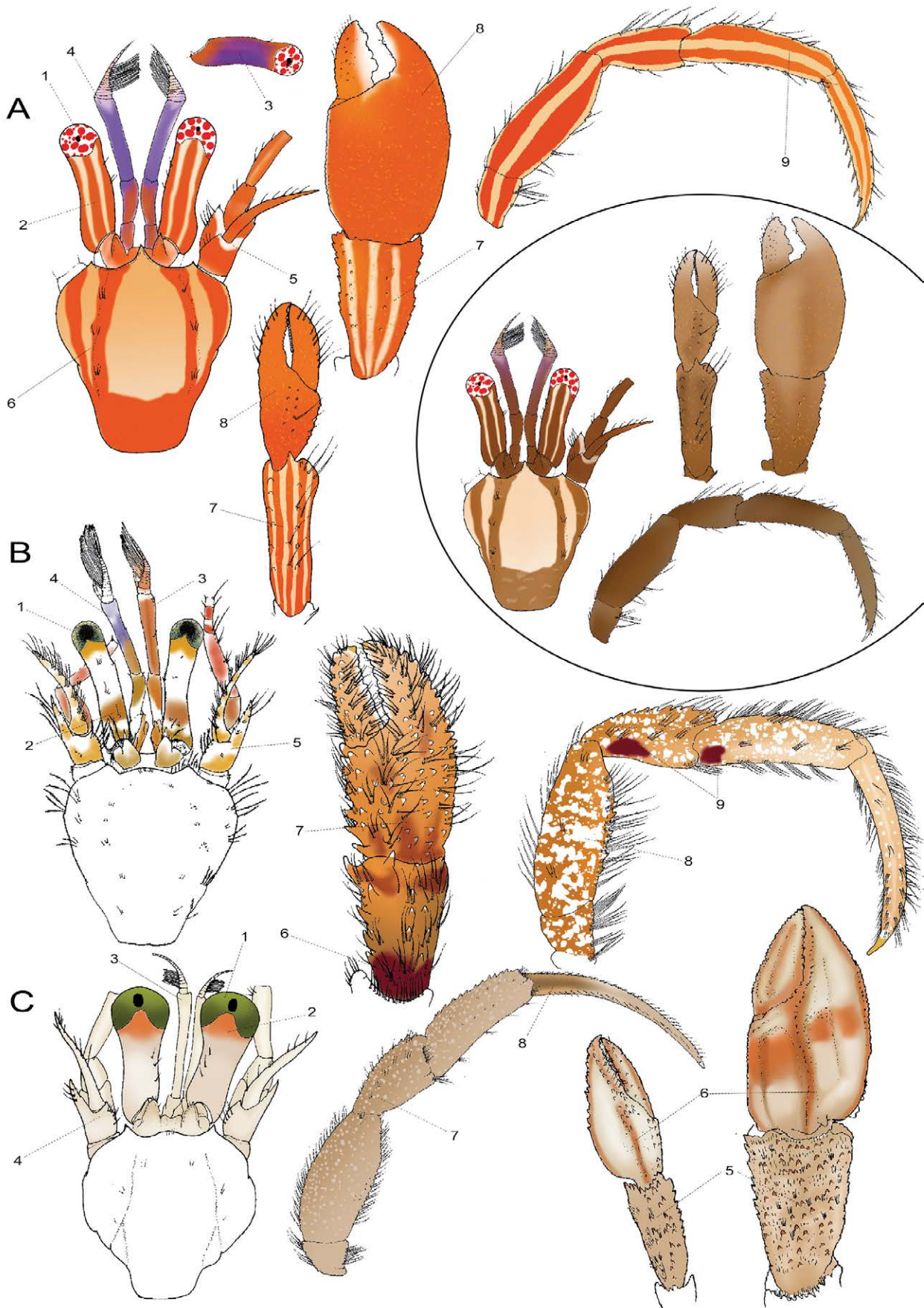


Fig. 9. – Colour patterns of *Pagurus* species: *P. chevreuxi*, Atlantic variety (A, 1-9); circled area corresponds to variations observed in Mediterranean specimens; *P. cuanensis*; (B, 1-9); *P. excavatus* (C, 1-8). All vectorial drawings modified from Ingle (1993).

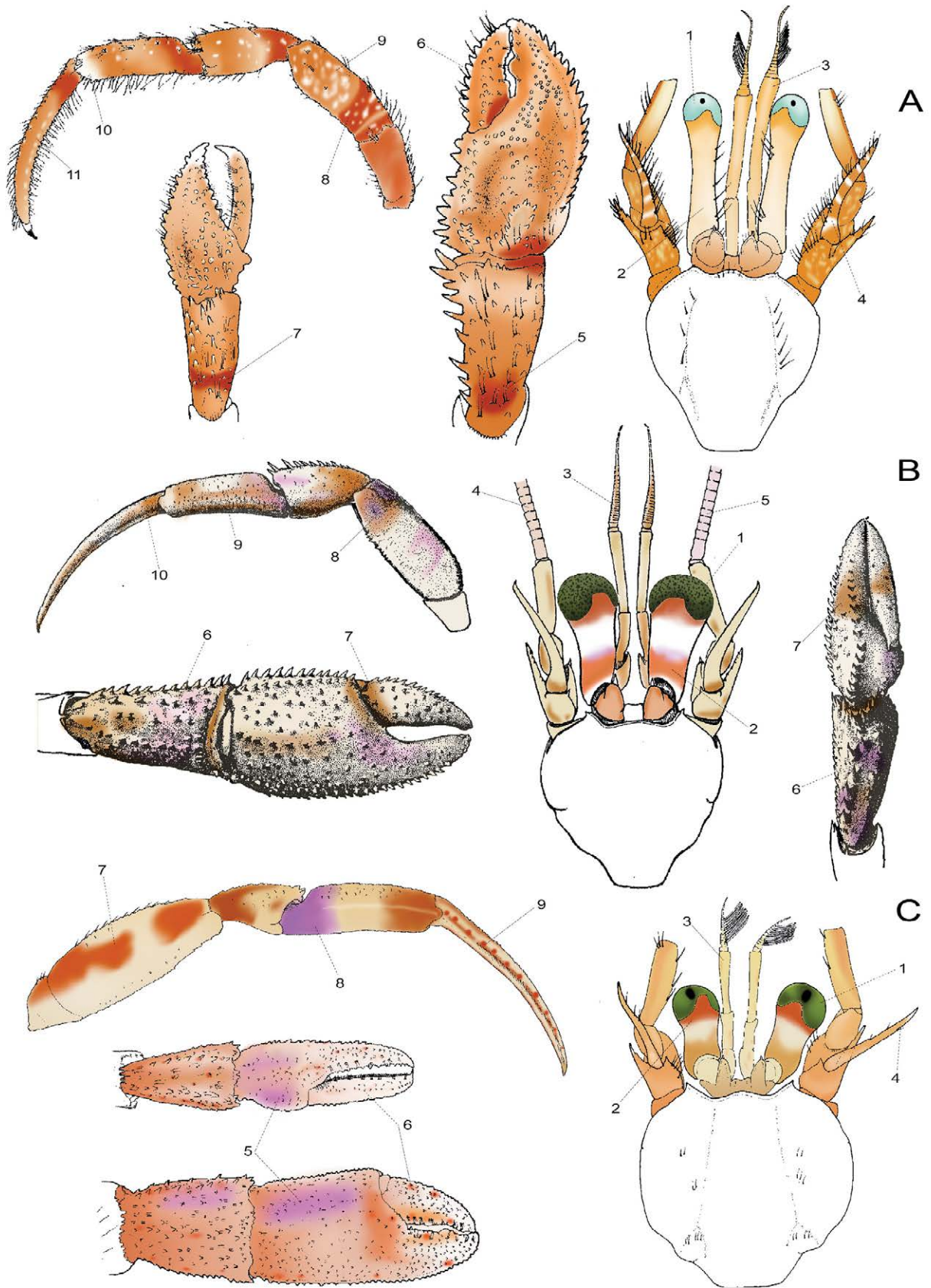


Fig. 10. – Colour patterns of *Pagurus* species: *P. forbesii* (A, 1-11); *P. mbizi* (B, 1-10); *P. prideaux* (C, 1-9). Vectorial drawings modified from A, C, Ingle (1993); B, Forest (1955).

Pagurus prideaux Leach, 1815
(Figs 10C, 20D)

Eyes (Fig. 10C.1-2). Oil green or siskin green corneas; ocular peduncles orange-coloured white with pale buff orange ring in proximal margin; vermilion red ring distally. **Antennules** (Fig. 10C.3) pale cream yellow tinged with buff orange dorsally. **Antennae** (Fig. 10C.4) cream yellow tinged with buff orange especially in proximal and lateral areas; acicle with white tip. **Chelipeds** (Fig. 10C.5-6) both with a similar pattern; buff orange to reddish orange with small, scattered vermilion spots especially conspicuous on fingers; violet purple stains near dorsal margin of carpus and palm; distal part of fingers whitish. **Pereiopods 2-3** (Fig. 10C.7-9) cream yellow; vermilion red stains on dorsal margin of ischium, proximal and distal margins of merus; darker stains on proximal half of carpus and distal part of propodus; violet purple ring in proximal area of propodus; dactylus cream yellow with wood brown line along the middle zone and a series of vermilion red spots over it.

Pagurus pseudosculptimanus García-Muñoz,
Cuesta and García-Raso, 2014
(Fig. 11A)

Eyes (Fig. 11A.1-2). Oil green corneas; ocular peduncles pale buff orange, darker on proximal margin. **Antennules** (Fig. 11A.3) pale buff orange tinged with vermilion red on proximal segment 1. **Antennae** (Fig. 11A.4) buff orange tinged with tile red. **Chelipeds** (Fig. 11A.5-7) both with a similar pattern; brownish orange with some whiter areas; indigo blue areas on distal part of merus, proximal and distal parts of carpus and palm, where they extend forward in a line medially; another indigo blue smaller stain on base of dactylus; bigger rounded tubercles of palm as well as central area of carpus orpiment orange; vermilion red patches almost completely covering the fingers; distal part of fingers white. **Pereiopods 2-3** (Fig. 11A.8-10) cream yellow; brownish orange rings on proximal part of carpus, and proximal and distal part of merus and propodus; dactylus oil green with brownish orange proximal part, and wood brown ring near distal margin followed by small white ring.

Pagurus pubescens Krøyer, 1838
(Figs 11B, 20F)

Eyes (Fig. 11B.1-2). Corneas pistachio green spotted in black; ocular peduncles tile red tinged with rose red, with orpiment orange spots aligned dorsally; small bright buff orange patch on distal margin, beneath corneas. **Antennules** (Fig. 11B.3) reddish orange, fading on distal part of segment 3. **Antennae** (Fig. 11B.4) tile red, tinged with orpiment orange in some areas of basal segments, and lateral margins of segments 4-5 and flagellum. **Chelipeds. Right** (Fig. 11B.5-6) with ischium, merus and carpus orpiment orange with some paler areas; palm lighter, with medial area of palm and fingers whitish; bigger spines and mesial distal angle

tinged with orpiment orange. **Left** (Fig. 11B.7) similar to right, but with a white ring on carpus medially. Tuberculated ridges on both chelipeds tinged with bright orpiment orange; corneous claws. **Pereiopods 2-3** (Fig. 11B.8-9) orange-coloured white; orpiment orange broad rings on proximal and distal margins of merus, carpus and propodus; dactylus with orpiment orange ring proximally, extending in a buff orange line medially.

Pagurus bernhardus (Linnaeus, 1758)
(Figs 11C, 20B)

The colour of the animal is whitish with wood brown patches when young but turning to a more yellowish brown when growing. Ocular peduncles in young specimens are vermilion red, and antennules saffron yellow (Fig. 11, circled area).

Eyes (Fig. 11C.1-2). Sienna yellow corneas; ocular peduncles white with siskin green broad ring occupying distal half, tinged with bluish green below corneas (in large individuals, this ring could be broader and tinged with orpiment orange). **Antennules** (Fig. 11C.3). Segments 1-2 berlin blue, somewhat hyaline; segment 3 and flagellum pale wood brown or very pale buff orange. **Antennae** (Fig. 11C.4) tile red or hyacinth red, darker on lateral margins. **Chelipeds** (Fig. 11C.5-6) both with a similar pattern; yellowish brown to honey yellow background, with broad brownish red medial band on carpus and propodus; this band is narrower in medial area of palm, extending to the tip of fingers; tubercles tinged with skimmed milk white or cream yellow (orpiment orange in large specimens). **Pereiopods 2-3** (Fig. 11C.7-8) from yellowish brown to almost greyish white; merus with brownish red patch covering almost all lateral surface; reddish orange series of spots along whole dorsal margin; carpus, propodus and dactylus with reddish orange lines laterally; dactylus with reddish orange lateral line. **Maxillipeds** (Fig. 11C.9) chestnut brown exopods with distal half sulphur yellow.

Pagurus pubescentulus (A. Milne-Edwards and
Bouvier, 1892)
(Fig. 12A)

Eyes (Fig. 12A.1-2). Ocular peduncles orange-coloured white, with brownish orange ring near proximal margin and reddish orange ring distally. **Antennules** (Fig. 12A.3) orange-coloured white; brownish orange ring on proximal segment 1; reddish orange rings on proximal part of segment 2 and distal part of segment 3; flagellum tinged with reddish orange. **Antennae** (Fig. 12A.4). Brownish orange basal segments and acicle, fading towards segment 5. **Chelipeds. Right** (Fig. 12A.5-6). Reddish orange carpus, fading distally to white; palm deep buff orange, usually covered by encrusting organisms giving an oil green aspect and hiding the tubercles; fingers whitish distally. **Left** (Fig. 12A.7) similar to right but with palm flesh red or orange-coloured white. **Pereiopods 2-3** (Fig. 12A.8-10)

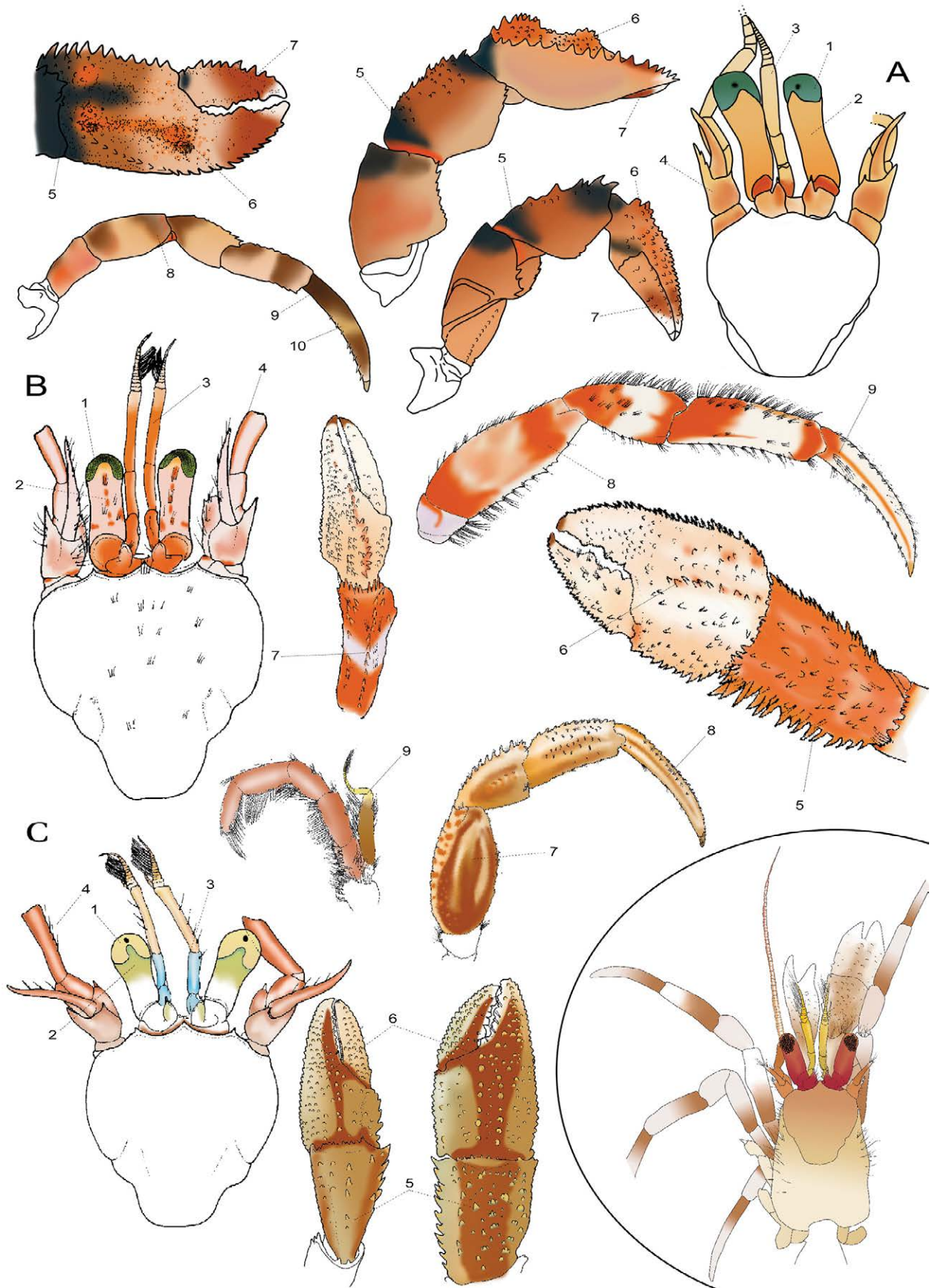


Fig. 11. – Colour patterns of *Pagurus* species: *P. pseudosculptimanus* (A, 1-10); *P. pubescens* (B, 1-9); *P. bernhardus* (C, 1-9; circled area corresponds to a juvenile). Vectorial drawings modified from A, García-Muñoz et al. (2014); B-C, Ingle (1993); juveniles of *P. bernhardus* (present work).

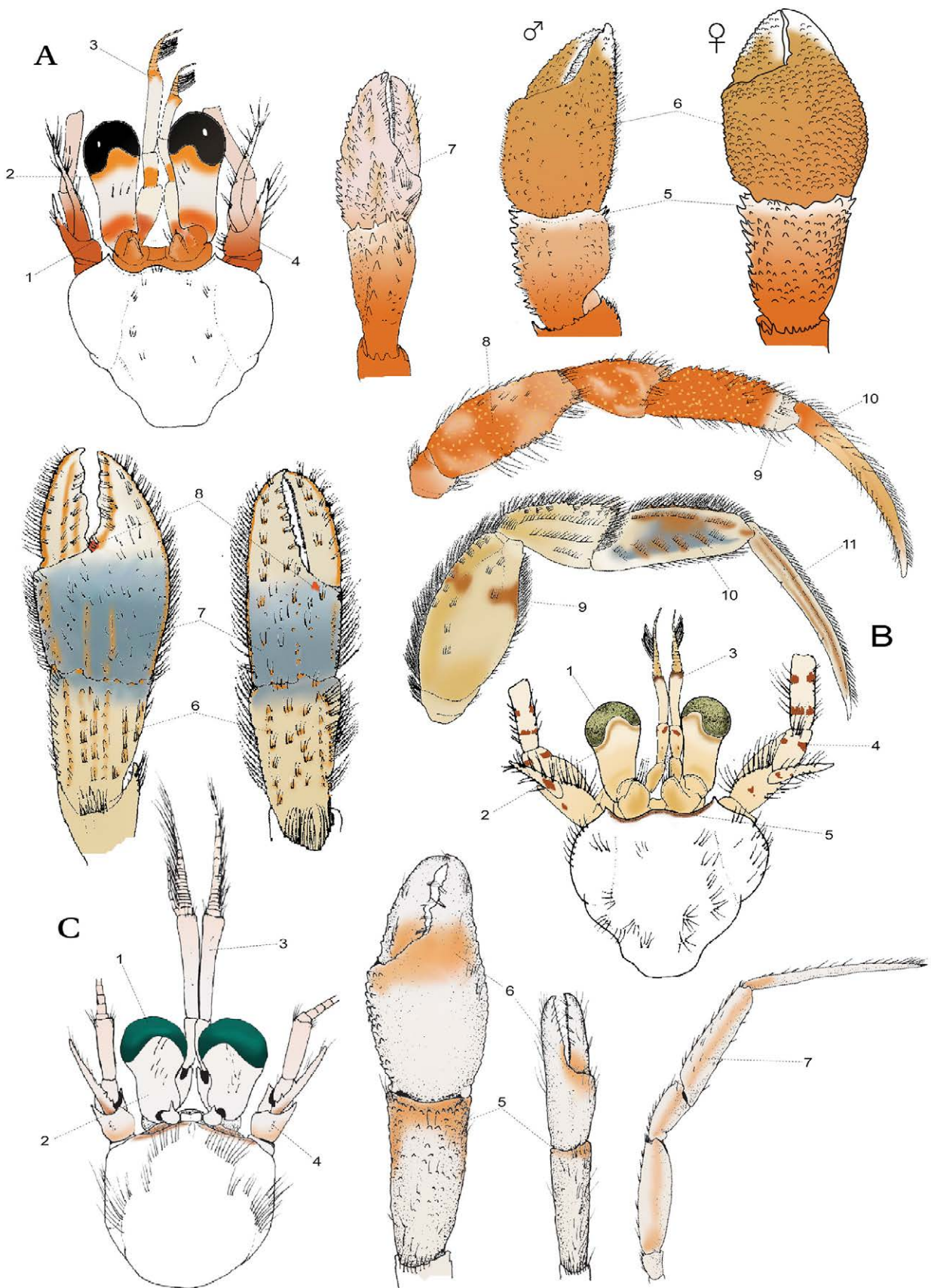


Fig. 12. – Colour patterns of Paguridae and Parapaguridae species: *Pagurus pubescentulus* (A, 1-10); *Spiropagurus elegans* (B, 1-11); *Strobopagurus gracilipes* (C, 1-7). Vectorial drawings modified from A-B, Ingle (1993); C, Lemaitre (2004).

reddish orange dotted with buff orange or cream yellow, with whitish areas on distal half of merus and carpus, almost snow-white on distal part of propodus; dactylus buff orange with reddish orange proximal part.

Spiropagurus elegans Miers, 1881
(Fig. 12B)

Eyes (Fig. 12B.1-2). Pistachio green corneas; ocular peduncles pale cream yellow, clearing distally; narrow wood brown ring near distal margin. **Antennules** (Fig. 12B.3) pale cream yellow with brownish red spots near distal margin of segment 2; segment 3 with brownish red ring distally; pale buff orange flagellum. **Antennae** (Fig. 12B.4) pale cream yellow with scattered brownish red spots, usually forming incomplete rings. **Shield** (Fig. 12B.5). Frontal margin with deep reddish brown border. **Chelipeds** (Fig. 12B.6-8) both with a similar pattern; cream yellow fading distally; spines and hair insertions orpiment orange, aligned longitudinally on carpus and palm; greyish blue areas on distal part of carpus and almost entire surface of palm; fingers whitish; dactylus with 2-3 orpiment orange parallel lines and single vermilion red spot proximally. **Pereiopods 2-3** (Fig. 12B.9-11) cream yellow with brown red incomplete ring on merus; propodus with brown red hair inserts and greyish blue area near ventral margin, with variable extension; dactylus cream yellow with two brown red parallel lines, dorsal one darker.

Family PARAPAGURIDAE Smith, 1882
Genus *Strobopagurus* Lemaitre, 1989
Strobopagurus gracilipes (A. Milne-Edwards, 1891)
(Figs 12C, 21C)

The background coloration can be whitish (Fig. 12C) or more reddish (Fig. 21C), although the same distinctive features remain.

Eyes (Fig. 12C.1-2). Olive green corneas; ocular peduncles yellowish white. **Antennules** (Fig. 12C.3) yellowish white tinged with tile red. **Antennae** (Fig. 12C.4) yellowish white tinged with tile red and some pale buff orange areas on proximal parts of basal segments and frontal margin of shield. **Chelipeds** (Fig. 12C.5-6) both with a similar pattern; yellowish white with pale buff orange on distal part of carpus and palm and proximal part of dactylus. **Pereiopods 2-3** (Fig. 12C.7) yellowish white; merus, carpus and propodus with pale lateral buff orange line medially; dactylus with pale buff orange patch proximally.

Genus *Parapagurus* Smith, 1879
Parapagurus pilosimanus Smith, 1879
(Figs 13A, 21A)

Eyes (Fig. 13A.1). Black corneas; ocular peduncles tile red tinged with reddish orange dorsally. **Antennules** (Fig. 13A.2) reddish orange on segments 1-2 with whitish distal parts; segment 3 bright red. **Antennae** (Fig. 13A.3-4) reddish orange, turning to brownish orange on segments 3-4; acicles buff orange.

Chelipeds (Fig. 13A.5-6) both with a similar pattern; orange-coloured white or pale buff orange, with proximal half of carpus reddish orange; palm buff orange or almost white. **Pereiopods 2-3** (Fig. 13A.7) uniformly deep reddish orange on the whole surface.

Parapagurus nudus (A. Milne-Edwards, 1891)

There is no information about the live colouration of this species.

Parapagurus alaminos Lemaitre, 1986
(Fig. 13B)

Eyes (Fig. 13B.1). Black corneas; ocular peduncles orange-coloured white tinged with very pale carmine red. **Antennules** (Fig. 13B.2) uniformly reddish orange. **Antennae** (Fig. 13B.3-4) tile red, lighter on basal segments, brighter acicle; segments 2-4 reddish orange. **Chelipeds** (Fig. 13B.5-6) both with a similar pattern; orange-coloured white or pale cream yellow with dull buff orange spots on distal part of palm and fingers. **Pereiopods 2-3** (Fig. 13B.7-8) buff orange with scarlet red areas on distal margin of ischium and propodus, proximal and distal parts of merus and carpus (also red on ventral margin) and dactylus.

Parapagurus abyssorum (Filhol, 1885)
(Fig. 13C)

Eyes (Fig. 13C.1). Black corneas; ocular peduncles orange-coloured white. **Antennules** (Fig. 13C.2) uniformly pale buff orange. **Antennae** (Fig. 13C.3-4) buff orange tinged with vermilion red; vermilion red flagellum. **Chelipeds** (Fig. 13C.5) both with a similar pattern; vermilion red background tinged with orpiment orange. **Pereiopods 2-3** (Fig. 13C.6-7) vermilion red tinged with orpiment orange, especially on distal part of segments, except dactylus which is orange proximally turning to red distally.

Genus *Oncopagurus* Lemaitre, 1996
Oncopagurus bicristatus (A. Milne-Edwards, 1880)
(Figs 14A, 21B)

Eyes (Fig. 14A.1). Black corneas; ocular peduncles yellowish white tinged with pale violet purple dorsally. **Antennules** (Fig. 14A.2) uniformly orange-coloured white. **Antennae** (Fig. 14A.3) uniformly orange-coloured white. **Shield** (Fig. 14A.4) yellowish white with lateral areas tinged with reddish orange and medial part violet purple. **Chelipeds** with yellowish white background. **Right** (Fig. 14A.5-6) merus with proximal 3/4 reddish orange fading distally; cream yellow carpus with reddish orange proximal half; pale buff orange areas on medial palm surface. **Left** (Fig. 14A.5, 7) reddish orange on proximal 3/4 of carpus and proximal margin of palm. **Pereiopods 2-3** (Fig. 14A.8-10) yellowish white; ischium and merus with violet purple proximal half, fading distally; proximal 1/3 of carpus and proximal half of propodus reddish orange; dactylus uniformly yellowish white.

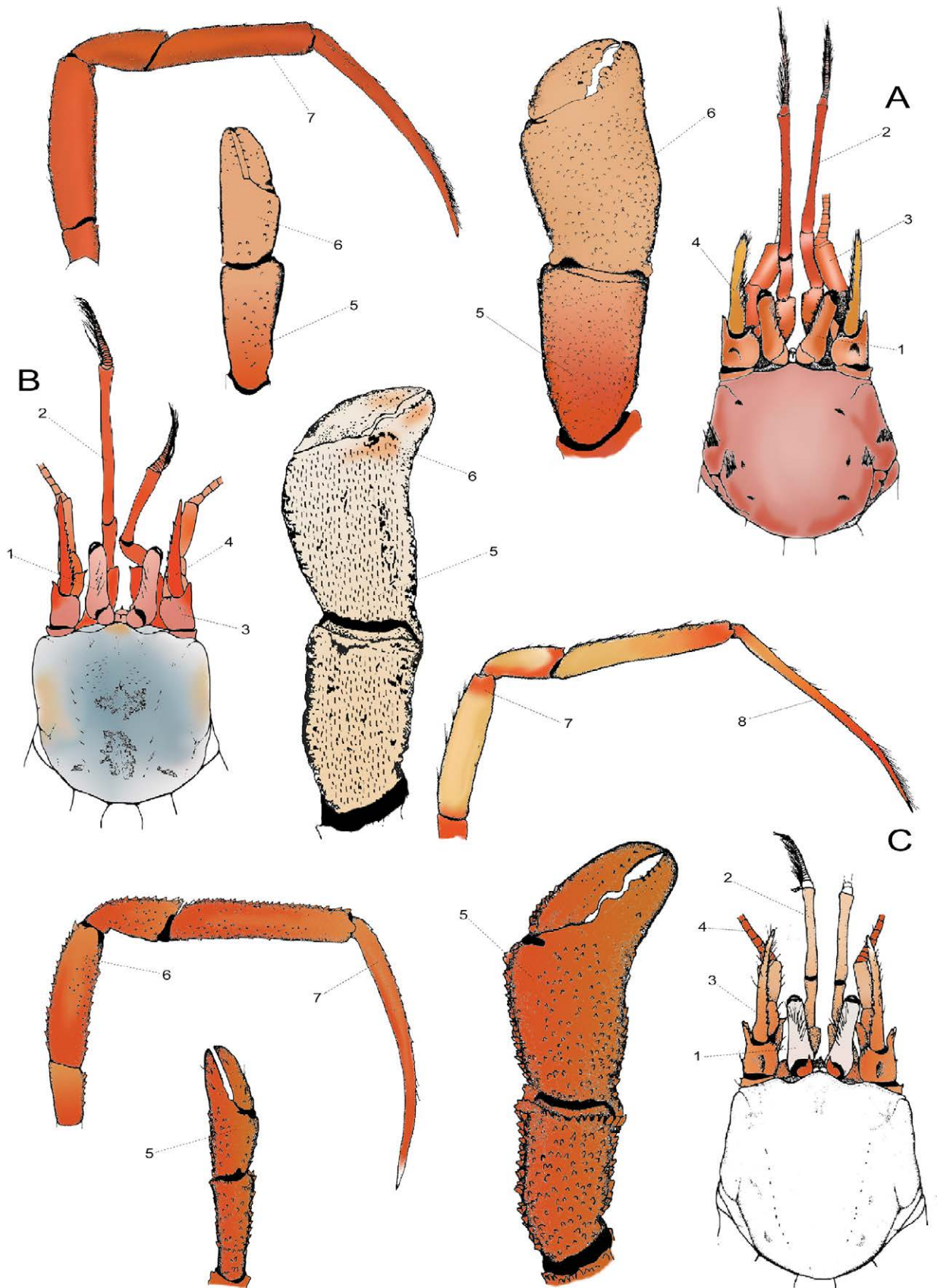


Fig. 13. – Colour patterns of *Parapagurus* species: *P. pilosimanus* (A, 1-7); *P. alaminos* (B, 1-8); *P. abyssorum* (C, 1-7). All vectorial drawings modified from Lemaitre (1989).

Genus *Paragiopagurus* Lemaitre, 1996
Paragiopagurus ruticheles (A. Milne-Edwards, 1891)
 (Figs 14B, 21D)

Eyes (Fig. 14B.1-3). China blue corneas with small velvet black square spots arranged in concentric lines, denser proximally; ocular peduncles pale reddish orange tinged with diffuse tile red area and an orpiment orange line dorsally; broad deep reddish orange line ventrally. **Antennules** (Fig. 14B.4) uniformly translucent pale buff orange. **Antennae** (Fig. 14B.5) pale buff orange tinged with reddish orange on basal segments. **Chelipeds** (Fig. 14B.6) both with a similar pattern; uniformly reddish orange, with no evident areas of different colour or intensity. **Pereiopods 2-3** (Fig. 14B.7) uniformly pale buff orange.

Genus *Sympagurus* Smith, 1883
Sympagurus acinops Lemaitre, 1989
 (Fig. 14C)

Eyes (Fig. 14C.1). Velvet black reduced corneas; ocular peduncles peach blossom red. **Antennules** (Fig. 14C.2) hyaline Berlin blue with wood brown ring on proximal margin of segments 2-3. **Antennae** (Fig. 14C.3) peach blossom red with some darker areas. **Shield** (Fig. 14C.4) deep peach blossom red, darker on frontal margin. **Chelipeds. Right** (Fig. 14C.5-6) with rose red background fading distally, and scattered wood brown stains. **Left** (Fig. 14C.7-8) similar to right, but generally whiter with palm usually snow-white. **Pereiopods 2-3** (Fig. 14C.9-10) peach blossom red, more intense on ischium and merus, fading towards dactylus; distal half of propodus and entire dactylus almost snow-white.

Identification key to Iberian hermit crabs based on live colouration

Left cheliped bigger than right or both similar in size A
 Right cheliped clearly bigger B
 A.1 Arterial blood red spots covering the ocular peduncles, shield, palm of chelipeds and dactylus of preiopods 2-3 (Fig. 1A) *Calcinus tubularis*
 – Body parts not covered by arterial blood red spots ..
 A.2
 A.2 Ocular peduncles with triangular dorsal patch, broadened proximally and running then along inner surface reaching the base of the corneas (Fig. 2A-D) .
 *(Diogenes)* A.3
 – Ocular peduncles with other type of pattern (e.g. Figs 3A-D; 1B-C) A.6
 A.3 Verditer blue spot on dorsal face of antennal segment 4; general colouration reddish orange or greenish white, with chestnut brown, usually incomplete rings on merus and carpus of left cheliped and pereiopods 2-3 (Fig. 2A) *Diogenes curvimanus*
 – Without verditer blue spot on antennal segment 4; reddish spot in proximal area of antennal acicle or without spot but all segments tinged with reddish orange (Fig. 2B-D) A.4

A.4 Chelipeds uniformly deep orange-coloured brown, with spines and tubercles brownish red; antennules with reddish orange distal ring on segment 3; antennal acicles tinged with reddish orange; shield with three paired brownish red stains on dorsal margin; carpus of chelipeds without transversal stripes (Fig. 2D)
 *Diogenes erythromanus*
 – Chelipeds not uniformly deep orange-coloured brown; antennules without defined distal ring A.5
 A.5 Antennal acicles with a vermilion red stain; shield with two distinctive brownish red longitudinal stains; narrow vermilion red stripes on carpus of chelipeds medially; hand with chestnut brown patches (Fig. 2C)
 *Diogenes pugilator*
 – Antennal acicles with chestnut brown stain; chelipeds and pereiopods 2-3 with umber brown transversal stripes over a greenish background; palm and fingers or chelipeds with orpiment orange spines (Fig. 2B) -
 *Diogenes armatus*
 A.6 Ocular peduncles with well-defined colour rings (Fig. 3A, B) *(Dardanus)* A.7
 – Ocular peduncles without colour rings, just differences in colouration (Figs 1B, C; 3C, D) A.8
 A.7 Ocular peduncles with three scarlet red rings; antennules violet purple tinged with red; antennae ranging proximo-distally from reddish orange to violet purple; palm of chelipeds with scarlet red stripes with edge of scales violet purple and reddish orange hairiness (Fig. 3A) *Dardanus arrosor*
 – Ocular peduncles with four scarlet red rings; antennules saffron yellow, reddish orange laterally; antennal segments 3-5 saffron yellow; chelipeds with broad peach blossom red ring on merus; tubercles of hands with peach blossom red base and black tips; pereiopods 2-3 with peach blossom red rings on merus, carpus and propodus (Fig. 3B) *Dardanus calidus*
 A.8 Ocular peduncles with one unique colour fading distally; bluish corneas; chelipeds with reddish tubercles and distinctive stain on inner distal face of merus with apical scarlet red half outlined in white and basal part blue (Fig. 3C-D) *(Paguristes)* A.9
 – Ocular peduncles reddish orange proximally, turning to oil green distally; black corneas spotted in white; chelipeds with whitish-bluish tubercles (Fig. 1B, C) ..
 *(Clibanarius)* A.10
 A.9 Chelipeds with vermilion red stain on the inner lateral surface of the palm; dactylus of pereiopods scarlet red with one distal and one subdistal white ring; corneas vivid azure blue (Fig. 3D) *Paguristes rubropictus*
 – Chelipeds without a vermilion red stain on the inner lateral surface of the palm; pereiopods reddish orange with apical white and subapical scarlet red rings on dactylus; corneas greenish blue (Fig. 3C) *Paguristes eremita*
 A.10 Fingers of chelipeds with arterial blood red stripes outlined in ultramarine blue, tubercles of chelipeds also blue; dactylus of pereiopods with scarlet red lines on a white background; exopods of maxillipeds dark chocolate red with ultramarine blue ring on tip and base of flagellum; ocular peduncles with proximal 1/4 reddish orange (Fig. 1B) *Clibanarius erythropus*
 – Fingers of chelipeds with distal scarlet red patch; oil green tubercles with white tips on chelipeds; dactylus

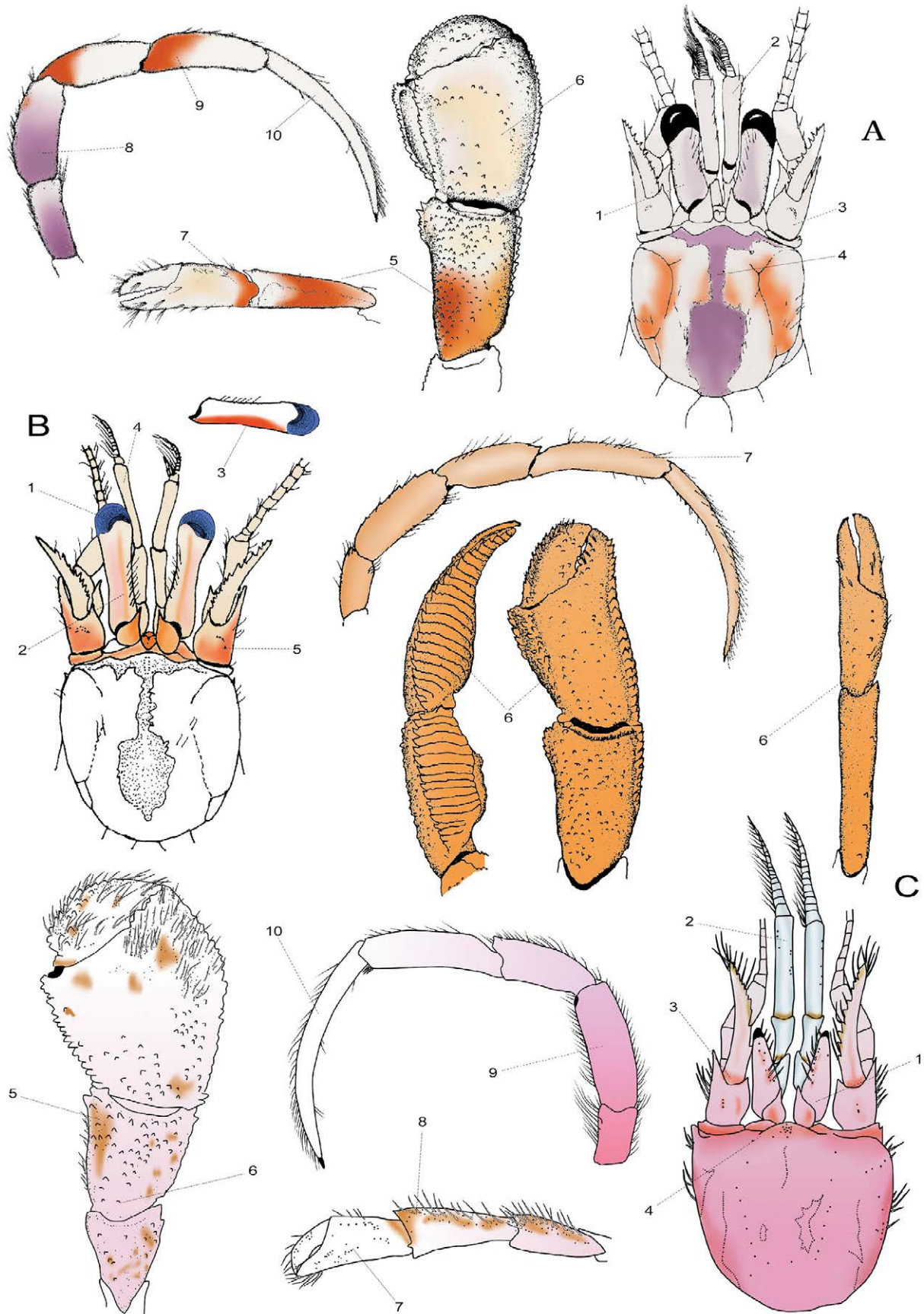


Fig. 14. – Colour patterns of Parapaguridae species: *Oncopagurus bicristatus* (A, 1-10); *Paragiopagurus ruticheles* (B, 1-7); *Sympagurus acinops* (C, 1-10). Vectorial drawings modified from A, Lemaitre (2014); B, Lemaitre (2013); C, present work.

- of pereopods saffron yellow with scarlet red proximal, distal and dorsal areas; exopods of maxillipeds dark chocolate with white ring on tips and base of flagellum; ocular peduncles with proximal 2/3 reddish orange (Fig. 1C) *Clibanarius aequabilis*
- B.1 Chelipeds and pereopods 2-3 with a well-defined pattern made up of longitudinal lines (Figs 7C; 8A; 9A) B.2
- Chelipeds and pereopods 2-3 pattern different than longitudinal B.4
- B.2 Primrose yellow ocular peduncles, with proximal chestnut brown ring and a thinner one under the verdigris green corneas; line pattern on shield, chelipeds and pereopods 2-3 is bluish lilac purple mixed with other colours (Fig. 8A) *Pagurus anachoretus*
- Ocular peduncles and corneas with different colouration as above; longitudinal pattern not including bluish lilac purple B.3
- B.3 Ocular peduncles reddish orange, with three arterial blood stripes on outer side; scarlet red patches on distal 2/3 of antennular segment 3 and antennal acicle; pattern on chelipeds and pereopods 2-3 with scarlet red lines over a reddish orange background (Fig. 7C) *Nematopagurus longicornis*
- Ocular peduncles orpiment orange with longitudinal straw yellow stripes on ocular peduncles and usually also on shield, chelipeds and pereopods 2-3; corneas white spotted in red; imperial purple antennular segment 3 (Fig. 9A) *Pagurus chevreuxi*
- B.4 Markedly reduced corneas (e.g. Figs 7A; 14C) .. B.5
- Corneas not markedly reduced B.9
- B.5 General colour pinkish with most areas fading to white (Figs 7A; 14C) B.6
- General colour uniformly reddish or reddish orange (Fig. 13A-C) (*Parapagurus*) B.7
- B.6 Chelipeds with rose red background fading distally to snow-white broad palm, with scattered wood brown stains; pereopods 2-3 peach blossom red fading towards dactylus (Fig. 14C) *Sympagurus acinops*
- Scarlet red corneas; palm of right cheliped not proportionally broadened, with rose red background fading distally; carpus and propodus of pereopods 2-3 with faint distal wood brown areas (Fig. 7A) *Catapaguroides microps*
- B.7 Chelipeds and pereopods 2-3 uniformly reddish orange or vermilion red, sometimes with small orange areas (Fig. 13A, C) B.8
- Chelipeds orange-coloured white or pale cream yellow; ocular peduncles orange-coloured white tinged with pale carmine red; buff orange pereopods 2-3 with short scarlet red distal areas (Fig. 13B) *Parapagurus alaminos*
- B.8 Ocular peduncles orange-coloured white; antennules uniformly pale buff orange; chelipeds and pereopods 2-3 vermilion red with some orpiment orange areas especially on distal part of segments (Fig. 13C) *Parapagurus abyssorum*
- Ocular peduncles tile red tinged with reddish orange; antennules reddish orange on segments 1-2 with whitish distal parts, segment 3 bright red; carpus of chelipeds reddish orange proximally; palm buff orange or almost white (Fig. 13A) *Parapagurus pilosimanus*
- B.9 Ocular peduncles with longitudinal patterns, not rings (Figs 4C; 7B; 11B; 14B) B.10
- Ocular peduncles with or without rings, never longitudinal patterns (e.g. Figs 4A, B; 5A; 6B; 11A) . B.13
- B.10 Ocular peduncles with thin continuous or dotted line (Figs 11B, 14B) B.11
- Ocular peduncles with broad scarlet red bands combined with clearer ones (Figs 4C; 7B) B.12
- B.11 Ocular peduncles with thin orpiment orange line dorsally; broad deep reddish orange line ventrally (Fig. 14B)..... *Paragiopagurus ruticheles*
- Ocular peduncles with longitudinal row of orpiment orange dots dorsally (Fig. 11B) ... *Pagurus pubescens*
- B.12 Emerald green corneas dotted in scarlet red; ocular peduncles scarlet red with thick longitudinal cream yellow lines; auricula purple antennular segment 3 (Fig. 7B) *Cestopagurus timidus*
- Corneas pistachio green with scarlet red dots; scarlet red ocular peduncles with white spots usually forming complete stripes dorsally; auricula purple antennular flagellum (Fig. 4C) *Anapagurus chiroacanthus*
- B.13 Ocular peduncles without well-defined rings, at most a diffuse area with different tone on distal or proximal part (e.g. Figs 6B; 10A, 11A) B.14
- Ocular peduncles with well-defined rings, complete or incomplete (e.g. Figs 4A, B, D; 5B, C; 6C) ... B.21
- B.14 Ocular peduncles without clear different colour, mostly uniform (Figs 5A; 6B; 11A; 12C; 14A) .. B.15
- Ocular peduncles with areas of different tone, resembling colour rings (but not well delimited) (Figs 6A; 8C; 10A)..... B.19
- B.15 Ocular peduncles whitish with subtle stains of different colour over it (Figs 5A; 6B; 12C; 14A) B.16
- Ocular peduncles, antennules and antennae buff orange; oil green corneas; chelipeds brownish orange with proximal carpus and palm indigo blue; bigger tubercles of palm orpiment orange; vermilion red patches in fingers (Fig. 11A) *Pagurus pseudosculptimanus*
- B.16 Ocular peduncles tinged with pale violet purple dorsally; shield with violet purple medial part and reddish orange laterals; reddish orange proximal carpus of right chelipeds and carpus-propodus of pereopods 2-3 and left cheliped (Fig. 14A) *Oncopagurus bicristatus*
- Ocular peduncles and shield without violet purple areas; chelipeds and carpus-propodus of pereopods 2-3 with different pattern B.17
- B.17 Yellowish white ocular peduncles with olive green dilated corneas and pale buff orange patches on antennae and distal part of carpus and palm of chelipeds; buff orange line on lateral surface of pereopods 2-3 (Fig. 12C) *Strobopagurus gracilipes*
- Corneas not expanded, ocular peduncles, antennules and antennae with different patterns; pereopods 2-3 with transversal stains, not only longitudinal B.18
- B.18 Corneas outlined and spotted in gamboge yellow; antennules orange-coloured white with brownish red and distal orange rings on segment 3; chestnut brown broad patch on palm of right cheliped fading backwards (Fig. 6B) *Anapagurus petiti*
- Corneas duck green dotted in black; antennules and antennae orange-coloured white, with wood brown areas in both; chelipeds with brownish red

- ring near distal half of merus and proximal areas of the same colour on propodus and dactylus of pereopods 2-3 (Fig. 5A)..... *Anapagurus curvidactylus*
- B.19 Ocular peduncles with darker area placed distally (Figs 6A; 10A) B.20
- Ocular peduncles tile to flesh red with darker area placed on proximal 3/4; general colour tile red or flesh red; chelipeds with orpiment orange spots on merus, carpus and propodus, and proximal and distal areas of pereopods 2-3 (Fig. 8C) *Pagurus carneus*
- B.20 Emerald green corneas; ocular peduncles pale buff orange, darker on distal margin; small vermilion red stains on proximal carpus, propodus and dactylus of right cheliped and rings of the same colour on carpus of left cheliped and all segments of pereopods 2-3 (Fig. 10A).....*Pagurus forbesii*
- Corneas oil green; ocular peduncles yellowish white with orpiment orange area distally fading backwards, and ocular acicles with deep brownish orange distal area; chelipeds and pereopods 2-3 orpiment orange (Fig. 6A) *Anapagurus longispina*
- B.21 Ocular peduncles with at least two well-defined rings, complete or incomplete (e.g. Figs 4A-B; 5B, C; 6C) B.25
- Ocular peduncles with only one well-defined ring (Figs 8B; 9C; 11C; 12B) B.22
- B.22 Ocular peduncles with proximal reddish orange ring, occasionally with diffuse reddish orange band under the corneas; in rose red variety, proximal ring is almost imperceptible; palm of chelipeds with central and lateral ridges reddish orange (Fig. 8B)... *Pagurus alatus*
- Ocular peduncles with distal ring only (Figs 9C; 11C; 12B) B.23
- B.23 Ocular peduncles with tile red distal ring; chelipeds pale wood brown with deep reddish brown spines; palm ridges and depressions tinged with yellowish brown (Fig. 9C) *Pagurus excavatus*
- Ocular peduncles with distal ring of different colour (Figs 11C; 12B) B.24
- B.24 Ocular peduncles pale cream yellow with narrow wood brown ring near distal margin; brownish red ring on antennular segment 3 and incomplete rings on antennae; proximal half of chelipeds palm greyish blue (Fig. 12B) *Spiropagurus elegans*
- Ocular peduncles whitish with broad siskin green ring distally; sienna yellow corneas; antennules hyaline berlin blue, with segment 3 pale wood brown; chelipeds yellowish brown with a broad brownish red central band on carpus and propodus; tubercles of chelipeds tinged in white, cream yellow or orange in larger individuals (Fig. 11C) *Pagurus bernhardus*
- B.25 Antennules with longitudinal lines dorsally (Figs 4A; 5B) B.26
- Antennules with another pattern but not longitudinal lines (Figs 4B, 5C; 6C; 9B; 10B, C; 12A)..... B.27
- B.26 Corneas honey yellow dotted with red; with a chestnut brown ring surrounding the base of corneas, extending backwards dorsally, reaching mid-length of ocular peduncles; antennules long, gallstone yellow, with wood brown lines on dorsal and ventral margins; chocolate red rings in merus of chelipeds and maxillipeds (Fig. 5B) *Anapagurus hyndmanni*
- Ocular peduncles with hyacinth red stripes near proximal margin, forming an almost complete ring; yellowish brown ring near distal margin; saffron yellow bands on antennular segment 1-2; segment 3 with longitudinal reddish orange dorsal line; ocular peduncles, corneas, antennules and antennae dotted in lemon yellow (Fig. 4A) *Anapagurus alboranensis*
- B.27 Ocular peduncles with distal ring orange, clearer than proximal ring (Figs 9B; 12A) B.28
- Ocular peduncles with distal ring red, of the same tone or darker than proximal ring (Figs 4B, D; 5C; 6C; 10B, C) B.29
- B.28 Antennules with reddish orange rings on proximal part of segment 2 and distal part of segment 3; ocular peduncles with brownish orange proximal ring and distal reddish orange ring; general colour reddish orange (Fig. 12A) *Pagurus pubescentulus*
- Distal half of antennular segment 2 and entire segment 3 deep orange-coloured brown; ocular peduncles with proximal wood brown ring, distal reddish orange; vermilion red areas on the very setose carpus-propodus of chelipeds and pereopods 2-3 (Fig. 9B) *Pagurus cuanensis*
- B.29 Some purplish areas on chelipeds and pereopods 2-3; antennules without evident rings (Fig. 10B, C) B.30
- Chelipeds and pereopods 2-3 with red bands and lines; antennules spotted or ringed (Figs 44B, D; 5C; 6C) . B.31
- B.30 Ocular peduncles with pale buff orange ring proximally and vermilion red distally; chelipeds buff orange with vermilion spots and violet purple areas; pereopods 2-3 with vermilion red areas over a cream yellow background; propodus with proximal violet purple patch; dactylus with a series of vermilion red spots medially (Fig. 10C) *Pagurus prideaux*
- Ocular peduncles with reddish orange ring near proximal margin and diffuse peach blossom red band above it; hyacinth red ring distally; pale buff orange chelipeds and pereopods 2-3 with diffuse peach blossom red areas (Fig. 10B) *Pagurus mbizi*
- B.31 Antennules with distal ring well-defined B.32
- Antennules with red and yellow spots, without rings; corneas pistachio green dotted in black; ocular peduncles with proximal and distal tile red rings; carpus of chelipeds and pereopods 2-3 orange-coloured white with tile red bands (Fig. 4B) . *Anapagurus bicorniger*
- B.32 Antennules translucent with hyacinth red spots dorsally forming distal rings on segments 2-3; ocular peduncles with proximal buff orange and reddish orange distal rings; palm of chelipeds with distinctive Y-shaped reddish orange patch medially; carmine red spots on ischium of pereopods 2-3 and reddish orange rings on merus and propodus; all segments dotted in yellow (Fig. 5C) *Anapagurus laevis*
- Chelipeds without the distinctive Y-shaped patch; ocular peduncles with rings of similar colour B.33
- B.33 Ocular peduncles with hyacinth red rings; antennular segment 3 with proximal and medial dorsal hyacinth red stains, and distal ring of the same colour; fingers of chelipeds with scarlet red subdistal ring; pereopods 2-3 whitish with longitudinal hyacinth red stains (Fig. 4D) *Anapagurus breviaculeatus*
- Tile red ocular peduncles with proximal, medial and distal vermilion red rings; antennules with brownish

purple red dorsal stripe on segment 3 ending in proximal and apical (tridentate) rings; fingers of chelipeds tinged with brownish orange, without well-defined rings; pereopods 2-3 with proximal and distal vermilion red rings on merus and propodus, with distal angles of all segments tinged in saffron yellow (Fig. 6C) *Anapagurus pusillus*

DISCUSSION

The application of modern techniques to taxonomy, has led to the identification of numerous new issues related to the identification and delimitation of taxa. With the spread of the integrative taxonomy perspective, and especially with the application of molecular techniques, concepts like “sibling”, “cryptic/pseudocryptic species”, “species-complex”, and even “convergent evolution”, have been gaining presence in the literature, showing that clusters of morphologically very similar but genetically different species are much more common than previously thought (Macpherson and Machordom 2005, Cornils and Held 2014, García-Muñoz et al. 2014, Negri et al. 2014, Craig and Felder 2021, Fitriani et al. 2022, Sultana et al. 2022). Modern taxonomy has allowed us to explore these problematic aspects, establishing a solid ground for validating or discarding certain taxonomic features and allowing us to select those reflecting evolutionary value.

The study of colour patterns in hermit crabs as a tool in taxonomy has been validated and successfully applied in recent studies for differentiation of very closely related species (Poupin and Lemaitre 2003, Malay and Paulay 2010, Poupin and Malay 2009, Negri et al. 2014, Lemaitre et al. 2018, Felder et al. 2019), although for most of the species within Paguroidea this information is still unknown. Differences in colouration make the separation straightforward in some species that are morphologically very similar. This is the case of the genus *Clibanarius*, which includes two morphologically very close species with

in the study area, with very evident patterns on each species that are visible even when the animal is partially retracted in the shell, especially on the dactylus of pereopods 2-3 and the stripes of the maxillipeds (Fig. 1B, C). This circumstance was already noticed by Santaella (1974), who included in his work a very detailed description of the live colour of *C. aequalis*. His description, still valid according with the present revision, has been modified and adapted to meet the general purpose of this work. Among the *Diogenes* species, primarily found in intertidal or shallow subtidal habitats, five species are included within the study area. These species have long been considered variations of the highly polymorphic *D. pugilator* (Forest and Guinot 1956, Ingle 1993, Noël 2016). Recent studies have demonstrated that there are in fact different species, which can be separated on the basis of several morphological characters that are not always easy to recognize and show a certain degree of intraspecific variation (Almón et al. 2022a, 2022b). However, despite the possible variations that may occur, general colour patterns are consistently different between the four species for which this information is available. The two species of *Dardanus* recorded in the area are also morphologically close, but the number and design of the stripes on the ocular peduncles, the colouration of the antennae and antennules and the differences in coloration of the chelipeds (Fig. 3A, B) are characters that are easily seen in live specimens, even when semi-retracted in their shells, and that can therefore facilitate their identification. The genus *Paguristes* is represented in the study area by two species, *P. eremita* and *P. rubropictus*. The status of *P. rubropictus* is still controversial (Ingle 1993), because the morphological differences from *P. eremita* are usually small and have even often been considered to fall within the intraspecific variability of *P. eremita*. Individuals from the Canary Islands reported as *P. rubropictus* were included in this work for comparative purposes. Beyond the subtle morphological differences that are often very difficult



Fig. 15. – Different colour patterns of *Diogenes pugilator* chelipeds. Vectorial drawings are originals from Almón et al. (2022a).

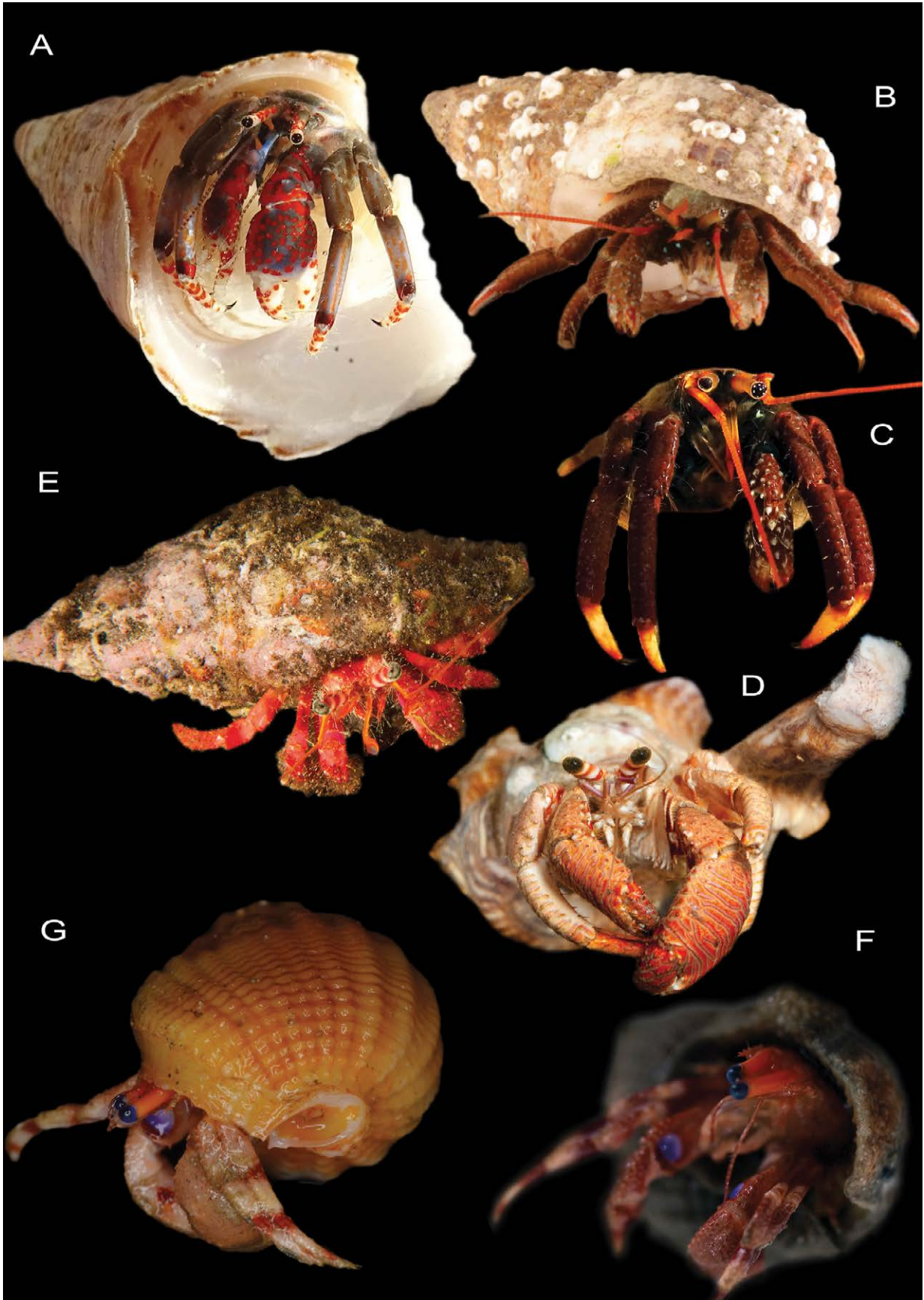


Fig. 16. – Colour photographs of species belonging to the family Diogenidae. A, *Calcinus tubularis* (IEOCD-BR/317); B, *Clibanarius erythropus* (IEOCD-BR/325); C, *Clibanarius aequabilis* (IEOCD-BR/326); D, *Dardanus arrosor* (IEOCD-BR/354); E, *Dardanus calidus* (IEOCD-BR/361); F, *Paguristes eremita* (IEOCD-BR/372); G, *Paguristes rubropictus* (IEOCD-BR/381).

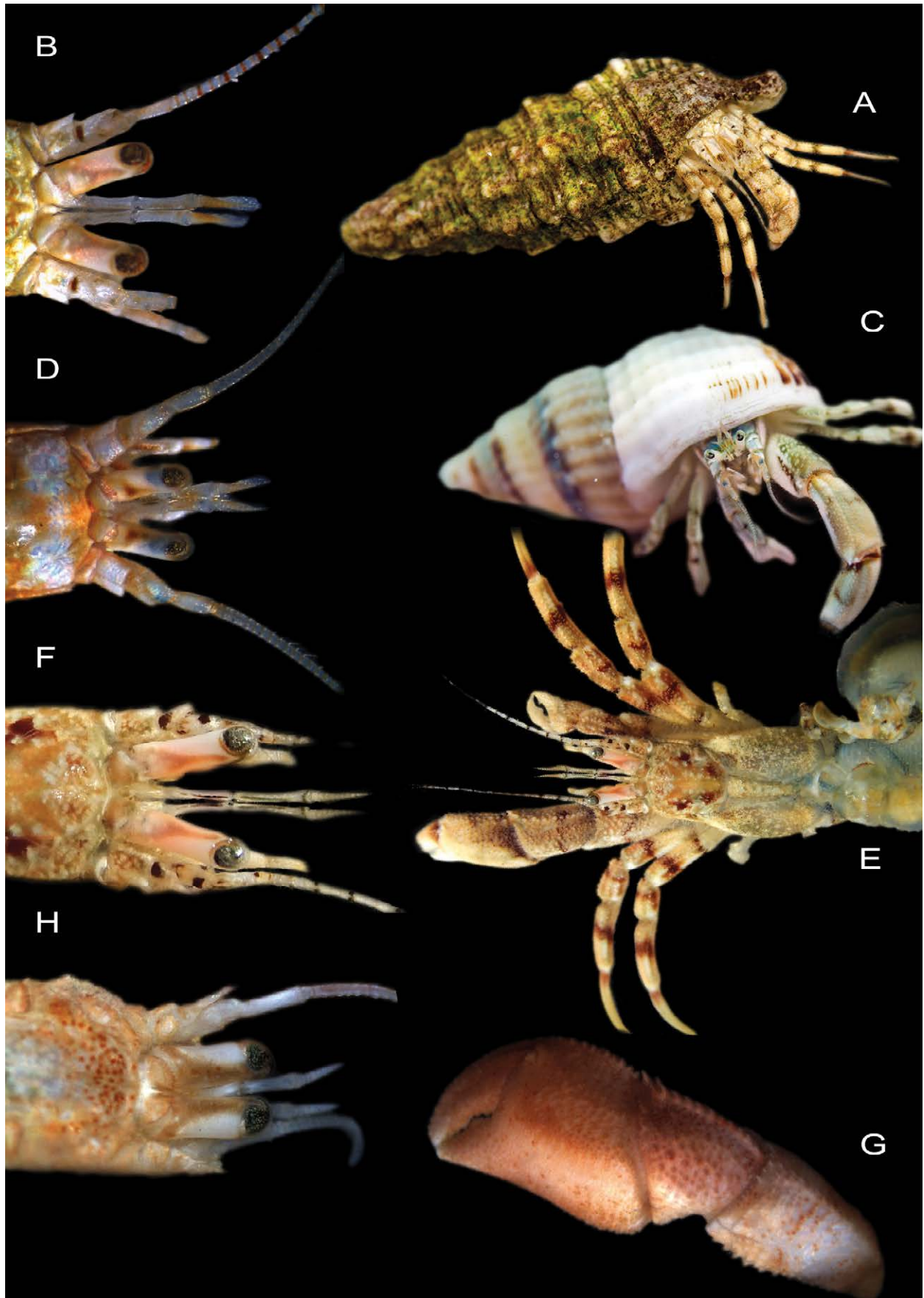


Fig. 17. – Colour photographs of the species of the genus *Diogenes*. A, B, *Diogenes armatus* (MNHN-IU-2019); C, D, *Diogenes curvimanus* (ZSMA2019 398); E, F, *Diogenes pugilator* (IEOCD-BR/2669); G, H, *Diogenes erythromanus* (IEOCD-BR/2680).



Fig. 18. – Colour photographs of species of the genus *Anapagurus* studied. A, *Anapagurus alboranensis* (IEOCD-BR/3041); B, *Anapagurus hyndmanni* (IEOCD-BR/3069); C, *Anapagurus breviaculeatus* (IEOCD-BR/3048); D, *Anapagurus chiroacanthus* (© Fredrik Pleijel); E, *Anapagurus petiti* (IEOCD-BR/313); F, *Anapagurus pusillus* (IEOCD-BR/316); G, *Anapagurus laevis* (IEOCD-BR/3096); H, *Anapagurus curvidactylus* (© Jacinto Pérez).

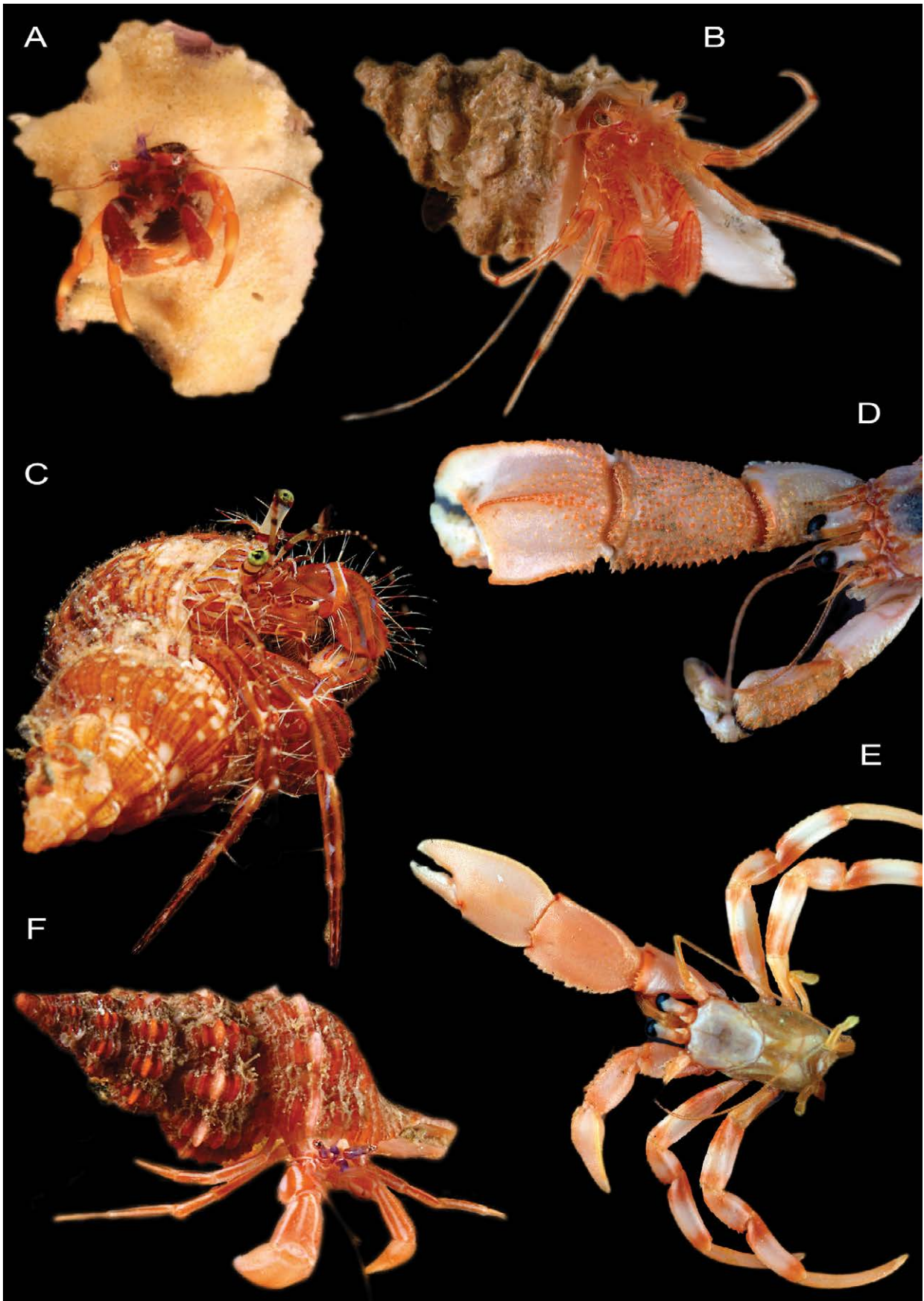


Fig. 19. – Colour photographs of species belonging to the family Paguridae. A, *Cestopagurus timidus* (© Jacinto Pérez); B, *Nematopagurus longicornis* (© Jacinto Pérez); C, *Pagurus anachoretus* (IEOCD-BR/285); D, *Pagurus alatus* (IEOCD-BR/3170); E, *Pagurus carneus* (IEOCD-POR13/286); F, *Pagurus chevreuxi* (IEOCD-BR/287).

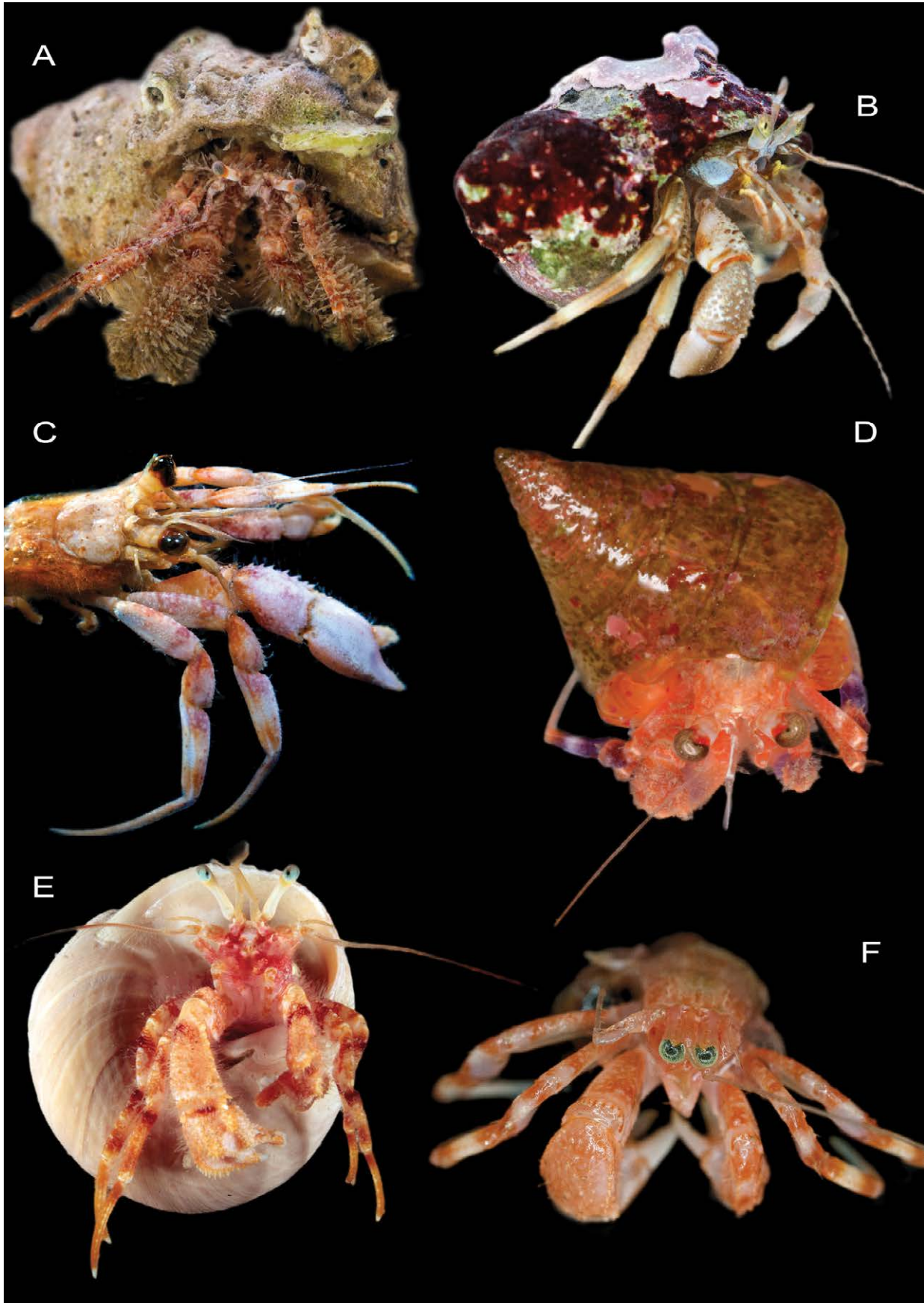


Fig. 20. – Colour photographs of species belonging to the family Paguridae. A, *Pagurus cuanensis* (IEOCD-BR/3163); B, *Pagurus bernhardus* (IEOCD-BR/3185); C, *Pagurus mbizi* (IEOCD-BR/3180); D, *Pagurus prideaux* (IEOCD-BR/3166); E, *Pagurus forbesii* (© Jacinto Pérez); F, *Pagurus pubescens* (IEOCD-BR/3200).

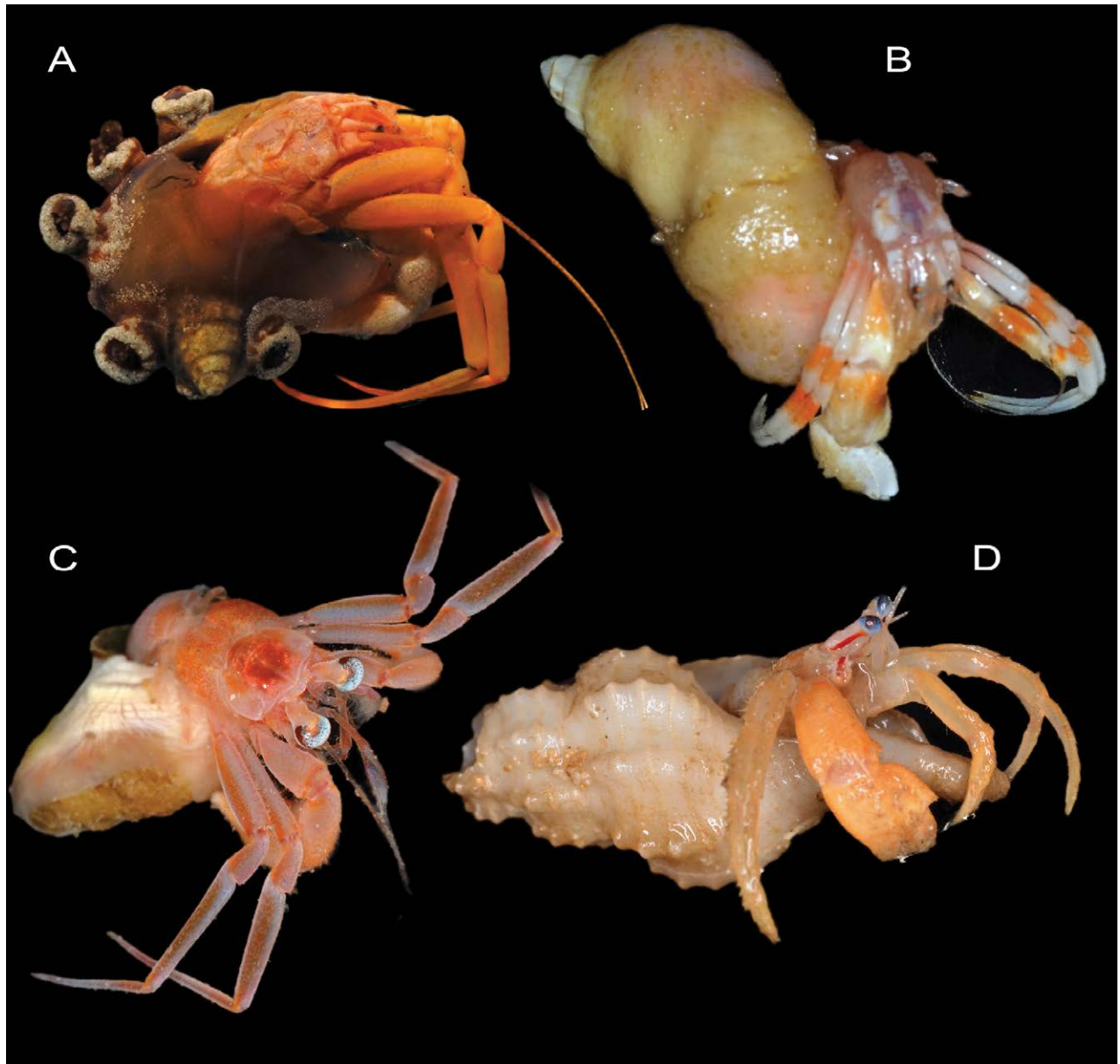


Fig. 21. – Colour photographs of species belonging to the family Parapaguridae. A, *Parapagurus pilosimanus* (IEOCD-BR/3195); B, *Oncopagurus bicristatus* (INFUECO1112); C, *Strobopagurus gracilipes* (IEOCD-BR/3193); D, *Paragiopagurus ruticheles* (IEOCD-BR/3197).

to observe, the most evident distinguishing feature is related to the colour (Santaella 1973). *P. rubropictus* has a vermillion red patch on the inner lateral surface of the hand, at the base of the mobile finger (Fig. 3C, D), which is absent in *P. eremita* (Forest 1954). In addition to this, several new characters that can help to differentiate the species have been included here, such as the colouration of the corneas and the colour pattern of pereopods 2-3.

The genus *Anapagurus* has been specially challenging for taxonomists owing to the small size of the specimens, the similarity between species and the morphological variability of some of the body parts within species (Ingle 1993, García-Gómez 1994). By introducing the colour dimension, identification of the species can be more easily achieved in most cas-

es, because unique patterns have been defined for 10 of the 12 species recorded in European waters (Figs 4-6), which represents more than 50% of the total number worldwide (Lemaitre and McLaughlin 2022). Although it is a valid premise for all species to a greater or lesser degree, some examples of species with different chromatic varieties, sometimes very pronounced, were found especially among the *Anapagurus* and *Pagurus* species. This is the case of *A. laevis*, *A. bicorniger*, *A. hyndmanni*, *P. alatus*, *P. cuanensis* and *P. prideaux*. All have shown a high variability in specimens coming from different areas and even within the same one, probably associated with the habitat type. There is a “whitish” variety that affects especially pereopods 2-3 and the male right and left chelipeds, which show a whitish background with more clear spots and pat-

terns, and a more reddish orange variant, in which the overlapping patterns become darker and less defined. New colour variations have recently been identified on the left chelae of the species *D. pugilator* (Fig. 15), which is an example of the variability inherent to some species. Nevertheless, for most of the species included in this study, certain colour characters have shown low variability, allowing those that can be preferably used as “identifying marks” to be highlighted, even in species with high variability in the general background colour. The perception of colours can also vary depending on the light conditions, the live stage of the individuals, the environment in which they live and their diet, among other factors. Therefore, the descriptions should be taken as an overview guide that is subject to some margin of variation.

The definition of valuable colorimetric species-defining characters involves an intense work of photography collection aligned with laboratory work to confirm the identities of the specimens under study. Most of the descriptions included in the present work are based on abundant material and are therefore considered solid. However, for the rarer species, the scarce available material has been used to give an educated guess of what it is considered to be the reality. Therefore, when new information becomes available, some descriptions will be completed and improved. Once these tasks are fulfilled, field work would be very much facilitated by the implementation of colourimetric patterns as an identification tool.

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APPENDIX

Appendix 1. – Summary of most relevant specimens and web references analyzed for the identification of the unique colour patten for each species.

Species	Locality	Country	Voucher number	Online Ressources	Sex
<i>Calcinus tubularis</i>	Tenerife, Canary Islands	Spain	IEOCD-BR/317		2M,1F
	off Cabo Girao, Madeira	Portugal		© Peter wirtz	1M
	Alboran Sea	Spain		https://litoraldegranada.ugr.es	-
<i>Clibanarius erythropus</i>	El Chato, Cádiz	Spain	IEOCD-BR/324		1F
	Cabo Estai, Vigo	Spain	IEOCD-BR/325		2M
<i>Clibanarius aequabilis</i>	Mar Menor	Spain		https://canalmarmenor.carm.es/	-
	Güímar, Canary Islands	Spain	IEOCD-BR/326		3M,1F
	La Graciosa, Canary Islands	Spain	IEOCD-BR/327		3M,2F
<i>Diogenes curvimanus</i>		Spain		https://www.biodiversidadcanarias.es/	-
	Doñana N.P., Huelva	Spain	IEOCD-BR/2587		1M
	Ribeira, Galicia	Spain	ZSMA2019 398		1F
<i>Diogenes armatus</i>	Cantabrian Sea	Spain		https://www.asturnatura.com	-
	Torregorda, Cádiz	Spain	MNHN-IU-2019		2M
	Bajo la Cabezuela, Cádiz	Spain	IEOCD-BR/2624		1F
<i>Diogenes pugilator</i>	Lagoa da Albuferia, Sesimbra	Portugal	IEOCD-BR/2647		1M
	Frontignan	France	IEOCD-BR/2669	© Christoph Schubart	1M
	La Carihuela, Málaga	Spain	IEOCD-BR/2662		1F
<i>Diogenes erthromanus</i>	Barcelona	Spain	CBRICMD/ICMD 143/1998		1M
	Baños del Carmen, Málaga	Spain	IEOCD-BR/2680		1F
	Cabo Pino, Mijas	Spain	IEOCD-BR/2935		4M,4F
<i>Dardanus arrosor</i>	Off Kenitra	Maroc	CCDE-IEOCD/2578-2		1M
	Gulf of Cadiz	Spain	IEOCD-BR/330		1M
	Cabrera, Balearic Islands	Spain	IEOCD-BR/353		1M
<i>Dardanus calidus</i>	Gran Canaria, Canary Islands	Spain	IEOCD-BR/354		1M,1F
	Mediterranean	Spain	CBR-ICMD 18/2000		1M,1F
	S Fuerteventura, Canary Islands	Spain	IEOCD-BR/361		1M
<i>Paguristes eremita</i>	Alboran Sea	Spain		https://litoraldegranada.ugr.es	
	Off Marsa, Western Sahara	Western Sahara	IEOCD-BR/372		1M1F
	Off El Aaiún, Western Sahara	Western Sahara	IEOCD-BR/373		1F
<i>Paguristes rubropictus</i>	Calafuria, Livorno	Italy		https://www.naturamediterraneo.com/	?
	W Gran Canaria, Canary Islands	Spain	IEOCD-BR/381		?
	SW Gran Canaria, Canary Islands	Spain	IEOCD-BR/385		?
	E Gran Canaria, Canary Islands	Spain	IEOCD-BR/389		1F

Species	Locality	Country	Voucher number	Online Ressources	Sex
<i>Anapagurus alboranensis</i>	Calaburra, Mijas	Spain	IEOCD-BR/3040		1M
	Baños del Carmen, Málaga	Spain	IEOCD-BR/3041		1M
	Playa del Pozuelo, Granada	Spain	IEOCD-BR/3043		1F
<i>Anapagurus bicorniger</i>	Cape of La Nao, Denia	Spain	CBR-ICMD 001028		1M
	Baños del Carmen, Málaga	Spain	IEOCD-BR/3047		1M
	Gulf of Cadiz	Spain	IEOCD-BR/314		1F
<i>Anapagurus breviaculeatus</i>	Formentera, Balearic Islands	Spain	IEOCD-BR/3048		3M,1F
	Eivissa-NW Ibiza, Balearic Islands	Spain	IEOCD-BR/3049		3M
	La Línea, Cádiz	Spain	IEOCD-BR/3050		1M
<i>Anapagurus chiroacanthus</i>	Eivissa-NW Ibiza, Balearic Islands	Spain	IEOCD-BR/3054		1F
	Aguilas-Cartagena	Spain	IEOCD-BR/3058		5M,1F
	SW Sweden	Sweden	not preserved	© Fredrik Pleijel/SLU Artdatabanken	?
<i>Anapagurus curvidactylus</i>	W off Gorée Island	Senegal	USNM 22921	Chevreaux and Bouvier, 1892	1M
	Ría de Arousa, Galicia	Spain	not preserved	© Jacinto Pérez	?
<i>Anapagurus hyndmanni</i>	Ribeira, Galicia	Spain	IEOCD-BR/3066		2M
	Ribeira, Galicia	Spain	IEOCD-BR/3069		1F
	Petón Baixo, Galicia	Spain	IEOCD-BR/3063		4M
<i>Anapagurus laevis</i>	Off Luarca	Spain	IEOCD-BR/3082		1F
	Gulf of Cadiz	Spain	IEOCD-BR/3096		8M
	Porcupine Bank	Spain	IEOCD-BR/3083		2M,2F
<i>Anapagurus longispina</i>	Formentera, Balearic Islands	Spain	IEOCD-BR/3087		8M
	Eivissa-NW Ibiza, Balearic Islands	Spain	IEOCD-BR/3088		4M,1F
	South of Dakar	Senegal	IEOCD-BR/3086		1M
<i>Anapagurus petiti</i>	Gulf of Cadiz	Spain	IEOCD-BR/313		2M
	Baños del Carmen, Málaga	Spain	IEOCD-BR/3091		1F
	Calaburra, Mijas	Spain	IEOCD-BR/3090		1M
<i>Anapagurus pusillus</i>	off Cabo Girao, Madeira	Portugal	IEOCD-BR/316		3F
	Canary Islands	Spain	IEOCD-BR/306		1M
	Cabrera, Balearic Islands	Spain	IEOCD-BR/3052		2M
<i>Catapaguroides microps</i>	Taiwan	Taiwan		https://taieol.tw/	?
	Vanuatu	Vanuatu	MNHN- IU-2008-16293	https://science.mnhn.fr/	?
<i>Cestopagurus timidus</i>	Gulf of Cadiz	Spain	IEOCD-BR/328		1M
	Cabrera, Balearic Islands	Spain	IEOCD-BR/320		1M
	Ría de Arousa, Galicia	Spain	not preserved	© Jacinto Pérez	?
<i>Nematopagurus longicornis</i>	Maó, Menorca, Balearic Islands	Spain	ICMD000913	© Pere Abelló	?
	Aguilas-Cartagena	Spain	IEOCD-BR/392		1M
	N of Dakhla, Western Sahara	Western Sahara	IEOCD-BR/398		1F
	Ría de Arousa, Galicia	Spain	not preserved	© Jacinto Pérez	?

Species	Locality	Country	Voucher number	Online Ressources	Sex
<i>Pagurus anachoretus</i>	SE Fuerteventura, Canary Islands	Spain	IEOCD-BR/498		1F
	La Herradura, Granada	Spain	IEOCD-BR/285		2M,1F
<i>Pagurus alatus</i>	Alboran Sea	Spain	not preserved	©Luis Sánchez Tocino	?
	Mallorca, Balearic Islands	Spain	IEOCD-BR/3168		2F,1M
	Playa del Pozuelo, Granada	Spain	IEOCD-BR/3169		1F
<i>Pagurus carneus</i>	Porcupine Bank		IEOCD-BR/3170		2M,2F
	Porcupine Bank		IEOCD-POR13/286		1M
	Porcupine Bank		IEOCD-BR/3171		1M
	Porcupine Bank		IEOCD-BR/3172		1F,1?
<i>Pagurus chevreuxi</i>	Aguilas-Cartagena	Spain	IEOCD-BR/3159		1F
	Ría de Arousa, Galicia	Spain	IEOCD-BR/287		1M
<i>Pagurus cuanensis</i>	Ría de Arousa, Galicia	Spain	IEOCD-BR/290		1M
	Radazul, Tenerife, Canary Islands	Spain	IEOCD-BR/3162		1M
	Ría de Arousa, Galicia	Spain	IEOCD-BR/3163		1F
	Aguilas-Cartagena	Spain	IEOCD-BR/3164		1M
<i>Pagurus excavatus</i>	Galician continental shelf	Spain	IEOCD-BR/3175		3M
	Off Laredo	Spain	IEOCD-BR/3174		1M
	Canary Islands	Spain	IEOCD-BR/3173		1F
<i>Pagurus forbesii</i>	Off Santander	Spain	IEOCD-BR/3176		1M,1F
	Canary Islands	Spain	IEOCD-BR/3177		1F
	Formentera, Balearic Islands	Spain	IEOCD-BR/3178		2M,1F
<i>Pagurus mbizi</i>	Fuerteventura, Canary Islands	Spain	IEOCD-BR/3179		1M
	Off Tarfaya	Maroc	IEOCD-CCLME11/289		1M,1F
<i>Pagurus prideaux</i>	Formentera, Balearic Islands	Spain	IEOCD-BR/3180		1M
	Porcupine Bank		IEOCD-BR/3165		1M
	Ría de Arousa, Galicia	Spain	IEOCD-BR/3166		2M
	Off Ribadeo	Spain	IEOCD-BR/3167		2M
<i>Pagurus pseudosculptimanus</i>	NW of La Güera, Western Sahara	Western Sahara	IEOCD-BR/3181		2F
	NE of Dakhla, Western Sahara	Western Sahara	IEOCD-BR/3182		2M,1F
	Málaga	Spain	MNCN 20.04/9148-49	García-Muñoz et al. 2014	1M,1F
<i>Pagurus pubescens</i>	Eivissa-NE, Balearic Islands	Spain	IEOCD-BR/3183		1M
	Flemish Cap	Canada	IEOCD-BR/3200		1M,1H
	Flemish Cap	Canada	IEOCD-BR/3201		1M
<i>Pagurus bernhardus</i>	Porcupine Bank		IEOCD-BR/3184		2F
	Aguiño, Galicia	Spain	IEOCD-BR/3186		3M,1F
	Cocho das dornas, Vigo	Spain	IEOCD-BR/3185		1M

Species	Locality	Country	Voucher number	Online Ressources	Sex
<i>Pagurus pubescentulus</i>	Off La Güera, Western Sahara	Western Sahara	IEOCD-BR/3187		1F
	off Lequeitio	Spain	IEOCD-BR/3188		1M
	Canary Islands	Spain	IEOCD-BR/3189		1F
<i>Spiropagurus elegans</i>	NW of Nouakchott, Mauritania	Mauritania	IEOCD-BR/3190		1M,1F
	North of Safi, Maroc	Maroc	IEOCD-BR/3191		1M,2F
	SW of Tarfaya, Western Sahara	Western Sahara	IEOCD-BR/3192		1M
<i>Strobopagurus gracilipes</i>	North of Casablanca	Maroc	IEOCD-BR/3193		3M,2F
	Off Rabat	Maroc	IEOCD-BR/3194		2M,1F
	Indo-Pacific	Indo-Pacific		Lemaitre R. 2004	
<i>Parapagurus pilosimanus</i>	Porcupine Bank		IEOCD-BR/3195		1M
	Off Bissagos Islands	Guinea-Bissau	IEOCD-BR/3196		3M
	Caribbean Sea	Honduras	USNM 1151654	http://n2t.net/ark:/65665/340d97ed6-d7e7-4f14-9a28-5e014007f973	1F
<i>Parapagurus alaminos</i>	Rio Grande do Norte	Brazil		Lemaitre and Tavares, 2015	1M
	Guadeloupe Island	Southern Caribbean Sea	MNHN-IU-2013-18767	http://crustiesfroverseas.free.fr/illustration.php?n=4&irenavID=7210	?
<i>Parapagurus abyssorum</i>	Azores	Portugal		Milne-Edwards and Bouvier , 1899	?
<i>Oncopagurus bicristatus</i>	Fuerteventura, Canary Islands	Spain	C.O.Canarias (IEO-CSIC)	INFUECO1112	3?
<i>Paragiopagurus ruticheles</i>	Canary Islands	Spain	IEOCD-BR/3197		1F
	Canary Islands	Spain	IEOCD-BR/3198		2M
	Canary Islands	Spain	IEOCD-BR/3199		1M,1F
<i>Sympagurus acinops</i>	Gulf of Mexico	Gulf of Mexico		Felder et al. 2014	1F
	Taiwan	Taiwan		https://taieol.tw/pages/126644	?