Taxonomic study of the *Pagurus forbesii* "complex" (Crustacea: Decapoda: Paguridae). Description of *Pagurus pseudosculptimanus* sp. nov. from Alborán Sea (Southern Spain, Western Mediterranean Sea).

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ABSTRACT

The study of hermit crabs from Alboran Sea has allowed recognition of two different morphological forms under what had been understood as *Pagurus forbesii*. Based on morphological observations with various species of *Pagurus*, and molecular studies, a new species is defined and described as *P. pseudosculptimanus*. An overview on species of *Pagurus* from the eastern Atlantic and Mediterranean Sea is provided.

Key words: Pagurus, new species, Mediterranean, eastern Atlantic.

Introduction

More than 170 species from around the world are currently assigned to the genus *Pagurus* Fabricius, 1775 (Lemaitre and Cruz Castaño 2004; Mantelatto *et al*. 2009; McLaughlin 2003, McLaughlin *et al.* 2010). This genus is complex because of there is high morphological variability and similarity among some species, and has been divided in groups (e.g. Lemaitre and Cruz Castaño 2004 for eastern Pacific species; Ingle, 1985, for European species) with difficulty (Ayón-Parente and Hendrickx 2012). This difficulty has lead to taxonomic problems, although molecular techniques have been recently used to elucidate some species (Mantelatto *et al.* 2009; Da Silva *et al*. 2011).

Thirteen species are present in eastern Atlantic (European and the adjacent African waters) (Ingle 1993; Udekem d'Acoz 1999; Froglia, 2010, MarBEL Data System - Türkay 2012, García Raso et al., in press) but only nine of these (the first ones mentioned below) have been cited in the Mediterranean Sea, all of them are present in the study area (Alboran Sea, southern Spain). These are: *Pagurus alatus* Fabricius, 1775; *Pagurus excavatus* (Herbst, 1791); *Pagurus prideaux* Leach, 1815; *Pagurus pubescentulus* (A. Milne-Edwards and Bouvier, 1892), *Pagurus mbizi* (Forest, 1955); *Pagurus cuanensis* Bell, 1846; *Pagurus forbesii* Bell, 1846; *Pagurus anachoretus* Risso, 1827; *Pagurus chevreuxi* (Bouvier, 1896); *Pagurus irregularis* (A. Milne-Edwards and Bouvier, 1892); *Pagurus carneus* (Pocock, 1889); *Pagurus bernhardus* (Linnaeus, 1758) and *Pagurus pubescens* Krøyer, 1838.

Within the European species of *Pagurus* only *P forbesii* and *P cuanensis* are characterized by having long eyestalks and the males with four left pleopods 2-5 (Zariquiey Álvarez 1968, Ingle 1993). These two species also show a wide eastern

Atlantic distribution, and are found in British Isles, Ireland, Norway to Africa: Senegal and South Africa respectively, and in the Mediterranean Sea.

We have identified two different morphologies associated with the hermit crab *Pagurus forbesii*, in large samples from the Alboran Sea. Thus, the aim of the present study is to clarify the situation, based on morphological and molecular data.

Pagurus forbesii was described by Bell in "*A history of British Crustacea* IV", dated 1846, although this publication (part) was on sale during the last week of December 1845; and 1853: 186) (Ingle 1993), and the type locaty is Falmouth (UK). Latter was referred by Henderson (1886: 72) as *Eupagurus*. On the other hand, Lucas described *Pagurus sculptimanus* (1846: 32, Pl 3, Fig. 6). These two taxa were considered belonging to one species and referred to as: *Eupagurus sculptimanus* by - Heller (1863: 162, Pl 5, Fig 9), - Chevreux and Bouvier (1892: 104, Pl II, Figs 18-29), - Bouvier (1896: 149, Fig 13), - Milne Edwards & Bouvier 1900: 226, - Bouvier (1940: 131, Figs 74, 87), - Pesta (1918: 242, Fig 74,) - Selvie (1921: 19, Pl .V, Figs 4-8), - Nobre (1931: 206, Figs 112-113), - Nobre (1936: 129, Figs 105, 108), - Forest (1955: 125), Forest (1961:232) - Zariquiey Álvarez (1946: 121, Fig. 149), - Zariquiey Álvarez (1952: 291); and as *Pagurus sculptimanus* by - Forest (1957: 426 and 1958: nomencl.), - Allen (1967: 22, fig. pag. 92), - Zariquiey Álvarez (1968: 246, Figs 12c, 89c, 90h), and - Turkay (1976: 33). However, Ingle in 1985 (page 765, Figs 2,8,18,46,57,63) highlighted the priority of the name *forbesii*, and in 1993 (page 133, Figs 105-108 and 472 p) made a complete description of the species with good figures from a specimen of Plymouth (UK), close to the topotypical locality (Falmouth, UK).

Comments on the most important references, captures and bibliographic references to these species are given in the Discussion.

Material and Methods

Area of study (Fig. 1). The study area is located on the Spanish coast of Málaga, in "Calahonda" a Site of Community Importance "Calahonda" (code ES6170030, Official Journal of the E.U. of 21.09.2006), included in Natura 2000 network, northern Alborán Sea (Westernmost Mediterranean Sea). The coordinates of the sampling station (in front of "Torre de Calahonda", Mijas) are 36º 28.0' N - 04º 42.3' W, in a depth of 25 m.

As result of its location, near the Straits of Gibraltar, in the area a mixture of Atlantic (inflow) and Mediterranean (outflow) waters exists. These water flows, together with the geomorphology of the basin, generate singular hydrodynamic conditions (gyres, fronts, up-welling, ...) (Lacombe and Tchernia 1972, Lanoix 1974, Parrilla and Kinder 1987, Heburn and La Violette 1990, Perkins *et al*. 1990, Sarhan *et al.* 2000) which contribute to the coexistence of Mediterranean and Atlantic species, European and African, and enhance the existence of a hotspot of European biodiversity (García Raso *et al.* 2010).

Sampling methodology. The samples analyzed were taken in November 2004, February and May 2005, on soft bottoms, at 25 m, using a small heavy rock dredge, with a rectangular frame of 42 × 22 cm and a net with a mesh size of 4.0 mm (knot to knot). Trawling time was 5 minutes for each haul at a speed of about 2 knots.

DNA extraction, amplification, sequencing and data analysis. Total genomic DNA was extracted from pereiopods muscle tissue of specimens of *Pagurus forbersi* and *P. pseudosculptimanus* preserved in 70-100% ethanol. The DNeasy Blood and Tissue Kit of Qiagen (Qiagen, Valencia, CA, USA) was used for DNA extraction. Fragments of

mitochondrial DNA from the large subunit rRNA (16S) and from the cytochrome oxidase subunit I (Cox1) genes were amplified with polymerase chain reaction (PCR) using the primers: 16S ar-L (5'-CGCCTGTTTATCAAAAACAT-3') and 16S br-H (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi *et al,* 1991) for 16S rRNA, and LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAATCA-3') (Folmer *et al,* 1994) for Cox1. PCRs were conducted in a 25 μl volume reactions containing 1 μl of both forward and reverse primers (10 μM), 2.5 μl of dNTP (2 mM), 4 μl of magnesium chloride (25 mM), 0.25 μl of Qiagen DNA polymerase, 5 μl of "Q-solution" (5x), and 2.5 μl of Qiagen buffer (10x) (Qiagen Taq PCR Core Kit). Amplification of Cox1 was performed with an initial denaturation for 5 min at 94ºC, followed by 35 cycles of 1min at 94ºC, 30 s at 44ºC (annealing temperature) and 1 min at 72ºC with a final extension of 7 min at 72ºC. The 16S amplification began with an initial denaturation for 5 min at 95ºC followed by 35 cycles of 30 s at 94ºC, 30 s at 44ºC (annealing temperature), 1 min at 72ºC with a final extension of 7 min at 72ºC. PCR products were sent to Bioarray Ltd. (Elche, Alicante, Spain) to be purified and then two-direction sequencing.

Sequences were edited using Chromas version 2.0 computer software, and manually aligned with the software ESEE version 3.2s (based on Cabot and Beckenbach 1989), excluding primer regions. The obtained DNA sequences for Cox1 were compared with sequences from the other European *Pagurus* species available in public databases (Genbank), and two pagurids, *Calcinus tubularis* (Linnaeus, 1767) and *Dardanus arrosor* (Herbst, 1796), were used as outgroups. Localities of these sequences, museum catalogue numbers, and Genbank accession numbers (including those for outgroups species) are listed on Table 1. A similar comparison has been not

made with 16S sequences due to a lower number of species available in Genbank for this genetic marker.

The best-fitting model of nucleotide substitution was selected by testing alternative models of evolution using the software MrModeltest version 2.2 (Nylander, 2004). A Bayesian inference analysis (BI) was run for ten million generations with four chains (three heated and one cold) with 1 out of every 5000 trees sampled; this Bayesian Analysis was performed with MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) using the optimal model estimated by MrModeltest and supplying its obtained model parameters as dirichlet parameter values in MrBayes. Burn-in values were estimated graphically by plotting the log-likelihood values in Microsoft Excel.

Morphological study. A comparative morphological study of the specimens collected has been made, and for the species a description and illustrations are provide. These ones have been compared with bibliographical information. In addition, the syntypes of *P. sculptimanus*, the only one synonymy of *P. forbesii*, have been examined for discard its validity as a different species.

The holotype of the new species *P. pseudosculptimanus*, and DNA vouchers paratypes are deposited at the Museo Nacional de Ciencias Naturales (CSIC), Madrid; two specimens have been sent to the Muséum National d'Histoire Naturelle (MNHN) du Paris, and the others are kept at the Department of Animal Biology, University of Malaga.

Results

A total of 200 specimens belonging to the "complex" *P. forbesii* - *Pagurus sculptimanus* were analyzed.

Cox1 data analysis. Sequences of 16S obtained for *P. forbesii* and *P. pseudosculptimanus* consist of 522 bp and present a divergence of 3.64%, in accord with divergence found among other congeners at the interspecific level (see Mantelatto et al., 2009). These sequences have been deposited in Genbank (accession number pending).

The length of the Cox1 sequences obtained in this study were 658 bp, but some of the sequences from Genbank were shorter (a minimum of 518 bp). The data sets consisted of 15 sequences, and a GTR+I+G model, selected by hLRT, was selected as the best-fitting evolutionary model by MrModeltest and implemented for subsequent Bayesian analysis. The resulting consensus tree with BI posterior probabilities is shown in Fig. 2.

These molecular data confirm the valid of the new species *P. pseudosculptimanus*, which it is clearly separate from the *a priori* closer related species like *P. forbesii*. The mtDNA of Cox1 gene is widely applied for genetic characterization and identification of species, and in the Fig. 2 the distances respect to *P. forbesii* are clear, although it is early to point out relationships with the rest of European species. The position of *P. cuanensis* and *P. prideaux* are not resolved while a strong supported relationship is observed in the clades of *P. bernhardus* and *P. pubescens*, and *P. alutus* and *P. forbesii*, respectively. These relationships are not reflecting the currently taxonomy (groups) based on adult morphology, but as pointed out above it is early for phylogenetic conclusions when the species composition of the analysis is incomplete and only one genetic marker is used.

Morphology. The description of *P. forbesii* is given for comparative purposes and to complete the one provided by Ingle (1993) (variability and data not cited)Also, those characters that allow us to differentiate both species are highlighted

Pagurus forbesii Bell, 1845

Eupagurus forbesii - Henderson (1886: 72).

Pagurus forbesii - Ingle 1985: 765, Figs 2,8,18,46,57,63, - Ingle 1993: 133, Figs 105-108, - Sandberg and McLaughlin 1998: 62, Fig. 18.

Pagurus sculptimanus Lucas 1846: 32, Pl 3, Fig. 6, - Allen 1967: 22, fig. page 92, - Zariquiey Álvarez 1968: 246, Figs. 12c, 89c, 90h.

Eupagurus sculptimanus - Heller 1863, - Milne Edwards and Bouvier 1990: 226, - Selvie 1921: 19, Pl .V, Figs 4-8, - Nobre 1931: 206, Figs 112-113.

Material studied: St. Calahonda Malaga, Spain, 36º 28.0'N - 04º 42.3'W, 25 m., 25-26/11/2004: 8 ♀♀ - 9♂♂, 09/02/2005: 21 ♀♀ - 17♂♂, 18/05/2005: 38 ♀♀ - 23♂♂. Genbank accession number ######## (pending). Oran harbor, Algeria: 3 ♂♂, syntypes of *Pagurus sculptimanus* Lucas 1846 (collections Muséum National d'Histoire Naturelle Paris: MNHN-IU-2008-15134 (=MNHN-Pg343), MNHN-IU-2009-3929 (=MNHN-Pg343) y MNHN-IU-2009-3930 (=MNHN-Pg343).

Description. Cephalothoracic shield (Figs. 3A, 11A). Antero medial frontal margin not protruding and rounded off, with blunt antero-lateral processes. The cervical groove is deep and distinct. Long eyestalk with cornea slightly expanded. Ratio total length / maximum width (cornea) about 2.8 - 3.0. They reach nearly to the tip of the antennal peduncle and of the 3º joint of antennular peduncle. Shield carapace length / eyestalk total length = 1.0 - 1.1. Sub-triangular ocular acicles, with a sub-marginal apical spine.

Antennules (Fig. 3B). The first segment with an outer medial spine. Ration length / width (in middle) 3º segment = 6.2-6.3. Ratio 3º / 2º segment length = 2.1. Endopod 8-segmented.

Antenna (Fig. 3C). Segment 1 with an outer sub-distal spine, sometime as obtuse process or absent, and with another ventro-inner distal spine. Strong dorso-outer process of the second segment of the antennal peduncle with 2 teeth on its inner edge, not reaching beyond proximal half of segment 4. Antennal acicle slightly curved, does not reaching the middle of the 5º segment, and does not reaching the base of the cornea (less frequently reach it, but not beyond cornea extremity).

Oral appendices: Mandibles as figure 3D, with a palp tri-segmented. Maxillules (Fig. 3E) - Endopod distally expanded into inner elongated lobe usually with two apical long setae and with outer distal part expanded in a rounded broad lobe. Maxillae - as figure 2F. Maxillipeds 1 (Fig. 3G) - exopod peduncle broadened proximally. Maxillipeds 2 - as figure 3H. Maxillipeds 3 - (Fig 3I) outer distal margin of carpus and merus without spines; crista dentata (ischium) with 16-18 teeth and one accessory tooth, and basipod wiht 2 teeth.

Right cheliped (Fig. 4A, 11B,C,D) much larger than the left. It is very characteristic. In lateral view the upper surface is in a plane, while the ventral surface is convex. It acts as a lid to close the mouth of the shell. It shows three deep dorsal depressions; the largest is in the outer part, on the palm and fixed finger, it is widest in the middle, just opposite to the base of the dactylus. The second depression is in the proximal part of the palm, lies towards the inner edge, being widest in the basal zone. Both are separated by a well-marked blunt ridge, which runs from the proximal outer part of the palm (starting at the outer side of the strong medial or outer proximal prominence) to the basal inner part of fixed finger, following an inclined line. The third

depression is defined by the fingers, each one has a rounded median ridge and from this the surface slope rapidly downwards so as to form a marked hollow between the fingers. There are two proximal tuberculate-spinous prominences: a medial, sometime called outer, and an inner tubercle smaller. The outer margin of the hand is convex, with a row of strong and distinct teeth on its total length. The inner margin, from the base of the protopod to the base of the dactylus, is almost straight, only the dactylus curves towards the fixed finger near the tip, and with tubercles or teeth well developed. The dorsal surface is thickly studded with low rounded flat tubercles. The ventral surface of the hand is almost smooth, with few tubercles. The fingers end in yellow claws. The carpus presents the upper (dorsal) surface granulate-denticulate with 1-2 rows of long and strong curved teeth in inner margin. Merus with upper surface smooth, ventral granulate with teeth on the distal part more developed in distal outer and inner margins. Ischium with a ventral keel with a row of 8-14 small teeth, and with 1 distal-outer-medial small tooth.

The left cheliped (Figs. 4B,C,D,E 11D) is much smaller than right. Dactylus longer than half palm and fixed finger length. The fingers end in yellow claws. The base on fixed finger is much broader than dactylus at is base. Dorsal surface of palm convex transversally in its central part and with the outer margin concave, which shows a deep rounded depression with the outer row of strong teeth oriented upwards. Palmar upper surface with rounded granules more developed in the upper central part and mainly on a proximal prominence which present strong tubercles. The upper surface and outer margin of the dactylus is practically smooth, with a few tubercles. The cutting edge of the dactylus is furnished with a long row of slender transparent spins. Carpus with a dorsal - outer row of 5-6 long and strong curved teeth, ventral area granulate sometime with some spines and with long setae. Merus with well developed ventral teeth and long

setae, 5-6 strong teeth in inner margin and with tubercles and smaller teeth in ventral and ventral outer part. Ischium with a ventral inner keel with 11-13 small teeth and with 1-2 outer- distal-lateral small tooth.

P2 left (Figs. 5A,B) - Ratio merus / ischium length = about 3.3 - 3.5. Merus: ventrally with strong ventral teeth, upper face smooth, unarmed. Capus with 7 - 8 upper teeth (mainly visible from inner view). Propodus with some (4 - 7) small dorsal teeth (see from inner view), ventrally smooth. Dactylus with articulate spines, but without teeth. P2 right (Fig. 5C) - Ratio mero / ischium length = about 3.5 - 4.0. Ischium: ventral face smooth or with small tubercles sometime some spinous. Merus with ventral teeth in all its extension in general (6 - 7), stronger in the anterior margin; upper face smooth, unarmed. Capus with 8 upper teeth (mainly visible from inner view). Propodus with 8 - 9 strong teeth on dorsal margin. Dactylus with slender articulate spines, but without teeth.

P3. P3 longer than P2. P3 left (Figs. 5D, 11E) - Ratio merus / ischium length = about 1.6. Ischium and merus dorsaly and ventraly smooth. Carpus with an antero-dorsal tooth sometime following by other 3 smaller (inner view). Propodus smooth dorsally and with ventral tubercles and teeth (7 - 11), the latter mainly in the half distal part. Dactylus with ventral articulate spines and with strong teeth extending from distal to proximal part. The left P3 dactylus is wider than the left P2 one. P3 right (Fig. 5E) - Ratio merus / ischium length = about 1.6 - 1.7. Ischium, merus, carpus and propodus dorsally and ventrally smooth. Dactylus with only articulate spines, without teeth (it is different to the left).

Anterior lobe of sternite of third pair of pereiopods (Fig. 3J) triangular to subtriangular and setose, with strong acute spines in all margins.

P4 (Fig 6A). It as usual. Dactylus with 14 - 15 ventral spiniform setae, ends in a long hyaline claw and propodus with a denticulate ventral area with row of spiniform setae.

P5 (Fig. 6B). It as usual, pseudochelate. Dactylus with 20 distal spines in distal margin. Distal-dorsal area of propodus with pseudochaeta.

Males pleopods (Figs. 6C,D,E,F). Males with four unpaired pleopods, Pl2 to Pl5, on the left side. Endopods well developed but measuring less than half of exopod length. Second pleopod smaller than 3, 4 and 5, witch are more or less similar in size.

Uropods (Fig. 6G). Left about twice size of right and, both, with pseudochaeta on the distal part of endopod and exopod.

Telson (Fig. 3G) well bilobed with medial cleft. The left lobe is slightly larger than right and with 12 and 10 distal subacute processes, largest outermost.

Distribution: Eastern Atlantic: British Isles, Ireland - Norway, to Morocco, Madeira (Desertas Island), Canary Islands and ¿to Senegal?, and Mediterranean Sea.

P. pseudosculptimanus sp. nov.

Euagurus sculptimanus - Chevreux and Bouvier 1892: 104, Pl II, Figs 18-29, - Bouvier 1896: 149, Fig 13, - Bouvier 1940?, - Forest 1955: 125.

Material studied: "Calahonda" Mijas littoral - Málaga (Alboran Sea, Spain), 36º 28.0'N - 04º 42.3'W, 25 m. 25-26/11/2004: 4 ♀♀ - 4♂♂, 09/02/2005 (2 samples): 17 ♀♀ - 13♂♂, and 18/05/2005: 27 ♀♀ - 19♂♂.

Type material: specimens of 18/05/2005: 27♀♀ - 19♂♂. Holotype: adult male, carapace shield length 3.8 mm, 18/05/2005, cat no. 20.04/9147 MNCN (CSIC) Madrid. Paratypes: 2 males, deposited at the MNCN (CSIC) Madrid (see Table 1, Genbank

accession number ####### pending), 3 specimens deposited at MNHN Paris and 40 in the Department of Biología Animal, University of Málaga.

Description. Cephalothoracic shield (Fig. 7A). Antero medial frontal margin not protruding and rounded off, with blunt antero-lateral processes. Cephalothoracic shield practically as long as wide, ratio lenght / width 1.01 - 0.9. The cervical groove is deep and distinct. Long and narrow eyestalk with cornea slightly expanded. Ratio total length / maximum width (cornea) about 2.5 - 2.7 (shorter than *P. forbesii*). They reach nearly to the tip of the antennal peduncle and about the middle of the 3º joint of antennular peduncle. Shield carapace length / ocular peduncle total length = 1.3. Sub-triangular ocular acicles, with a sub-marginal apical spine and with the inner face a little convex.

Antennules (Fig. 7B).The first segment with an outer medial spine. Ration length / width 3º segment = 3.3 - 3.6. Ratio 3º / 2º segment length = 1.5. Endopod 8-segmented.

Antenna (Fig. 7C). Segment 1 with an outer sub-distal spine and with another ventro-inner distal spine. Strong dorso-outer process of the second segment of the antennal peduncle with 3 teeth on its inner edge, not reaching beyond proximal half of segment 4. Antennal acicle slightly curved, does not reaching the middle of the 5º segment, and reach or overreach the base of the cornea but not beyond it extremity.

Oral appendices: Mandibles (Figure 7D) with palp tri-segmented. Maxillules (Fig. 7E), endopod distally expanded into inner elongated lobe usually with an apical long setae and with outer distal part expanded in a rounded broad lobe. Maxillae as figure 7F, with subdistal setae (3 - 4) on the palpus. Maxillipeds 1 (Fig. 7G), exopod peduncle broadened proximally, distal part of endopod reaching the half of exopod peduncle. Maxillipeds 2, as figure 7H. Maxillipeds (Fig 7I), outer distal margin of

carpus and merus without spines; proximal dorso-inner margin of ischium with two sub-acute processes, crista dentata with 16 - 17 sub-acute processes and one accessory distal tooth; basipod wiht 2 teeth.

Right cheliped (Figs. 8A, 11F,G,H) much larger than the left. It is very characteristic. In lateral view the edge of upper surface are in a plane, with a central ridge separating two laterals areal (sometime too concaves). The distinct central blunt ridge runs following a straight line, from a strong proximal-central tubercle to a medium palmar one, behind the basal inner part of fixed finger (it does not exist in *P. forbesi*). Both prominences are higher than the central blunt ridge (in different grade). A third smaller proximal inner prominence appears on the propodus. The straight ridge defines two depressions (sometime well conspicuous) with different morphologies to the ones of *Pagurus forbesii*, an outer large depression and other inner smaller with a more or less similar wide in its proximal and distal zones. A third depression is defined by the fingers, each one has a rounded median ridge and from this the surface slope rapidly downwards so as to form a hollow between the fingers. The upper palmar surface presents rounded granules, which could be developed as tubercles in the prominences. The outer margin of the hand is convex, with a row of strong and distinct teeth on its total length. The inner margin, from the base of the protopod to the tip of the dactylus, is almost straight, only the dactylus curves towards the fixed finger near the tip, and also with a row of strong and well developed blunt teeth. The ventral surface of the hand is almost smooth, with few tubercles. The fingers end in yellow claws. The upper (dorsal) surface of carpus is denticulate with teeth. Merus with upper surface smooth, and with the distal ventral margin denticulate. Ischium with a ventral keel with small denticles and setae, and with a row of small tubercles with setae (5) in the distal-outer-medial part.

The left cheliped (Figs. 8B, 11I) is much smaller than right. Dactylus longer than half palm and fixed finger length. The fingers end in yellow claws. The base on fixed finger is much broader than dactylus at is base. Dorsal surface of palm convex transversally in its central part and with the proximal outer margin concave, which shows a feeble depression with the outer row of strong teeth oriented upwards. Palmar upper surface with rounded granules little more developed in the upper central part and mainly on a proximal prominence which present tubercles. The cutting edge of the dactylus is furnished with a long row of slender transparent spines. Carpus dorsally spinous with a medial row of 4 - 6 strong teeth, ventral area granulate with long setae. Merus with ventral tubercles and teeth, more developed in the distal outer and inner margins, and long setae. Ischium with a ventral inner keel with a row of 10 - 12 small teeth and setae and with some small outer- distal-lateral tubercles.

P2 left (Fig. 9A) - Ratio merus / ischium length = about 3.7 - 4.0. Merus: with some (2 - 3) distal-ventral teeth, upper face smooth, unarmed. Capus with 4 - 7 upper teeth. Propodus with small dorsal spinous tubercles (9), ventrally smooth. Dactylus with articulate spines, but without teeth. P2 right (Fig. 9B) - Ratio merus / ischium length = about 4.5 - 5.0. Ischium smooth. Merus with some small ventral-distal teeth (1 - 2 or 3), upper face smooth. Capus with 6 - 10 upper strong teeth. Propodus with 9 - 11 teeth on dorsal margin. Dactylus with slender articulate spines, but without teeth.

P3. P3 longer than P2. Left (Figs. 9C, 11I) - Ratio merus / ischium length = about 1.3 - 1.4. Ischium and merus dorsaly smooth. Carpus with 1 - 3 distal-upper tooth. Propodus smooth dorsally and with some denticulate tubercles (3 - 6) in the ventral-distal part. Dactylus with ventral articulate spines extending from distal to proximal part, but without teeth. P3 right (Fig. 9D) - Ratio mero/ischium length = about 1.6-1.8. Ischium and merus smooth, merus sometime with small articulate spines. Carpus and

propodus ventrally smooth, dorsally with small denticles (or absents). Dactylus with articulate spines, but without teeth.

Anterior lobe of sternite of third pair of pereiopods (Fig. 9E) subtriangular and setose, with strong acute spines in distal margins.

P4 (Fig. 10A). It as usual. Dactylus with 14 - 15 ventral spiniform setae, ends in a hyaline blunt claw. Outer ventral area of propodus with numerous statulate to subacute pseudochaeta.

P5 (Fig. 10B). It as usual. Dactylus spatulate with 24 spines in distal margin. Propodus with distal-upper area with pseudochaeta.

Males with four pleopods, Pl2 to Pl5, on the left side. In Pl2 (Fig. 10C) the endopods is absent, or too reduced as a small projection "lamina"; in the Pl3 to Pl5 (Figs. 10D,E,F) the endopods measure less than half of exopod length.

Uropods. Left about twice size of right and, both, with pseudochaeta on the distal part of endopod and exopod.

Telson (Fig. 10G) bilobed with medial cleft. The left and right lobes are more or less similar in size, the left is slightly larger than right, and with about 11 - 14 distal subacute processes, largest outermost.

Etymology. the species name is a combination of the words "sculptimanus", in allusion to the morphology of large cheliped, and "pseudo", based on the invalidity of this name (synonymy of *Pagurus forbesii*) given to some specimens in old references.

Distribution. Mediterranean Sea: Spain (in Alborán Sea between 15-25 m depth) and East Atlantic Ocean: Morocco to Senegal (see discussion).

The principal morphological differences, easily observable, between *P. forbesii* and *P. pseudosculptimanus* are in the morphology of right cheliped (central ridge and tubercles) (Fig. 11C,D - F,G,H) and the dactylus of left P3 (with strong teeth in *P. forbesii*) (Fig. 11 E - I). Other differences are in the ratios length / width of the eyestalks (total length / maximum width (cornea)), and in the 3º segment of antennular peduncle (length / width (in the middle)).

Habitat and species associated. The species inhabits in the continental shelf, in medium sandy bottoms with bioclasts, "detritic bottoms": Characteristics: 0.250 < Q50 < 0.500 (Q50 = 0.466). % clay (% < 0.063) = 2.5. % gravel (% >2.00) = 8.8. % bioclasts (% > 6.30) = 3.5. % organic material = 1.97± 0.41 sd.

Other species of hermit crabs found in this bottom, at 25 m depth, were (by abundances): *Diogenes pugilator* (Roux, 1829), *Anapagurus hyndmanni* (Bell, 1845), *Paguristes eremita* (Linnaeus, 1767), *Dardanus arrosor* (Herbst, 1796), *Pagurus cuanensis* Bell, 1845, *Anapagurus alboranensis* Garcia-Gomez, 1994, *Calcinus tubularis* (Linnaeus, 1767), *Pagurus prideaux* Leach, 1815, *Pagurus excavatus* (Herbst, 1791), *Anapagurus chiroacanthus* (Lilljeborg, 1856), *Anapagurus petiti* Dechancé & Forest, 1962, *Dardanus calidus* (Risso, 1827) and *Cestopagurus timidus* (Roux, 1830).

Discussion

Bell (1845 and 1853: page 186) described *Pagurus forbessi* in the British Isles, but with few details and poor figures; however, the figure of the right hand shows an inclined central keel, which make it possible to recognize and characterize the specimen. In 1846 Lucas (1846, page 32, Pl 3, Fig. 6) described (also incompletely) *Pagurus sculptimanus* however, according to some of the data in the text and the figure of the right cheliped

(which shows a somewhat inclined central keel and only two basal tubercles on the hand), this new species must be considered a synonym of *P. forbesii*. This conclusion has been confirmed after checking the three syntypes of Lucas, from Oran (Fig. 12). Milne Edwards and Bouvier (1990, page 226, as *Eupagurus sculptimanus*) mentioned five specimens from Madeira (Desertas Islands, 100-150 m) and one from the Canary Islands (182 m) with abundant granulations on the distal half part of the propodus and on almost the entire length of the dactylus of the posterior left ambulatory leg; which is more a distinctive feature of *P. forbesii*. Selvie (1921, page 19, Pl V, Figs 4-8) (as *Eupagurus sculptimanus*) makes a good description and better figures of the specimens of this species from the Aran Islands, west Ireland, showing the morphology of the right cheliped and P3 leg (dactylus). Others authors such as Nobre (1931: page 206, Figs. 112-113) and Allen (1967, page 22, Figure page 92) give a limited description, but these descriptions and/or the figures (the morphology of the right cheliped (hand) showing a somewhat inclined central keel, and with only two basal tubercles) allow us to assign these specimens to *P. forbesii*. Heller (1863, page 162, Fig. 9 in lamina 5) give a poor figure and refer the species from Adriatic Sea. A good figure from this Sea was given by Sandberg & McLaughlin (1998, pages 62-66, Fig. 18). Ingle in 1995 make good description and figures (1985, page 765, figures 2, 8, 18, 46, 57, 63) and 1993 (1993, pages 133-136, Figs. 105-108), but these were some differences between them; in 1985 mentioned a "lower margin of dactylus of pereiopod 3 with subacute teeth and spines", but in 1993 these teeth were not mentioned (perhaps because only the right legs were considered).

On the other hand, the description and figures of some specimens from Africa identified as *P. sculptimanus* show a large cheliped with different morphologies. Chevreux and Bouvier (1892, page 104, Pl II, Figs 18-29), as *Eupagurus*, in Figure 18

showed the cheliped of specimens from Gorè Island (Senegal) with two tubercles, one proximal and one basal, with a central straight ridge, and two lateral not very marked depressions. This figure is in accordance with the new species. They, also, do not refer to the existence of teeth on the dactylus of the left P3. Forest (1955), in a study of the genus *Eupagurus* from the intertropical eastern Atlantic, mentioned in the key that *P. sculptimanus* had a cheliped with a longitudinal strong ridge, with one thick basal tubercle and other behind the dactylus. These two tubercles were also mentioned by Zariquiey Álvarez (1968, page 246) in the key (copy from other authors?), although the figures of the three leg (12c), right cheliped (89c) and the sternite of third pair of pereiopods (90h) are belonging to *P. forbesii*.

Clément (1875) described a variety of *Pagurus sculptimanus*: *P. s.* var. *complanatus*, but it is a junior synonym of *P. cuanensis*.

In addition, there are other references which cannot be assigned to a particular species. It because the authors provide figures that are not originals but rather copies of figures from other authors (Pesta 1918: 242, Fig 74, copied the figure of Chevreux and Bouvier; Bouvier 1940: 132, Figs 74, 87, used the figures of Bouvier 1896). Moreover, there are studies without descriptions and figures, and which only mention catches or references to others papers (such as Milne Edwards and Bouvier 1892; Rathbun 1900, Alcok 1905, Forest 1966, Turkay 1976).

However these data have allowed us to determine (although partially) the possible distribution of the two species, indicated in the Results section.

As an overview of the east Atlantic hermit crabs, and in addition to the European and adjacent African *Pagurus* species mentioned in the Introduction, Forest (1955, 1956, 1966, 1978) referred the following species in African waters: in 1955 *P. alcocki* (Balss, 1911), *P. carneus*, *P. cuanensis, P. sculptimanus*, *P. similimanus* (Balss, 1921),

P. souriei (Forest, 1952), *P. triangularis* (Chevreux and Bouvier, 1892), *P. pubescentulus*, *P. variabilis*, *P. pulchellus* (A. Milne-Edwards and Bouvier, 1892), *P. alatus*, *P. mbizi* (Forest, 1955), *P. pycnacanthus* (Forest, 1955), and *P. prideaux*; in 1956 a new species was described from Côte de l'Or: *P. gordonae* (Forest, 1956) (in this paper *P. cuanensis* was cited as *P. spinimanus* Lucas 1846); in 1961 some of the above species were referred again; in 1966 two new species were described from the "Campagne de la Calypso dans le Golfe de Guinée aux iles Principe, Säo Tomé et Annobon": *P. anachoretoides* Forest, 1966 and *P. fimbriatus* Forest, 1966 and latter in 1978, *Pagurus laurentae* Forest, 1978.

Finally, another species from South Africa waters must be added (Barnard 1950, Kensley 1981, McLaughlin and Forest, 1999, among others): *Pagurus liochele* (Barnard, 1947) (it was described as *Pylopagurus*, and also cited as *Pagurus barnardi* Forest, 1966). The reference of *P. spinulentus* (Henderson, 1888) (as *Eupagurus*) must not be considered because the Hendrerson species is different to the ones from South Africa, which are next to *P. prideaux* (see Forest 1955, MacLaughlin and Forest 1999). Other species cited in this area (mentioned above) are: *P. alcolcki*, *P. alatus* (as *E. variabilis*), *P. triangularis* (as *Eupagurus*), *P. cuanensis* (as *Eupagurus*, = *E. placens* Stebbing, 1924) and *P. prideaux*. The references *Eupagurus zebra* Henderson, 1893 and *Eupagurus deprofundis* Stebbing, 1924 must not be considered because they belong to others genera: *Pylopaguropsis* and *Propagurus* respectively.

Within the Atlantic species (African and the European), the following species have relatively long eyestalks, with cornea that are not too expanded: *P. cuanensis*, *P. forbesii*, *P. anachoretus*, *P. chevreuxi*, *P. irregularis*, *P. alcocki*, *P. similimanus*, *P. souriei*, *P. triangularis*, *P. gordonae P. anachoretoides*, *P. fimbriatus, P. liochele* and *P. pseudosculptimanus*. However, within these only the males of *P. cuanensis*, *P.*

forbesii, P. irregularis and *P. pseudosculptimanus* have four pleopods (the males of *P. excavatus* and *P. pycnacanthus* also have four pleopods but they have short eyestalks with expanded cornea). In addition, out of these latter species only *P. forbesii* and *P. pseudosculptimanus* n. sp. are able to join the chelipeds to form a more or less opercular system, such as a lid to close the mouth of the shell. In *P. forbesii* the inner edge of the right cheliped is joined with the central ridge of the left cheliped (Fig. 13). A similar structure is found in the new species, *P. pseudosculptimanus* (Fig. 12B, C), and also, in the African species *P. alcocki* (although it is somewhat different, see Fig. 12D), however, as mentioned above, the males of this last species only have three pleopods.

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Table 1. Localities, data of accession number of collections, and genetic database accession number for Cox1 sequences of the specimens used in the data set. Abbreviations: MB, as referred in Table 7 by Matzen et al. (2011); MNCN, Museo Nacional de Ciencias Naturales (CSIC), Madrid; UF, Invertebrate Collections of the Florida Museum of Natural History, University of Florida.

Species	Locality	Catalogue No.	Genbank accession number
			Cox1
Pagurus alatus 1	Algarvia (Portugal)	MB89000415	JN107575
Pagurus alatus 2	Algarvia (Portugal)	MB89000463	JN107577
Pagurus bernhardus	Wales (UK)	MB89000491	JN107579
Pagurus cuanensis	Azores (Portugal)	no data	JN107584
Pagurus excavatus 1	Costa de Prata (Portugal)	MB89000268	JN107586
Pagurus excavatus 2	Sicily (Italy)	MB89000078	JN107588
Pagurus forbesii 1	Calahonda, Málaga (Spain)	MNCN (pending)	pending
Pagurus forbesii 2	Calahonda, Málaga (Spain)	MNCN (pending)	pending
Pagurus prideaux 1	Sicily (Italy)	MB89000086	JN107593
Pagurus prideaux 2	Bear Island Slide (Norway)	MB89000493	JN107594
Pagurus pseudosculptimanus 1	Calahonda, Málaga (Spain)	MNCN (pending)	pending
Pagurus pseudosculptimanus 2	Calahonda, Málaga (Spain)	MNCN (pending)	pending
Pagurus pubescens	Svalbard (Norway)	MB89000490	JN107602
Calcinus tubularis	Madeira (Portugal)	UF8361	FJ620332
Dardanus arrosor	Sicily (Italy)	MB89000494	JN107572

Explanation of figures

Figure 1. Study area and sampling station: Calahonda Málaga, 36º 28.0' N - 04º 42.3' W, 25 m.

Figure 2. Topology of Bayesian tree with consistency values of Bayesian reconstruction based on 658 bp of the Cox1 gene sequences, showing inferred phylogenetic relationships within the European representatives of the genus *Pagurus*, with represent of the pagurids *Calcinus tubularis* and *Dardanus arrosor* as outgroups. Number close to nodes indicates Bayesian posterior probabilities (Pp ≥ 50).

Figure 3. *Pagurus forbesii*. A - Cephalothoracic shield and ocular peduncles. B - Left antennular peduncle (outer view) and distal part with endopod and exopod. C - Antenna, left dorsal view and detail of proximal segments (ventral view). D - Left mandible (outer view). E - Left maxillule (outer view). F - Left maxilla (outer view). G - Right first maxilliped (outer view). H - Left second maxilliped (inner view). I - Left third maxilliped (inner view). J - Sternal plate. All scales 1 mm. Setation not shown.

Figure 4. *Pagurus forbesii*. A - Right cheliped (outer view) and detail of basal segments. B to E - Left cheliped (B general inner view; C and D: details of palm in outer and dorsal views, and E: details of isquium and merus). All scales 1 mm. Setation not shown.

Figure 5. *Pagurus forbesii*. A - Left second pereiopod (outer view). B - Carpus and propodus of left second pereiopod (inner view). C - Right second pereiopod (inner view). D - Left third pereiopod (outer view) and detail of carpus (inner). E - Right third pereiopod (inner view). All scales 1 mm. Setation not shown.

Figure 6. *Pagurus forbesii*. A - Left fourth pereiopod and details of propodus and dactylus. B- Left fifth pereiopod and detail of dactylus. C to F - Pleopods 2-5. G - Uropods and telson (dorsal view). All scales 1 mm. Setation not shown.

Figure 7. *Pagurus pseudosculptimanus* n.sp. A - Anterior part of body. B - Right antennule (outer view). C - Antenna, right dorsal view and of proximal segments in ventral view. D - Right mandible (outer view). E - Left maxillule (inner view). F - Left maxilla (outer view). G - Left first maxilliped (inner view). H - Right

second maxilliped (inner view). I - Right third maxilliped (outer view). All scales 1 mm. Setation not shown.

Figure 8. *Pagurus pseudosculptimanus* n.sp. A - Right cheliped (outer view) and detail of basal segments (inner view). B - Left cheliped (inner view) and details (palm in outer and dorsal views). All scales 1 mm. Setation not shown.

Figure 9. *Pagurus pseudosculptimanus* n.sp. A - Left second pereiopod (inner view). B - Right second pereiopod (inner view). C - Left third pereiopod (inner view). D - Right third pereiopod (inner view). E - Sternal plate. All scales 1 mm. Setation not shown.

Figure 10. *Pagurus pseudosculptimanus* n.sp. A - Left fourth pereiopod (outer view). B - Left fifth pereiopod (outer view). C - Pleopod 2 (from two specimens). D to F- Pleopods 3-5. G - Telson (dorsal view). All scales 1 mm. Setation not shown.

Figure 11. *Pagurus forbesii*: A to E. A - Cephalothoracic region (dorsal view). B, C, D - Right cheliped (lateral and dorsal views). E - Dactylus and distal part of propodus of left P3 (lateral view). *Pagurus pseudosculptimanus* n.sp.: F to I. F, G, H - Right cheliped (dorsal and lateral views). I - Dactylus and distal part of propodus of left P3 (lateral view).

Figure 12. *Pagurus forbesii*, syntypes of *Pagurus sculptimanus* Lucas (reference MNHN-IU-2008-15134 (=MNHN-Pg343), Muséum d'Histoire Naturelle du Paris). A Right cheliped (dorsal view of propodus and dactylus). B - Right cheliped (inner view). D - Left third pereiopod (outer view).

Figure 13. Junction of both chelipeds to close the mouth of the shell in A - *Pagurus forbesii*, B - *Pagurus pseudosculptimanus* sp. n. and C - *Pagurus alcocki*.

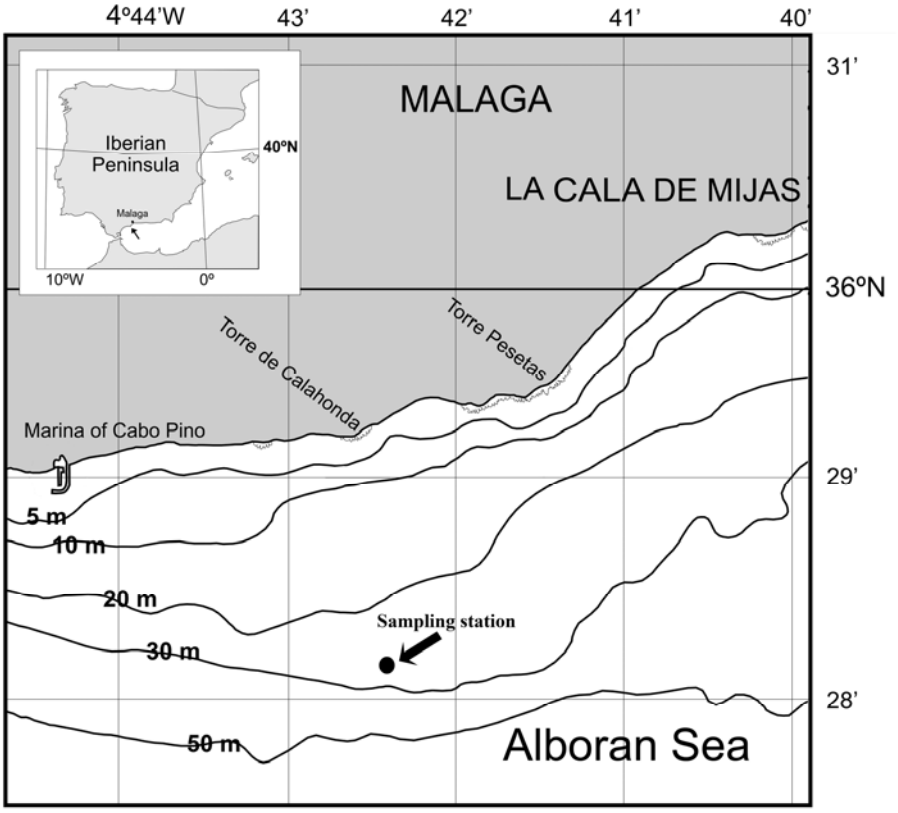
4º44'W
43'
42'
41'
40'
31'
36ºN
29'
28'
MALAGA
LA CALA DE MIJAS
Iberian
Peninsula
40ºN
Malaga
10ºW
0º
Torre de Calahonda
Torre Pesetas
Marina of Cabo Pino
5 m
10 m
20 m
30 m
50 m
Sampling station
Alboran Sea

Fig.1

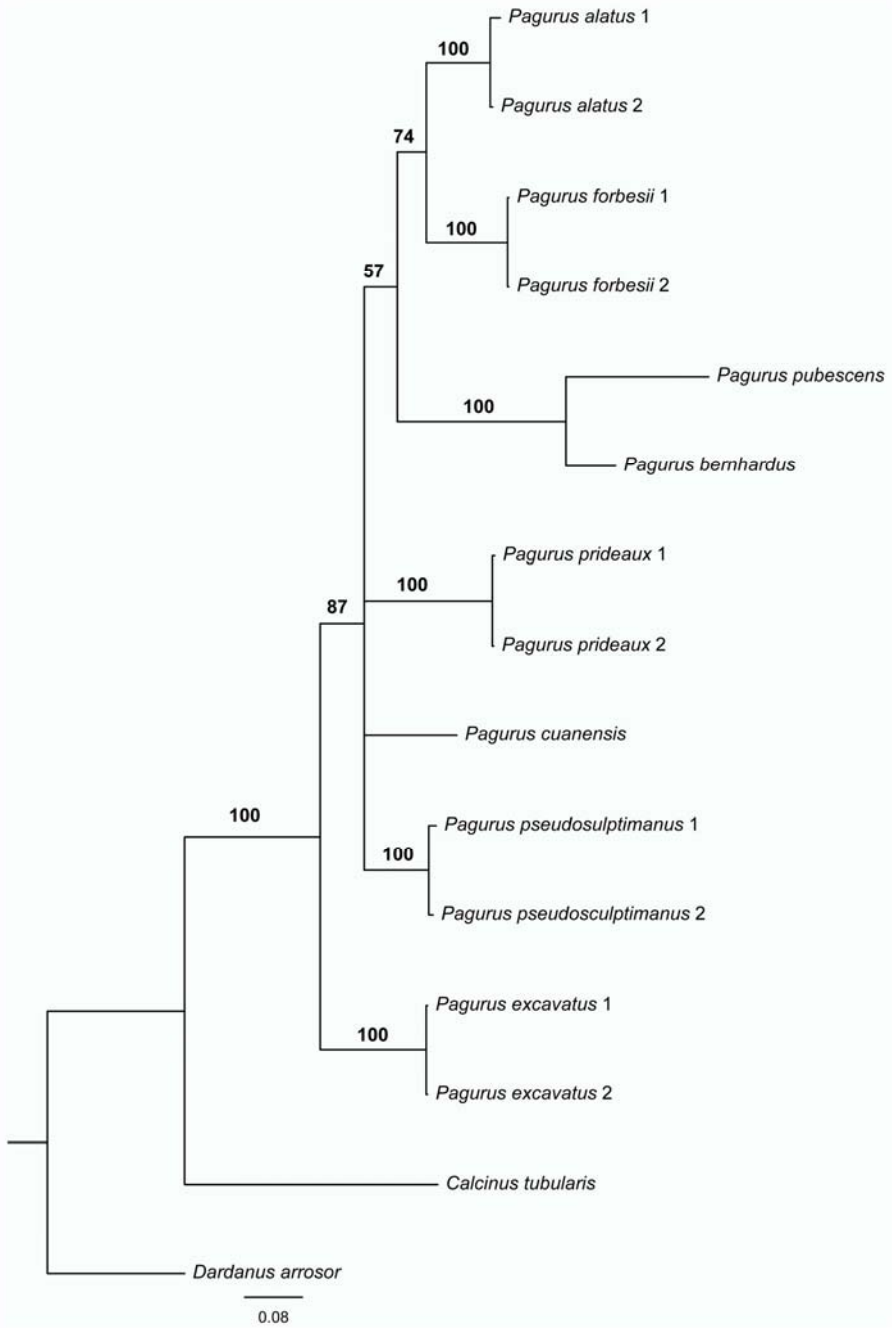
Pagurus alatus 1
100
Pagurus alatus 2
74
Pagurus forbesii 1
100
Pagurus forbesii 2
57
Pagurus pubescens
100
Pagurus bernhardus
Pagurus prideaux 1
100
87
Pagurus prideaux 2
Pagurus cuanensis
100
Pagurus pseudosulptimanus 1
100
Pagurus pseudosculptimanus 2
Pagurus excavatus 1
100
Pagurus excavatus 2
Calcinus tubularis
Dardanus arrosor
0.08

Fig. 2

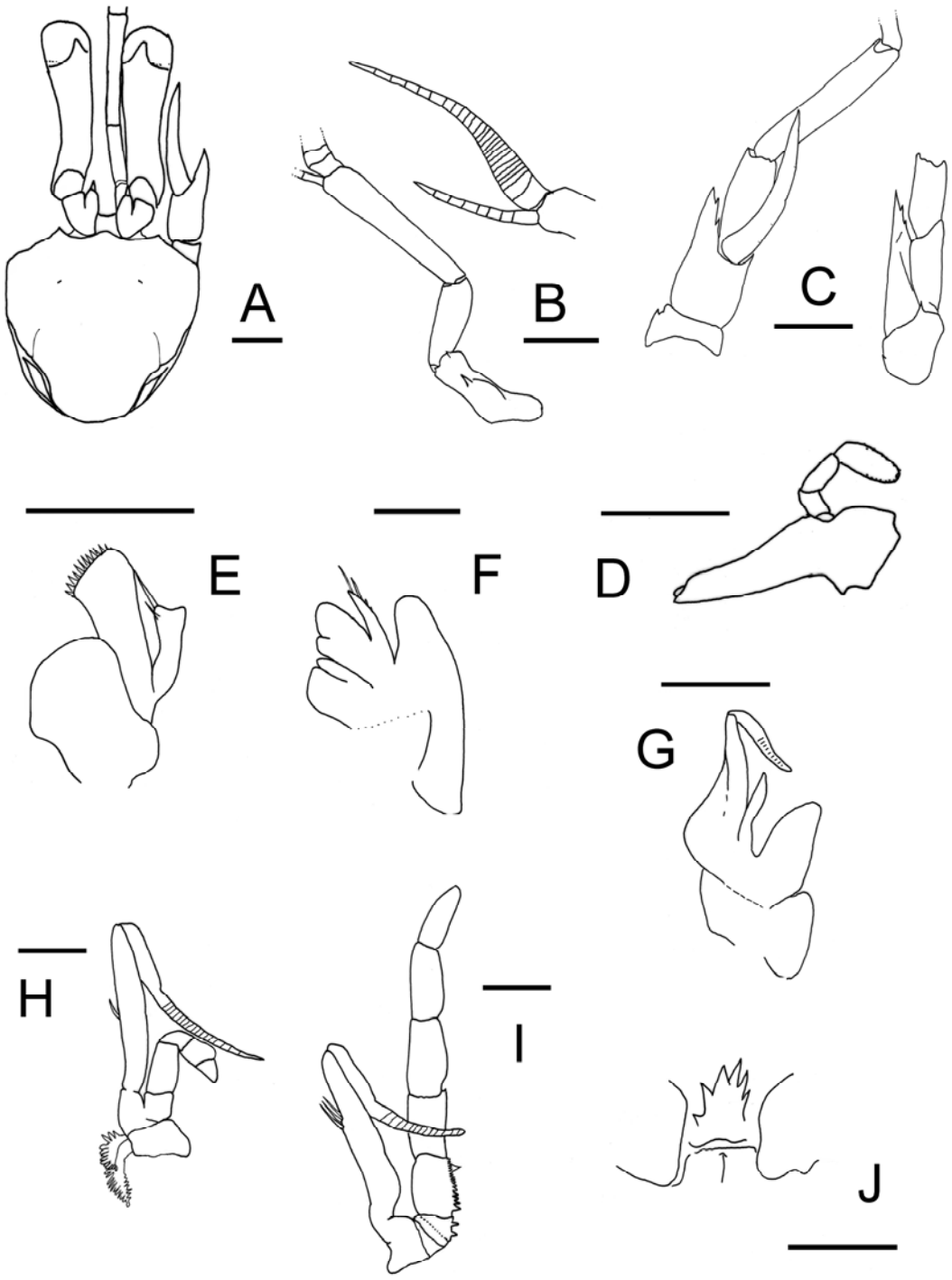

Fig.3

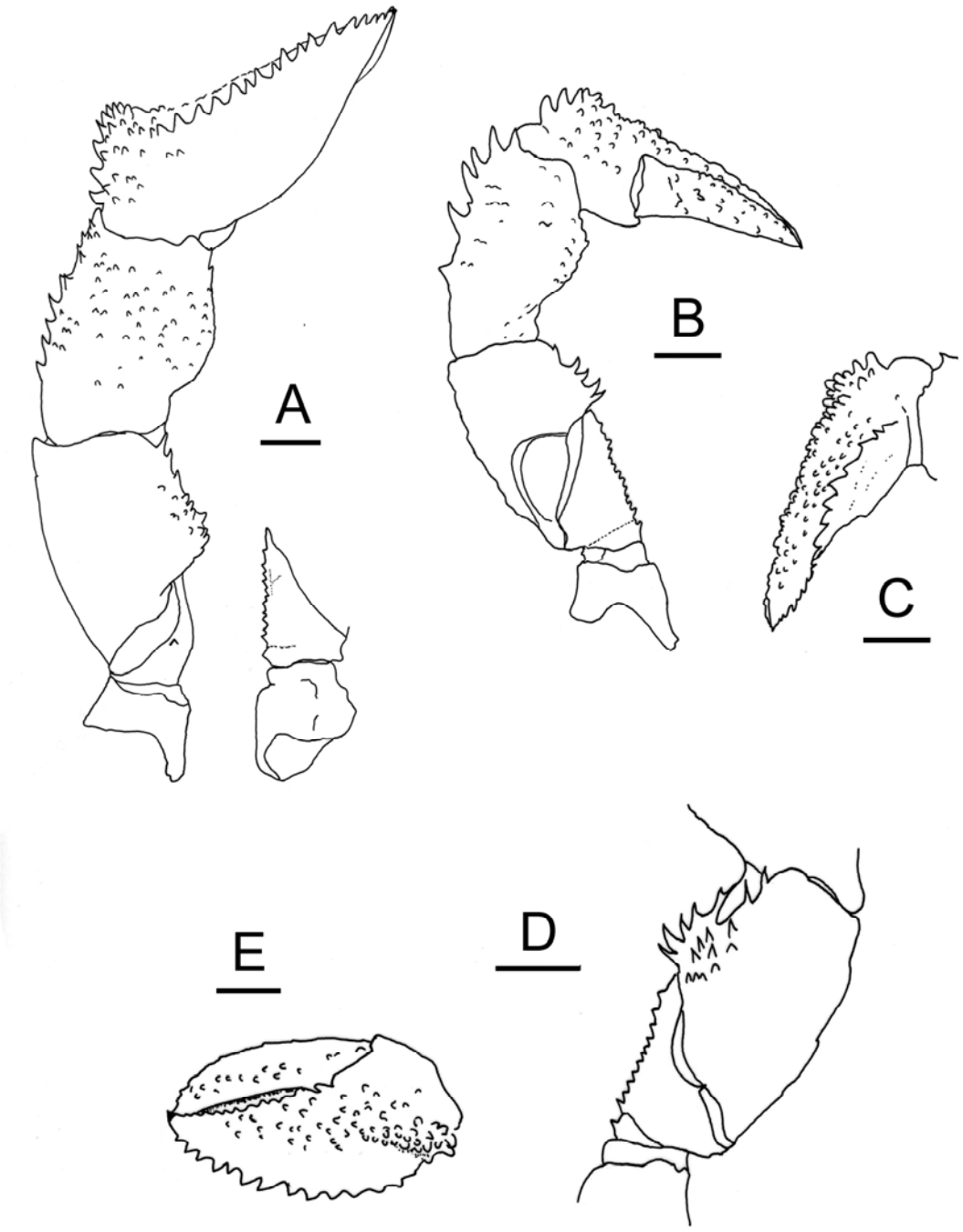

Fig. 4

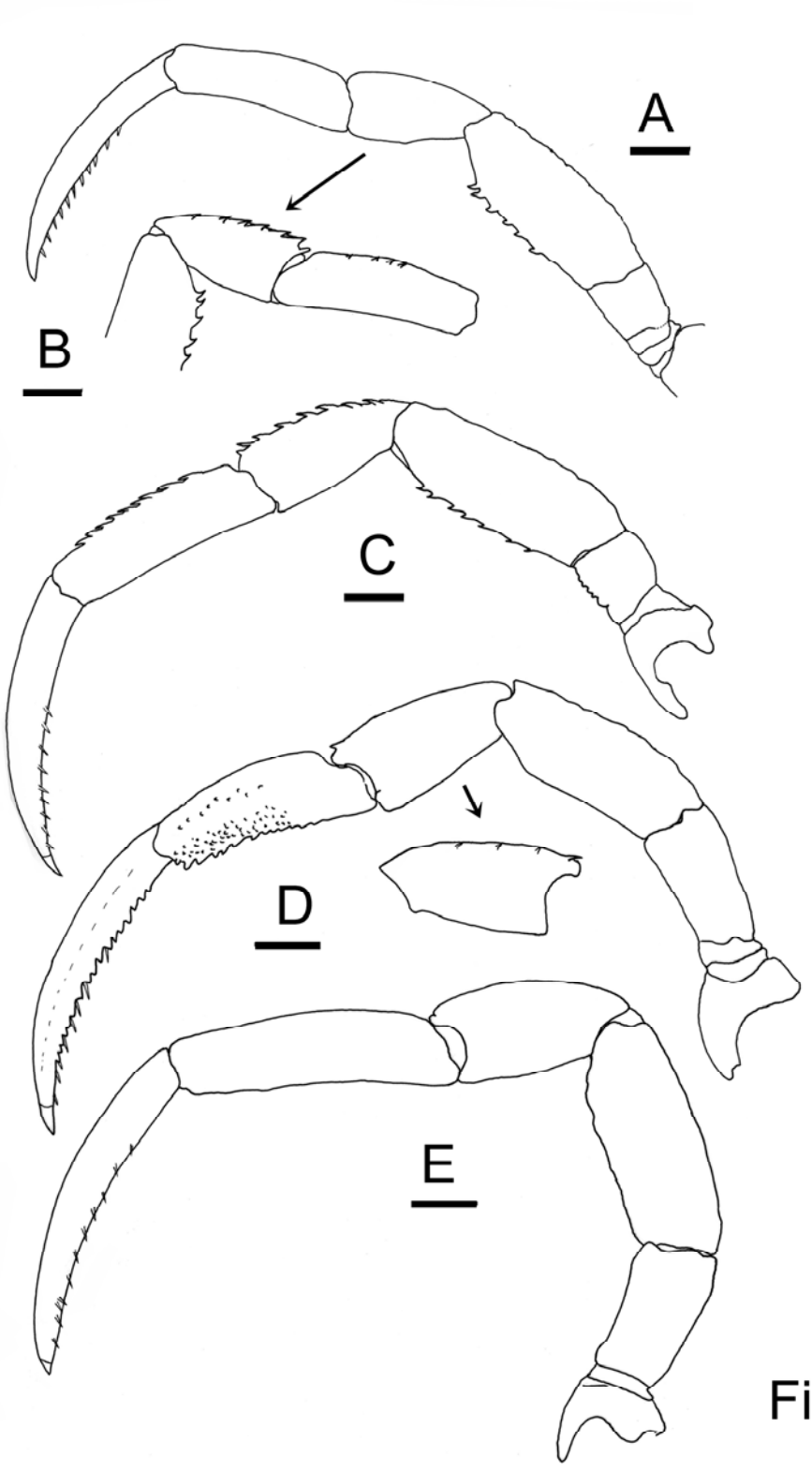

Fig.5

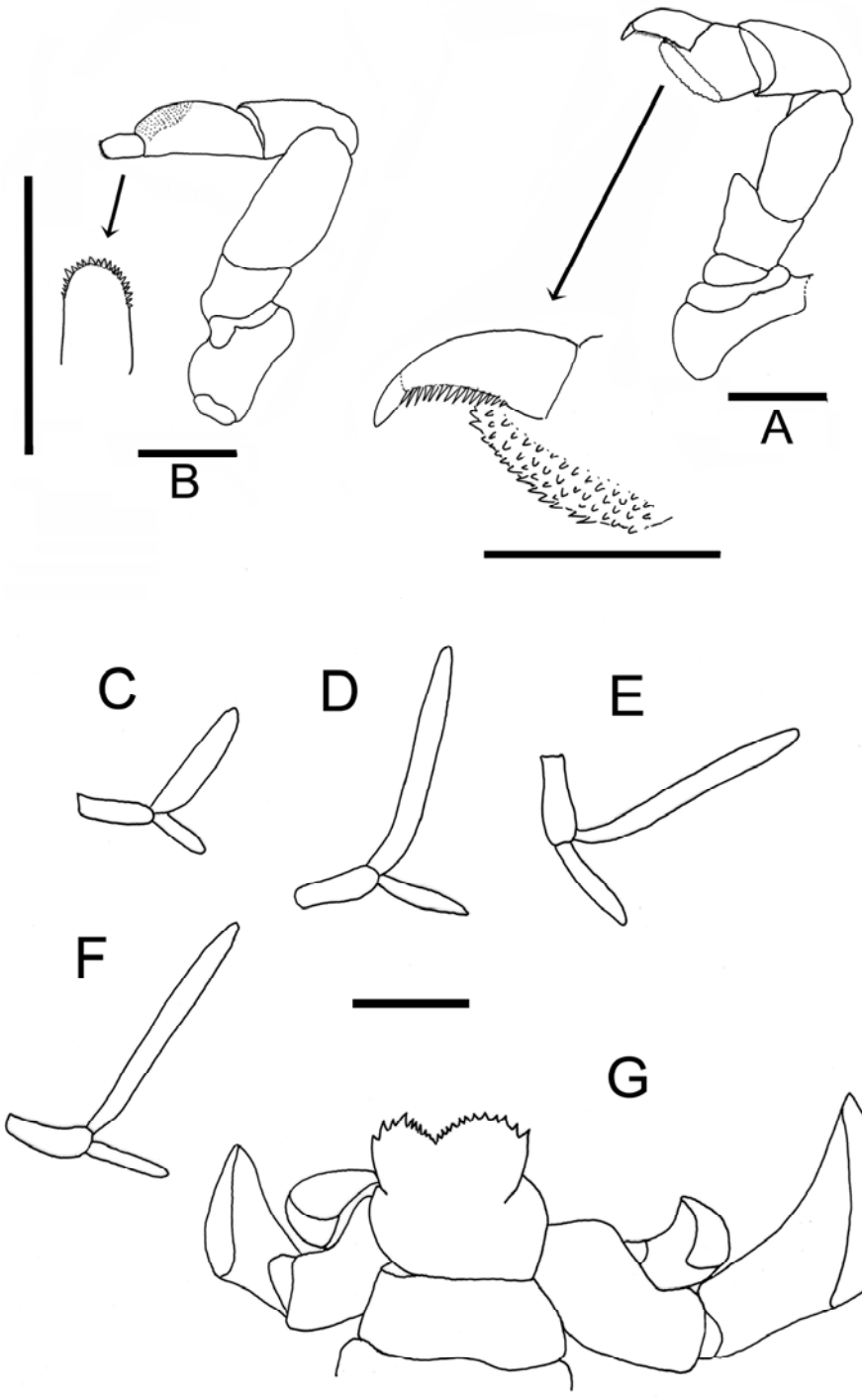

Fig.6

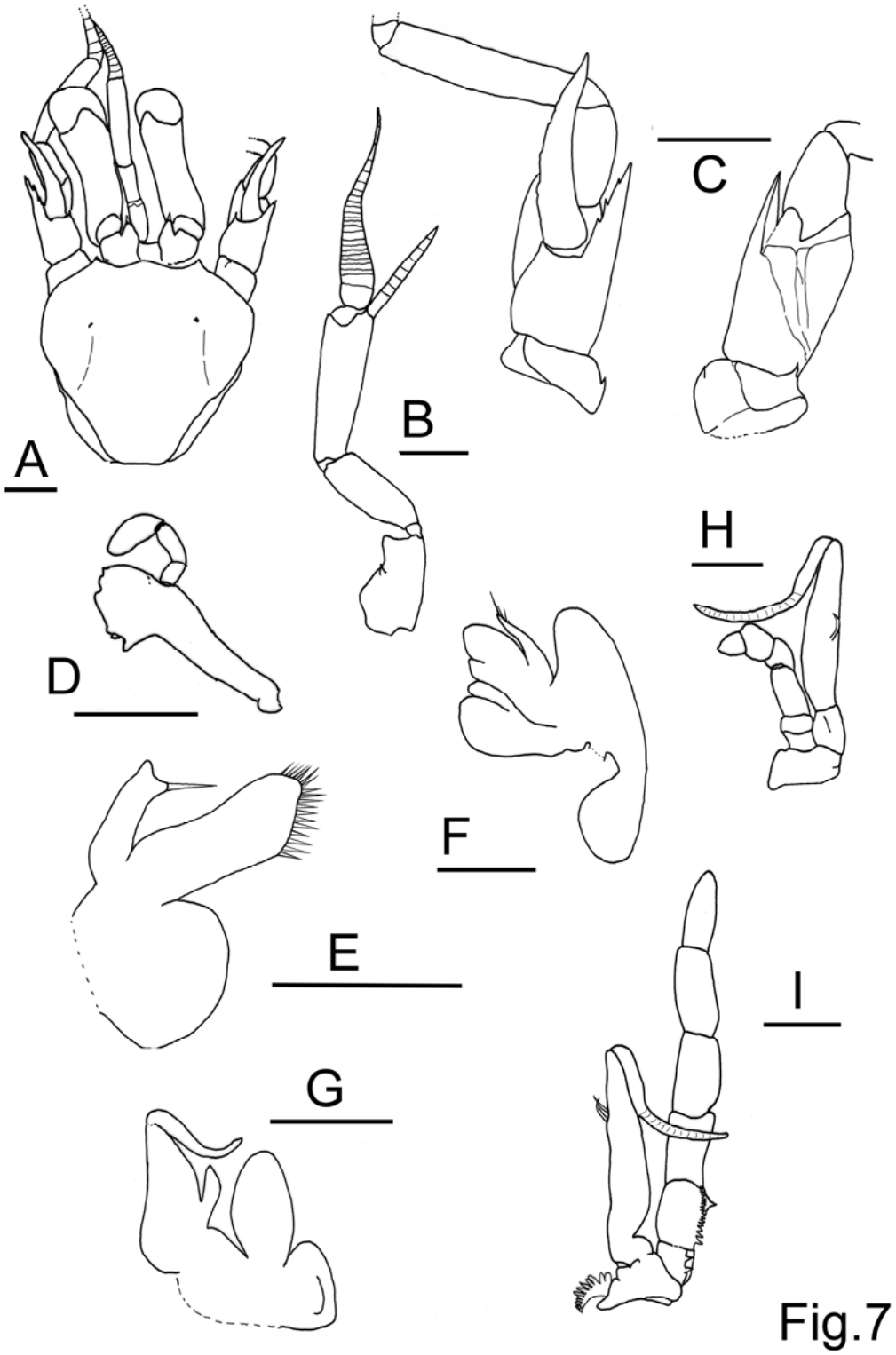

Fig.7

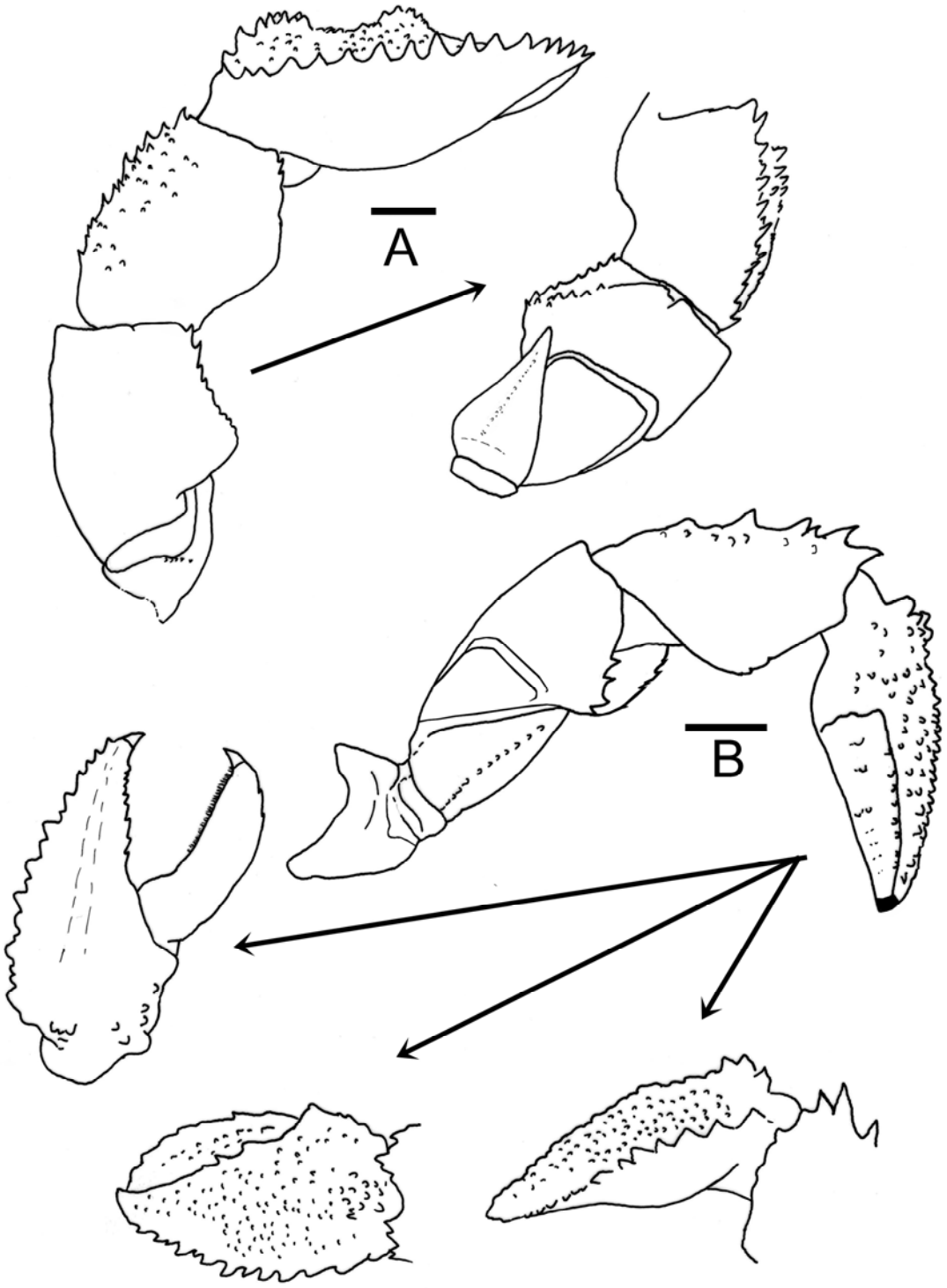

Fig.8

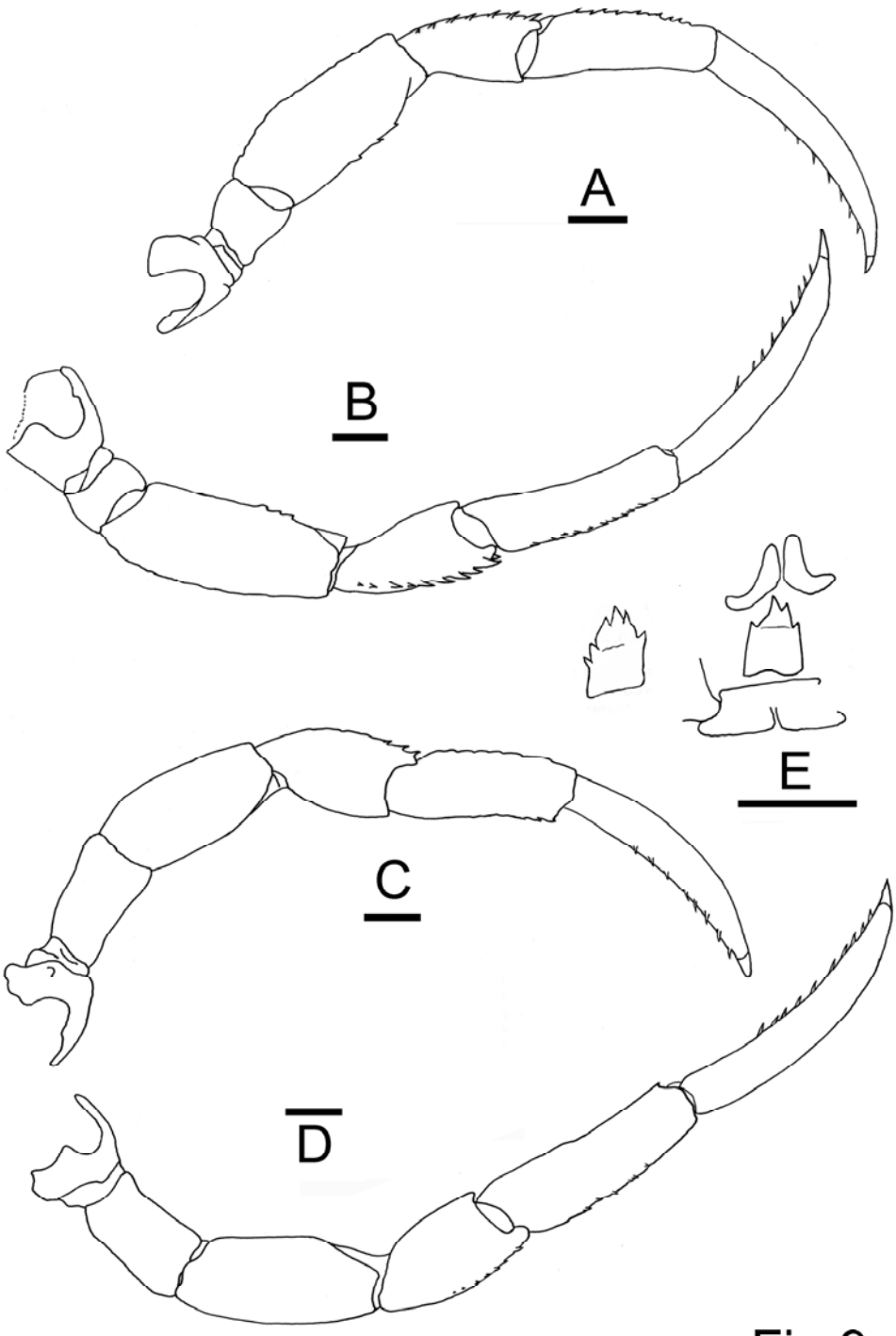

Fig.9

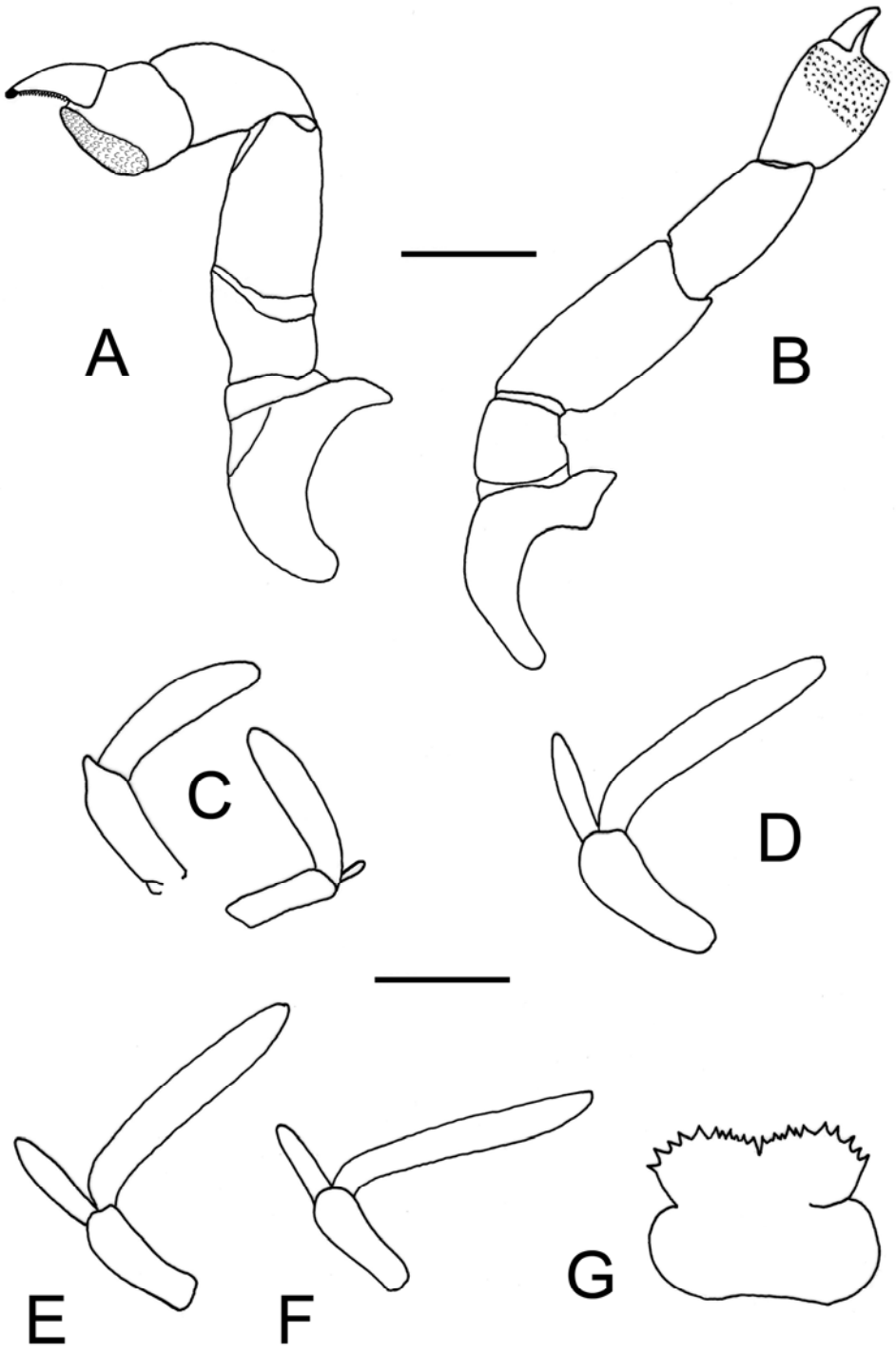

Fig.10

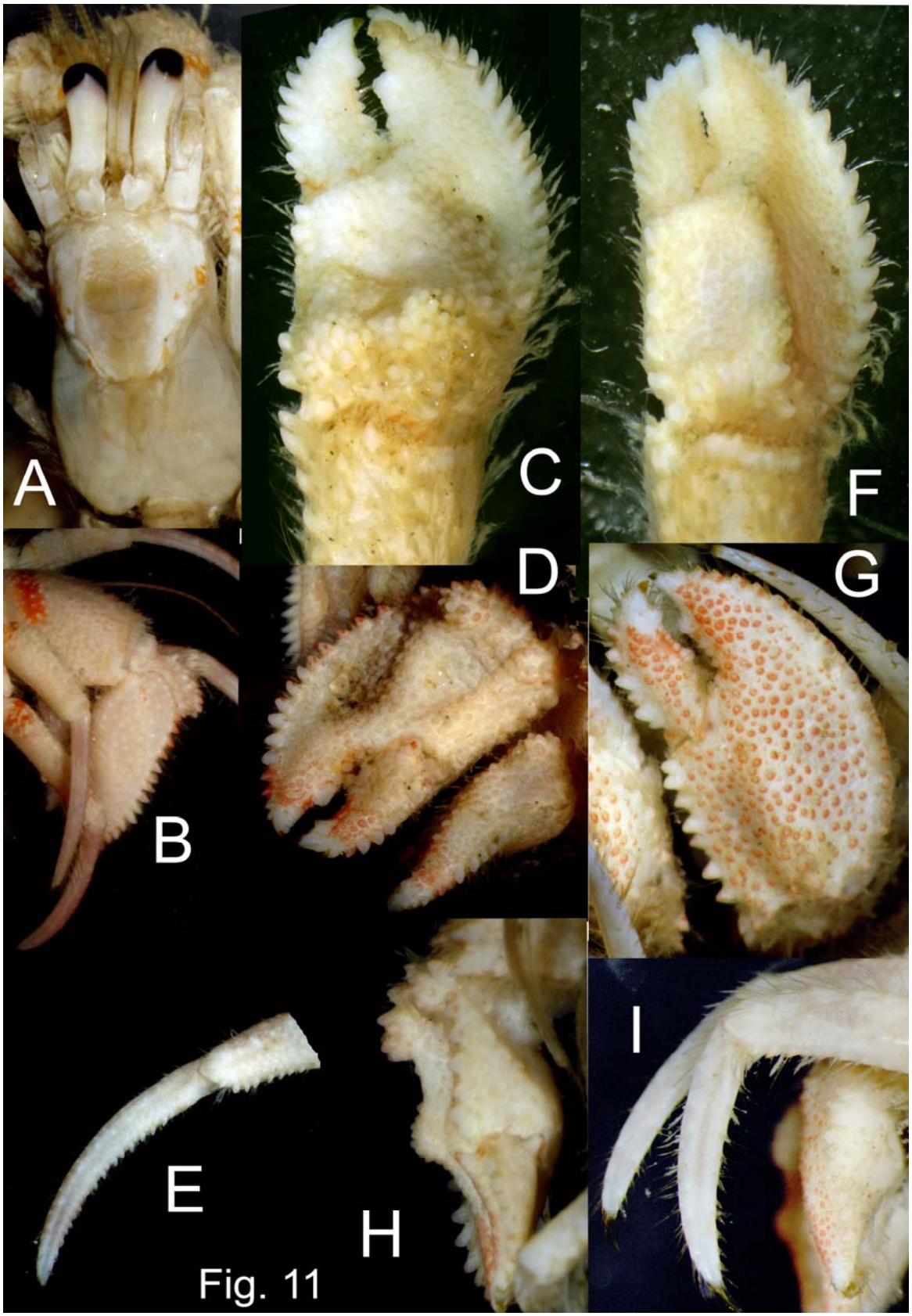

Fig. 11

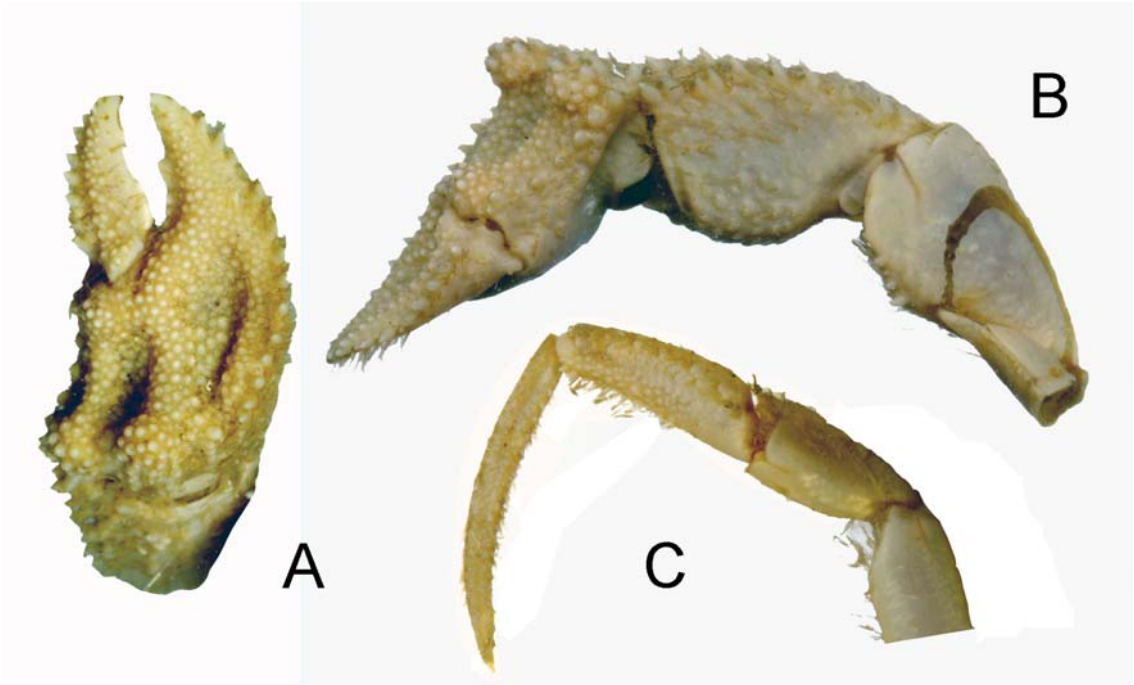
A
B
C


Fig.12
A
B
C