

European and Mediterranean Thalassinidea (Crustacea, Decapoda)

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ABSTRACT

All genera and species from Europe and the Mediterranean are diagnosed or redescribed, differentiating characters are illustrated and an identification key is provided. A review of literature and biological information is included, and a classification, with two new genera, is proposed. The superfamily Axiioidea comprises the Axiidae, with *Axius stirhynchus*, *Calocarides coronatus*, *Levantocaris hornungae*; and the Calocarididae with *Calastacus laevis* and *Calocaris macandreae*. The Callianassoidea include the Callianassidae, Ctenochelidae, Laomediidae and Upogebiidae. The Callianassidae contain three subfamilies. The Callianassinae have three species placed in *Callianassa*: *C. acanthura*, *C. subterranea* and *C. truncata*; three other species are assigned to a new genus, *Pestarella* n. gen.: *P. candida* n. comb., *P. tyrrhena* n. comb. and *P. whitei* n. comb. *Pestarella* n. gen. species have an operculiform Mxp3, a telson rounded in posterior half, and no Plp1-2 in male. The little known species *Calliapagurops charcoti* is placed in the Callichirinae. The Eucalliicinae contain two species: *Calliax lobata* and *Calliaxina punica* n. comb., type species of a new genus, *Calliaxina* n. gen. Species of *Calliaxina* n. gen. possess a rostrum with pointed tip, an operculiform Mxp3 with exopod, the P1 equal and similar, and Plp1-2 with *appendix interna* in both male and female. The Ctenochelidae have one subfamily, Gourretinae with *Gourretia denticulata*. The Laomediidae are represented by one species, *Jaxea nocturna*, and the Upogebiidae by seven species: *Gebiacantha talismani*, *Upogebia deltaura*, *U. mediterranea*, *U. nitida*, *U. pusilla*, *U. stellata* and *U. tipica*.

KEY WORDS

Crustacea,
Decapoda,
Thalassinidea,
Europe,
Mediterranean,
new genera,
revision.

RÉSUMÉ

Thalassinidea (Crustacea, Decapoda) d'Europe et de Méditerranée.

Une diagnose (ou redescription) de tous les genres et espèces d'Europe et de la Méditerranée est présentée et les caractères différentiels sont figurés. Une revue des données bibliographiques et biologiques est incluse ; une classification, comportant deux genres nouveaux, et une clé sont proposées. La superfamille Axiioidea comprend les Axiidae, avec *Axius stirhynchus*, *Calocarides coronatus*, *Levantocaris hornungae*, et les Calocarididae, avec *Calastacus laevis* et *Calocaris macandreae*. Les Callianassoidea se composent des Callianassidae, Ctenochelidae, Laomediidae et Upogebiidae. Les Callianassidae contiennent trois sous-familles. Les Callianassinae ont trois espèces placées dans *Callianassa*: *C. acanthura*, *C. subterranea* et *C. truncata* ; trois autres sont attribuées à un nouveau genre, *Pestarella* n. gen. : *P. candida* n. comb., *P. tyrrhena* n. comb. et *P. whitei* n. comb. Les espèces de *Pestarella* n. gen. ont un Mxp3 operculiforme, un telson arrondi dans sa partie postérieure et pas de Plp1-2 chez les mâles. L'espèce peu connue, *Calliapagurops charcoti*, est placée dans les Callichirinae. Les Eucalliicinae contiennent deux espèces : *Calliax lobata* et *Calliaxina punica* n. comb., espèce type d'un genre nouveau, *Calliaxina* n. gen. Les espèces de *Calliaxina* n. gen. possèdent un rostre à extrémité pointue, un Mxp3 operculiforme muni d'exopode, les P1 égaux et les Plp1-2 avec *appendix interna* dans les deux sexes. Les Ctenochelidae ont une sous-famille, Gourretinae, avec *Gourretia denticulata*. Les Laomediidae sont représentées par une espèce, *Jaxea nocturna*, et les Upogebiidae par sept espèces : *Gebiacantha talismani*, *Upogebia deltaura*, *U. mediterranea*, *U. nitida*, *U. pusilla*, *U. stellata* et *U. tipica*.

MOTS CLÉS

Crustacea,
Decapoda,
Thalassinidea,
Europe,
Méditerranée,
nouveaux genres,
révision.

INTRODUCTION

The European and Mediterranean Thalassinidea are a small group of decapod crustaceans currently comprising 23 species, excluding a new axiid that would have been described by M. de Saint Laurent. They have never been subject to an overall revision; uncertainty and confusion still exist for a number of species, especially in the Upogebiidae. On the other hand, several important works on the taxonomy and phylogeny of the Thalassinidea have been published in recent years: de Saint Laurent (1973), de Saint Laurent & Le Loeuff (1979), Sakai & de Saint Laurent (1989), Manning & Felder (1991), Poore (1994), Sakai (1999a), Tudge *et al.* (2000). Various classification systems have been proposed, sometimes with large differences, which meant that choices had to be made concerning the taxonomy of the European and Mediterranean fauna.

The first objective of this paper is to define the species. All species and genera from Europe and the Mediterranean are diagnosed, with redescrptions where necessary, and illustrated; extensive synonymies are given from taxonomic and biological literature. Characteristics of higher taxa can be found in the Discussion and in the Key.

A classification of the European and Mediterranean Thalassinidea, which includes two new genera, is presented. Different views concerning taxa are discussed.

MATERIALS AND METHODS

All materials of European and Mediterranean Thalassinidea currently present in the Muséum national d'Histoire naturelle, Paris (MNHN), The Natural History Museum, London (NHML) and the Rijksmuseum of Natural

History, Leiden (RMNH) were examined during the course of this study. Additional specimens came from the Museum of Comparative Zoology, Harvard (MCZ), the Museum of Copenhagen (ZMUC), the Museum of Victoria (NMV), the Natural History Museum, Vienna (NHMW), the Senckenberg Museum, Frankfurt (SMF), the Swedish Museum of Natural History, Stockholm (SMNH), the Smithsonian Institution, Washington DC (USNM), as well as from the personal collections of Cédric d'Udekem d'Acoz (d'Udekem d'Acoz, now deposited in the MNHN), and of Prof. Athanasios Koukouras (A.U.TH, deposited in the Museum of the Zoology Department, Aristoteleio University of Thessaloniki).

It has not been possible to locate the types for about a third of the species studied, nor was it possible to ascertain that they were lost. An effort has been made to clarify problems concerning the identity of these species, but no neotypes have been selected.

The measurements given in the description are: carapace length (cl.) measured from the tip of the rostrum (in the Callianassoidea) or the base of the rostrum, at the orbital margin (in the Axiioidea) to the posterior border of the carapace; total length (tl.) measured from the tip of the rostrum (in the Callianassoidea) or the base of the rostrum (in the Axiioidea) to the posterior border of the telson.

Most specimens belonging to the MNHN and a few from other institutions were measured. The carapace length is given for all whereas the total length is only given for types and figured specimens.

Figured specimens and appendages were stained with a weak solution of chlorazol black, sometimes with a drop of lactic acid added.

If not otherwise stated, the rostrum, the anterior part of the carapace, the telson and the uropods are figured in dorsal view and appendages in lateral view.

In the list of synonymies, the original names given to a species are presented first, in chronological order while other names are in alphabetical order. References preceded by an asterisk (*) deal

with larvae, those preceded by the symbol ° refer to a mention of the species in a list, without detail.

ABBREVIATIONS

A1	antennule;
A2	antenna;
Md	mandible;
Mx1	maxillule;
Mx2	maxilla;
Mxp1-3	maxillipeds 1-3;
P1-5	pereopods 1-5;
Plp1-5	pleopods 1-5.

The following terminology used may need clarification:

For axiids, A2 acicle = antennal scale.

For callianassids (adapted from Manning & Felder 1991), dorsal oval (e.g., Figs 8A; 13A) is defined by a groove or furrow that delimits an oval anterior portion of the carapace; posteriorly, it is delimited by the cervical groove.

Mxp3: pediform (Fig. 21E) means ischium-merus length more than three times merus width; subpediform (Fig. 9D) means ischium-merus length about two to three times merus width; operculiform (e.g., Figs 12G; 13G) means ischium-merus length less than twice merus width.

Dorsal plate on uropodal exopod (e.g., Figs 8G; 9F) is an antero-dorsal thickening terminating posteriorly in a dorsal setal row near the posterior border.

For upogebiids, lateral ridges (e.g., Figs 24A; 26A) are the upper longitudinal toothed crests of the gastric region, on either side of the rostrum.

DISCUSSION

Examination of the European and Mediterranean Thalassinidea supports Poore's (1994) view about assigning the Axiidae and Callianassidae into separate superfamilies, the Axiioidea and Callianassoidea. Members of the two families share a chelate P2 and the presence of an *appendix interna* on Plp3-5 but differ in many features. A number of presumably plesiomorphic characteristics are found in the Axiioidea: *linea thalassinica* absent; rostrum large and armed with teeth or

spines; antennal acicle large; Mxp3 slender with a strong tooth crest on mesial surface; suture present on the uropodal exopod, among others. The Axioidea are probably the least evolved of the two superfamilies and Forest & de Saint Laurent (1981: 53) pointed out the characters shared with the primitive Glypheoidea. In the European and Mediterranean fauna, nevertheless, they represent an homogeneous group as compared with the Callianassoidea.

The superfamily Callianassoidea, as stated by Poore (1994), is defined by one unquestionable synapomorphy: posterior margin of carapace soft and without ridges. All European and Mediterranean members also have the *linea thalassinica* present on the carapace. Yet there are differences between the families as reflected in the key below: the rostrum is small (in Callianassidae and Ctenochelidae) or large (in Laomediidae and Upogebiidae); the Mx2 scaphognathite has long setae on the posterior lobe (in Laomediidae) or lacks them (in Upogebiidae, Callianassidae and Ctenochelidae); P2 is chelate (in Callianassidae and Ctenochelidae) or simple (in Laomediidae and Upogebiidae); pleopods either bear an *appendix interna* (in Callianassidae and Ctenochelidae) or do not (in Laomediidae and Upogebiidae); uropodal exopod and endopod either both have suture (in the Laomediidae) or lack it (in Upogebiidae, Callianassidae and Ctenochelidae). Among the four families of European Callianassoidea, the Laomediidae are most similar to the Axioidea by virtue of the large rostrum, the Mx2 scaphognathite with long posterior setae, the morphology of Mxp3 with a strong toothed crest on mesial surface of ischium and the presence of a suture on the uropodal exopod. Poore (1994) considered them, with the Upogebiidae, the least derived of the Callianassoidea.

The Upogebiidae possess numerous autapomorphies including the broad rostrum with lateral gastric ridges, *appendix interna* and *masculina* absent from pleopods and the uropodal endopod distally truncate. The Callianassidae share a carapace with dorsal oval; P3 propodus with heel on proximal corner; Plp1 and 2 sexually modified; and uropodal exopod with dorsal setose plate.

The Ctenochelidae differ by having no dorsal oval on the carapace, no dorsal plate on the uropodal exopod and a different form of the Mxp3. Phylogenetic relationships of thalassinid families are presented in a cladogram and discussed by Poore (1994). Given the small number of species studied and distributed among few families, this work proposes no changes to this phylogeny. A classification of the European and Mediterranean Thalassinidea including two new genera, *Pestarella* n. gen. and *Calliaxina* n. gen., both belonging to the Callianassidae, is presented, followed by a key.

SPECIES OF EUROPEAN AND MEDITERRANEAN THALASSINIDEA

Infraorder THALASSINIDEA Latreille, 1831

Superfamily AXIOIDEA Huxley, 1879

Family AXIIDAE Huxley, 1879

Genus *Axius* Leach, 1815

Axius stirrhynchus Leach, 1815, type species

Genus *Calocarides* Wollebæk, 1909

Calocarides coronatus (Trybom, 1904), type species

Genus *Coralaxius* Kensley & Gore, 1982

Coralaxius nodulosus (Meinert, 1877), type species

Genus *Levantocaris* Galil & Clark, 1993

Levantocaris hornungae Galil & Clark, 1993, type species

Family CALOCARIDIDAE Ortmann, 1891

Genus *Calastacus* Faxon, 1893

Calastacus laevis de Saint Laurent, 1972

Genus *Calocaris* Bell, 1846

Calocaris macandreae Bell, 1846, type species

Superfamily CALLIANASSOIDEA Dana, 1852

Family CALLIANASSIDAE Dana, 1852

Subfamily CALLIANASSINAE Dana, 1852

Genus *Callianassa* Leach, 1814

Callianassa acanthura Caroli, 1946

Callianassa subterranea (Montagu, 1808), type species

Callianassa truncata Giard & Bonnier, 1890

- Genus *Pestarella* n. gen.
Pestarella candida (Olivi, 1792) n. comb.
Pestarella tyrrhena (Petagna, 1792) n. comb., type species
Pestarella whitei (Sakai, 1999) n. comb.
- Subfamily CALLICHIRINAE Manning & Felder, 1991
 Genus *Calliapagurops* de Saint Laurent, 1973
Calliapagurops charcoti de Saint Laurent, 1973, type species
- Subfamily EUCALLIACINAE Manning & Felder, 1991
 Genus *Calliax* de Saint Laurent, 1973
Calliax lobata (de Gaillande & Lagardère, 1966), type species
 Genus *Calliaxina* n. gen.
Calliaxina punica (de Saint Laurent & Manning, 1982) n. comb., type species
- Family CTENOCHOLIDAE Manning & Felder, 1991
- Subfamily GOURRETINAE Sakai, 1999
 Genus *Gourretia* de Saint Laurent, 1973
Gourretia denticulata (Lutze, 1937), type species
- Family LAOMEDIIDAE Borradaile, 1903
 Genus *Jaxea* Nardo, 1847
Jaxea nocturna Nardo, 1847, type species
- Family UPOGEBIIDAE Borradaile, 1903
 Genus *Gebiacantha* Ngoc-Ho, 1989
Gebiacantha talismani (Bouvier, 1915), type species
 Genus *Upogebia* Leach, 1814
Upogebia deltaura (Leach, 1815)
Upogebia mediterranea Noël, 1992
Upogebia nitida (A. Milne-Edwards, 1868)
Upogebia pusilla (Petagna, 1792)
Upogebia stellata (Montagu, 1808), type species
Upogebia tipica (Nardo, 1869)

KEY TO SPECIES OF EUROPEAN AND MEDITERRANEAN THALASSINIDEA

1. *Linea thalassinica* absent. A1 with article 3 about as long as article 2. Rostrum large. Mx2 scaphognathite with long setae on posterior lobe. P1 and P2 chelate. Plp2-5 similar, all with *appendix interna*. Uropodal exopod with suture Axioidea (2)
 — *Linea thalassinica* present. A1 usually with article 3 longer than article 2. Rostrum small or large. Mx2 scaphognathite with or without long setae on posterior lobe. P1 chelate or subchelate, P2 chelate or simple. Pleopods with or without *appendix interna*. Uropodal exopod and endopod both with suture or both without suture Callianassoidea (6)
2. Eyestalk differentiated, cornea rounded. Plp2 m with *appendix masculina* not fused with endopod. Gonochoristic Axiidae (3)
 — Eyestalk short, hardly mobile, cornea slightly flattened, contiguous to carapace, unpigmented. Plp2 with *appendix masculina* fused with endopod. Hermaphroditic .. Calocarididae (5)
3. Rostrum triangular with obtuse tip, lateral border with small round teeth, lateral carina unarmed, short median carina terminating near anterior third of gastric region. A2 acicle reaching mid-length of article 3 of peduncle 4
 — Rostrum triangular with pointed tip, lateral border and lateral carina with spines, median carina terminating near posterior third of gastric region, submedian carina present. A2 acicle spike-like reaching distal border of article 3 of peduncle *Calocarides coronatus*

4. Faint submedian carina on gastric region. Abdominal segments 3-5 with lateral tufts of setae. Mxp3 endopod with lower distal spine on merus. P1 unequal, dissimilar. Plp2-5 rami broad. Two dorsal spines on telson, posterior border convex *Axius stirrhynchus*
- No submedian carina on gastric region; no lateral setae on abdominal segments 3-5. Mxp3 endopod with three or four lower spines on ischium and merus. P1 subequal. Plp2-5 rami narrow. Four dorsal spines on telson, posterior border rounded *Levantocaris hornungae*
5. Rostrum pointed, lateral border unarmed except for large suborbital spine. Lateral carina short. Median carina extending posteriorly to cervical groove; no post-cervical carina. A2 acicle slender, elongate. P1 with fingers about as long as palm. Telson with no spinous dorsal carinae, no median spine on posterior border *Calastacus laevis*
- Rostrum pointed, lateral border and lateral carine with spines. Median carina extending posteriorly to whole length of carapace. A2 acicle small. P1 with fingers longer than palm, often twice as long. Telson with pair of dorsal spinous carinae and median spine on posterior border *Calocaris macandreae*
6. *Linea thalassinica* lateral to antennae, straight antero-posteriorly on carapace 7
- *Linea thalassinica* depressed anteriorly. Rostrum broad, obtuse. Gastric region with lateral ridges. A1 with article 3 longer than article 2. P1 chelate or subchelate, P2 simple. Pleopods without *appendix interna* or *masculina*; Plp1 absent in males, uniramous in females; Plp2 similar to Plp3-5. No suture on uropods Upogebiidae (17)
7. Rostrum large, pointing distally. No lateral ridges on gastric region, *linea thalassinica* well defined. A1 with article 3 longer than article 2. Mx2 scaphognathite with several thickened setae on posterior lobe. P1 chelate, P2 simple. Pleopods without *appendix interna* or *masculina*; Plp1 absent in males, uniramous in females; Plp2 similar to Plp3-5. Suture on both rami of uropods Laomediidae, *Jaxea nocturna*
- Rostrum obsolete or a spike. No lateral ridges on gastric region. A1 with article 3 longer than article 2 (except for *Calliaxina* n. gen.). No long setae on posterior lobe of Mx2 exopod. Both P1 and P2 chelate. Plp2 different from Plp3-5, sexually modified, with or without *appendix interna* or *masculina*; Plp3-5 with *appendix interna*. No suture on uropods 8
8. Mpx3 ischium-merus pediform; ischium with prominent toothed crest on mesial surface; dactylus digitiform. Carapace lacking dorsal oval. Uropodal exopod lacking dorsal plate Ctenochelidae, Gourretinae, *Gourretia denticulata*
- Mpx3 ischium-merus subpediform or operculiform; no prominent toothed crest on mesial surface of ischium. Uropodal exopod with dorsal plate Callianassidae (9)
9. Mxp3 dactylus digitiform. Carapace with dorsal oval 10
- Mxp3 dactylus ovate. Carapace lacking dorsal oval Eucalliicinae (16)

10. Mxp3 propodus at least 1.5 times as long as broad, lower border straight or weakly convex. Carapace with well defined dorsal oval *Callianassinae* (11)
 — Mxp3 propodus ovate, less than 1.5 times as long as broad, lower border strongly convex. Carapace trispinous, with faint dorsal oval *Callichirinae*, *Calliapagurops charcoti*
11. Telson squarish in posterior half, posterior border flattened, with fine median spinule; male Plp1 small, uniramous, male Plp2 absent or vestigial *Callianassa* (12)
 — Telson rounded in posterior half, posterior border convex, unarmed; male Plp1 and Plp2 absent *Pestarella* n. gen. (14)
12. Mxp3 subpediform. Eye cornea indistinct. Lateral border of uropodal endopod unarmed *Callianassa subterranea*
 — Mxp3 operculiform. Eye cornea distinct, disk-shaped. Lateroposterior border of uropodal endopod with spine 13
13. Lateroposterior border of telson with large acute spine, same spine on lateroposterior border of uropodal endopod and near base of uropodal exopod *Callianassa acanthura*
 — No large spine on lateroposterior border of telson, spinule on lateroposterior border of uropodal endopod, minor P1 with lower median spinule on merus *Callianassa truncata*
14. Telson about as long as wide, uropodal endopod and exopod weakly exceeding telson. Meral hook of major P1 rounded; carpus of minor P1 wider proximally than distally, wider than propodus *Pestarella tyrrhena* n. comb.
 — Telson wider than long, uropodal endopod and exopod greatly exceeding telson. Meral hook of major P1 with pointed distal tip; carpus of minor P1 not wider proximally than distally, not wider than propodus 15
15. A1 peduncle not longer than that of A2. Mxp3 propodus about 1.5 times as long as wide, lower border convex. Telson less than 1.5 times as wide as long *Pestarella candida* n. comb.
 — A1 peduncle longer than that of A2. Mxp3 propodus slender, twice as long as wide, lower border nearly straight. Telson about 1.5 times as wide as long *Pestarella whitei* n. comb.
16. Mxp3 subpediform, without exopod. P1 unequal, dissimilar *Calliax lobata*
 — Mxp3 operculiform, with exopod. P1 subequal, similar *Calliaxina punica* n. comb.
17. Infrarostral spines present, several spines and spinules on anterolateral border of carapace *Gebiacantha talismani*
 — No infrarostral spines, anterolateral border of carapace unarmed or with spine *Upogebia* (18)

- 18. Anterolateral border of carapace unarmed 19
 - Anterolateral border of carapace with spine 21
- 19. Pleuron of first abdominal segment pointed postero-ventrally, article 3 of A2 peduncle with lower spine *Upogebia deltaura*
 - Pleuron of first abdominal segment rounded postero-ventrally, article 3 of A2 peduncle unarmed 20
- 20. Rostrum triangular elongate, both P1 and P2 merus with upper subdistal spine, telson about as long as wide *Upogebia mediterranea*
 - Rostrum triangular, no upper subdistal spines on P1 and P2 merus, telson wider than long *Upogebia nitida*
- 21. A pleurobranch on P5 (can break off), P1 carpus with median distal spine on mesial border, dactylus with upper conical proximal tooth *Upogebia stellata*
 - No pleurobranch on P5, no median distal spine on mesial border of P1 carpus, no upper conical tooth on dactylus 22
- 22. Rostrum less than 1.5 times as long as wide, four or five teeth on lateral border, P1 merus with spines and spinules on proximal half of lower border, telson wider than long *Upogebia pusilla*
 - Rostrum over 1.5 times as long as wide, six to eight teeth on lateral border, P1 merus with spines and spinules on two-thirds or whole lower border, telson subquadrate *Upogebia tipica*

SYSTEMATICS

Infraorder THALASSINIDEA Latreille, 1831
 Superfamily AXIOIDEA Huxley, 1879

Family AXIIDAE Huxley, 1879

TYPE GENUS. — *Axius* Leach, 1815, by original designation.

REMARKS

Recent major works dealing with axiids include: Sakai & de Saint Laurent 1989; Kensley 1989; Poore 1994 (as part of the phylogeny of the Thalassinidea families); Sakai 1994.

Examination of European materials supports the view of Kensley (1989) and Poore (1994) rather than those of Sakai & de Saint Laurent (1989) and Sakai (1994) in resurrecting the family

Calocariidae Ortmann, 1891. In this family of hermaphrodites, the *appendix masculina* is presumably fused to the median portion of the Plp2 endopod which is densely setose or spinose mesially. The distal portion of the Plp2 endopod is large, and similar to that of the exopod, in *Calocaris macandreae* (Fig. 7D); it is less defined in *Calastacus laevis* (Fig. 5I).

This work does not give as much importance as did Sakai & de Saint Laurent (1989) to the thoracic sternite of P4 since its morphology does not vary much in the species studied, except for the presence of a spine on the lateral border (Fig. 11), and in its size. These are indicated in the diagnosis.

A species probably not belonging to the European fauna but often mentioned in the past, *Coralaxius nodulosus* (Meinert, 1877) (better known as *Axius nodulosus* Meinert, 1877), is briefly treated.

Genus *Axius* Leach, 1815

TYPE SPECIES. — *Axius stirrhynchus* Leach, 1815 by monotypy.

DIAGNOSIS. — Rostrum triangular, margin armed, extending to gastric region. Anterolateral margin of carapace unarmed. Gastric region slightly convex; one short median and two short submedian carinae present; cervical groove well defined to whole length. Abdominal pleura ventrally rounded, that of somite 2 broadest, that of somites 3-5 with lateral tufts of setae. Telson longer than wide with dorsal spines; posterior border convex with median spine. Eyestalk subglobose, cornea pigmented; antennal acicle large. Mx2 scaphognathite with long setae on posterior lobe. Mxp3 endopod pediform, with prominent toothed crest on ischium, P1 unequal; P2 chelate; P5 subchelate.

Exopod on Mxp1-3; single epipod on Mxp1-3 and P1-4; single podobranch on Mxp2, Mxp3 and P1-3; single rudimentary arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-4; single pleurobranch on P1-5 (small on P5, sometimes a rudiment).

Male Plp1 uniramous, unsegmented, female Plp1 uniramous, two-segmented; male Plp2 biramous with *appendix interna* and *appendix masculina*, female Plp2 biramous with *appendix interna*. Uropodal exopod with inconspicuous transverse suture near posterior border.

Axius stirrhynchus Leach, 1815

(Figs 1; 2)

Axius stirrhynchus Leach, 1815: 343; 1816: pl. 33. — Bell 1846: 228, 1 fig. — White 1847: 70; 1850: 32. — Stebbing 1893: 187. — Holthuis 1962: 252. — Sinel 1907: 217.

Axiopsis mediterranea Caroli, 1921a: 254, fig. 1, pl. 9 figs 1-4, pl. 10 figs 5-16.

Callianassa bisulcata Risso, no date: Ms, fig. (f).

Axia stirrhynchus – ? Gibert i Olivé 1920: 51, 1 fig.

Axiopsis (Axiopsis) mediterranea – de Man 1925b: 70.

Axius stirrhynchus – Desmarest 1825: 207, pl. 36 fig. 1. — H. Milne Edwards 1837a: 311; 1837b: 131, pl. 48 fig. 2. — White 1857: 25. — Norman 1868: 177; °1907: 357. — Carus 1885: 490. — Lovett 1885: 16. — Kœhler 1886: 59. — Norman & Scott 1906: 13. — Norman 1907: 357. — Sinel 1907: 217. — Schlegel 1912: 237. — Selbie 1914: 89, pl. 14 figs 1-4. — Caroli 1921a: 254; 1921b: 241. — *Webb 1921: 406, pl. 3 figs 3, 6. — Monod 1931: 119, 123, fig. 6E. — °Delphy & Magne 1938: 84. — Bouvier 1940: 93, fig. 65. — Zariquiey Alvarez 1946: 103,

fig. 131; 1968: 223, fig. 88a. — Drensky 1951: 213. — *Kurian 1956: 72, fig. 141. — Gordon 1957: 249. — *Bourdillon-Casanova 1960: 99, fig. 35. — Holthuis 1962: 247; 1977: 57, pl. 5, fig. a. — *O'Ceidigh 1962: 163. — ICZN 1964: 341. — Bourdon 1965: 15. — Allen 1967: 17, 57 (key), 89 (fig.). — °Štević 1969: 128; 1990: 214. — *Thiriou 1976: 349, 367. — Beaubrun 1979: 69, figs 44, 73. — Moncharmont 1979: 69. — d'Udekem d'Acoz 1986: 101, fig. 1; 1989: 175; 1995: 47, fig. 1; 1999: 153, fig. on cover. — Sakai & de Saint Laurent 1989: 27, fig. 7. — Moyses & Smalton 1990: 517, fig. 10.12. — Dworschak 1992: 214. — °Koukouras *et al.* 1992: 223. — Frogliia 1995: 7. — Hayward *et al.* 1995: 432, fig. 8.51 (part). — Falcia & Minervini 1996: 143, 1 fig. — *Barnich 1996: 130, figs 28, 66. — Astall *et al.* 1997b: 668. — Pinn *et al.* 1999a: 103, figs 1H, 2A; 1999b: 1461, figs 1B, 4, tabs 1-6. — *González-Gordillo *et al.* 2001: 279. — Livory 2001: 30. — *Martin 2001: 75, 1 fig. — °Turkey 2001: 289.

Axius (Axius) stirrhynchus – Borradaile 1903: 537. — de Man 1925b: 11.

TYPE MATERIAL. — Lectotype: Plymouth, Devonshire, south coast of England, ♀ dried (figured by Leach 1815) (NHML 261b); paralectotype: Sidmouth, Devonshire, 1 ♀ dried (NHML 261a), by present designation.

MATERIAL EXAMINED. — **Great Britain.** Plymouth, Devonshire, ♀ lectotype cl. 20.5 mm, tl. 70.5 mm (NHML 261b); Sidmouth, Devonshire, ♀ paralectotype cl. 10.5 mm, tl. 33 mm (NHML 261a).

France. English Channel, French coast, Pointe du Château, N of Tréguier (Côtes d'Armor), intertidal, P. Noël coll., 28.II.1994, 1 ♀ cl. 22.5 mm, tl. 70 mm, 1 ♂ cl. 20.5 mm, tl. 63.5 mm (figured) (MNHN Th 1322); P. Noël and C. d'Udekem d'Acoz coll., 27.II.1994, 1 ♂ cl. 14 mm (MNHN Th 1408). — Cherbourg, dredge, in mud, S. Godefroy coll., 11.XI.2001, 1 ♀ cl. 21 mm, tl. 64 mm (MNHN Th 1414). — Dinard, Baron de St Joseph coll., 2 ♂♂ cl. 20 mm, tl. 61.5 and 62 mm (figured) (MNHN Th 151). — St-Vaast-la-Hougue, Bouvier coll., 1 damaged ovigerous ♀ (MNHN Th 150). — Bay of Mont-St-Michel, Y. Gruet coll., 24.IV.1967, 1 ♀ cl. 9 mm (MNHN Th 611). — Locality?, Gruet coll., 31.I.1968, 1 ♀ cl. 7.5 mm (MNHN Th 606); Gruet coll., 13.XII.1966, 1 ♂ cl. 8.5 mm (MNHN Th 608); Gruet coll., 8.VIII.1962, 1 young ♂ cl. 7 mm (MNHN Th 624). — Gruet coll., locality, date?, 1 ♀ cl. 12.5 mm (MNHN Th 627). — North coast of Brittany, Bourdon coll., 1 broken ♀ cl. 15 mm (MNHN Th 540).

Atlantic, Chausey Island, under rock, intertidal, A. Crosnier, B. Richer de Forges, R. Manning coll., 28.VIII.1992, 1 young ♀ cl. 13 mm, tl. 36 mm (figured) (MNHN Th 1321); J.-C. Hureau and C. Ozouf coll., 28.III.1994, 1 ♀ cl. 14.5 mm (MNHN Th

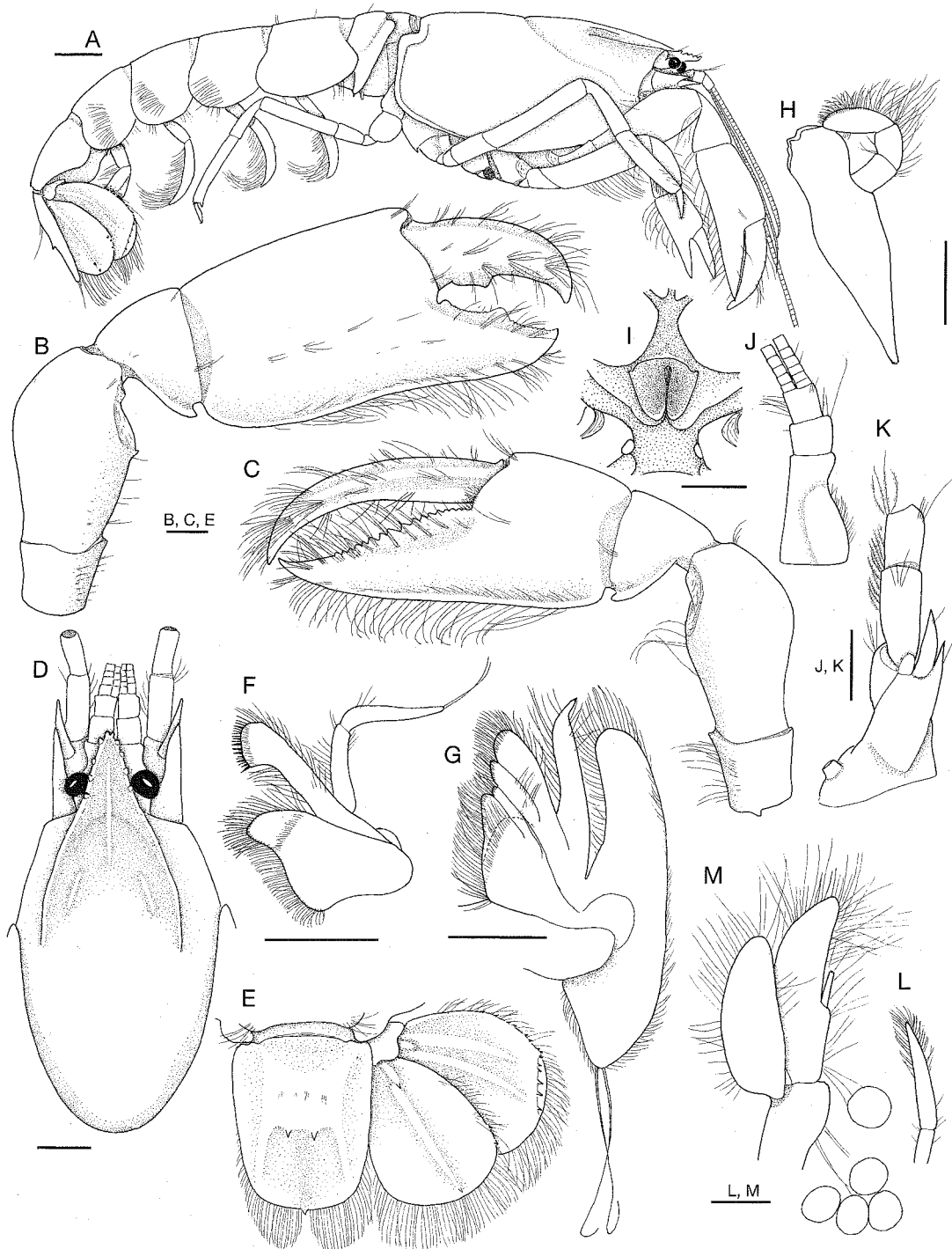


FIG. 1. — *Axis stirhynchus* Leach, 1815; **A**, young ♀ from Chausey, France (MNHN Th 1321), lateral view; **B**, **C**, **E-H**, **J-M**, ♀ from Pointe du Château, N of Tréguier, France (MNHN Th 1322); **D**, **I**, ♂ from Dinard, France (MNHN Th 151); **B**, **C**, right and left pereopod 1; **D**, anterior part of carapace; **E**, telson and uropods; **F**, **G**, maxillule and maxilla; **H**, mandible; **I**, thoracic sternite 4, ventral view; **J**, **K**, antennule and antenna; **L**, **M**, female pleopod 1-2. Scale bars: 2 mm.

1409). — West of Chausey Island, under rocks, A. Crosnier, B. Richer de Forges, P. Clark, R. Manning coll., 28.VIII.1992, 1 ♂ (NHML 1992.1344).

DISTRIBUTION. — Atlantic: southwest of Scotland (Allen 1967), Ireland (Selbie 1914; O'Ceidigh 1962), southwest of North Sea (d'Udekem d'Acoz 1996). English Channel, English coast (Norman 1868; Leach 1815; Norman & Scott 1906; Gordon 1957); English Channel, French coast (Martin 2001). Atlantic: Chausey Island; French coast of the Bay of Biscay (Delphy & Magne 1938); ?Atlantic coast of Morocco (Beaubrun 1979).

Mediterranean: south of Catalonia (Gibert i Olivé 1920), Banyuls (Thiriot 1976), Nice (Holthuis 1977), bay of Naples (Caroli 1921a), Adriatic (Dworschak 1992; Kurian 1956), Aegean sea (Drensky 1951).

A distribution map was presented by d'Udekem d'Acoz (1996).

DIAGNOSIS

Rostrum (Fig. 1D) with blunt apex, four to six small round teeth on lateral margin, latter continued posteriorly to unarmed lateral carina. Eye with cornea rounded, well pigmented. Gastric region slightly convex, cervical groove present to whole length; median carina terminating distally near tip of rostrum, posteriorly near anterior third of gastric region, two short submedian carinae. Abdominal pleuron 1 pointed ventrally in young specimens (Fig. 1A) rounded in large ones; pleuron 2 broadest, pleura 3-5 with lateral tufts of setae; thoracic sternite of P4 unarmed or with minute lateral spine (Fig. 1I). Telson (Fig. 1E) slightly longer than wide, pair of dorsal spines on posterior half, convex posterior border with median spine.

A2 acicle large (Fig. 1K) reaching middle of fourth article of peduncle. Md (Fig. 1H) cutting edge smooth. Mx1 (Fig. 1F) endopod with distal article sickle-shaped; Mx2 (Fig. 1G) scaphognathite bearing pair of long posterior setae. Mxp1 (Fig. 2A) endopod slender, exopod with distal flagellum, epipod with large posterior lobe. Mxp2 (Fig. 2B) exopod with distal flagellum overreaching distal border of merus. Mxp3 (Fig. 2C) endopod carrying prominent ischial toothed crest (Fig. 2D), one or two lower distal spines on merus; exopod with distal flagellum.

P1 (Fig. 1B, C) slightly stouter in male than in female, unequal; larger cheliped with fixed finger

and dactylus both bearing triangular tooth near middle of cutting edge; smaller cheliped with fixed finger bearing round and acute teeth on cutting edge, dactylus unarmed. P2 (Fig. 2H) chelate, fixed finger and dactylus with pectinate cutting edge. P3 (Fig. 2I), P4 (Fig. 2J) simple, latter with small spiniform setae on lateral surface of propodus and dactylus. P5 (Fig. 2K) subchelate.

Male Plp1 (Fig. 2E) small, unsegmented; male Plp2 (Fig. 2F) with *appendix interna* and *appendix masculina*. Female Plp1 (Fig. 1L) two-segmented; female Plp2 (Fig. 1M) with *appendix interna*. Male and female Plp3-5 (Fig. 2G) with *appendix interna*.

Uropod (Fig. 1E) endopod and exopod about as long as telson with spinules on lateral external border, an unobvious suture near posterior border of exopod.

Colour

General colour: pale reddish-brown (Bell 1846). Dull pink (d'Udekem d'Acoz pers. comm.); a colour photograph is presented in d'Udekem d'Acoz (1999: cover).

Size

Largest specimens in material examined: cl. 20.5-22.5 mm, tl. 63.5-70 mm. Largest size reported: tl. 72 mm (Selbie 1914; Moyses & Smaldon 1990).

ECOLOGY AND BIOLOGY

This species is known as difficult of capture as it retreats to its burrows when disturbed (d'Udekem d'Acoz 1995). It occurs intertidally from *Fucus serratus* zone to about 34 m depth where it burrows in coarse muddy sand with the entrance often hidden under a large rock (d'Udekem d'Acoz 1995, 1999). It is rare in the Atlantic, uncommon in the British Isles (Moyes & Smaldon 1990), very rare in the Mediterranean. It is found in Plymouth under stone in mud where its larvae occur in the plankton in summer and early autumn (Gordon 1957). The species spawns at Roscoff, France, in July and August (Schlegel 1912). Larvae are rare in the

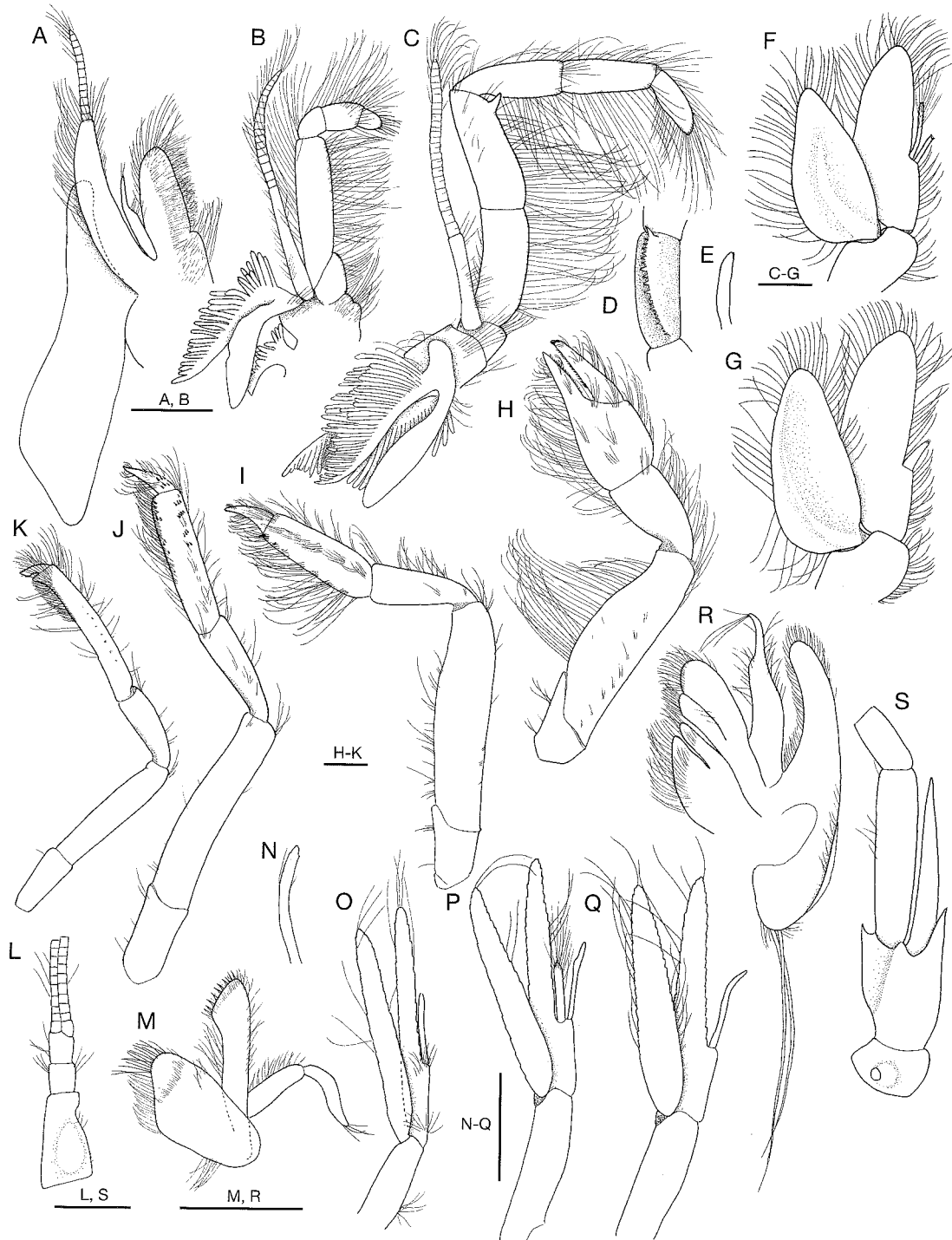


FIG. 2. — A-K, *Axius stirhynchus* Leach, 1815, from Pointe du Château, N of Tréguier, France (MNHN Th 1322); A-D, H-K, ♀; E-G, ♂; A, B, maxilliped 1 and 2; C, D, maxilliped 3 and mesial view of ischium; E-G, male pleopod 1-3; H-K, pereopod 2-5; L-S, *Calocarides coronatus* (Trybom, 1904), from Bohuslan, Sweden (SMNH 5221); L, M, P-S, ♂; N, O, ♀; L, antennule; M, maxillule; N, O, female pleopod 1 and 2; P, Q, male pleopod 2 and 3; R, maxilla; S, antenna. Scale bars: 2 mm.

plankton of Roscoff but are more frequent in Banyuls, France, in summer (Thiriot 1976), and common in July-September, off the French coasts of the English Channel (Martin 2001).

The branchial morphology, gill area and gill ultrastructure were dealt with by Astall *et al.* (1997b); the diet by Pinn *et al.* (1998b); the gut morphology and gut microflora by Pinn *et al.* (1999a); mouth part setal fringes by Pinn *et al.* (1999b).

REMARKS

An amendment to *stirhynchus* of the original incorrect spelling *stiryinchus* was proposed to the ICZN by Holthuis (1962) and validated under the plenary powers (ICZN 1964).

The species has been quoted by several authors as having no suture on the uropod exopod. A suture actually exists, as revealed by Bouvier (1940) and Sakai & de Saint Laurent (1989) but is often inconspicuous and placed near the posterior border of the exopod.

An illustration of this species from Nice in Risso's manuscript notes, under the name *Callianassa bisulcata*, was discussed by Monod (1931) and Holthuis (1977). Both contended that Risso's figure (fig. f) could hardly represent any other species in the area than *Axius stirhynchus*. The telson, correctly depicted with a convex posterior border and a pair of dorsal spines, confirms this view.

Genus *Calocarides* Wollebæk, 1909

TYPE SPECIES. — *Euconaxius coronatus* Trybom, 1904, subsequent designation by Sakai & de Saint Laurent (1989).

DIAGNOSIS. — Rostrum slender, triangular, pointed at tip; margin carrying a row of teeth and continuous backward to lateral carina of gastric region. Anterolateral margin of carapace usually unarmed. Gastric region convex with one median and two submedian carinae; cervical groove present to whole length. Abdominal pleura rounded ventrally, lacking lateral tufts of setae. Telson subsquare or longer than wide, with slight dorsal carinae; posterior border convex bearing median spinule.

Eyestalk subglobose, pigmented or not; antennal acicle prominent, elongated. Mx2 scaphognathite bearing

pair of long posterior setae. P1 unequal, P2 chelate, P3-5 simple.

Exopod on Mxp1-3; single epipods on Mxp1-3 and P1-4; single rudimentary podobranch on Mxp3 and P1-3; paired arthrobranch on Mxp3 and P1-4.

Male Plp1 absent, female Plp1 uniramous; male Plp2 slender, biramous, with *appendix interna* and *appendix masculina*, female Plp2 with *appendix interna*.

Uropodal exopod with transverse suture.

Calocarides coronatus (Trybom, 1904)

(Figs 2; 3)

Euconaxius coronatus Trybom, 1904: 384, pl. 20 figs 1-10, 13, 14, pl. 21 figs 1-8.

Euconaxius crassipes Trybom, 1904: 390, pl. 20 figs 11, 12.

?*Axius* (*Neaxius*) *laevis* Bouvier, 1915: 182. — de Man 1925b: 13 (key).

Axiopsis (*Calocarides*) *coronatus* — de Man 1925b: 6, 67, 71 (key).

Axiopsis (*Calocarides*) *crassipes* — de Man 1925b: 6, 67, 71 (key).

Calocarides coronatus — Wollebæk 1909a: 3. — Bals 1925: 209; 1926: 26. — Grieg 1927: 43. — Poulsen 1941: 216, fig. 4. — Bouvier 1940: 97. — Christiansen 1955: 1; 1972: 40, fig. 45; 2000: 231. — *Elofsson 1959: 1, figs 1-20. — Brattegard 1966: 45, fig. 1, tabs 1, 2. — Allen 1967: 57 (key), 89 (fig.). — Sakai & de Saint Laurent 1989: 80, fig. 20. — Noël 1992: 79. — °Cartes *et al.* 1994: 137. — °García Raso 1996: 738. — Kensley 1996: 56. — °Brattegard & Christiansen 1997: 220. — d'Udekem d'Acoz 1999: 153. — *González-Gordillo *et al.* 2001: 279. — °Türkay 2001: 289.

Calocarides crassipes — Wollebæk 1909a: 23, pls 1-7.

TYPE MATERIAL. — Whereabouts unknown.

MATERIAL EXAMINED. — Norway. Nordfjord, 556-578 m, T. Brattegard leg., 18.VI.1983, 2 ♂♂, 4 ♀♀ (1 ovig. cl. 13.5 mm, tl. 40 mm) (SMF 11835).

North Sea. Skagerrak, N Skagen, 320 m, F. S. Alkor coll., 22.VII.1987, 1 ovig. ♀ cl. 17 mm, tl. 49 mm (SMF 19774); S Arendal, 441-448 m, F. S. *Valdivia*, 25.II.1987, 1 damaged spec. (SMF 25687).

Sweden. W coast, Kosterfjord, Sv. Hydr. Kom. Expedition, 220-230 m, F. Trybom coll., 12.VIII.1901, 1 ♂ cl. 14 mm, tl. 43 mm (figured) (SMNH 1186); about 230 m, 6.VII.1902, 1 ♂, 1 ♀ (SMNH 1189). — Bohuslan, W of Hällö, 90 fms (162 m), B. Wingård coll., 1.1939, 1 ♂ cl. 15.5 mm, tl. 49 mm (figured), 1 ♀ cl. 14.5 mm, tl. 44.5 mm (figured), 1 ♂ broken cl. 15 mm, tl. 46.5 mm (SMNH 5221).

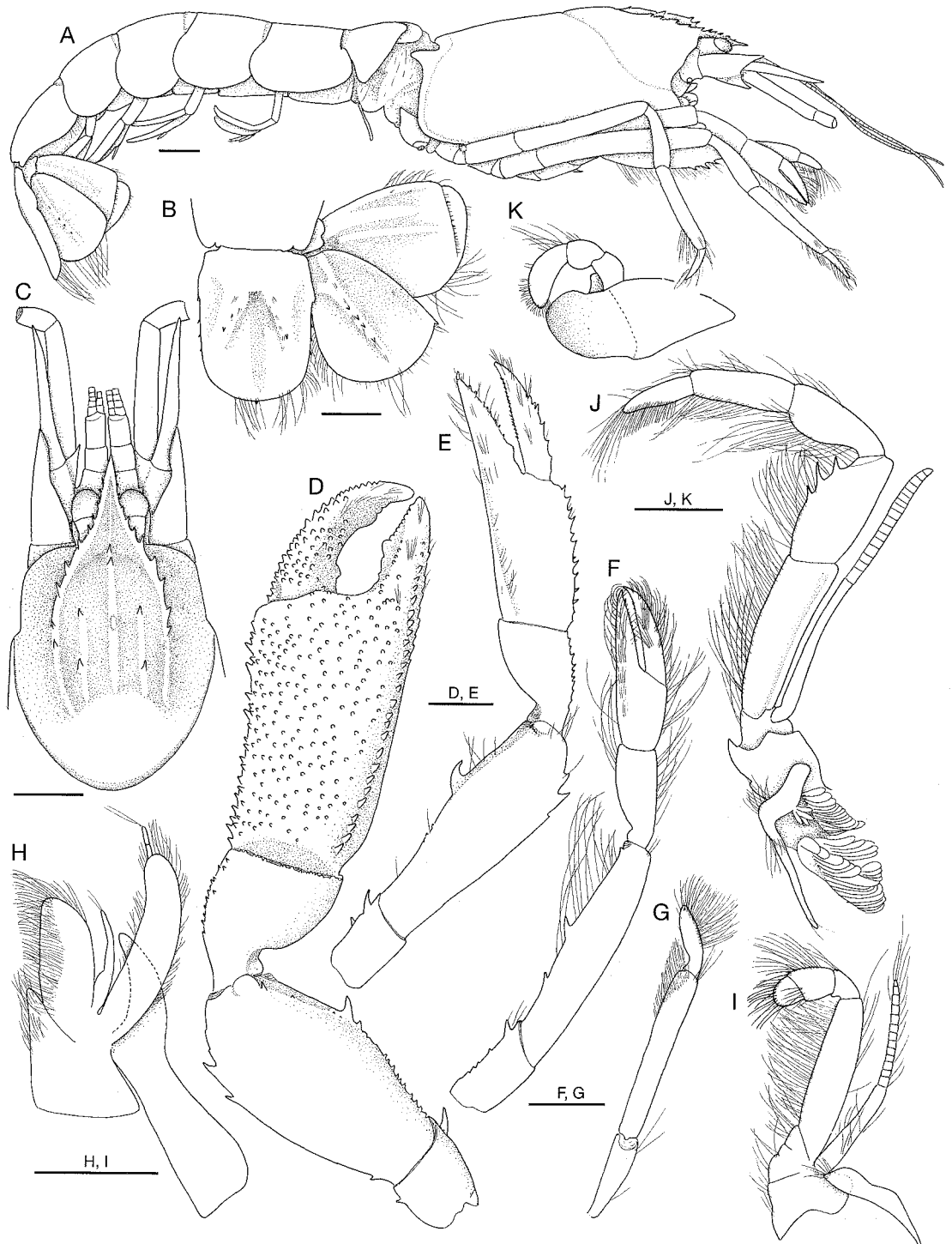


FIG. 3. — *Calocarides coronatus* (Trybom, 1904); **A-F**, ♂ from Kosterfjord, Sweden (SMNH 1186); **G-K**, ♂ from Bohuslan, Sweden (SMNH 5221); **A**, lateral view, pereopod 1 and 5 omitted; **B**, telson and uropods; **C**, anterior part of carapace; **D**, **E**, right and left pereopod 1; **F**, **G**, pereopod 2 and distal part of pereopod 5; **H**-**J**, maxilliped 1-3; **K**, mandible. Scale bars: 2 mm.

Mediterranean. Alboran Sea, BALGIM Exped., stn CP 127, 35°35.4'N, 3°48.5'W, 720 m, 18.VI.1984, 1 ♀ cl. 5 mm, tl. 14.5 mm (MNHN Th 1179). — Catalan Sea slope, 1 ♂ cl. 7 mm, tl. 18.5 mm.

DISTRIBUTION. — North Sea, Norway, Sweden, Denmark (Poulsen 1941; Sakai & de Saint Laurent 1989). Mediterranean: Alboran Sea (García Raso 1996), Catalan coast (Cartes *et al.* 1994).

DIAGNOSIS

Rostrum (Fig. 3C) triangular, slender, pointed at tip, reaching beyond eye; lateral rostral margin continuous with lateral carina, together with 11-13 spines, smaller distally. Eye nearly reaching middle of rostrum; eyestalk cylindrical, cornea distal, rounded, unpigmented. Gastric region weakly convex, cervical groove well defined; median carina with one or two spines near anterior border of gastric region, submedian carinae with two spines. Pleuron of abdominal somite 1 narrow, ventrally rounded; pleura of somites 2-5 ventrally rounded (Fig. 3A), all unarmed; thoracic sternite of P4 with minute spine. Telson (Fig. 3B) 1.3 times as long as proximal width, with denticles on lateral border, pair of slight dorsal carinae diverging distally, each with one or two spinules, posterior margin convex with median spinule.

A2 (Fig. 2S) acicle large, acute, reaching approximately distal margin of fourth article of peduncle. Md (Fig. 3K) cutting edge smooth. Mx1 (Fig. 2M) endopod with distal article sickle-shaped; Mx2 (Fig. 2R) scaphognathite bearing pair of long posterior setae. Mxp1 (Fig. 3H) endopod slender, exopod with two-articulate distal flagellum, epipod with truncate posterior lobe. Mxp2 (Fig. 3I) exopod with multiarticulate distal flagellum overreaching distal border of merus. Mxp3 (Fig. 3J) endopod with three to five lower distal spines on merus; exopod with multiarticulate distal flagellum.

P1 unequal in adult male, subequal in young male and female. Larger P1 of adult male (Fig. 3D) stout and spinous, with fingers about one-third as long as palm, dactylus well curved; smaller P1 of adult male (Fig. 3E.) as well as both P1 of young male and female, more slender, laterally compressed, with fingers about as long as palm, dactylus slightly curved. All P1 with lower distal spine on ischium, two or three upper subdistal

spines and one lower median spine on merus, upper spines and spinules on carpus, propodus and dactylus. P2 (Fig. 3F) chelate, with lower spine on ischium, one or two lower spines on merus. P3, P4 and P5 (Fig. 3G) simple.

Male Plp1 absent (with exception); male Plp2 (Fig. 2P) with *appendix interna* and *appendix masculina*; exopod and endopod slender. Female Plp1 (Fig. 2N) of one article, slender; female Plp2 (Fig. 2O) with *appendix interna*. Male and female Plp3-5 (Fig. 2Q) with *appendix interna*.

Uropod (Fig. 3B) endopod and exopod about as long as telson; endopod with spine on latero-posterior border and median carina bearing three or four spinules; a suture with spiniform setae near posterior border of exopod.

Colour

Body and pereopods pale dull brown, eyes brownish white, eggs dark brown (d'Udekem d'Acoz pers. comm.).

Size

Type material of tl. 21-52 mm (Trybom 1904); adult males in present material of cl. 14-15.5 mm, tl. 43-49 mm; ovigerous females of cl. 13.5-17 mm, tl. 40-49 mm. Largest size reported: ♂ tl. 57 mm (Wollebæk 1909a; Christiansen 1955), ♀ tl. 53 mm (Christiansen 1955). Specimens from the Mediterranean are smaller: cl. 5 mm and 7 mm, tl. 14.5 and 18.5 mm.

ECOLOGY AND BIOLOGY

The species lives in soft muddy bottom and deep waters, 162-578 m (present material), 440-460 m in Denmark (Poulsen 1941) or 400-424 m in Norway (Wollebæk 1909a).

An extensive study in Norwegian waters by Brattegard (1966) reveals that this species is a mud eater, living in a depth range of 225-670 m. It is found together with *Calocaris macandreae*; the latter dominates in shallow waters while *C. coronatus* does at depths of 500 m and below. *C. coronatus* has been collected in sediments of Md < 7.6 µm, at temperatures of about 6-7.5°C and salinity of 35‰. Ovigerous females are recorded from March to November, all from depths

exceeding 340 m. Egg-laying occurs during February-March; the eggs are carried for about 10 months and hatch in November-December.

The larvae attributed to *Calocarides coronatus* and described by Elofsson (1959) were obtained from the Korstfjord (western Norway) over a muddy bottom, at 600 m depth. The development presumably includes at least three larval stages.

REMARKS

This deep water species is likely to be distributed from the north of Europe to the Mediterranean although it has not been reported from the British Isles or the European Atlantic coast so far. The specimens studied by Cartes *et al.* (1994) and García Raso (1996), though smaller, agree well with those from the north. Cartes (pers. comm.) also stated that *C. coronatus* was regularly found in Mediterranean waters, always at bathyal depths.

In most of the material examined, Plp1 are absent in males as always previously reported. One exception nevertheless exists and small Plp1 are present in one specimen figured here (Fig. 3A).

There is uncertainty about the synonymy of *Axius* (*Neaxius*) *laevis* Bouvier, 1915 with *Calocarides coronatus* as proposed by Sakai & de Saint Laurent (1989: 82). The holotype and only known specimen of the former species is a young female in poor condition, of 20 mm in total length, with a broken rostrum and collected off the Moroccan coast (25°29'N, 18°18'W). It was partly figured (Sakai & de Saint Laurent 1989: fig. 21) but unfortunately is now missing in the MNHN collection. Sakai & de Saint Laurent (1989) stated that "Bouvier's species *laevis* is to be included in *coronatus* because the dorsal region of the carapace and the abdomen are identical with those of *coronatus*". Yet the original description (Bouvier 1915: 182, 183) and Sakai & de Saint Laurent's figure (1989: fig. 21A-D) show several differences: 1) in A2 peduncle of *Axius laevis*, the upper distal spine of the second article reaches the middle of the antennal acicle (in *C. coronatus*, the same upper distal spine reaches one-third of the antennal acicle); 2) in *A. laevis*, the A2 acicle is two-thirds as long as the fourth article, the latter terminating approximately at the level of the A1 peduncle

(Sakai & de Saint Laurent 1989: fig. 21B) (in *C. coronatus*, the A2 acicle is about as long or slightly longer than the fourth article, the latter far overreaching the A1 peduncle, Figs 2S; 3C); 3) in the original description or figure by Sakai & de Saint Laurent, there is no mention of submedian carinae and spines (these are present in *C. coronatus*, Fig. 3C); and 4) the telson is over 1.5 times as long as wide, with four or five spinules on the lateral border, the subdistal one largest in *A. laevis* (telson 1.3 times as long as wide in *C. coronatus*, with no spinule on the lateral border, Fig. 3B).

Also doubtful is the assignment to *Calocarides coronatus* ("by geographical reason", Sakai & de Saint Laurent 1989: 79) of materials previously identified as *Calocarides longispinis* (McArdle, 1901) by Stebbing (1910: 367), Barnard (1950: 503, fig. 93d-f), Kensley (1981: 30), and two males in the MNHN collection. The three former materials were from South Africa while the MNHN specimens (MNHN Th 1044 and 1045) were collected off Namibia (26°26'S, 14°25'E and 20°1'S, 11°38'E respectively). The latter are very similar to specimens of *C. coronatus* but differ in: 1) their larger size, tl. 72.5 mm and 73 mm; 2) both P1 are laterally compressed, with upper and lower longitudinal rows of spines and spinules on merus, numerous tubercles on lateral surface; 3) larger P1 with fingers over two-thirds as long as the palm, dactylus nearly straight; and 4) large acute spines along the carinae of the telson and uropodal endopod.

Genus *Coralaxius* Kensley & Gore, 1982

TYPE SPECIES. — *Axius nodulosus* Meinert, 1877 (= *Coralaxius abelei* Kensley & Gore, 1982), subsequent designation by Kensley (1994).

Coralaxius nodulosus (Meinert, 1877)

Axius nodulosus Meinert, 1877: 212. — Stephensen 1910: 276, figs 1-5. — de Man 1925b: 18. — Bals 1926: 26. — Poulsen 1941: 208, fig. 2.

Coralaxius abelei Kensley & Gore, 1982: 1278, figs 1-6.

"?*Axiopsis nodulosus*" – Borradaile 1903: 539.

Coralaxius nodulosus – Sakai & de Saint Laurent 1989: 11. — Kensley 1994: 814, 822. — d’Udekem d’Acoz 1999: 153.

REMARKS

This species was first described as *Axius nodulosus* by Meinert in 1877 from a single specimen of 9 mm in total length from the North Sea off Nymindagab, and has never been discovered again. Stephensen (1910: figs 1-4) depicted both P1, left P2, P4 of the type as well as the telson and uropods. Poulsen (1941: 209, fig. 2) reviewed and figured it in detail. Poulsen (1941: 213) believed that the specimen was a postlarva or a grown-up thalassinidean, but differed in one or more characters from all known postlarvae and young thalassinideans in the area. Likewise, no similarities are found between this specimen and the larvae referred to *Calocarides coronatus* (second stage, tl. 10 mm including rostrum), studied later by Elofsson (1959).

Sakai & de Saint Laurent (1989) assigned the species to the genus *Coralaxius* Kensley & Gore, 1982. Meinert’s specimen resembles the type species of *Coralaxius*, *C. abelei* Kensley & Gore, 1982 (from Florida and the Caribbean) in: 1) the short rostrum; 2) the morphology of both major and minor P1; 3) the morphology of P2; 4) the biunguiculate P4; and 5) the telson and uropods (see Stephensen 1910: figs 1-5 and Poulsen 1941: fig. 2 as compared with Kensley & Gore 1982: figs 1-6 and Kensley 1994: figs 5, 6).

Kensley (1994: 814), describing more materials of *Coralaxius*, considered further that Meinert’s specimen was “unquestionably a mature male of *Coralaxius abelei*” (the species name *nodulosus* has therefore priority over *abelei*), that it “came from the Caribbean and the collection data became confused at some point”. Kensley’s argument seems convincing, and as *C. nodulosus* has not been collected again in the North Sea or European waters for over a century, it is likely to be an alien to the European fauna.

Genus *Levantocaris* Galil & Clark, 1993

TYPE SPECIES. — *Levantocaris hornungae* Galil & Clark, 1993, by monotypy.

DIAGNOSIS. — Rostral triangular, margin with denticles, short median carina present, lateral carina unarmed. Eye with reduced pigmentation, anteriorly flattened, eyestalk rounded. Antenal acicle as a well developed spike. Mx2 scaphognathite with long posterior seta. Mxp3 with toothed crest on mesial surface of ischium. First pereopod chelate, subequal, P2 chelate, P3-5 simple.

Exopod on Mxp1-3; single epipod on Mxp1-3 and P1-4; single podobranch on Mxp1-3 and P1-3; paired arthrobranch on Mxp3 and P1-4; single pleurobranch on P2-4.

Male Plp1 slightly dilated subdistally, male Plp2 with *appendix interna* and *appendix masculina*. Telson longer than wide, bearing dorsal spines; posterior border convex with median spine. Uropodal exopod with transverse suture.

Levantocaris hornungae Galil & Clark, 1993

(Fig. 4)

Levantocaris hornungae Galil & Clark, 1993: 48, figs 1-4. — d’Udekem d’Acoz 1999: 154. — °Turkey 2001: 289.

Axiella or Axiidae n. sp. — Noël 1992: 80, *nomen nudum*.

TYPE MATERIAL. — Holotype: ♂, 50 km NW of Haifa, Israel (NHML 1992: 608).

MATERIAL EXAMINED. — Israel. 50 km NW of Haifa, 33°00’N, 34°35’E, 1400 m, B. Galil coll., 17.XII.1991, 1 ♂, holotype, cl. 11 mm, tl. 25.3 mm including rostrum (figured) (NHML 1992: 608).

DISTRIBUTION. — Mediterranean: Israel (Galil & Clark 1993), Catalan coast (de Saint Laurent pers. comm.), in deep waters: 1400 m (Galil & Clark 1993).

DIAGNOSIS (partly after Galil & Clark 1993)

Rostrum (Fig. 4B) elongate, triangular, dorsal surface concave, lateral margin with two or three denticles, continuous posteriorly to unarmed lateral carina. Eyestalk less than half rostrum length, cornea unpigmented. Gastric region slightly convex, carrying short, unarmed median carina, cervical groove well defined. Abdominal somites (Fig. 4A) unarmed, pleura ventrally rounded, pleuron 2 largest. Telson (Fig. 4G) over 1.6 times as long as proximal width, proximal half with two pairs of dorsal spines; three to five spinules on lateral border, posterior border convex with median spine.

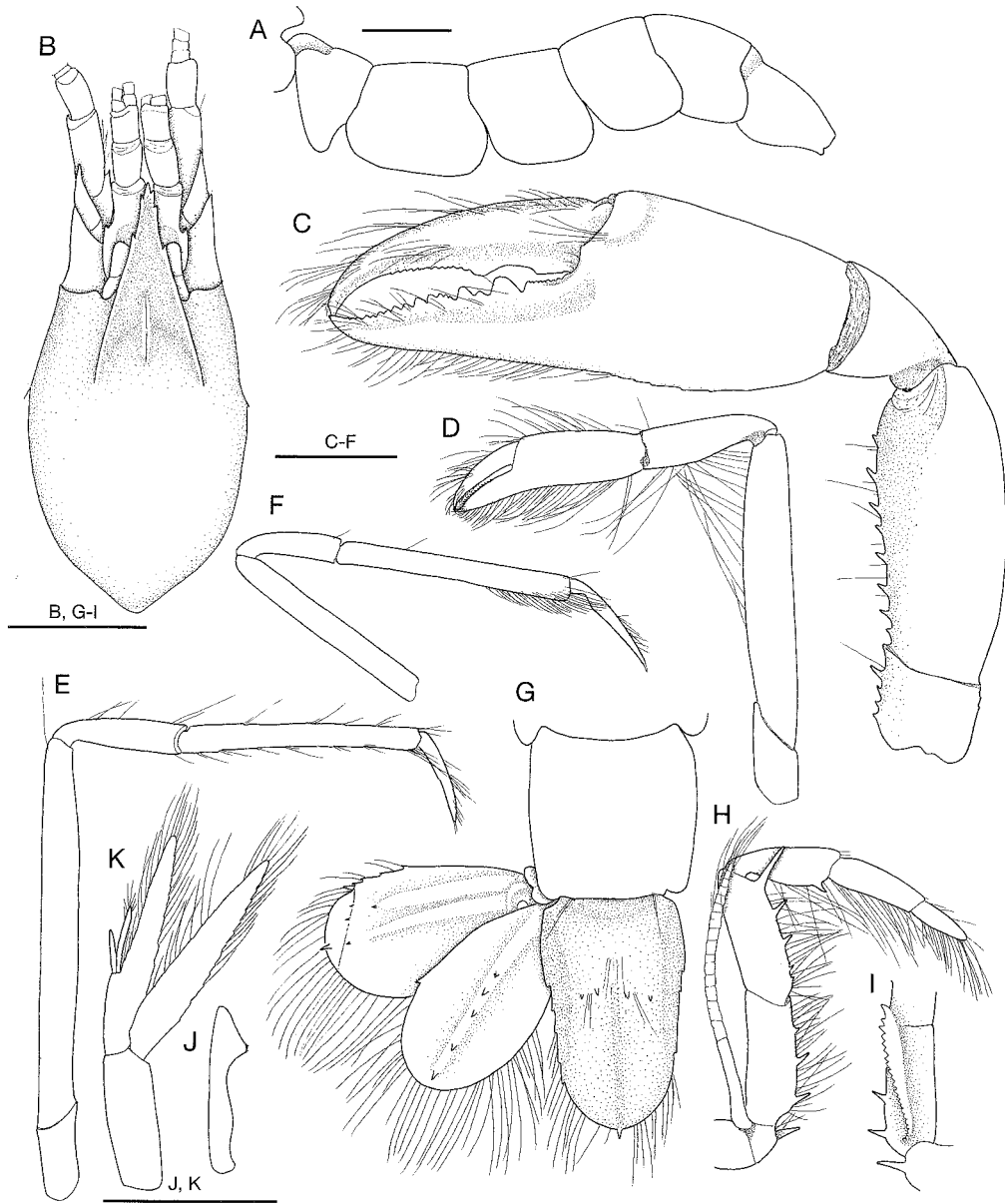


FIG. 4. — *Levantocaris hornungae* Galil & Clark, 1993, holotype, ♂ from Haifa, Israel (NHML 1992: 608); **A**, abdomen, lateral view; **B**, anterior part of carapace; **C**, **D**, pereopod 1 and 2; **E**, **F**, pereopod 3 and distal part of pereopod 5; **G**, telson and uropods; **H**, **I**, maxilliped 3 and mesial view of ischium; **J**, **K**, pleopod 1 and 2. Scale bars: 2 mm.

A2 acicle (Fig. 4B) reaching approximately middle of fourth article of A2 peduncle. Md, Mx1, Mx2 (see Galil & Clark 1993: fig. 2c, d, e respectively) as figured: Md cutting edge smooth, Mx1 with sickle-shaped endopod, Mx2 scaphognathite

with long posterior seta. Mxp1 (Galil & Clark 1993: fig. 3a, b) with large epipod; exopod bearing distal segmented process tipped with setae. Mxp2 and Mxp3 (Galil & Clark 1993: fig. 3c, d; see also Fig. 4H, I): Mxp2 with long and slender

exopod, Mxp3 with prominent toothed crest on mesial surface of ischium, three spines on lower border of ischium and merus, distal largest.

P1 (Fig. 4C) chelate, subequal. Ischium and merus with spines on lower border, propod with fixed finger nearly as long as palm, cutting edge bearing large and small round teeth; dactylus curved distally with denticles on distal half of cutting edge. P2 (Fig. 4D) chelate, unarmed, fixed finger and dactylus with pectinate cutting edge. P3-5 (Fig. 4E, F) simple, slender.

Branchial formula (after Galil & Clark 1993): single epipod on Mxp1-3 and P1-4; single podobranch on Mxp1-3 and P1-3; paired arthrobranch on Mxp3 and P1-4; single pleurobranch on P2-4.

Male Plp1 (Fig. 4J) slightly dilated subdistally bearing cluster of minute hooks on mesial border. Male Plp2 (Fig. 4K) with *appendix interna* and *appendix masculina*.

Uropod (Fig. 4G) about as long as telson, endopod with subdistal spine on lateral border and four or five dorsal spines; exopod with denticles and subdistal spine on lateral border, a suture near posterior border.

Colour

White (Galil & Clark 1993).

Size

Holotype of cl. 11 mm, tl. 25.3 mm (Galil & Clark 1993).

REMARKS

As the holotype is the only known specimen and in poor condition, the morphology of mouth appendages and the branchial formula are here given according to Galil & Clark (1993) (unchecked).

According to de Saint Laurent (pers. comm.), the material of "*Axiella* n. sp.", a *nomen nudum* mentioned by Noël (1992: 80), from the Catalan coast, belongs to this species. It is deposited in the Institut de Ciències del Mar de Barcelona (Dr Joan Cartes) but is not available for study at present. This material will be treated in a later work, with additional data on ecology and distribution.

Family CALOCARIDIDAE Ortmann, 1891

TYPE GENUS. — *Calocaris* Bell, 1846, by original designation.

Genus *Calastacus* Faxon, 1893

TYPE SPECIES. — *Calastacus stilirostris* Faxon, 1893, by monotypy.

DIAGNOSIS. — Rostrum slender, pointed at tip, margin unarmed and continuous to gastric region. Anterolateral margin of carapace unarmed. Gastric region convex, fine median dorsal carina present, cervical groove well defined dorsally. Telson longer than wide, lacking dorsal carinae; posterior border rounded, median spine absent.

Eyestalk short, cornea flattened. Antennal acicle prominent, elongated.

P1 slightly unequal, P3 and P5 coxae with gonopore. Hermaphroditic.

Exopod on Mxp1-3; single epipod on Mxp2, Mxp3 and P1-4; single podobranch (rudiment) on Mxp3 and P1-3; rudiment of arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-4. No pleurobranch.

Plp1 uniramous, two-segmented, distal segment spatulate, bearing rudiment of *appendix interna*. Plp2 biramous with small *appendix interna* and with *appendix masculina* presumably fused to endopod. Uropodal exopod with transverse suture.

Calastacus laevis de Saint Laurent, 1972

(Fig. 5)

Calastacus laevis de Saint Laurent, 1972: 348, figs 1-10. — Kensley 1989: 961; 1996: 161. — Sakai & de Saint Laurent 1989: 60. — Noël 1992: 79. — d'Udekem d'Acoz 1999: 152. — °Türkyay 2001: 289.

TYPE MATERIAL. — Holotype: Northern Spain, 43°43.5'N, 4°27'W, hermaphroditic (MNHN Th 152).

MATERIAL EXAMINED. — **France.** Capbreton, south of Bay of Biscay, 43°37,78'N, 1°43,91'W, NO Côtes de la Manche, CNRS-INSU, stn K, 639-645 m, mud, SEDICAN I Exp., 20.V.2000, 1 spec. damaged cl. 10 mm (Sorbe, personal collection).

Northern Spain. 43°43.5'N, 4°27'W, 950-1000 m, mud, *Thalassa* Exp., stn 377, 7.X.1970, 1 spec. cl. 14.5 mm, tl. 39 mm, holotype, right P1, P2 present (MNHN Th 152).

DISTRIBUTION AND ECOLOGY. — Bay of Biscay, SW France, northern Spain, in mud, 639-1000 m.

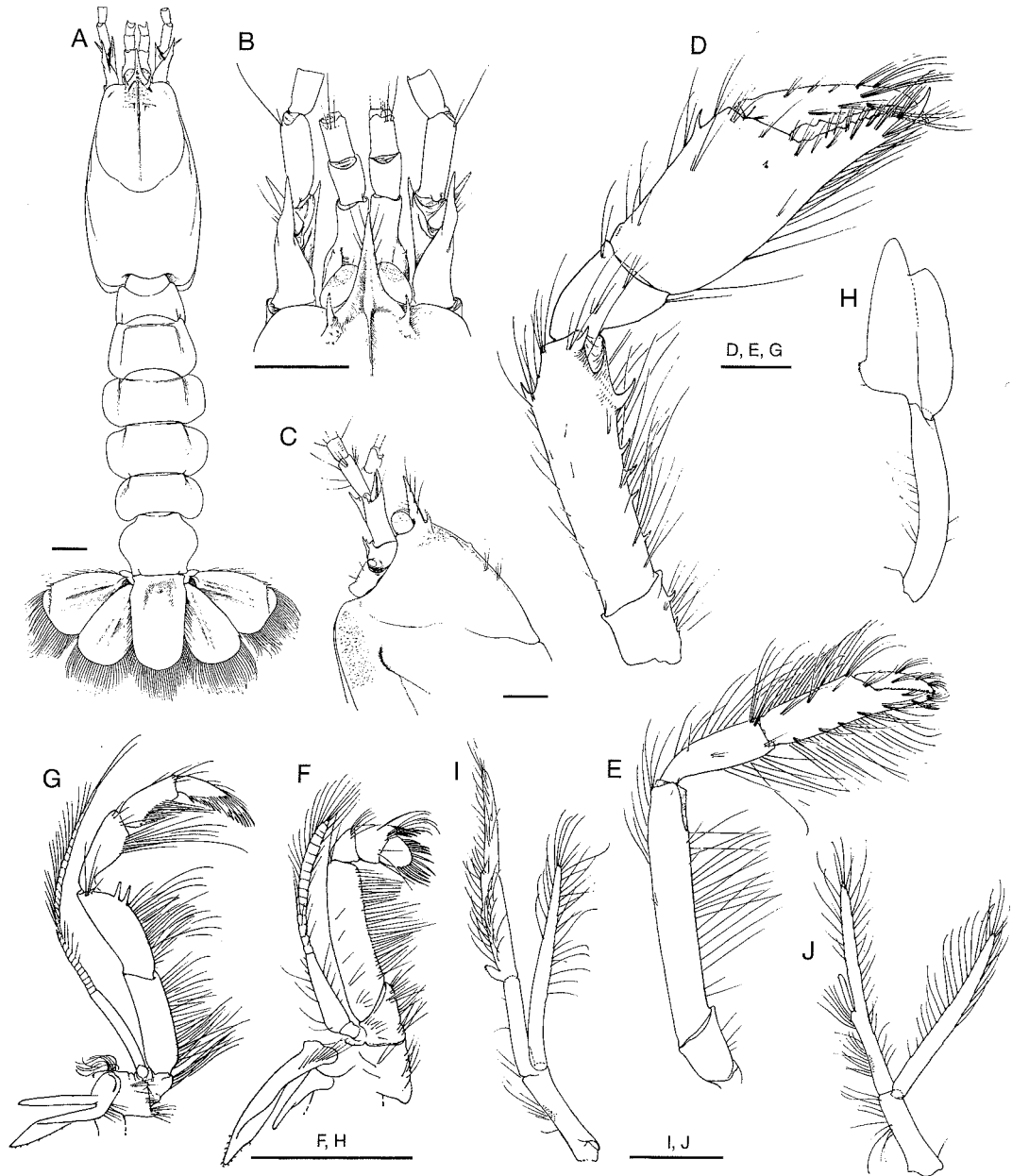


FIG. 5. — *Calastacus laevis* de Saint Laurent, 1972, holotype hermaphroditic from Northern Spain (MNHN Th 152) (figures from de Saint Laurent 1972); A, dorsal view; B, C, anterior part of carapace, dorsal and lateral view; D, E, pereopod 1 and 2; F, G, maxilliped 2 and 3; H-J, pleopod 1-3. Scale bars: 2 mm.

DIAGNOSIS (from de Saint Laurent 1972)
 Carapace (Fig. 5C) laterally compressed, dorsally rounded; cervical groove weakly defined dorsally, very faint on sides. Rostrum (Fig. 5B) slender,

lateral margin unarmed, continuous posteriorly to short lateral carina bearing large spine at base. Fine dorsal carina from base of rostrum to cervical groove with faint tubercle near anterior third.

Abdominal somites (Fig. 5A) unarmed, pleura rounded ventrally, third somite largest; thoracic sternite of P4 with minute spine. Telson (Fig. 5A) about 1.5 times as long as wide, unarmed, posterior border rounded.

Eye hardly mobile (Fig. 5B) nearly fused to carapace, cornea slightly flattened anteriorly, unpigmented. A2 acicle slender, reaching approximately middle of fourth article of A2 peduncle. Mxp2 (Fig. 5F) as figured. Mxp3 (Fig. 5G) with two lower distal spines on merus.

Right P1 (Fig. 5D) long and stout. Merus with five lower spines, larger distally, and upper subdistal spine. Carpus unarmed. Propodus with upper subdistal spine; external surface of palm with spinule behind articulation with dactylus. Fixed finger and dactylus about as long as palm, strongly curved at tip. P2 (Fig. 5E) much smaller than P1, unarmed. Gonopores wide open on coxae of P3 and P5.

Branchial formula (from de Saint Laurent 1972): single epipod on Mxp2, Mxp3 and P1-4; single podobranch (rudiment) on Mxp3 and P1-3; rudiment of arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-4.

Plp1 (Fig. 5H) of two articles, distal dilated with bunch of minute hooks on mesioproximal border representing vestigial *appendix interna*. Plp2 (Fig. 5I) endopod of two articles with short *appendix interna* articulated at base of second article, latter more densely setose proximally than on distal half. Plp3-5 (Fig. 5J) *appendix interna* articulating near midlength of endopod.

Uropods (Fig. 5A) about as long as telson, lateral border of endopod and exopod with one and two distal spinules respectively; a suture near posterior border of exopod.

Colour

Unknown.

Size

Holotype of cl. 14.5 mm, tl. 39 mm (de Saint Laurent 1972); other material: cl. 10 mm.

REMARKS

De Saint Laurent (1972) reported that the holotype bears numerous setae and remnants of egg

envelopes on the pleopods indicating that it was ovigerous shortly before capture.

Genus *Calocaris* Bell, 1846

TYPE SPECIES. — *Calocaris macandreae* Bell, 1846, by original designation.

DIAGNOSIS. — Rostrum triangular, margin bearing spines. Gastric region convex, median dorsal carina present, extending to posterior border of carapace; cervical groove well defined to whole length. Abdominal pleura rounded ventrally, lateral setae absent. Telson longer than wide, lateral border with spinules, pair of dorsal carinae present, posterior border rounded, with or without median spine.

Eyestalk hardly mobile, cornea flattened anteriorly, unpigmented. Antennal acicle reduced. Mx2 scaphognathite with single posterior seta.

P1 equal; propodus with dorsal distal spine, fixed finger and dactylus slender, compressed, longer than palm. P2 chelate, much smaller than P1, P3-5 simple. Coxa of P3 and P5 with gonopore. Hermaphroditic.

Exopod on Mxp1-3; single epipod on Mxp1-3 and P1-4; reduced podobranch on Mxp2, Mxp3 and P1-3; single arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-4.

Plp1 uniramous, of two articles, distal expanded; Plp2 biramous, with *appendix interna* and with *appendix masculina* presumably fused to endopod; Plp3-5 with *appendix interna*. Uropodal exopod with transverse suture.

Calocaris macandreae Bell, 1846

(Figs 6; 7)

Calocaris Macandreae Bell, 1846: 233, 1 fig. — White 1850: 33. — *Sars 1884: 180, pls 2, 6, 7. — Carus 1885: 490. — Stebbing 1893: 190. — Adensamer 1898: 621. — *Lo Bianco 1903: 187. — Norman & Scott 1906: 12. — Hansen 1908: 41. — Stephensen 1910: 277. — Selbie 1914: 92, pl. 14, figs 5-7. — Bouvier 1917: 119, pl. 11 figs 5, 6. — de Man 1925a: 140, fig. 7. — Balss 1925: 209. — °Zariquiey y Cenarro 1935: 7.

Calocaris Macandrae – Bull 1933: 48, figs 1-18.

Calocaris Macandrei – White 1857: 99, pl. 8, fig. 4.

Calocaris (Calocaris) Macandreae – Borradaile 1903: 539. — de Man 1925b: 116.

Calocaris Mc Andreea – Bouvier 1940: 96.

Calocaris macandreae – Kirk 1879: 401. — Sars 1884: 166, pl. 2. — Lovett 1885: 16. — Ortmann 1891: 50,

pl. 1 fig. 5. — Anderson 1897: 97. — Adensamer 1898: 621. — Appelhöf 1906: 132. — Lagerberg 1908: 51, pl. 1 fig. 17. — *Lo Bianco 1909: 603. — Wollebæk 1909a: 251, figs 1-6, pls 15-17; 1909b: 251. — Björck 1913: 1, figs 1-6, pl. 1. — Pesta 1918: 191, fig. 59. — Caroli 1921a: 241; 1921b: 264. — Runnström 1925: 14, pls 1, 2. — Balss 1926: 26. — Grieg 1927: 34. — Miranda y Rivera 1933: 21. — Gustafson 1934: 16. — Poulsen 1941: 214, fig. 3. — *Gurney 1942: 242, fig. 97. — Zariquiey Alvarez 1946: 104, fig. 132; 1952: 19; 1968: 225, fig. 88b. — Holthuis 1950: 108, fig. 38; 1958: 8, fig. 5; 1962: 246. — Christiansen 1955: 5; 1972: 40, fig. 46; 2000: 230, fig. 1, tabl. 1. — Soot-Ryen 1955: 1. — Gordon 1959: 191. — *Bourdillon-Casanova 1960: 101, figs 36, 37. — Buchanan 1963: 729, figs 1-15, tabl. 1. — ICZN 1964: 340. — Forest 1965: 347. — Picard 1965: 104. — Squires 1965: 10. — Allen 1967: 17, 57, 89 (fig.). — *Štević 1969: 128; 1990: 214. — Christiansen 1972: 40, fig. 46. — Frogli 1976: 76; *1995: 7. — Kattoulas & Koukouras 1974: 344. — *Thiriot 1976: 349. — Beaubrun 1979: 70, figs 45, 46. — Moncharmont 1979: 70. — García Raso 1983: 318; *1996: 738. — Riedl 1983: 482, pl. 177, 2 figs. — Nash *et al.* 1984: 425, figs 1-3, pls 1-3. — Atkinson 1986: 356, figs 1K, 2A. — Holthuis & Heerebout 1986: 62, fig. 82. — Moore 1986: 31. — Thessalou-Legaki 1986: 182. — Atkinson & Taylor 1988: 212, fig. 1h. — Manning & Frogli 1982: 323. — Sakai & de Saint Laurent 1989: 56. — Moyses & Smaldon 1990: 117, fig. 10.12. — Dworschak 1992: 215. — *Koukouras *et al.* 1992: 223. — Noël 1992: 79. — Kocaraş & Katagan 1993: 35. — *Pipitone & Tumbiolo 1993: 361. — Anderson *et al.* 1994: 515, figs 1-5. — Cartes *et al.* 1994: 136, tabs 2, 3. — *Diez *et al.* 1994: 47. — Galil & Goren 1994: 47. — Hayward *et al.* 1995: 432, fig. 8.51 (part). — Falciai & Minervini 1996: 143, 1 fig. — *Barnich 1996: 131, fig. 65. — Astall *et al.* 1997b: 675, pl. 1a, tabs 1-5. — *Brattegard & Christiansen 1997: 220. — Hughes & Atkinson 1997: 640. — Johns *et al.* 1997: 127, figs 1-4, tabl. 2. — Pinn *et al.* 1998a: 243, fig. 1A; 1998b: 211, figs 1B, 2B; 1999a: 103, figs 2B-D, 3H, 4A, 4B, 5F; 1999b: 1461, figs 1E, 2, 3, tabs 1-6. — Taylor *et al.* 1999: 163, figs 1, 2, tabs 1-4; 2000: 265, figs 1-3, tabs 1-6. — d'Udekem d'Acoz 1999: 153. — Widdicombe *et al.* 2000: 371, figs 1-8, tabs 1-3. — *González-Gordillo *et al.* 2001: 279. — *Türkay 2001: 289.

Non *Calocaris macandreae* – Alcock & Anderson 1894: 163. — Alcock 1901: 189. — Whiteaves 1901: 257 (= *Calocaris templemani* Squires, 1965), also Rathbun 1929: 25, fig. 33. — Moen & Svensen 1999: 233, 1 fig. (= *Upogebia*, probably *U. stellata* (Montagu, 1808)).

TYPE MATERIAL. — Holotype: Loch Fyne, Scotland, 80 fms (144 m), dried (NHML 48.20).

MATERIAL EXAMINED. — **Norway.** Trondheimsjorden, Vanvik. coll., S. Bock, 1.X.1945, 1 spec. (SMNH

5838). — Gullmarfjord, 150 m, 26.IX.1969, 7 spec. (4 ovig.) cl. 12.5-15 mm, tl. 38.5-41.5 mm (SMF 28970). — Northeast Atlantic, palaeartic region, RV *Sarsia*, anchor dredge, 1000 m, J. D. George coll., 17.VII.1973, 2 spec. (1 juv.) (NHML 1977.575). — Trondheims Fjord, SW of Rissen, Strømmen, 650 m, dredge, excursion Leiden Biologists, 28.VIII.1961, 1 spec. (RMNH D 17159). — Trondheims Fjord, off Stranden, 63°34'N, 9°48'E, 7-50 m, dredge, excursion Leiden Biologists, 28.VIII.1961, 1 spec. (RMNH D 17160). — Oslofjord, E of Bastö, SE of Harten, 125-150 m, 8.V.1962, leg. Ståleson, don. Mrs J. Indrehus, c. 10 spec. (RMNH D 17384). — Stjörn fjord near Trondheims Fjord, N of Flessa lighthouse, stn 9, 200 m, trawl, excursion Leiden Biologists, 21-26.VIII.1963, c. 100 spec. (9 ovig.) (RMNH D 19506). — Trondheimsfjord near Rissen, 550 m, trawl, excursion Leiden Biologists, 24.VIII.1963, stn 19, 9 spec. (3 ovig.) (RMNH D 19548). — Stjörn fjord near Trondheimsfjord near Frengsbugeten, 12-50 m, dredge, excursion Leiden Biologists, 20.VIII.1963, stn 8, 6 spec. (2 ovig.) (RMNH D 19870). — Tromsø Flatanger, off Kvaløy, *Gunnerus*, stn 8, 375-380 m, 31.VIII.1951, leg. E. Sivertsen, 3 spec. (RMNH D 21492). — Trondheimsfjord, off Rissen, 50-300 m, rocks and corals, excursion Leiden Biologists, stn 210, 27.VIII.1965, 24 spec. (RMNH D 21826). — Trondheimsfjord near Kivnaebnes, 50-200 m, rocks with corals, dredge, excursion Leiden Biologists, stn 123, 30.VIII.1965, 1 spec. (RMNH D 24375). — Stjörn fjord near Trondheimsfjord, S of Stjörna, 220 m, trawl, excursion Leiden Biologists, stn 108, 25.VIII.1965, 1 spec. (RMNH D 24378); 150-200 m, agassiz trawl, clay, excursion Leiden Biologists, stn 105, 24.VIII.1965, c. 100 spec. (1 ovig.) (RMNH D 24987). **North Sea.** Mid North Sea, 58°15.86'N, 0°41.64'E-58°16.10'N, 0°40.95'E, 146 m, F. S. *Valdivia*, 29.I.1987, 10 spec. (SMF 25682); 55°20.54'N, 0°4.69'W-55°20.57'N, 0°3.37'W, 101 m, F. S. *Valdivia*, 4.II.1987, 1 spec. (SMF 25683). — East Bergenbank, 296 m, F. S. *Valdivia*, 2.III.1987, 2 spec. (SMF 25685). — Skagerrak, S Larvik, 218-244 m, F. S. *Valdivia*, 26.II.1987, 3 spec. (SMF 25684); 164.3-179.3 m, F. S. *Gauss*, 5.VI.1986, 33 spec. (SMF 25686). — SW of Fladengrund-Rinne, 130.6 m, F. K. Senckenberg, 22.VII.1989, 3 spec. (SMF 20646). — Skagerrak, F. S. *Gauss*, 164.3-179.3 m, 5.VI.1986, 5 spec. (SMF 28337); F. S. *Poseidon*, 3 spec. (SMF 28338). — Farne Deep, 80-100 m, 16.VI.1971, leg. G. R. Heerebout, c. 36 spec. (18 ovig.) (RMNH D 27237). — 58°12.5'N, 0°0'E, 140 m, 15.VII.1912, *Wodan* Wn.97, donated by the Netherlands Institute of Sea Research, 1 spec. (RMNH D 29693). — E Scotland, 58°15.7'N, 1°30.6'W, 143 m, 3.X.1990, F. S. *Valdivia*, 1 spec. (SMF 28340). — Fladengrund, 56°12.7'N, 0°12'W, 133 m, 5.X.1990, F. S. *Valdivia*, 1 spec. (SMF 28341).

Sweden. c. 120 km N of Göteborg, Kristineberg marine Research station coll., IX.1976, U. Pettke leg., 19 spec. (SMF 28339). — Gullmar, Tofna, Bohuslän,

- Kristinebergs Zoologische Station coll., 1894, 3 spec. (RMNH D 15220). — Off Dalsvik near Lysekil, mouth of Gullmarfjord, 45-50 m, ringtrawl, excursion Leiden Biologists, 16.IX.1961, 20 spec. (RMNH D 17131). — E of Tova, Gullmarfjord near Lysekil, 50 m, mud, excursion Leiden Biologists, 15.IX.1961, 10 spec. (RMNH D 17140). — Gullmarfjord near Smörkullen, dredge, 50 m, excursion Leiden Biologists, 18.IX.1961, 1 spec. (RMNH D 17158). — Gullmarfjord off Lysekil, 35 m, ringtrawl, excursion Leiden Biologists, 11.IX.1963, stn 65, 6 spec. (RMNH D 19871). — Gullmarfjord, W of Store Bornö, NW of Uddevalla, 50 m, dredge, excursion Leiden Biologists, 10.IX.1963, stn 56b, 2 ovig. spec. (RMNH D 19872). — Gullmarfjord, SW of Gåsklävan lighthouse, 10-50 m, rocks and shell gravel, dredge, excursion Leiden Biologists, stn 136, 7.IX.1965, 2 spec. (1 ovig.) (RMNH D 24374). — Gullmarfjord, SW of Smörkullen, 40-60 m, mud, agassiz trawl, excursion Leiden Biologists, stn 162, 14.IX.1965, 4 spec. (1 ovig.) (RMNH D 24376). — Gullmarfjord, Finnsbobukten, 40-50 m, mud, agassiz trawl, excursion Leiden Biologists, stn 137, 8.IX.1965, 1 spec. (RMNH D 24377).
- Great Britain.** Scotland, Loch Fyne, 80 fms (144 m), holotype dried spec. cl. 14.5 mm, tl. 41 mm (NHML 48.20); Sound of Lorn, 50-100 fms (90-180 m), 3.X.1988, 2 spec. (NHML 1971.14); Loch Duich, 60 fms (108 m), J. Murray coll., 31.X.1887, 1 spec. (NHML 94.9.18.40); Cumbrey Deep, Millport Marine Station coll., 17.X.1949, 1 spec. (NHML 1950.9.29.11); Area YY 10C, 135 m, Marine Laboratory Aberdeen coll., 5.V.1951, 6 spec. (NHML 1951.9.5.3-7); Loch Carron, 50-60 fms (90-108 m), J. Murray coll., 7 spec. (NHML 1892.1.30.47), 60 fms (108 m), 2 spec. (NHML 94.9.18.39); Loch Fyne, 105 fms (189 m), J. Murray coll., 3 spec. (NHML 1892.1.30.1-3); Kilchattan Bay, Clyde area, 17.V.1948, 5 spec.; 6.X.1948, 1 spec. (NHML 1949.1.18.39-42). — Isle of Man, 11.5 miles (18.4 km) off Bradda, 65 fms (117 m), mud, J. Gordon coll., VII.1960, 3 spec. (NHML 1960.VII.25.151-152). — Wales, Loch Aber, 80 fms (144 m), J. Murray coll., 4 spec. (NHML 94.10.8.75-78). — Ireland, National Museum of Ireland coll., 3 spec. (1 ovig.) (NHML 1921.5.27.101-103).
- France.** Bay of Biscay, *Thalassa*, 1970, stn W 397, 43°55'8 N, 5°9'W, 770-800 m, 2 spec. cl. 9.5 mm and 10 mm (MNHN Th 164); stn?, 1 spec. cl. 10.5 mm (MNHN Th 166), 4 spec. cl. 9-10 mm (MNHN Th 163). — *Thalassa*, stn 486, 43°40,1'N, 8°50.4'W, 490 m, 8.VIII.1967, 2 spec. cl. 10 mm and 11 mm (MNHN Th 153); stn 460, 43°35.6'N, 8°57.2'W, 290 m, 7.VIII.1967, 2 spec. cl. 10.5 mm (MNHN Th 154). — Banyuls, RV *Lacaze-Duthiers*, beam trawl, 500 m, P. Noël coll., 18.V.1976, 55 spec. cl. 5-12.5 mm (MNHN Th 1404); Sollaud coll., ES 30, 3 spec. (MNHN Th 1360); J. M. Amouroux coll., 2 spec. cl. 10 mm and 11 mm (MNHN Th 1411); ECO-MARGE, A14, 653 m, 23.I.1984, 38 spec. cl. 8.5-11.5 mm; 4 spec. (figured) cl. 10.5-12 mm, tl. 31.5-33 mm (MNHN Th 1320); 620-711 m, 2.VIII.1985, 28 spec. cl. 6.5-12 mm, 1 spec. (figured) cl. 10 mm, tl. 29 mm (MNHN Th 1406); 815-900 m, 2.VIII.1985, 10 spec. cl. 6-12 mm (MNHN Th 1405). — Gulf of Lion (off Banyuls), 42°41'N, 3°45'E, dredge, 410-420 m, P. Noël coll., 8 spec. cl. 6.5-10.5 mm (MNHN Th 1412). — Marseille, *Travailleur*, 555 m, mud, 4.VII.1881, 1 spec. (poor condition) cl. 7.5 mm (MNHN Th 156); 647 m, 1 spec. (poor condition) cl. 6 mm (MNHN Th 159). — Canyon of Cassidaigne (E of Marseille), dredge, 300 m, H. Zibrowius coll., 21.VI.1969, 3 spec. cl. 8-10 mm (MNHN Th 172); 320-360 m, H. Zibrowius coll., 23.XI.1978, 1 spec. cl. 11 mm (MNHN Th 634). — Bay of Roquebrune (near Monaco), 300-420 m, mud, trawl, 25.X.1964, leg E. Gilat, 1 spec. (RMNH D 19873).
- Atlantic.** *Thalassa*, stn 440, 48°41.4'N, 10°21.5'W, soft mud, 860 m, 26.X.1973, 2 spec. cl. 4 mm and 7 mm (MNHN Th 344); leg. Frank, 1879, 1 spec. (RMNH D 1428).
- Spain.** Rosas, from fishermen, J. Gordon coll., 9.VIII.1954, 1 spec. (NHML 1955.2.28.91). — Catalan coast, R. Zariquiey pres., 2 spec. (NHML 1954.12.30.94-95); Catalan coast, leg. et don R. Zariquiey, 1 spec. (RMNH D 4983); trawl, leg. et don. R. Zariquiey y Cenarro, 1934, 3 spec. (RMNH D 6204), 1935, 3 spec. (RMNH D 6205).
- Mediterranean.** A. Longhrin coll., 1 spec. (NHML 70.35).
- Italy.** Gulf of Taranto, stn 288, 95 m, clay, 23.VIII.1966, leg. A. Vatova, 1 spec. (RMNH D 24379).
- Greece.** Aegean Sea, Cape Athos, SE of Moni Megistis Lavras, 750-800 m, 10.VIII.1975, 1 spec. (A.U.TH P 4527).
- Morocco.** Off Cape Baba, 300 fms (540 m), R. N. Rofendon coll., 1 spec. (NHML 1906.12.3-4).
- Senegal.** Dakar, 675 m, 13.VIII.1958, 5 ovig. spec. cl. 10-12 mm, tl. 31-35 mm, 4 non ovig. (MNHN Th 226). — 16°48'N, 16°45'W, 600-700 m, P. Doutre coll., 2.X.1958, 4 ovig. spec. cl. 11 mm and 11.5 mm, 2 non ovig. (MNHN Th 225).

DISTRIBUTION. — Eastern Atlantic (from the North Sea to the Gulf of Guinea in the south): North Sea, S of Iceland (Hansen 1908), Norway (Soot-Ryen 1955), Sweden, Scotland, Ireland, Wales, east coast of Great Britain (Moore 1986); west coast of France, southern Portugal and southwestern Spain (García Raso 1996), Gulf of Guinea (Beaubrun 1979).

Mediterranean: Alboran Sea (García Raso 1983, 1996), eastern Mediterranean (Bouvier 1917; Montcharmont 1979), Adriatic (Pesta 1918; Štević 1990; Dworschak 1992); Aegean Sea (Kattoulas & Koukouras 1974); Sea of Marmara (Kocataş & Katagan 1993); Sicilian Channel (Pipitone & Tombiolo 1993); Israel (Galil & Goren 1994).

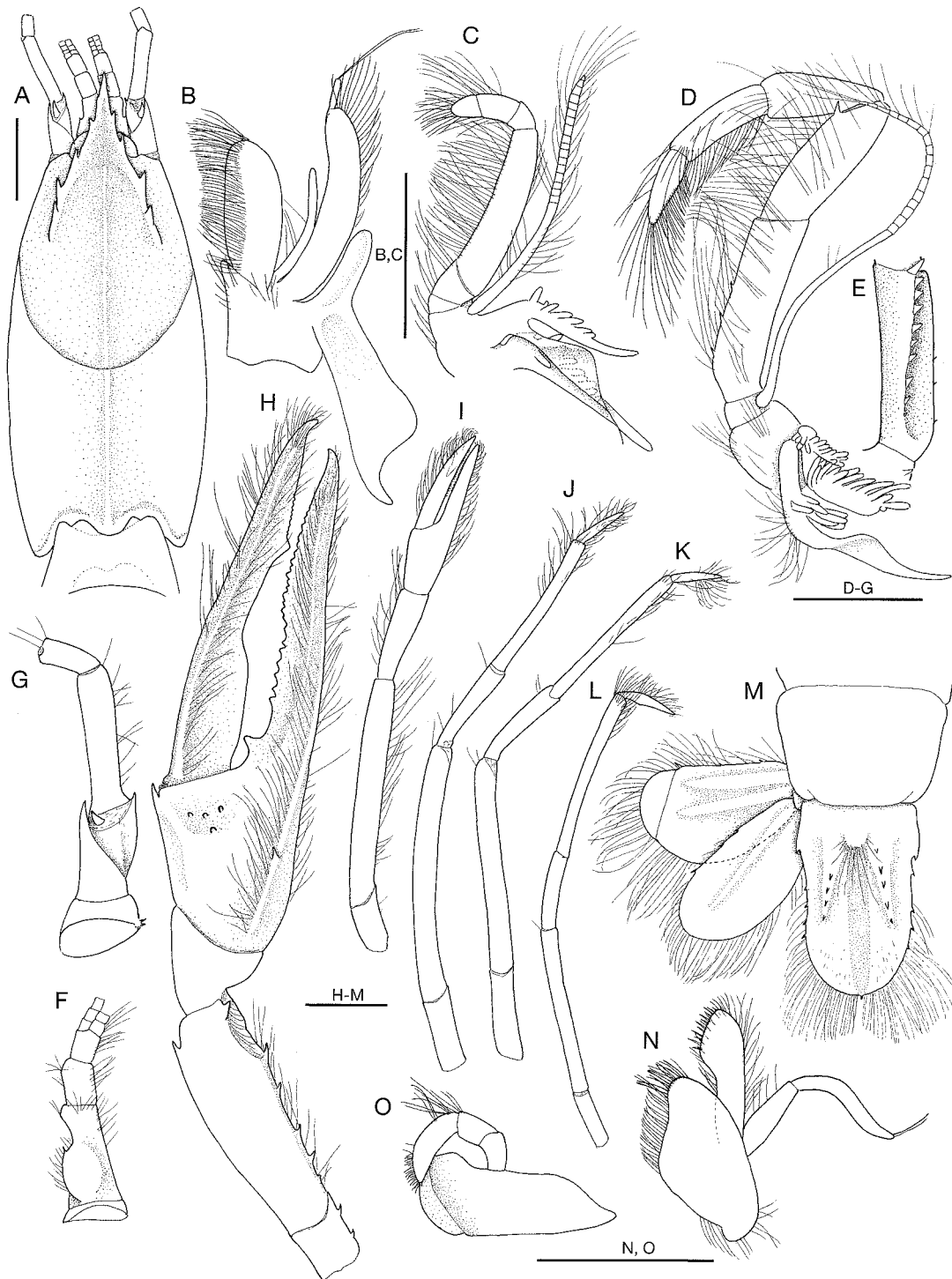


FIG. 6. — *Calocaris macandreae* Bell, 1846, hermaphroditic, from Banyuls, France; **A, H-L**, MNHN Th 1406; **B-G, M-O**, MNHN Th 1320; **A**, carapace; **B, C**, maxilliped 1 and 2; **D, E**, maxilliped 3 and mesial view of ischium; **F, G**, antennule and antenna; **H-L**, pereopod 1-5 respectively; **M**, telson and uropods; **N**, maxillule; **O**, mandible. Scale bars: 2 mm.

DIAGNOSIS

Rostrum (Fig. 6A) triangular with pointed tip; lateral margin continued posteriorly to lateral carina bearing together four to six spines. Gastric region slightly convex, cervical groove well defined, fine median carina terminating anteriorly near base of rostrum, extending posteriorly to whole length of carapace. Abdominal somites unarmed (Fig. 7A), pleura rounded ventrally, thoracic sternite of P4 unarmed. Telson (Fig. 6M) approximately 1.5 times as long as wide, dorsal surface with slight median longitudinal groove and pair of slight dorsal carinae pointing posteriorly and bearing spinules; lateral border also with spinules and median spinule on rounded posterior border.

Eyestalk (Fig. 6A) not differentiated, hardly mobile, cornea flattened anteriorly, unpigmented. A2 acicle (Fig. 6G) small. Md (Fig. 6O) cutting edge smooth. Mx1 (Fig. 6N) endopod with distal article sickle-shaped; Mx2 (Fig. 7B) scaphognathite bearing single long posterior seta. Mxp1 (Fig. 6B) endopod slender, exopod with distal article, epipod with large posterior lobe. Mxp2 (Fig. 6C) exopod with multiarticulate distal flagellum far overreaching distal border of merus. Mxp3 (Fig. 6D, E) endopod with two to four lower proximal spinules and prominent toothed crest on mesial surface of ischium, one or two lower subdistal spines on merus; exopod with multiarticulate distal flagellum.

P1 (Fig. 6H) equal, not sexually dimorphic, dactylus and fixed finger much compressed, approximately of same length, 1.5-3 times (usually twice) as long as palm, both with slight longitudinal carinae, fixed finger with large proximal tooth and dactylus with smaller subdistal tooth on cutting edge. P2 (Fig. 6I) much smaller than P1, chelate, with fingers about 1.5 times as long as palm. P3-5 (Fig. 6J-L) simple, slender, as figured. Both male and female gonopore present together on specimens of about 6.5 mm and over in carapace length.

Plp1 (Fig. 7C) of two articles, distal expanded with hooks on small mesiodistal lobe. Plp2 (Fig. 7D) with setose *appendix masculina* presumably fused to median part of endopod, *appendix inter-*

na at its base. Plp3-5 (Fig. 7E) with *appendix interna* at about one-third of mesial border of endopod.

Uropod (Fig. 6M), endopod and exopod about as long as telson with spinules on lateral external border, a suture near posterior border of exopod.

Colour

Delicate pink or orange, white in alcohol (Bell 1846; d'Udekem d'Acoz pers. comm). A coloured lithography is presented in Bouvier (1917: pl. 11, figs 5, 6).

Size

Specimens are larger in northern areas than in the south: the types from Loch Fyne, Scotland, are of about 2 inches (50 mm) (Bell 1846); ovigerous specimens from Norway of cl. 12.5-15 mm, tl. 38.5-41.5 mm (SMF 28970).

In Banyuls, France, largest specimens have cl. 10.5-12 mm, tl. 31.5-33 mm.

ECOLOGY AND BIOLOGY

The species is the most common thalassinidean in Norwegian waters, living in soft bottoms, between 15-580 m, and is most abundant below 50-100 m (Christiansen 2000). It occurs in soft bottoms, between 13-88 m, and is also collected at 310 m in Danish waters (Poulsen 1941). In muddy parts of the Clyde Sea area, it can be found everywhere and occasionally in stomach contents of cod, at 35-190 m (Allen 1967). It is a characteristic species of deep muddy bottoms in Marseille area (Pérès & Picard 1964; Picard 1965).

Aspects of biology studied

General biology (Buchanan 1963); hermaphroditism (Wollebæk 1909b); burrow and burrowing behaviour (Nash *et al.* 1984); physiological ecology of burrowing (Atkinson & Taylor 1988); anaerobic metabolism during anoxia (Anderson *et al.* 1994); branchial morphology, gill area and gill ultrastructure (Astall *et al.* 1997b); sulphide metabolism (Johns *et al.* 1997); particle size selectivity and resource partitioning (Pinn *et al.* 1998b); diet (Pinn *et al.* 1998a); gut morphology

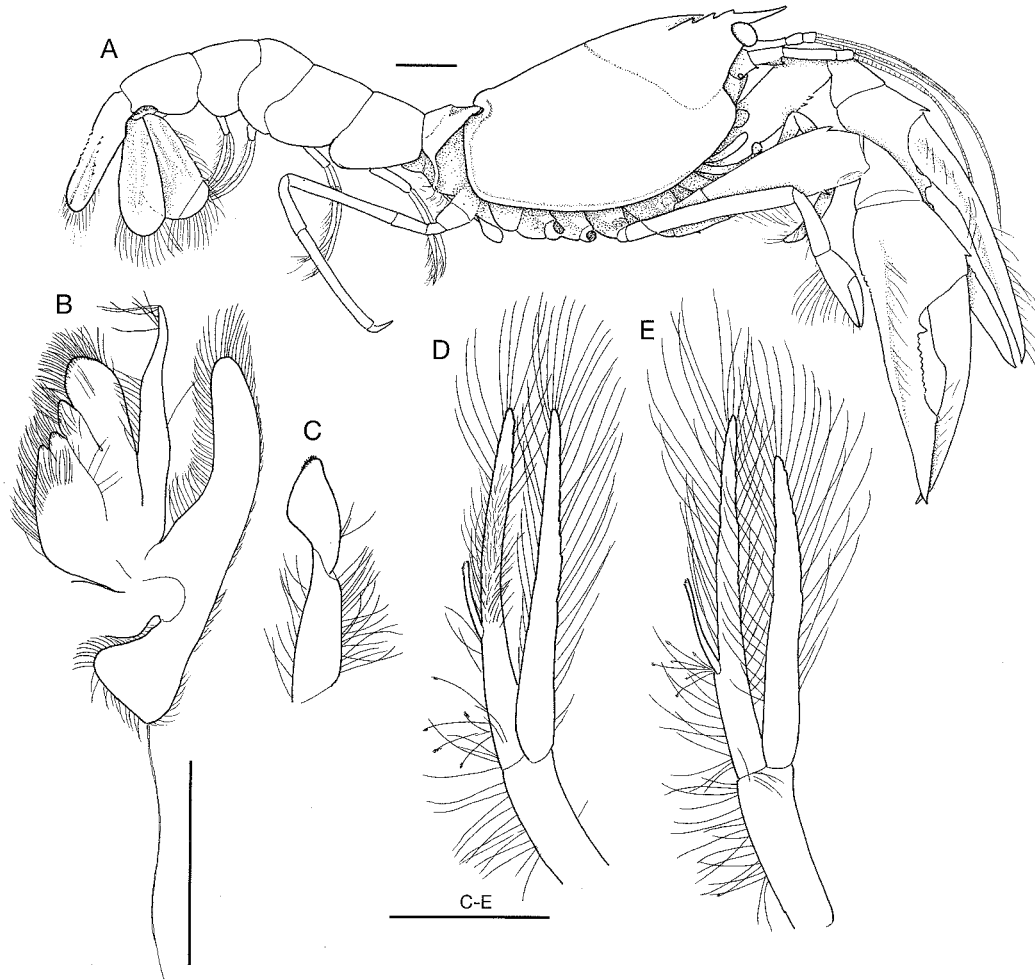


FIG. 7. — *Calocaris macandreae* Bell, 1846, hermaphroditic, from Banyuls, France (MNHN Th 1320); **A**, lateral view, pereopod 3 and 4 omitted; **B**, maxilla; **C-E**, pleopod 1-3. Scale bars: 2 mm.

and gut microflora (Pinn *et al.* 1999a); mouth part setal fringes (Pinn *et al.* 1999b); effects of sulphide and thiosulphide on the respiratory properties of the haemocyanin (Taylor *et al.* 1999); oxygen transporting properties of the haemocyanin (Taylor *et al.* 2000); bioturbation (Widdicombe *et al.* 2000).

REMARKS

The genus *Calocaris* and the species *Calocaris macandreae* were first published in Bell's book *A History of the British Stalked-Eyed Crustacea* (1844-

1853: 231-235). These pages were included in Part V of the book according to Gordon (1959) who also pointed out, on the authority of Dr H. O. Bull, that although "parts IV, V, VI were dated 1st January (of 1846, 1847, 1848 respectively), they did in fact appear in the market by Christmas, 7 to 10 days earlier".

The genus *Calocaris* with the type species *Calocaris macandreae* were proposed to be placed on the Official list (Holthuis 1962) and validated under the ICZN plenary powers in 1964 (ICZN 1964).

Calocaris macandreae has been reported from the Arabian Sea and the Bay of Bengal, off Sri Lanka (Alcock 1901), and also from the Gulf of St Lawrence, Canada (Whiteaves 1901).

Comparison of Alcock's description with the present material of *Calocaris macandreae* confirms Selbie's view (1914) that the Indian specimens belong to a closely related but separate species. The same must be said of those reported by Alcock & Anderson (1894: 163) from the Indian fauna. The specimen taken by Whiteaves was assigned to a new species, *Calocaris templemani* Squires, 1965 reported from Hermitage Bay, Newfoundland (Squires 1965) and probably also those from the Atlantic Canada, described by Rathbun (1929: 25, fig. 33).

Male and female gonopores appear together on young adults of *Calocaris macandreae* confirming Buchanan (1963) view that the species is not a protandric hermaphrodite.

Superfamily CALLIANASSOIDEA Dana, 1852

Family CALLIANASSIDAE Dana, 1852

Subfamily CALLIANASSINAE Dana, 1852

TYPE GENUS. — *Callianassa* Leach, 1814, subsequent designation by Manning & Felder (1991).

REMARKS

Four major works on the Callianassidae and Ctenochelidae of the Callianassoidea have been published recently: Manning & Felder (1991), Poore (1994, as part of a phylogeny of the Thalassinidea), Sakai (1999a), Tudge *et al.* (2000), the latter with a cladistic analysis. Various classification systems have been proposed sometimes with large differences. Reexamination of materials has been necessary and choices have been made concerning the taxonomy of European Callianassidae and Ctenochelidae.

This work uses the familial and subfamilial divisions proposed by Tudge *et al.* (2000) and adopts the alternative suggested by these authors which is to provisionally leave the genus *Callianassa* as a polyphyletic group. The diagnosis of *Callianassa* s.l. is given below.

The species *Callianassa acanthura* Caroli, 1946, *Callianassa truncata* Giard & Bonnier, 1890 and *Necallianassa berylae* Heard & Manning, 1998 were placed by Heard & Manning (1998) in the new genus *Necallianassa* on the ground of lateral spines on the telson and the uropodal endopod. These spines are however much smaller in *C. truncata* (Fig. 11D) than in the other two species (Fig. 8G). Furthermore, *Necallianassa berylae* has a large rostral spine which is absent in the other two species, and in both *C. truncata* (Fig. 11I) and *N. berylae*, female Plp2 bears a distal *appendix interna* on the endopod and lacks it in *C. acanthura* (Fig. 8O). The latter character is regarded as of generic importance.

In summary, *Necallianassa berylae*, the type species, possesses a large rostral spine, large acute lateral spines on the telson and uropods and an *appendix interna* on female Plp2.

C. acanthura differs by having no rostral spine, no *appendix interna* on female Plp2.

C. truncata differs by having no rostral spine, no large acute spines on the telson and uropods.

Although Sakai (1999a: 128) synonymised *Necallianassa* with *Callianassa*, this genus can be diagnosed using the characters mentioned above for the type species. But the inclusion of *C. acanthura* and *C. truncata* does not seem justified. Both species are reassigned to the genus *Callianassa* s.l.

The species *Callianassa candida* (Olivi, 1792), *C. tyrrhena* (Petagna, 1792) and *C. whitei* Sakai, 1999 and two others from the eastern Atlantic are separated into a new genus, *Pestarella* n. gen.

Genus *Callianassa* Leach, 1814

TYPE SPECIES. — *Cancer Astacus subterraneus* Montagu, 1808, by original designation.

DIAGNOSIS. — Carapace with dorsal oval, lacking rostral carina and posterodorsal cardiac prominence. Eyestalk short, flattened dorsoventrally; cornea subdistal, dorsal or dorsolateral. Mxp1 with anteriorly truncate epipod, endopod minute. Mxp2 with small epipod. Mxp3 lacking exopod, subpediform or operculiform; propodus not expanded ventrally, less than three times as wide as dactylus, latter digitiform, at least twice as long as wide.

P1 unequal, usually with meral hook, P2 chelate, P3 and P4 simple, P5 subchelate. P3 lacking or bearing reduced lower proximal heel on propodus.

Exopod on Mxp1-2; single arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-5.

Plp1 and Plp2 often absent or rudimentary in male, larger in female; female Plp2 biramous. Plp3-5 with stubby, projecting *appendix interna*. Uropodal exopod with dorsal plate.

REMARKS

The genus *Callianassa* is provisionally considered a polyphyletic group, with the species included as listed in Tudge *et al.* (2000). Sakai (1999a) proposed a much broader concept of the genus as he synonymised several genera erected by Manning & Felder (1991) with *Callianassa*. Although his action is not considered fully justified, the genera established by Manning & Felder (1991), focusing on American callianassids, probably need to be reconsidered, especially in view of their global use. Examination of the abundant, highly diverse material from the Indo-Pacific, together with a detailed phylogenetic analysis is desirable to show the true relationships between species and provide a solid base for their grouping. This however is beyond the scope of this work.

Nevertheless a number of additional characters, besides those given by Tudge *et al.* (2000), are suggested to be useful in the taxonomic study of this genus. Taking the three European *Callianassa* species as an example, it can be noted that, though they all fit the diagnosis of the genus as given above, *C. subterranea* has a slender minor P1 (Fig. 9C) not compressed laterally, with the carpus four or five times as long as wide; the P3 (Fig. 9J) propodus not ovate, with the lower border dentate; the third segment of Md palp (Fig. 9M) of same width throughout and the basal endite of Mx1 (Fig. 10A) approximately rounded distally.

By contrast, *C. acanthura* and *C. truncata* have the minor P1 (Fig. 8D) slightly compressed laterally, with the carpus less than twice as long as wide; the P3 propodus ovate (Fig. 8F) with the lower border regularly curved; the third segment of Md palp (Fig. 8K) narrowing distally and the basal endite of Mx1 (Fig. 8E) of inverted-triangle shape with an expanded distal border bearing spiniform setae.

These characters were not considered by Tudge *et al.* (2000) in their analysis but are probably of phylogenetic significance; those of *C. acanthura* and *C. truncata* are presumably apomorphic.

Callianassa acanthura Caroli, 1946

(Fig. 8)

Callianassa acanthura Caroli, 1946: 66, figs 1a, 2. — Holthuis 1953: 94, fig. 5. — Monchartmont 1979: 71. — de Saint Laurent & Božić 1976: 21, figs 3, 11, 19, 25, 30. — Türkay 1982: 225; °2001: 289. — °Türkay *et al.* 1987: 92. — °Koukouras *et al.* 1992: 223. — Noël 1992: 81. — °Froglia 1995: 7. — Falciai & Minervini 1996: 147, 3 figs. — d'Udekem d'Acoz 1996: 54, 56. — Abed-Navandi & Dworschak 1998: 605, figs 1-8. — Sakai 1999a: 14, 128 (addendum). — °Türkay 2001: 289.

Callianassa (Trypaea) acanthura – Zariquiey Alvarez 1968: 229.

Necallianassa acanthura – Heard & Manning 1998: 883. — d'Udekem d'Acoz 1999: 155.

TYPE MATERIAL. — Lectotype: ♂, Naples, Italy, E. Caroli coll., received V.1959, don. Zoological Station Naples (RMNH D 15212 a); paralectotype: ♂ (RMNH D 15212 b), by present designation.

MATERIAL EXAMINED. — Italy. Naples, E. Caroli coll., 2 ♂♂ lectotype cl. 11 mm, tl. 43 mm (figured), and paralectotype cl. 8 mm, tl. 36 mm (RMNH D 15212 a and b); Gulf of Naples, E. Caroli don., 1 ♂ (RMNH D 6588).

Croatia. Adriatic, Kornati, Zirje Island, 3 m, D. Abed-Navandi coll., 17.IX.1997, 1 ♂, 1 ♀ cl. 10 mm (figured) (NHMW 15372).

Greece. NW Pogonia, 1.5 m, C. d'Udekem d'Acoz coll., 12.VII.1993, 1 ♀ cl. 8.5 mm, tl. 36.5 mm (figured) (MNH Th 1400); Lesbos (Aegean sea), C. d'Udekem d'Acoz coll., 12.VII.1992, 1 ♂ cl. 10.5 mm (MNH Th 1401), 1 ♀ cl. 10 mm (d'Udekem d'Acoz).

OTHER MATERIAL EXAMINED. — *Necallianassa berylae* Heard & Manning, 1998, South Carolina, 1 ♂ cl. 2.5 mm, 1 ♀ cl. 4.5 mm (paratypes, USNM 260885); Georgia, 1 ♂ cl. 3.2 mm (paratype, USNM 260888).

DISTRIBUTION. — Mediterranean: Adriatic (Abed-Navandi & Dworschak 1998), Naples, Aegean, Ionian sea (d'Udekem d'Acoz 1996).

DIAGNOSIS

Carapace (Fig. 8A) with dorsal oval; rostrum approximately triangular with blunt tip, rostral

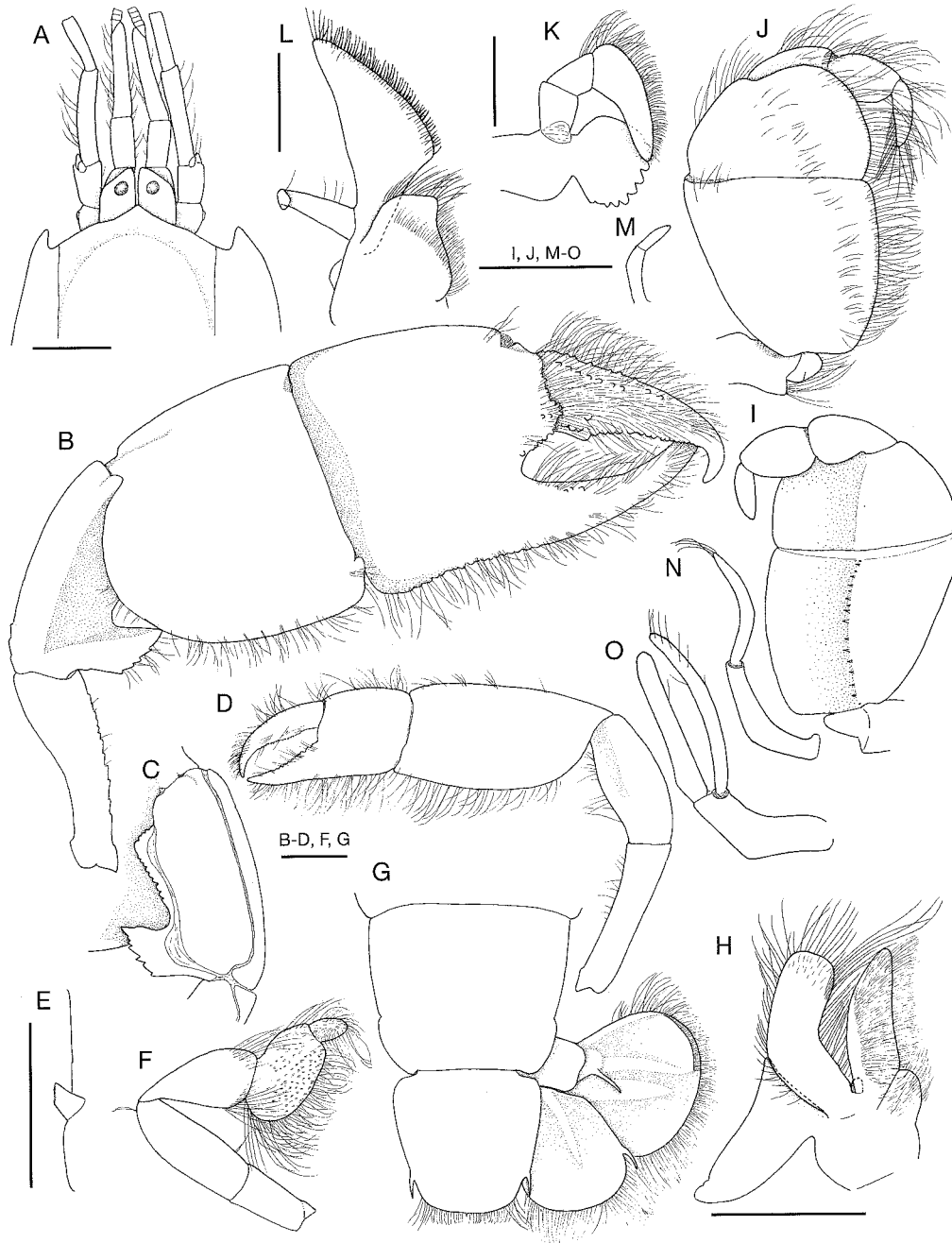


FIG. 8. — *Callianassa acanthura* Caroli, 1946; **A-D, F, G, M**, lectotype, ♂ from Naples, Italy (RMNH D 15212 a); **E, H-L**, ♀ from Pogonia, Greece (MNHN Th 1400); **N, O**, ♀ from Zirje island, Croatia (NHMW 15372); **A**, anterior part of carapace; **B, C**, major pereopod 1 and merus in mesial view; **D**, minor pereopod 1; **E**, *appendix interna* on mesial border of pleopod 3; **F**, pereopod 3; **G**, telson and uropods; **H**, maxilliped 1; **I, J**, maxilliped 3, mesial and lateral view; **K**, mandible; **L**, maxillule; **M**, male pleopod 1; **N, O**, female pleopod 1 and 2. Scale bars: **A-J, M-O**, 2 mm; **K, L**, 1 mm.

spine absent. Telson (Fig. 8G) about as long as proximal width, a little narrower distally, lateral border weakly convex with long curved subdistal spine, posterior border weakly rounded with median spinule.

Eyestalk (Fig. 8A) short; cornea dorsal, subterminal, disk-shaped. A1 peduncle slightly shorter than that of A2. Md (Fig. 8K) with three-segmented palp, last segment pointing distally. Mx1 (Fig. 8E) with basal endite of inverted-triangle shape, bearing spiniform setae. Mx2 with large endopod. Mxp1 (Fig. 8H) with small endopod, epipod without anterior lobe. Mxp3 (Fig. 8I, J) operculiform, ischium-merus length about 1.5 times merus width, ischium with *crista dentata* of 14-16 spines on mesial surface; propodus 1.5 times as long as wide; dactylus digitiform, 1.5 times to twice as long as wide.

P1 unequal in adult male, subequal in young male and female with both chelipeds similar to minor cheliped of adult male. Male major P1 (Fig. 8B) with lower border of merus convex on distal half (Fig. 8C) bearing small rounded teeth; meral hook pointed distally and denticulate on proximal border; carpus and propodus unarmed; dactylus with curved tip and densely setose near base. Male minor P1 (Fig. 8D) slender with carpus 1.7-1.8 times as long as wide and twice as long as propodus; both fixed finger and dactylus with denticulate cutting edge. P3 (Fig. 8F) propodus with lower border rounded, no proximal heel. P4 propodus slender, over three times as long as wide.

Male Plp1 (Fig. 8M) small, two-articulated; male Plp2 absent. Female Plp1 (Fig. 8N) uniramous, two-articulated; female Plp2 (Fig. 8O) biramous, exopod longer than endopod. Plp3-5 biramous, foliaceous, *appendix interna* (Fig. 8E) small, narrowing distally, partly embedded, the rest projecting from inner border of endopod.

Uropod (Fig. 8G) as long as telson; exopod with long proximal spine, dorsal plate with setal distal row at short distance from posterior border; endopod with long lateral subdistal spine.

Colour

Body whitish in living specimens, white P1; tailfan mottled with whitish or dull-yellowish dots

and spots that are characteristic of the species (d'Udekem d'Acoz 1986).

Tailfan and eyestalk orange, ripe ovaries red (Dworschak pers. comm.).

Size

Medium: cl. 8.5-11 mm, tl. 36-43 mm.

ECOLOGY

The species lives in muddy sand, at 2-3 m depth (Caroli 1946), or in a mixture of mud and fine or coarse sand, at 1-1.5 m, together with *C. truncata* or *U. pusilla* (d'Udekem d'Acoz 1996), or in pure sand, at 0.5 m depth (Türkyay 1982). It is abundant on sublittoral sandy bottoms of the Kornati Archipelago and near Rovinj, in fine or medium sand, at 3-6 m depth, associated with the fish *Trachinus* sp. and *Bothus* sp. (Abad-Navandi & Dworschak 1998).

REMARKS

This species, together with *Necallianassa berylae* Heard & Manning, 1998, can be distinguished from all other callianassids by the presence of large acute spines on the lateroposterior border of the telson and uropodal endopod, as well as proximally on the uropodal exopod. Spines are present on the lateroposterior border of the telson in a few other species, e.g., *C. truncata* or *C. intermedia* de Man, 1905 (see Sakai 1999a: 128) but in none of these are they so large (about one-fifth length of telson and uropodal endopod in *C. acanthura*) and acute.

Among its European and Mediterranean congeners, *C. acanthura* is close to *C. truncata* but differs essentially in: 1) the large acute spines on the telson and uropods, as mentioned above; and 2) the absence of an *appendix interna* on female Plp2.

Callianassa subterranea (Montagu, 1808)

(Figs 9; 10)

Cancer Astacus subterraneus Montagu, 1808: 89, pl. 3 figs 1, 2.

Callianassa helgolandica Lutze, 1938: 174, figs 52-61.

Callianassa pestae – Lutze 1937: 6, figs 1-6; 1938: 167, figs 10-21.

- Callianassa subterranea* – Leach 1815: 343; 1816: pl. 32. — Desmarest 1825: 205, pl. 36 fig. 2. — White 1847: 70; 1857: 94, pl. 7 fig. 2. — Bell 1846: 219, 1 fig. — °Lafont 1868: 522. — A. Milne-Edwards 1870: 80, 101. — °Fischer 1872: 428. — Stalio 1877: 106. — °de Folin & Périer 1879: 211. — Stossich 1880: 206. — Van Beneden 1884: 647. — Carus 1885: 489. — Kœhler 1886: 59. — Bonnier 1887: 247. — Ortmann 1891: 55, pl. 1, fig. 10. — Adensamer 1898: 620. — °Graeffe 1902: 69. — °Norman 1907: 357. — Sinel 1907: 216. — Lagerberg 1908: 53, pl. 1, fig. 15. — *Lo Bianco 1909: 603. — Schlegel 1912: 238, 250. — *Boraschi 1921: 6, pl. 1 fig. 2. — *Webb 1921: 403, pl. 3, figs 2, 5. — Miranda y Rivera 1933: 21. — Gustafson 1934: 14. — Lutze 1938: 170, figs 28-51. — Poulsen 1941: 229, figs 10-12. — *Gurney 1942: 244, fig. 98. — Zariquiey Alvarez 1946: 106. — *Rees 1955: 74, fig. 4.5 (part). — Holme 1966: 433, fig. 23 (part). — Allen 1967: 57, 90 (fig.). — Naylor 1972: 69. — °Pastore 1976: 107. — °Christiansen 1972: 41, fig. 49; 2000: 234. — de Saint Laurent & Božić 1976: 17, figs 1, 9, 17, 28. — *Thiriot 1976: 350, 367. — de Saint Laurent & Le Lœuff 1979: 52, fig. 9c, e. — Moncharmont 1979: 71. — Domenech *et al.* 1981: 150. — Adema *et al.* 1982: 23, fig. 6a-c, map 4. — Christiansen & Greve 1982: 213. — Atkinson 1986: 358, fig. 1M. — Campbell & Nicholls 1986: 218, 1 fig. — Holthuis & Heerebout 1986: 62, fig. 83. — Moore 1986: 32. — Thessalou-Legaki 1986: 182; 1987: 457. — Witbaard & Duineveld 1989: 209-219, fig. 1. — Atkinson & Nash 1990: 403, figs 1, 2, tabs 1, 2. — Moyse & Smaldon 1990: 520, fig. 10.13 (part). — Števičić 1990: 217. — Manning & Felder 1991: 768, fig. 8. — Dworschak 1992: 203. — °Koukouras *et al.* 1992: 223. — Noël 1992: 81. — Lindley *et al.* 1993: 53. — °Diez *et al.* 1994: 47. — Rowden & Jones 1994: 623, figs 1-5, tabs 1-3; 1995: 1155, figs 1-4, tabl. 1; 1997: 153, figs 1-3. — °Froggia 1995: 7. — Hayward *et al.* 1995: 432, fig. 8.52 (part). — Nickell & Atkinson 1995: 181, fig. 1, tabl. 1. — Falciai & Minervini 1996: 147, 4 figs. — Astall *et al.* 1997b: 669, 674, 675, fig. 1, tabs 1-5, pls 2, 4, 5. — Brattegard & Christiansen 1997: 220. — Hughes & Atkinson 1997: 639. — Johns *et al.* 1997: 127, tabs 1, 2. — Rowden *et al.* 1998: 1365, figs 1-4, pls 1-2; tabl. 1. — Christiansen & Stene 1998: 75. — Nickell *et al.* 1998: 735, 749, 754, figs 1-3. — Pinn *et al.* 1998b: 243, fig. 3; 1999a: 103, figs 1, 3, 4; 1999b: 1461, tabs 1-6. — Stamhuis *et al.* 1997: 156; 1998a: 43; 1998b: 197. — Stamhuis & Videler 1998: 2152. — d'Udekem d'Acoz 1999: 155. — Sakai 1999a: 19. — Hughes *et al.* 2000: 189, figs 1-5. — Öksnebjerg 2000: 78. — Taylor *et al.* 2000: 265, figs 1-3, tabs 1-3, 5, 6. — *González-Gordillo *et al.* 2001: 279. — Livory 2001: 33C. — Markham 2001: 196, tabs 1, 2. — *Martin 2001: 77, 1 fig. — °Türkay 2001: 289.
- Callianassa (Callianassa) subterranea* – Zariquiey Alvarez 1968: 229.
- Callianassa (Cheramus) subterranea* – Borradaile 1903: 545. — de Man 1928a: 6, pl. 1 figs 1-1h; 1928b: 27, 91, 92, 94, 97. — Makarov 1938 (English edition, 1962): 63, fig. 21. — Bouvier 1940: 101, fig. 67. — Gurney 1944: 82, figs 1A, 14, 15. — Gordon 1957: 249. — *O'Ceidigh 1962: 163.
- Callianassa tyrrhena* – Holthuis & Gottlieb 1958: 62, fig. 13.
- Cheramus subterraneus* – Colosi 1923: 6.
- Non *Callianassa subterranea* – H. Milne Edwards 1837a: 309; 1837b: 130, pl. 48 figs 3-3c (= *Pestarella tyrrhena* (Petagna, 1792) n. comb.). — Heller 1863: 202, pl. 6 figs 9-11 (= *P. tyrrhena* n. comb.). — Ortmann 1891: 55, pl. 1, fig. 10 (= *P. tyrrhena* n. comb.). — Giard & Bonnier 1890: 362, figs 1, 3 (= *P. candida* (Olivi, 1792) n. comb.).
- TYPE MATERIAL. — Lectotype: ♂, Kingsbridge Estuary, S Devon, Great Britain (NHML 1939.2.20.1); paralectotype: 1 ovig. ♀ (NHML 1939.2.20.2) by present designation.
- MATERIAL EXAMINED. — North Sea. Kettle Hole, southern North Sea, 23.III.1955, leg. et don. P. Smit, 1 broken spec. (RMNH D 10985). — Near Pit bouy, 17.III.1955, depth 150 ft, leg. et don. P. Smit, 1 chela (RMNH D 10986). — Bruine Bank near Winterton Twenties, c. 53°N, 3°E, 20-27.VIII.1960, leg. et don. J. Kruuk, 1 broken spec. (RMNH D 16614). — 53°41'45"N, 3°55'E, ms *Tridens*, haul 44, 12.VIII.1971, leg. G. R. Heerebout, 1 ♂ (RMNH D 29227).
- Great Britain. S Devon, 1 ♂ lectotype cl. 13 mm, tl. 52 mm (NHML 1939.2.20.1), 1 ♀ paralectotype cl. 12 mm, tl. 47.5 mm (NHML 1939.2.20.2); 2 spec., dried (NHML 260a, b). — Plymouth Sound, 1 ♂ cl. 11 mm, tl. 47 mm (figured), 1 ♂ cl. 9 mm, 2 ♀ ♀ cl. 10 mm and 10.5 mm, tl. 42.5 and 44.5 mm (figured), 3 ♀ ♀ (1 ovig.) cl. 10-10.5 mm (MNHN Th 211). — Lion Rock, Millport, Firth of Clyde, sandy mud, R. B. Pike coll., 2.IX.1959, 1 ♂, 1 juv. (NHML 1962.7.5.8-9). — English Channel, stn 107, MBA coll., 10 ♂ ♂, 6 ♀ ♀, 3 juv. (damaged) (NHML 1999.81-101); stn 44, 29 m, 2 ♂ ♂, 1 ♀ (NHML 1999.72-73); stn 152, 42 m, 1 ♂ without abdomen (NHML 1999.126); stn 103, 37 m, 1 ovig. ♀ (NHML 1999.74); stn 110, 51 m, MBA coll., 7 ♂ ♂, 1 ovig. ♀ (poor condition) (NHML 1999.102-114); stn 173, 54 m, MBA coll., 7 ♂ ♂, 1 ♀ (poor condition) (NHML 1999.127-138); stn 152, 42 m, 2 ♂ ♂, 1 abdomen of ♀ (poor condition) (NHML 1999.115-116). — Western Channel, MBA coll., 17.III.1970, 3 ♂ ♂, 2 ♀ ♀ (damaged) (NHML 1971.24). — Salcombe, Devon, spring low tides, P. Gibb coll., 26.III.1970, 1 ovig. ♀ (NHML 1971.23); R. Gurney coll., 21.III.1935, 3 ♂ ♂, 3 ♀ ♀ (damaged) (NHML 1947.3.18.723-725). — 1 mile S of Knight Errant muddy grounds, 22 fms, 8.III.1970,

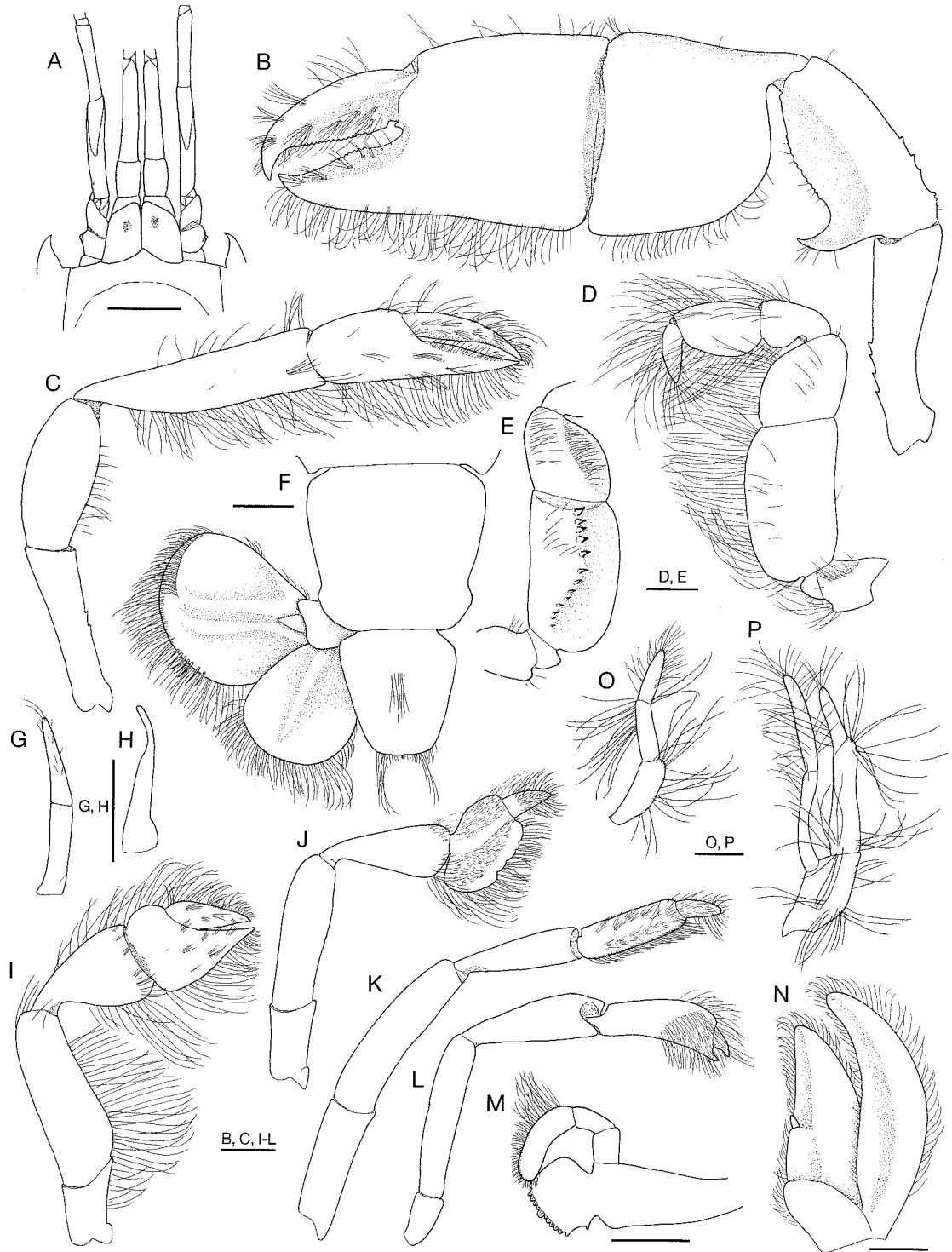


FIG. 9. — *Callianassa subterranea* (Montagu, 1808); **A**, ♀ from Plymouth, UK, anterior part of carapace (from de Saint Laurent & Božić 1976); **B-P**, from Plymouth, UK (MNHN Th 211); **B-E**, **I-P**, ♀; **F-H**, ♂; **B, C**, major and minor pereopod 1; **D, E**, maxilliped 3 and mesial view of ischium, merus; **F**, telson and uropods; **G, H**, male pleopod 1 and 2; **I-L**, pereopod 1-5; **M**, mandible; **N**, pleopod 3; **O, P**, female pleopod 1 and 2. Scale bars: A-E, G-M, O, P, 1 mm; F, N, 2 mm.

1 ♂, 1 ovig. ♀ (NHML not registered). — Jersey, 3 dried spec. (NHML 260d).

France. Roscoff, *Thalassa*, 1970, 1 juv. cl. 3 mm (MNHN Th 103), 1 ♀ cl. 5.5 mm, 1 juv. (MNHN Th 104), 1 juv. cl. 2 mm (MNHN Th 105), 1 damaged spec. (MNHN Th 106). — Grande Vasière, near Concarneau, Glémarec coll., 1 ♂ cl. 6 mm, 1 ♀ cl. 5 mm (MNHN Th 102); Glémarec coll., IV.1972, 2 ♂♂ cl. 4 and 8 mm (MNHN-Th 108), 1 ♂ just moulted cl. 10 mm (MNHN Th 109), 1 ♂ cl. 5.5 mm, 1 ♀ cl. 5 mm, 1 juv. (MNHN Th 110), 1 ♂ cl. 5.5 mm, 3 ♀♀ cl. 5-7 mm, 2 juv. (MNHN Th 111). — Bay of Biscay, 120-180 m, leg. Lagardère, 2 ♂♂ cl. 4.5 and 6 mm, 1 ovig. ♀ cl. 5.5 mm (MNHN Th 107). — Banyuls, mud with *Turritella*, 30 m, P. Noël coll., 3.VIII.1976, 1 juv. cl. 3 mm (MNHN Th 1349); VI.1977, 1 ♂ cl. 4.5 mm, 1 ovig. ♀ cl. 5 mm (MNHN Th 1350); mud, 90 m, 14.VI.1977, 1 ♂ cl. 4 mm (MNHN Th 1351).

Portugal. 42°9,4'N, 8°58,3'W, *Thalassa*, stn 819, 103 m, 21.X.1968, 1 juv. cl. 4 mm (MNHN Th 635).

Spain. Alboran sea, *Calypso*, 35°50'N, 3°19'W, muddy sand, 500 m, 3.IX.1958, 1 ♂ cl. 8 mm (MNHN Th 367).

Greece. *Calypso*, stn 1, dredge, 94 m, 27.IX.1977, 1 ♂, 1 ovig. ♀ cl. 4.5 mm (MNHN Th 625). — Aegean Sea, Strymonikos G., 25 m, 5.II.1977, 2 ♀♀ (A.U.TH P 1529).

Israel. Ascalon, bottomgrab, 54 m, 27.VII.1947, leg. A. Wirszubski, No. 590A, 1 juv. (RMNH D 13796); 30.IX.1947, leg. A. Wirszubski, No. 652, 2 juv. (RMNH D 13797). — Haifa Bay, stn 7, bottomgrab, 38 m, 7.VI.1955, leg. E. Gottlieb, No. 225, 1 juv. (RMNH D 13798); stn 9, bottomgrab, 42 m, 11.X.1954, leg. E. Gottlieb, No. 148, 1 ♀ (RMNH D 13799). — Nabi Junis, bottomgrab, 54 m, 18.VIII.1949, leg. A. Wirszubski, No. 787, 1 ♂ (RMNH D 13801). — Nahariya, bottomgrab, 70 m, 18.IX.1947, leg. A. Wirszubski, No. 638, 2 juv. (RMNH D 13802). — Tel Aviv, bottomgrab, 54 m, 12.XII.1949, leg. A. Wirszubski, No. 838, 1 juv. (RMNH D 13803). — Nabi Rubin, bottomgrab, 56 m, 24.V.1949, leg. A. Wirszubski, No. 741, 1 juv. (RMNH D 13804). — Rafan, bottomgrab, 36 m, 22.VI.1947, leg. A. Wirszubski, No. 545, 1 juv., broken (RMNH D 13805).

Dahomey. *Ombango*, dredge, 40 m, A. Crosnier coll., 9.X.1963, 1 juv. cl. 3.5 mm (MNHN Th 265).

DISTRIBUTION. — Eastern Atlantic: S Scandinavia (Gustafson 1934; Poulsen 1941; Christiansen & Greve 1982; Christiansen & Stene 1998), SW of Scotland (Allen 1967; Nickell *et al.* 1998), S of North Sea, English Channel, W coast of France, Dahomey. Mediterranean: France, Israel, Greece, Alboran Sea, Adriatic Sea.

C. subterranea is recorded on the Coast of Norway to 60°N from 5-7 m to 60-100 m (Christiansen 2000). According to de Saint Laurent & Božić (1976), the species is common in the northern part of its distribu-

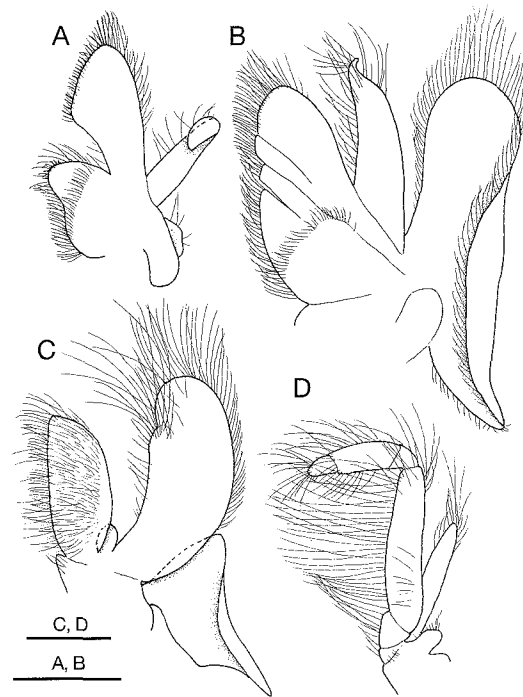


FIG. 10. — *Callianassa subterranea* (Montagu, 1808), ♀ from Plymouth, UK (MNHN Th 211); A, B, maxillule and maxilla; C, D, maxilliped 1 and 2. Scale bars: 1 mm.

tion range (Great Britain, Denmark, Norway), scarce along the atlantic coast of France and in the Mediterranean with smaller specimens living in deeper waters (35-500 m).

DIAGNOSIS

Carapace (Fig. 9A) with dorsal oval; rostrum approximately triangular with blunt tip, rostral spine absent. Telson (Fig. 9F) about as long as proximal width, narrowing distally, lateral border convex proximally, posterior border with median spinule. Eyestalk (Fig. 9A) short, cornea dorsal, indistinct. A1 peduncle shorter than that of A2. Md (Fig. 9M) with three-segmented palp, last segment of same width throughout. Mx1 and Mx2 (Fig. 10A, B) as figured. Mxp1 (Fig. 10C) with small rounded endopod, epipod without anterior lobe. Mxp2 (Fig. 10D) with short exopod. Mxp3 (Fig. 9D, E) subpediform; row of 13-15 spines on mesial surface of ischium, smaller proximally; propodus about 1.5 as long as wide; dactylus 2.5-3 times as long as wide.

Major P1 (Fig. 9B) stouter in male than in female, strong meral hook, curved anteriorly, smooth or with denticles on proximal border; carpus about as long as distal width, propodus slightly longer, cutting edge of fixed finger and dactylus unarmed or with small round teeth. Minor P1 (Fig. 9C) slender with carpus approximately four times as long as distal width. P2 (Fig. 9I) as figured. P3 (Fig. 9J) propodus with lower border dentate bearing separated tufts of setae, no proximal heel. P4 (Fig. 9K) propodus slender, nearly three times as long as wide. P5 (Fig. 9L) subchelate.

Male Plp1 (Fig. 9G) uniramous, male Plp2 (Fig. 9H) small, sometimes absent. Female Plp1 (Fig. 9O) uniramous, female Plp2 (Fig. 9P) biramous, exopod overreaching endopod.

Plp3-5 (Fig. 9N) biramous, foliaceous, *appendix interna* approximately cylindrical, partly embedded, distal half projecting from inner border of endopod. Uropodal endopod (Fig. 9F) about as long as telson; exopod longer, setal row of dorsal plate at short distance from posterior border.

Colour

Colour during life more or less orange, sometimes yellow on the sides and on the tail, the arms usually pink (White 1857); dorsal abdomen pale pink (Dworschak pers. comm.); white to light pink or light blue (Campbell & Nicholls 1986).

Size

♂ lectotype of cl. 13 mm, tl. 52 mm; ♀ paralectotype of cl. 12 mm, tl. 47.5 mm.

In the present material examined, specimens are larger in northern Atlantic, of cl. 10-13 mm, tl. 42-52 mm, smaller in southern Atlantic (e.g., France, Spain) and in the Mediterranean, of cl. 4-8 mm, ovigerous ♀ of cl. 4.5-5.5 mm.

ECOLOGY AND BIOLOGY

This species shows all the characteristics of a deposit feeder, according to Stamhuis *et al.* (1997). It is common in subtidal (10-80 m) muddy fine sands and muds (Adema *et al.* 1982; Dworschak 1992; Moysé & Smaldon 1990). In Plymouth, UK, larvae are very common in the plankton in summer and early autumn (Gordon 1957).

Its ecology and general biology including burrow structure in the North Sea were dealt with by Witbaard & Duinevelt (1989), Atkinson & Nash (1990), Rowden & Jones (1994, 1995).

Other aspects of biology studied

Burrow morphology and feeding behaviour (Nickell & Atkinson 1995); burrows and bioturbation (Rowden & Jones 1997); burrow architecture and burrow ventilation (Stamhuis *et al.* 1997; Stamhuis & Videler 1998); branchial morphology, gill area and gill ultrastructure (Astall *et al.* 1997b); sulphide metabolism (Johns *et al.* 1997); morphology of mouthparts and pereopods in relation to feeding, ecology and grooming (Nickell *et al.* 1998); morphology, motion and function of appendages (Stamhuis *et al.* 1998a); size selectivity and resource partitioning (Pinn *et al.* 1998b); optimal foraging and grain size selection (Stamhuis *et al.* 1998b); role in sediment turnover resuspension (Rowden *et al.* 1998); gut morphology and gut microflora (Pinn *et al.* 1999a); effects of burrows on sediments-water solute fluxes (Hughes *et al.* 2000); oxygen transporting properties of haemocyanin (Taylor *et al.* 2000).

REMARKS

As reported by de Saint Laurent & Božić (1976), the specimen from Helgoland assigned by Lutze (1938) to *Callianassa pestae* (p. 167, figs 10-21) as well as his new species *Callianassa helgolandica* (p. 174, figs 52-61) actually belong to *C. subterranea*. This is confirmed by the figures of their Mxp3, both subpediform (fig. 11, also part of fig. 26a, b for *C. pestae* and fig. 53 for *C. helgolandica*). On the other hand, Dworschak (1992: 205) contends that the specimen collected by the "Pola Expedition" (NHMW 6613) and mentioned by Adensamer (1898: 620) is in fact a juvenile of the present species, not of *Gourretia denticulata* (Lutze 1937).

There is variation in the length of major P1 carpus and propodus, also in the length and shape of the dactylus and fixed finger. This appears to be not linked with sex (Nickell *et al.* 1998).

Callianassa truncata Giard & Bonnier, 1890
(Fig. 11)

Callianassa truncata Giard & Bonnier, 1890: 362, figs 2, 4. — Caroli 1940: 73; 1946: 66, figs 1b, 3. — Holthuis 1953: 91, fig. 4. — *Bourdillon-Casanova 1960: 108. — Picard 1965: 38. — Lagardère 1966: 195, pls 2-5; 1973: 84. — *Faure 1970: 773. — de Saint Laurent & Božić 1976: 19, figs 2, 10, 18, 29. — Beaubrun 1979: 84, figs 56, 57, 62-64. — Monchartmont 1979: 72. — *Kocataş 1981: 162. — Mikashavidze 1981: 1417. — Thessalou-Legaki & Zenetos 1985: 309. — Thessalou-Legaki 1986: 183. — *Koukouras *et al.* 1992: 223. — Noël 1992: 81. — *Frogliia 1995: 7. — Falciai & Minervini 1996: 147, 4 figs. — d'Udekem d'Acoz 1996: 54. — Ziebis *et al.* 1996: 619, fig. 1. — Abed-Navandi & Dworschak 1997: 565, figs 1-8. — Sakai 1999a: 20. — *González-Gordillo *et al.* 2001: 279. — Markham 2001: 197. — *Türkay 2001: 289.

Callianassa italica Parisi, 1915: 64, figs 1, 2.

Callianassa (Trypaea) italica — de Man 1928a: 11, figs 5-5h; 1928b: 27, 101.

Callianassa (Trypaea) truncata — Borradaile 1903: 546. — de Man 1928b: 28, 101. — Bouvier 1940: 102, fig. 68. — Gurney 1944: 82, figs 1E, 3, 4. — Zariquiey Alvarez 1950: 81, fig. 1, pl. 6 figs 1-6, pl. 7 fig. 2; 1968: 229. — *Dolgopolskaia 1954: 186, figs 5-9; *1969: 316, pls 35-38.

Callianassa (Trypaea) truncata. — *Băcescu 1967: 229, fig. 104.

Necallianassa truncata — Heard & Manning 1998: 883. — d'Udekem d'Acoz 1999: 156. — Dworschak *et al.* 2000: 302. — *Lindley *et al.* 2001: 46. — Markham 2001: tabs 1, 2.

Pestaina truncata — Öksnebjerg 2000: 78 *nomen nudum*.

TYPE MATERIAL. — Whereabouts unknown.

MATERIAL EXAMINED. — **France.** Bay of Chingoudy (eastern Pyrénées), A. Chaud coll., V.1982, 2 ♂♂ cl. 9.5 and 10 mm, tl. 40 and 41 mm (figured), 6 ♂♂ cl. 10-11.5 mm, 2 ♀♀ (1 ovig.) cl. 9 mm (MNHN Th 653); III.1983, 1 ♂ cl. 9.5 mm (MNHN Th 658). — Noirmoutiers Island, Y. Gruet coll., 3.V.1973, 1 ovig. ♀ cl. 7 mm (MNHN Th 604); 2.VII.1973, 1 ovig. ♀ cl. 9 mm (MNHN Th 605).

Italy. Gulf of Naples, donated by E. Caroli, 3 ♂♂, 2 ♀♀ (RMNH D 6586). — South of La Gaiola, 100 m, in mud, 11.VIII.1963, don. J. A. W. Lucas, 1 small ♀ (RMNH D 9070). — Naples, collection E. Caroli, received III.1959 from Zoological Station Naples, 47 ♂♂, 23 ♀♀, 24 ovig. ♀♀ (RMNH D 12988).

Greece. Kreta, W of Souda Bay, C. d'Udekem d'Acoz coll., 14.VII.1987, 1 ♂ cl. 6 mm, 3 ovig. ♀♀ cl. 6-

6.5 mm (MNHN Th 1354); 15.VII.1987, 1 ♂ cl. 7.5 mm, 6 ♀♀ (3 ovig.) cl. 5.5-6.5 mm (d'Udekem d'Acoz). — Kalives Harbour, 11.VII.1987, 2 ovig. ♀♀ cl. 4.5 and 5 mm (d'Udekem d'Acoz). — Tersanas (west of Stavros), 15.VII.1987, 22 ♂♂ cl. 3.5-6 mm, 25 ♀♀ (2 ovig.) cl. 3-6.5 mm (d'Udekem d'Acoz). — Pogonia, 0.5-1.5m, C. d'Udekem d'Acoz coll., 12.VII.1993, 1 ♂ cl. 5 mm, 8 ♀♀ (7 ovig.) cl. 4-5.5 mm (MNHN Th 1415). — Georgiopolis, C. d'Udekem d'Acoz coll., 10.VII.1987, 7 ♂♂ cl. 5-9 mm, 12 ♀♀ (6 ovig.) cl. 5-8 mm (d'Udekem d'Acoz). **Morocco.** Leg. Institut scientifique chérifien, III.1966, 3 ♂♂ cl. 5-6.5 mm, 1 ♀ cl. 4.5 mm (MNHN Th 112). — Melilla, VI.1946, leg. J. Rutlant, R. Zariquiey Alvarez coll., 1 ♂ (RMNH D 35798a).

DISTRIBUTION. — Atlantic coast of France (Noirmoutiers Island, Bay of Biscay) to Atlantic coast of Morocco (de Saint Laurent & Božić 1976). Mediterranean: Greece, Italy, Melilla. Adriatic Sea (Abed-Navandi & Dworschak 1997), Ionian Sea (Thessalou-Legaki 1986; d'Udekem d'Acoz 1996), Aegean Sea (Kocataş 1981; Koukouras *et al.* 1992), southeast of Black Sea (Mikashavidze 1981).

DIAGNOSIS

Carapace (Fig. 11A) with dorsal oval, rostrum approximately triangular with blunt or slightly acute tip, rostral spine absent. Telson (Fig. 11D) about as long as proximal width, a little narrower distally; lateral borders weakly convex, latero-posterior corner with two transparent minute spines, posterior border with median spinule.

Eyestalk short (Fig. 11A), cornea dorsal, sub-terminal, disk-shaped. A1 peduncle approximately as long as that of A2. Md (Fig. 11F) with three-segmented palp, last segment tapering distally. Mx1 (Fig. 11G) with basal endite of inverted triangle, distal border widened bearing spiniform setae. Mxp3 (Fig. 11J, K) operculiform, length about 1.6-1.7 times merus width, ischium with row of 15-16 spinules on mesial surface; propodus about 1.6-1.7 times as long as wide; dactylus 1.8-2 times as long as wide.

P1 unequal in adult male and female, subequal in certain small specimens. Major P1 of male (Fig. 11C) with lower border of merus convex on distal half bearing small rounded teeth; meral hook pointed distally, denticulate on both proximal and distal border; carpus unarmed; propodus dentate on lower border; dactylus with curved tip and dense setae on proximal two-thirds and near

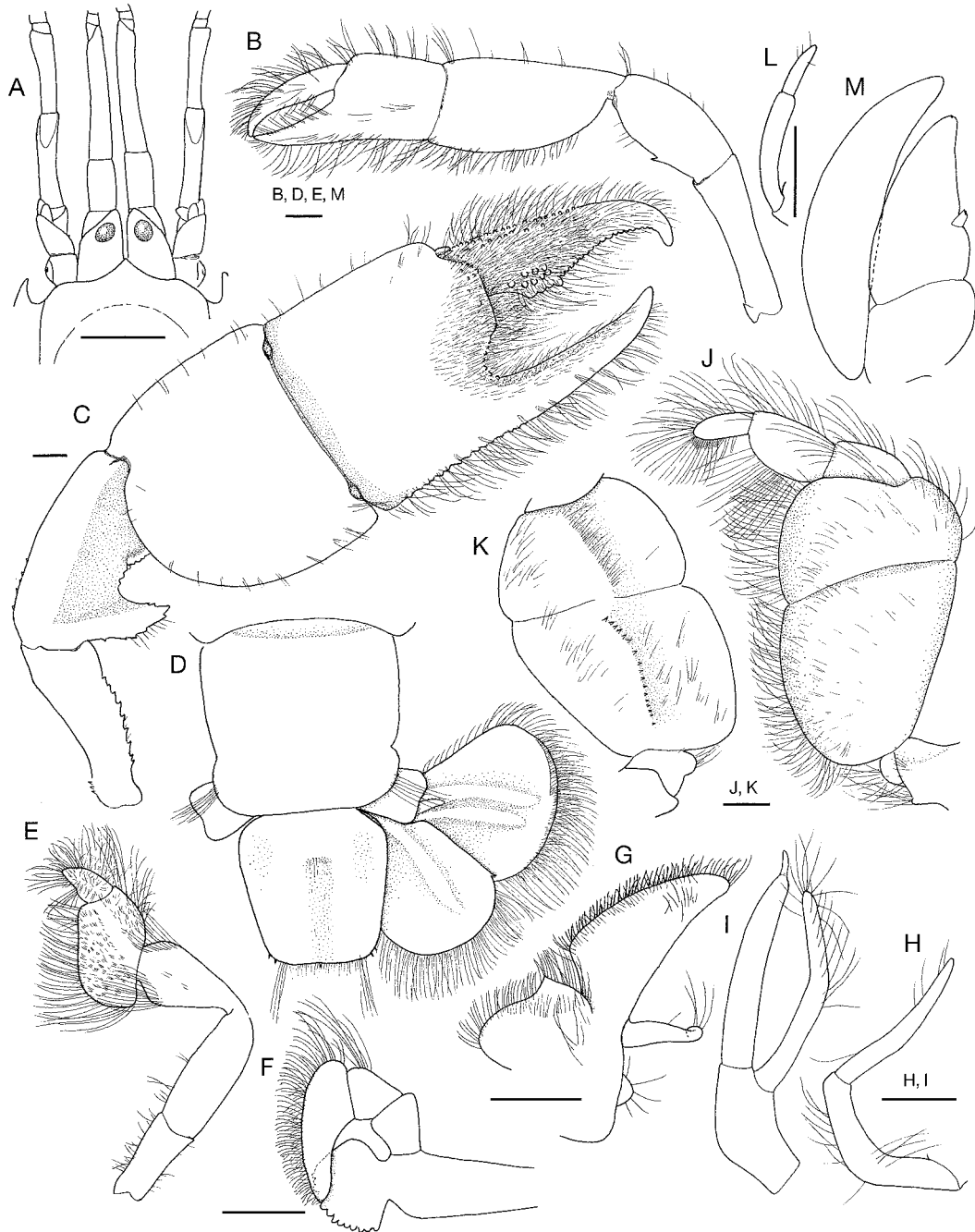


FIG. 11. — *Callianassa truncata* Giard & Bonnier, 1890; **A**, ♂ from Morocco, anterior part of carapace (from de Saint Laurent & Božić 1976); **B-M**, from Chingoudy Bay, France (MNHN Th 653); **B-G, J-M**, ♂; **H, I** ♀; **B, C**, minor and major pereopod 1; **D**, telson and uropods; **E**, pereopod 3; **F**, mandible; **G**, maxillule; **H, I**, female pleopod 1 and 2; **J, K**, maxilliped 3 and mesial view of ischium, merus; **L**, male pleopod 1; **M**, pleopod 3. Scale bars: 1 mm.

base of fixed finger. Major P1 of smaller male and of female similar to that of male but more slender, with fewer or very few setae (in female) on dactylus. Minor P1 (Fig. 11B) slightly compressed laterally, merus with median spine on lower border, carpus about 1.4-1.5 times as long as wide and 1.5 as long as propodus, lower border regularly curved. P3 (Fig. 11E) propodus approximately oval, with lower border rounded, no proximal heel. P4 propodus slender, over three times as long as wide.

Male Plp1 (Fig. 11L) small, male Plp2 absent. Female Plp1 (Fig. 11H) uniramous, female Plp2 (Fig. 11I) biramous, exopod about as long or slightly longer than endopod, latter with distal *appendix interna*. Pleopods 3-5 (Fig. 11M) foliaceous, *appendix interna* approximately cylindrical, slightly narrowing distally, partly embedded, partly projecting from inner border of endopod. Uropod (Fig. 11D) as long as telson; exopod with distal setal row of dorsal plate at short distance from posterior border; endopod with small lateral distal spine.

Colour

Body yellowish, abdomen dull yellow, pereopods whitish (d'Udekem d'Acoz 1996).

Creamy to yellowish on dorsal abdomen, chelipeds white, sometimes yellow, hepatopancreas orange-brown, ripe ovaries bright orange-red (Dworschak pers. comm.). A coloured photograph is presented in Ziebis *et al.* (1996).

Size

Medium: cl. 5.5-11.5 mm, largest specimens of cl. 9.5-11.5 mm, tl. 40-43 mm approx.

ECOLOGY

The species occurs in fine sand with or without mud, sometimes with pebbles. It seems to prefer fine sand and can be locally abundant (d'Udekem d'Acoz 1996). According to Picard (1965), *C. truncata* is characteristic of muddy bottoms along the coast of France. In the Bay of Biscay and nearby areas, specimens were captured in the littoral and at 44-57 m depth (Lagardère 1965).

REMARKS

De Saint Laurent & Božić (1976) cited a pair of fine spinules on each lateroposterior angle of the telson and a small laterodistal spine on the uropodal endopod as diagnostic characters for this species. It must be noted, however, that the spinules on the lateroposterior angle of the telson (figured in this work) are transparent and indistinct in most specimens. By contrast, the laterodistal spinule on the uropodal endopod is obvious. It makes a good distinguishing feature for the species in Europe, together with the lower meral spinule on the minor P1.

In certain populations of small size, e.g., MNHN Th 1415 from Pogonia, Greece, all females (eight specimens with seven ovigerous, cl. 4-5.5 mm) have their P1 subequal and similar to the minor P1 of males. This does not occur in larger specimens, e.g., those of cl. 8-9 mm.

Genus *Pestarella* n. gen.

Astacus Petagna, 1792: 418 (part).

Cancer Olivi, 1792: 51 (part).

Callianassa Leach, 1814: 400 (part).

TYPE SPECIES. — *Astacus tyrrhenus* Petagna, 1792, by present designation.

SPECIES INCLUDED. — *Astacus tyrrhenus* Petagna, 1792, *Cancer candidus* Olivi, 1792, *Callianassa rotundicaudata* Stebbing, 1902, *Callianassa convexa* de Saint Laurent & Le Lœuff, 1979, *Callianassa whitei* Sakai, 1999.

ETYMOLOGY. — The genus is named in honour of Dr Otto Pesta. The gender is feminine.

DIAGNOSIS

Carapace with dorsal oval, rostrum approximately triangular, rostral spine absent. Abdominal somite 2 about equal in length with abdominal somite 6; abdominal somites 3-5 with lateral tufts of setae. Telson rounded in posterior half.

Eyestalk short, flattened dorsoventrally; cornea distinct, disk-shaped. A1 peduncle as long or longer than that of A2. Mxp1 epipod truncate anteriorly; Mxp3 operculiform, a row of numerous spinules on mesial surface of ischium, dactylus digitiform; exopod absent.

Exopod on Mxp1-2; single arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-5. P1 unequal in male and female, major with meral hook. P3 propodus oval, no proximal heel. P4 propodus narrow; P5 subchelate. Male Plp1 and Plp2 absent; female Plp1 uniramous, female Plp2 biramous, Plp3-5 biramous, foliaceous in both sexes, *appendix interna* small, projecting from mesial border of endopod. Uropodal exopod with dorsal plate terminating in posterior setal row near or apart from posterior border.

REMARKS

The late Dr Ray Manning had intended to separate the two European species *Callianassa candida* and *C. tyrrhena* into a genus dedicated to Dr Otto Pesta. The present generic name fulfills that intention. The genus nevertheless has not hitherto been erected and the names *Pestaina truncata* and *Pestaina candida* used by Öksnebjerg (2000: 78) are *nomina nuda*.

In the subfamily Callianassinae of the Callianassidae, the new taxon is related to *Callianassa*. It differs by the telson rounded in posterior half, the operculiform Mxp3, and the absence of Plp1 and Plp2 in males.

Apart from *Pestarella whitei* n. comb., the four other species of this genus were placed in a small group within *Callianassa* by de Saint Laurent & Le Lœuff (1979: 96). They inhabit eastern Atlantic: three European species, *P. convexa* n. comb. from Senegal and *P. rotundicaudata* n. comb. from South Africa.

Pestarella candida (Olivi, 1792) n. comb.
(Fig. 12)

Cancer candidus Olivi, 1792: 51, pl. 3 fig. 3.

Gebios Davyanus Risso, 1822: 243.

Callianassa subterranea forma *pontica* Czerniavsky, 1884: 81 (part).

Callianassa (Callichirus) Pestae de Man, 1928a: 34, pl. 9 figs 16-16E; 1928b: 29, 111.

Callianassa algerica Lutze, 1938: 168, figs 22-26a, b, 27.

Callianassa candida – Giordani Soika 1943: 83 (part); 1946: 944. — Lewinsohn & Holthuis 1986: 20. —

°Koukouras *et al.* 1992: 223. — Dworschak 1992: 194; 1998a: 1535, figs 1, 3, 5-9 (part), tabl. 1; 1998b: 143. — Noël 1992: 81. — Falciai & Minervini 1996: 147, 4 figs. — d'Udekem d'Acoz 1996: 54; 1999: 154. — Sakai 1999a: 14, fig. 2. — *González-Gordillo *et al.* 2001: 279. — ?*Lindley *et al.* 2001: 46. — °Türkay 2001: 289. — Dworschak 2002: 64, figs 1a, b; fig. 2; tabl. 1 (part).

Callianassa laticauda – Heller 1863: 203.

Callianassa (Callichirus) laticauda – Pesta 1918: 204. — Bouvier 1940: 103, fig. 69.

Callianassa pestae – Manning & Štević 1982: 295. — García-Raso 1985: 21. — Froglija & Grippa 1986: 261.

Callianassa pestai – Holthuis 1953: 95, fig. 3. — *Dolgopolskaia 1969: 316, pls 32-34. — Mikashavidze 1981: 1417, fig. 2. — Türkay *et al.* 1987: 92.

Callianassa (Callichirus) pestai – Zariquiey Alvarez 1968: 230. — Kattoulas & Koukouras 1974: 344, fig. 1.

Callianassa pontica – *Dolgopolskaia 1954: 179, figs 1-4. — Štević 1972: 102. — de Saint Laurent & Božić 1976: 24, figs 5, 13, 21, 32. — Beaubrun 1979: 84, figs 58, 59, 68-70. — Monchartmont 1979: 71. — García Raso 1983: 323, fig. 3. — Thessalou-Legaki & Zenetos 1985: 311. — °Thessalou-Legaki 1986: 182.

Callianassa (Callichirus) pontica – Caroli 1946: 71; 1950: 190. — Makarov 1938: 73, 297, figs 27, 28. — Băcescu 1967: 231, fig. 105.

Callianassa (Callichirus) stebbingi – Pesta 1918: 101 (part), fig. 63.

Callianassa subterranea – Giard & Bonnier 1890: 362, figs 1, 3.

Callianassa tyrrhena – Forest & Guinot 1956: 31.

Pestaina candida – Öksnebjerg 2000: 78 *nomen nudum*.

Non *Callianassa pestae* – Lutze 1937: 6, figs 10-21; 1938: 167, figs 10-21 (= *C. subterranea* (Montagu, 1808)).

TYPE MATERIAL. — Neotype: ♀, from Kuvi Bay, south of Rovinj, Istria, Croatia, selected by Sakai 1999a (SMF 23572).

MATERIAL EXAMINED. — France. Banyuls, ex. collection Sollaud, No. ES 30, 1932, 2 ovig. ♀♀ cl. 14 and 16 mm, tl. 52 and 58 mm (figured) (MNHN Th 1358). — Villefranche, Old Harbour, *Travailleur*, 1886, 1 ♂ cl. 13 mm (MNHN Th 123). — Îles Cerbicales, Corsica, C. Monniot coll., VII.1994, 1 ♀ cl. 10.5 mm (MNHN Th 1348).

Portugal. Algarve, mudflat near Praia de Faro, just W of Faro, along lagoon, behind dunes, 2.XI.1974, excursion RMNH, stn 79, 1 ♂ (RMNH D 36281 as *Callianassa pestae*).

Spain. Cadaqués, NE Spain, VI.1950, leg. J. Fortuny, collection R. Zariquiey Alvarez, 2 ♂♂ (RMNH D 35799b as *Callianassa pestae*).

Italy. Naples, collection E. Caroli, received V.1959 from Zoological Station Naples, 7 ♂♂, 6 ♀♀ (RMNH D 13005, as *Callianassa pestae*). — Gulf of Naples, Italy, donated by E. Caroli, 2 ♀♀ (RMNH D 6587 as *Callianassa pontica*). — Lido di Staranzano, intertidal, P. Dworschak coll., 9.X.1984, 1 ♂, 2 ♀♀ (NHMW 6788). — Punta Sabbioni, Venice Lagoon, mud flat, P. Dworschak coll., 25.III.1989, 2 ♂♂, 1 ♀ (MNHW 6761). — Porto Cesareo, P. Parenzan coll., 1969, 1 ♀ cl. 10 mm (MNHN Th 214).

Adriatic. Norman coll., 1 ♂ (NHML 1997.322). — Kuvi, Rovinj, P. Dworschak coll., 11.VII.1997, 1 ♂, 1 ovig. ♀ (NHMW 15369).

Slovenia. Strunjan (near Piran), intertidal, P. Dworschak coll., IX.1985, 1 ♂, 1 ♀ (NHMW 6789).

Greece. Kreta, Stavros, C. d'Udekem d'Acoz coll., 4.VII.1987, 1 ♂, 1 ♀, 1 juv. (d'Udekem d'Acoz), 12.VII.1987, 2 ♂♂, 1 ♀ (d'Udekem d'Acoz); Kato Zakro, 21.VII.1987, 1 ♀ (d'Udekem d'Acoz). — Amvrakikos Kolpos, SE Koronissia, 2.5-3 m, C. d'Udekem d'Acoz coll., 16.VII.1993, 1 ♀ (d'Udekem d'Acoz). — SE Peloponesos, Epidavros Limeria, C. d'Udekem d'Acoz coll., 3.VII.1986, 1 ♂ (d'Udekem d'Acoz). — Khoklakos, Rhodos, don. Zoological Museum, Tel Aviv University, Israel, 13.X.1970, 2 ♂♂ (RMNH D 35802, as *Callianassa pestae*).

Israel. Haifa Bay, 11.VI.1963, leg. C. Lewinsohn, 1 ♂, 1 ♀ (RMNH D 35803 as *Callianassa pestae*).

Algeria. Castiglione, leg. R. Dieuzeide, V.1939 (material previously identified by Lutze as *Callianassa algerica*), 3 ♂♂ cl. 7.5-9 mm, 1 ♀ cl. 9 mm (MNHN Th 96); 21.VI.1931, 1 ♂ cl. 6.5 mm (MNHN Th 97); 23.IV.1929, 1 ♂ cl. 5 mm, 1 ♀ cl. 6 mm, 1 juv. cl. 4 mm (MNHN Th 98).

Morocco. Near Tanger, G. Buchet coll., 1901, 3 ♂♂ cl. 7.5-10 mm, 2 ♀♀ (1 ovig.) cl. 8 and 12 mm (MNHN Th 804).

Tunisia. Gulf of Tunis, R. B. Manning coll., 16.VIII.1973, 1 ♂, 1 ♀ cl. 9 mm, tl. 32 mm (figured) and 56 ♂♂, 37 ♀♀ cl. 6-9 mm, 40 juv. (MNHN Th 633); 1978, 1 ♂ cl. 12 mm (MNHN Th 626). — Les Bibans, Cherbonnier coll., 18.V.1955, 1 ♀ cl. 7 mm (assigned to *C. tyrrhena* by Forest & Guinot 1956) (MNHN Th 122). — Salammbô, Ingle & Manning coll., 18.II.1974, 1 ♂ (NHML 1997.320); on sand flat, 1 m or less, R. B. and B. A. Manning coll., 23.XI.1972, 7 juv. cl. 2.5-5 mm (MNHN Th 316). — Punic Port, Salammbô, M. de St Laurent coll., IX.1973, 7 ♂♂ cl. 6-13 mm, 2 ♀♀ cl. 7 mm, 5 juv. (MNHN Th 419); northern Punic Port, sandy mud, 5-20 cm, Manning, Forest and de Saint Laurent coll., 7.VIII.1973, 12 ♂♂ cl. 6-10 mm, 3 ♀♀ cl. 6.5-9 mm (MNHN Th 712).

DISTRIBUTION. — This species is mainly confined to the Mediterranean with a few specimens in nearby areas, Cadix Gulf in southern Spain (García Raso 1983, 1985) and Algarve, in southern Portugal.

DIAGNOSIS

Rostrum (Fig. 12A) with blunt tip. Telson (Fig. 12H) with proximal width about 1.3-1.5 times median length.

Eyestalk (Fig. 12A) with blunt tip or slightly pointed mesially, cornea disk-shaped, dorso-lateral or dorsal. Peduncles of A1 and A2 of approximately same length. Mxp1 (Fig. 12E) as figured. Mxp3 (Fig. 12F, G) propodus about 1.5 times as long as wide, lower border convex; ischium-merus length about 1.4-1.5 times merus width, dactylus digitiform, 2.5 to 3 times as long as wide.

Major P1 (Fig. 12D) merus with lower border straight or slightly convex; meral hook pointed distally, with denticles on lower border, posterior to distal point. Minor P1 (Fig. 12C) unarmed on lower border, carpus slightly narrower proximally than distally, about as wide as propodus and 1.6-2 times its length. Plp3-5 (Fig. 12I) with small *appendix interna*. Uropodal exopod (Fig. 12H) longer than distal width, dorsal plate with distal row of setae well apart from posterior border; endopod oblong, about 1.3-1.5 times length of telson, posterior border rounded.

Colour

Body creamy, tailfan sometimes yellowish, chelipeds always white (Dworschak pers. comm.).

Size

Medium, of cl. 6-16 mm, ovigerous ♀ of cl. 12-16 mm, tl. 50-58 mm.

ECOLOGY

Pestarella candida n. comb. was found in the Gulf of Tunis, in muddy sand with or without *Zostera*, at 20-30 m depth, together with *P. tyrrhena* n. comb. and *Upogebia pusilla* (de Saint Laurent & Manning 1982); but it occurs higher up in relation to intertidal level and in more muddy sediments (Dworschak 1992). It is also common in coarse sand or mud in the intertidal and shallow subtidal, at 7-9 m depth (García Raso 1983; Thessalou-Legaki & Zenetos 1985). Its burrow and functional morphology are reported in Dworschak (2002).

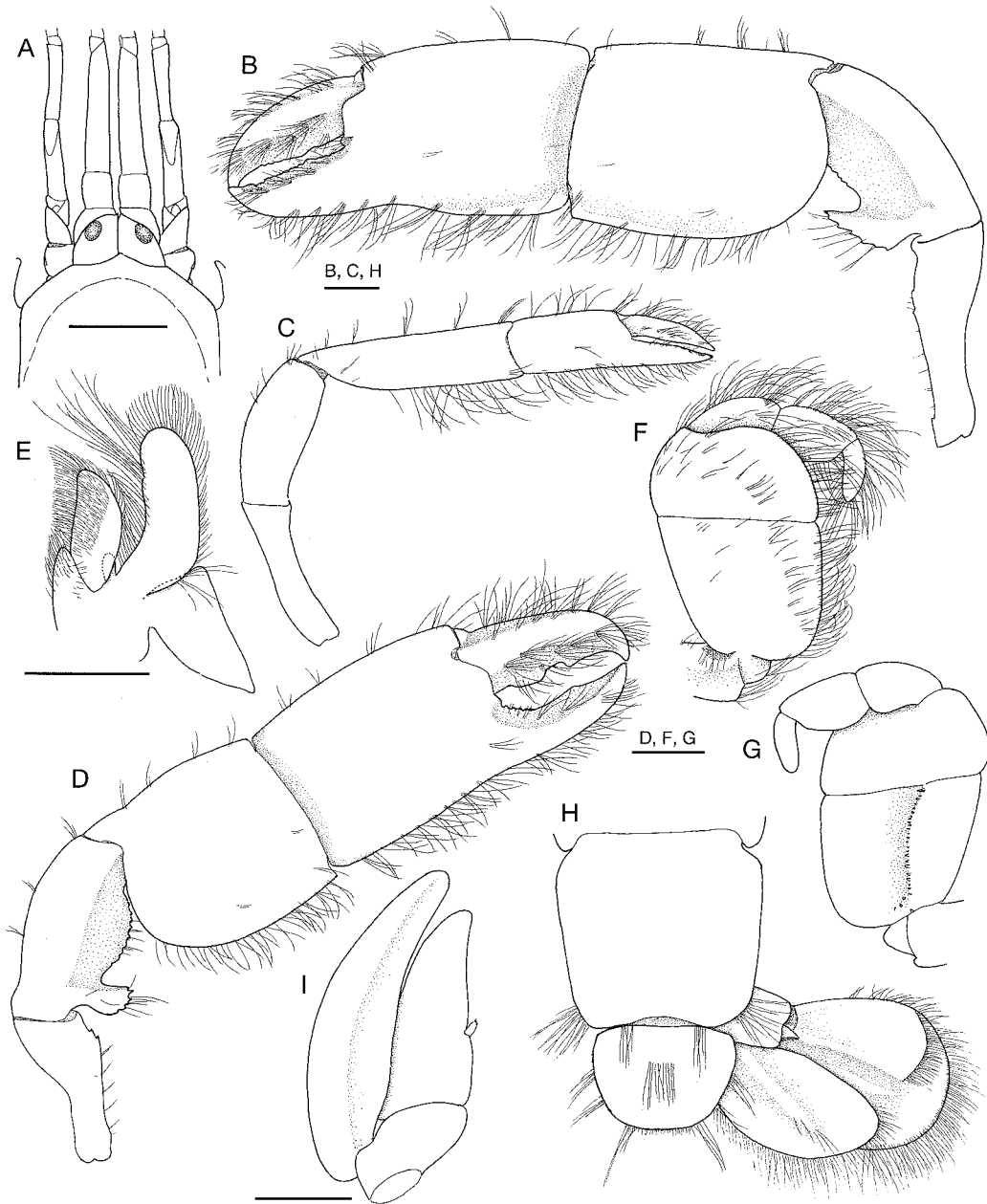


FIG. 12. — *Pestarella candida* (Olivi, 1792) n. comb.; **A**, ♀ from Castiglione, Algeria, anterior part of carapace (from de Saint Laurent & Božić 1976); **B, C, F-H**, ♀ from Banyuls, France (MNHN Th 1358); **D, E, I**, ♂ from Gulf of Tunis, Tunisia (MNHN Th 633); **B, D**, major pereopod 1; **C**, minor pereopod 1; **E**, maxilliped 1; **F, G**, maxilliped 3, lateral and mesial view; **H**, telson and uropods; **I**, pleopod 3. Scale bars: 2 mm.

REMARKS

This species has been known in the past under *Callianassa pontica* or *Callianassa pestae* (*pestai*) and the priority of these names was discussed by Holthuis (1953) and de Saint Laurent & Božić (1976). In 1986, Lewinsohn & Holthuis pointed out the priority of the name *candida*. Although both Dworschak (1992) and d'Udekem d'Acoz (1999) found Lewinsohn and Holthuis' arguments (based on the white chelipeds of the species) not quite convincing, especially given the rudimentary work by Olivi (1792), the name *candida* was used by both, and also in this work, for the sake of nomenclature stability. Sakai (1999a) selected a neotype (SMF 23572) for the species.

As reported by de Saint Laurent & Božić (1979: 26), a part of the material assigned by Lutze (1938) to *Callianassa algerica* and now deposited in MNHN (MNHN Th 96-98), belongs to the present species. The identity of the two forms is confirmed.

Variations occur in: 1) the eyestalk distal tip is blunt or mesiodistally produced; 2) the lower border of P1 merus is straight or convex; 3) the length ratios of carpus/propodus/fingers vary in both P1; and 4) the meral hook of the major cheliped is often relatively large with the lower border straight and a distinct pointed distal tip (Fig. 12B) or smaller with the lower border convex and the distal tip more discrete (Fig. 12D).

Besides characters given in the key, additional details differentiating *P. candida* n. comb. and its two congeners are presented under these latter species.

Pestarella tyrrhena (Petagna, 1792) n. comb.
(Figs 13; 14)

Astacus tyrrhenus Petagna, 1792: 418, pl. 5, fig. 3.

Callianassa laticauda Otto, 1821: 11; 1828: 345, pl. 21 fig. 3. — Stalio 1877: 107. — Stossich 1880: 206. — Carus 1885: 489. — Giard & Bonnier 1890: 365. — Caroli 1940: 73; 1946: 71; 1950: 189. — Zariquiey Alvarez 1946: 106. — Holthuis 1953: 91, fig. 2. — Picard 1957: 48. — Faure 1970: 773.

Callianassa sp. — Stebbing 1893: 184.

Callianassa (Callichirus) Stebbingi Borradaile, 1903: 547. — Selbie 1914: 100, pl. 14, figs 8-10.

Callianassa candida — Giordani Soika 1943: 83 (part).

Callianassa (Callichirus) laticauda — Borradaile 1903: 547. — Pesta 1918: 204. — de Man 1928a: 33, pl. 8 fig. 15-15d; 1928b: 28, 91, 92, 111. — Bouvier 1940: 102, fig. 69. — Gurney 1944: 82, figs 1D, 10, 11. — O' Céidigh 1962: 164.

Callianassa Stebbingi — Southern 1915: 35. — Steinitz 1933: 147.

Callianassa stebbingi — Bals 1926: 27. — Schellenberg 1928: 78, figs 59, 60. — Bodenheimer 1937: 281. — Lutze 1937: 6, figs 1-6; 1938: 165, figs 1-9. — Ott *et al.* 1976: 61, fig. 2 (part), tabl. 2, pls 1, 2 (part).

Callianassa (Callichirus) stebbingi — Pesta 1918: 201 (part).

Callianassa subterranea — H. Milne Edwards 1837a: 309; 1837b: 130, pl. 48 fig. 3-3 e. — Heller 1863: 202, pl. 6 figs 9-11. — Ortmann 1891: 55, pl. 1 fig. 10.

Callianassa tyrrhena — Holthuis 1947: 320, fig. 1; 1953: 91, 93, fig. 1; 1958: 8, fig. 4; 1977: 57; 1991: 252, 264, figs 457, 458. — Holthuis & Gottlieb 1958: 62 (part). — Bourdillon-Casanova 1960: 108. — Forest & Gantès 1960: 348. — Pérès & Picard 1964: 54. — Picard 1965: 59. — Bourdon 1965: 15. — Forest 1967: 6. — Le Gall 1969: 398, figs 1-4, tabs 1-5. — Pastore 1976: 107. — Thiriot 1976: 350, 367. — de Saint Laurent & Božić 1976: 22, figs 4, 12, 20, 31. — Glaçon 1977: 36. — Beaubrun 1979: 84, 90, figs 55, 60, 61, 66, 67. — de Saint Laurent & Le Lœuff 1979: 53. — Domenech *et al.* 1981: 149, figs 35, 36a, b. — Kocataş 1981: 162. — Adema *et al.* 1982: 26, fig. 7a-c. — Manning & Števcic 1982: 295. — García Raso 1983: 323, fig. 2. — Riedl 1983: 483, pl. 177, 2 figs. — Holthuis & Heerebout 1986: 62, fig. 83a. — d'Udekem d'Acoz 1986: 101, fig. 2; 1989: 176; 1996: 54; 1999: 155. — Thessalou-Legaki 1986: 182; *1990: 659, figs 1-5, tabs 1-4. — Dworschak 1987a: 421, fig. 1 (part); 1992: 206; 1998a: 1535, figs 1, 2, 4, 4-9 (part), tabl. 1; 1998b: 143, figs 1-4; 2000: 155, figs 1-6. — Thaker & Haritos 1989a: 63, figs 1-8; 1989b: 199, figs 1-7. — Moysse & Smaldon 1990: 520, fig. 10.13 (part). — Števcic 1990: 217. — Pérez Sánchez & Moreno Batet 1991: 189, 1 fig. — de Vaugelas 1991: 56, photo 1; 1998: 3, figs 1-3. — García Raso *et al.* 1992: 258. — Koukouras *et al.* 1992: 223; 1993: 195. — Noël 1992: 81. — Gruner 1993: 997, fig. 619. — Mayoral *et al.* 1994: 236. — Frogliani 1995: 7. — Gonzalez Pérez 1995: 136, photo 78. — Hayward *et al.* 1995: 432, fig. 8.52 (part). — Falcia & Minervini 1996: 147, 4 figs. — Ingle 1997: 78, fig. 7.3. — Thessalou-Legaki & Kiortsis 1997: 435, figs 1-4. — Thessalou-Legaki *et al.* 1997: 439, figs 1-3, tabs 1-3. — Sakai 1999a: 21. — Dworschak *et al.* 2000: 302. —

*González-Gordillo *et al.* 2001: 279. — Livory 2001: 33. — *Martin 2001: 78, 1 fig. — *Lindley *et al.* 2001: 46. — Markham 2001: tabl. 2. — °Türkay 2001: 289.

Callianassa (Callichirus) tyrrhena – Zariquiey Alvarez 1968: 230. — Monchartmont 1979: 72. — Neves 1974: 13, fig. 4.

Pestaina tyrrhena – Öksnebjerg 2000: 78 *nomen nudum*.

Non *Alpheus Tyrhenus* – Risso 1816: 94, pl. 2 fig. 2 (= *Pontonia pinnophylax* (Otto, 1821)).

Callianassa tyrrhena – Risso 1827: 54 (= *Pontonia pinnophylax* (Otto, 1821)). — Forest & Guinot 1956: 31; 1958: 10 (= *Pestarella candida* (Olivi, 1792) n. comb.). — Holthuis & Gotlieb 1958, fig. 13 (= *Callianassa subterranea* (Montagu, 1808)).

Callianassa stebbingi – Gottlieb 1953: 440 (= *Gourretia denticulata* (Lutze, 1937)).

Callianassa (Callichirus) stebbingi – Pesta 1918, fig. 63 (part) (= *Pestarella candida* (Olivi, 1792) n. comb.).

Callianassa (Callichirus) tyrrhena – Cottiglia 1983: 80, figs 27a, 30, 31 (= *Pestarella candida* (Olivi, 1792) n. comb.).

TYPE MATERIAL. — Whereabouts unknown.

MATERIAL EXAMINED. — **North Sea.** 53°10'N, 2°15'E, depth 20-22 fms, 16.IV.1963, don. Netherlands Institute of Sea Research, received VII.1973, 2 ♀♀ (RMNH D 29676). — Southern North Sea, 52°11'N, 4°21'E, 6-18.IX.1965, leg. D. Eisma, don. Netherlands Institute of Sea Research, 1 ♀ (poor condition, RMNH D 35804).

The Netherlands. Diepe Gat, 17 fms, in stomach *Raja clavata* (L.), don. Netherlands Institute of Sea Research, 1 ♀ poor condition (RMNH D 6203). — 30 miles NW of Ijmuiden, 7.VII.1950, leg. et don. Zoological Station Den Halder, 1 ♂ (RMNH D 7381). — Province of Zuid Holland, off Scheveningen, sand pumped from quadrant, 52°10'00.46"N, 4°02'28.81"E-52°12'00.02"N, 4°06'00.00"E-52°12'49.50"N, 4°04'52.08"E-52°10'59.90"N, 4°01'20.86"E, 2 broken ♀♀, several P1 (RMNH D 40764); c. 30 km off Scheveningen, sand pumped on the beach, H. L. Strack coll., 31.III.1991, 2 chela (RMNH D 40769). — Diepe Gat near Den Helder, 17 fms, 16.II.1951, from stomach of *Mustelus mustelus* (L.), leg. et don. Zoological Station Den Halder, 1 spec. (RMNH D 7634).

Great Britain. Jersey, Norman coll., 2 ♂♂, 2 ♀♀ (NHML 98.5.7.751.52). — Jersey, purchased 30.V.1950, 3 ♂♂, 1 ovig. ♀ (NHML 1950.8.22.13-17). — St Clement, Jersey, J. Sinel coll. (types of *Callianassa stebbingi*), 1 ♂, 1 ♀ (NHML 84.18). — St-Aubius Fort, Channel Islands, Jersey, R. Pike coll., 1 ♀ (NHML 1951.9.4.1-2).

France. Brittany, Pointe du Château, N of Tréguier, P. Noël coll., 28.II.1994, 2 ♂♂ cl. 9 and 15 mm, tl. 36.5 and 55.5 mm; 1 ♀ cl. 14 mm, tl. 57 mm (figured) (MNHN Th 1346). — St-Malo Bridge, N. Rabet coll., 1.VIII.1992, 1 ♀ cl. 13 mm, tl. 54.5 mm (figured) (MNHN Th 1345). — Réville, Normandie, J. I. Legrand coll., VII.1974, 1 ♀ cl. 12.5 mm (MNHN Th 422). — Wimereux, leg. R. P. Dolfus, 1905, 2 ♂♂ cl. 12.5 mm, 1 ♀ cl. 10 mm, and 1 ♀ cl. 12.5 mm, tl. 53 mm (figured) (MNHN Th 677). — Noirmoutiers, fine sand, Y. Gruet coll., 1.VII.1973, 1 ♂ cl. 15 mm (MNHN Th 600); 2.VII.1973, 1 ovig. ♀ cl. 13.5 mm (MNHN Th 601); 13.VIII.1972, 1 ♂ cl. 6 mm (MNHN Th 602); 1.VII.1973, 1 ovig. ♀ cl. 14 mm (MNHN Th 603). — Concarneau, Baron of St-Joseph coll., 1911, 1 ovig. ♀ cl. 13 mm (MNHN Th 227); Cabellou Beach, J. Forest coll., VIII. 1957, 1 ♂ cl. 10 mm (MNHN Th 781). — Rade of Brest, Point of Bindy, P. Noël coll., 23.I.1992, 2 ♂♂ cl. 5.5 and 8.5 mm (MNHN Th 1347). — Coutainville, Lessertisseur coll., IX.1962, 1 ♂ cl. 10.5 mm (MNHN Th 135). — Roscoff, F. Gentil coll., 1972, 1 ♂ cl. 12 mm, 1 ♀ cl. 9 mm (MNHN Th 221). — St-Servan, Brittany, Monot coll., 1 ♀ cl. 12.5 mm (MNHN Th 133); unknown coll., IV.1924, 1 ♀ cl. 10 mm (MNHN Th 555); E. Fischer coll., IX.1929, ex. coll. Sollaud, No. ES 33, 2 ♂♂ cl. 13 and 14.5 mm, 1 ♀ cl. 13.5 mm (MNHN Th 1364). — St-Malo, Vaillant coll., 2 ♀♀ cl. 7.5 and 8.5 mm (MNHN Th 132). — Dinard?, about 4.88 gr. W, 54.5 gr. N, 1930 (?), ex coll. Sollaud, No. ES 28, 1 ♀ cl. 12.5 mm (MNHN Th 1356). — Lancieux, about 4.99 gr. W, 52.2 gr. N, V.1927, ex coll. Sollaud, No. ES 36, 1 ♂, infested by isopod, with left Plp1 present (MNHN Th 1367). — Audierne, Finistère, Dr Piton don., No. 10.1924, 3 ♀♀ (2 ovig.) cl. 14-15 mm, 1 broken ♂ (MNHN Th 220). — Chausey Island, western Atlantic, northern area, flats exposed at low tides, A. Crosnier and P. Clark coll., IX.1992, 1 ♂, 4 ♀♀ (NHML 1992.1086). — Rocheneuf, between St-Malo and Mont-St-Michel, Ille-et-Vilaine, 20.VIII.1958, collection H. Nouvel, 1 ♀ (RMNH D 35806). — Mediterranean, 1 ♀ cl. 13.5 mm (MNHN Th 224).

Portugal. Olhão, C. d'Udekem d'Acoz coll., 18.VII.1988, 2 ♂♂ cl. 11 and 12 mm (d'Udekem d'Acoz). — Algarve, lagoon of Manta Rota, C. d'Udekem d'Acoz coll., 20.VII.1988, 1 ♂ cl. 8 mm, 3 ♀♀ cl. 9-11.5 mm (d'Udekem d'Acoz). — Algarve, mudflat near Praia de Faro, just W of Faro, 2.XI.1974, excursion RMNH, stn 79, 1 ♂, 3 ♀♀ (RMNH D 36278); 1 ♂, 3 ♀♀ (RMNH D 36279); 3.XI.1974, excursion RMNH, stn 80, 3 ♀♀ (RMNH D 36280). **Spain.** Playa Gentils in Cala de Cutip, N of Cabo de Creus, NE Spain, 12.VIII.1950, leg. et don. L. B. Holthuis, No. 127, 1 juv. (RMNH D 6735). — Playa Jonquet, N of Cadaqués, NE Spain, c. 0.5 m, sand and stones, 13.VIII.1950, leg. et don. L. B. Holthuis, No. 128, 1 juv. (RMNH D 6736). — Cala Junques, N of

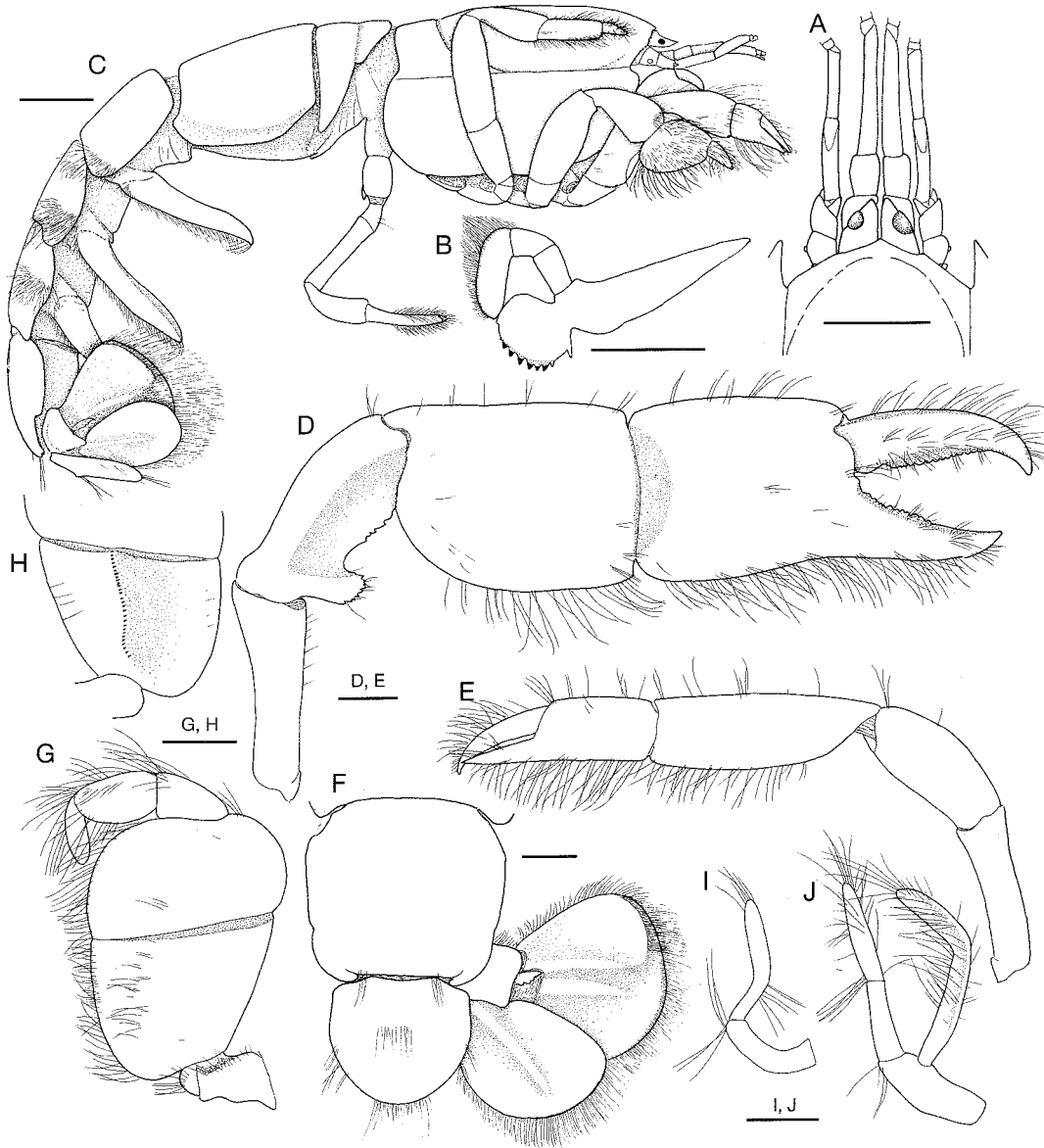


FIG. 13. — *Pestarella tyrrhena* (Petagna, 1792) n. comb.; **A**, ♂ from Morocco, anterior part of carapace (from de Saint Laurent & Božić 1976); **B**, **G**-**J**, ♀ from Wimereux, France (MNHN Th 677); **C**, ♂ from Pointe du Château, France (MNHN Th 1346); **D**-**F**, ♀ from St-Malo, France (MNHN Th 1345); **B**, Mandible; **C**, lateral view, pereopod 1 omitted; **D**, **E**, major and minor pereopod 1; **F**, telson and uropods; **G**, **H**, maxilliped 3 and mesial view of ischium; **I**, **J**, female pleopod 1 and 2. Scale bars: A, B, D-J 2 mm; C, 4 mm.

Port Lligat near Cadaqués, sand and stones, c. 0.2 m, 20.VIII.1959, leg. L. B. Holthuis, 1 juv. (RMNH D 15214). — Ria de Arosa, N of Cabo Cruz, stn 0.32, 23.VII.1962, low water mark, excursion Rijksmuseum van Natuurlijke Historie, 2 ♀♀ (RMNH D 18544). — Ria de Arosa, Peninsula Chazo, Playa

Barraña, sandy beach with some rocks, in burrows in sand between low and highwater marks, 7.VII.1963, excursion RMNH, stn 0.50, 2 ♂♂, 1 ♀ (RMNH D 20539); Ria de Arosa, Playa de Barrana, 10.VIII.1964, excursion RMNH, stn o.126, 1 ♂, 1 ovig. ♀ (RMNH D 23659); mouth of Ria de Arosa, Peninsula del

Grove, Punta San Vicente, littoral, burrowed in sand, 1.VI.1963, excursion RMNH, stn 0.44, 1 ♂ (RMNH D 20540). — Bay between Cadaqués and Cabo de Creus, Rierca de Junquet, 19.VIII.1950, leg. R. Zariquiey Alvarez, No. 1331, 3 ♂♂ (RMNH D 35805). — VIII.1951, leg. R. Zariquiey Alvarez, No. 1330, 1 ♀, 1 juv. (RMNH D 35807).

Italy. Porto Cesareo, P. Parenzan coll., 1969, 1 ovig. ♀ cl. 8.5 mm (MNHN Th 207). — Naples, 1920, C. Gravier, 1 ♀ cl. 13.5 mm (MNHN Th 125); Norman coll., 2 ♂♂, 2 ♀♀ (NHML 98.5.7.748-50); 1 ♂ (NHML 1910.2.4.91); 1 ♂, 1 ovig. ♀ (bought I.1925) (NHML 1950.1.2.113-114); 1876, leg. J. G. de Man, 3 ♂♂, 1 ♀, 2 ovig. ♀♀ (RMNH D 938); collection E. Caroli, received V.1959 from Zoological Station Naples, 23 ♂♂, 12 ♀♀, 4 ovig. ♀♀ (RMNH D 13007). — Gulf of Naples; V.1924, leg. et don. G. Stiasny, 1 ♀ (RMNH D 2391 as *Callianassa laticauda*); V.1957, leg. et don. J. H. Stock, Zoologisch Museum, Amsterdam, 4 ♂♂ (RMNH D 15213).

Greece. Kreta, Kato Zakro, C. d'Udekem d'Acoz coll., 21.VII.1987, 1 ♂ cl. 6 mm, 1 ovig. ♀ cl. 9 mm (d'Udekem d'Acoz). — Tersanas, W of Stavros, 2.VII.1987, 1 ♂ cl. 7 mm, 1 ♀ cl. 6 mm (d'Udekem d'Acoz). — Stavros, 4.VII.1987, 1 ovig. ♀ cl. 8.5 mm, 1 juv. (d'Udekem d'Acoz); 11.VII.1987, 2 ♂♂ cl. 6 and 9 mm, 1 juv. (d'Udekem d'Acoz). — Ormos Livadi, 9.VII.1987, 3 ♂♂ cl. 6-10 mm, 1 ovig. ♀ cl. 9 mm (d'Udekem d'Acoz). — W of Goudouras, 19.VII.1987, 4 ♂♂ cl. 6-11 mm (d'Udekem d'Acoz). — Island of Lesbos, Gavatas, C. d'Udekem d'Acoz coll., 8.VII.1992, 1 ♂ cl. 6.5 mm (d'Udekem d'Acoz). — Aegean Sea, *Calypso*, stn 779, NE of Salamina, 90-100 m, 21.IX.1955, Saronikos G., 1 ♀ (A.U.TH P 3505).

Israel. Tantura, 6.VII.1952, don. Tel Aviv Institute of Natural Sciences, 1 ♂ (RMNH D 13800). — Mediterranean coast near Tantura, S of Haifa, in rock-pools, 0-2 m, with Pro-nox fish poison, 3.V.1962, leg. A. Ben-Tuvia, E. Gilat and L. B. Holthuis, 2 ♂♂ (RMNH D 18545).

Morocco. 1 km S of Oued Yquem, 22 km S of Rabat, along highway Rabat-Casablanca, rocky coast with sandy lagoon, 19.X.1974, excursion RMNH, No. 39, 9 ♂♂, 2 ♀♀ (RMNH D 36277). — SPMOPO 1974, stn 034, Morocco, atlantic coast, on highway Rabat-Casablanca, south of Rabat, 19.X.1974, Exc. RMNH 1974, 1 ♀ (RMNH D 38482). — SPMOPO 1974, stn 038, 0-0.2 m deep, rock pools. 20.X.1974, Exc. RMNH 1974, 1 ♂ (RMNH D 38483).

Tunisia. R. B. Manning coll., 12.VIII.1973, 13 juv. (MNHN Th 1344). — Salammbô, grass flats, in sand, Manning, Forest and de Saint Laurent coll., 19.VIII.1973, 3 ♂♂ cl. 7-12.5 mm, 3 ♀♀ cl. 12-14 mm (MNHN Th 711).

Guinea. Témara, îles de Los, H. Gantès coll., No. 852, 14.III.1952, 1 ♀ cl. 11 mm (MNHN Th 131); No. 1696, 14.V.1953, 1 ♂ cl. 9.2 mm, 1 ♀ cl. 10 mm

(MNHN Th 128); No. 2312, 24.II.1955, 1 moult, broken (MNHN Th 129).

OTHER MATERIAL EXAMINED. — *Pestarella convexa* n. comb., Gambia, south of Cape of Bald, 18 m, unknown collector, 31.III.1954, 1 ovig. ♀ cl. 5 mm, tl. 24 mm (holotype), 1 ♂ tl. 24 mm, 1 ♀ tl. 18 mm (paratypes) (MNHN Th 617). — Mauritania *N'Diogo*, stn 61, in boulders, B. Richer de Forge coll., 18.IV.1982, 3 ovig. ♀♀ cl. 8-9.5 mm (MNHN Th 723).

Pestarella rotundicaudata n. comb., South Africa, Kowie, Port Alfred, A. Panther coll., V.1896, 1 ♂ cl. 8.5 mm (NHMW 6619).

DISTRIBUTION. — From Southern North Sea, Eastern Atlantic: Ireland (Selbie 1914), English Channel, Atlantic coasts of France, Spain, Portugal, Morocco to Guinea. Mediterranean including Adriatic (Števcíć 1990; Dworschak 1992) and Corsica (de Vaugelas 1991, 1998).

DIAGNOSIS

Carapace (Fig. 13A) with blunt tip, no rostral spine. Abdominal segments (Fig. 13C) unarmed, second largest, segments 3-5 with lateral tufts of setae. Telson (Fig. 13F) about as long as proximal width.

Eyestalk with blunt distal tip; cornea distinct, dorso-lateral or dorsal. A1 peduncle slightly longer than A2 peduncle (Fig. 13A). Md (Fig. 13B), Mxp1, Mxp2 (Fig. 14F, G) as figured; Mxp3 operculiform (Fig. 13G, H), ischium-merus length about 1.3-1.4 times merus width, propodus 1.5-1.7 times as long as wide, lower border convex; dactylus digitiform.

Major P1 (Fig. 13D) slightly stouter in male; meral lower border straight or slightly convex; meral hook with rounded, denticulated lower border. Minor P1 (Fig. 13C) unarmed, carpus slightly wider proximally than distally, wider than propodus.

P2-5 (Fig. 14B-E) as figured, P3 propodus with lower border slightly dentate.

Female Plp1 (Fig. 13I) uniramous, two-articulated; female Plp2 (Fig. 13J) biramous, endopod two-articulated. Uropodal exopod (Fig. 13F) about as long as proximal width, dorsal plate with distal row of setae at short distance and indistinct from posterior border; endopod slightly longer than telson.

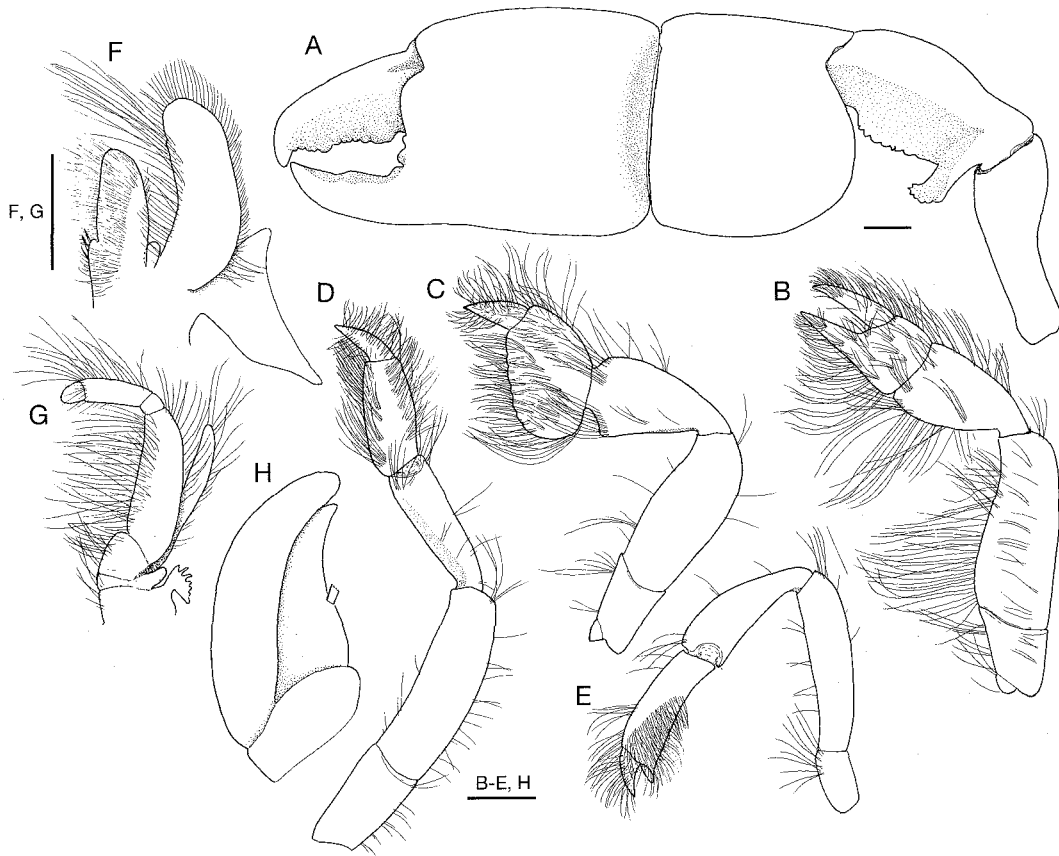


FIG. 14. — *Pestarella tyrrhena* (Petagna, 1792) n. comb.; **A**, ♂ from Pointe du Château, France (MNHN Th 1346), pereopod 1; **B-E**, ♀ from St-Malo, France (MNHN Th 1345), pereopod 2-5; **F-H**, ♀ from Wimereux, France (MNHN Th 677); **F, G**, maxilliped 1 and 2; **H**, pleopod 3. Scale bars: 2 mm.

Colour

General colour of body similar to that of *P. candida* n. comb., creamy with a slight tint of pink, tailfan sometimes yellowish, chelipeds usually slightly to bright pink (but sometimes completely white), ripe ovaries yellow to orange (Dworschak pers. comm.; d'Udekem d'Acoz 1999). A coloured photograph is presented in Perez Sanchez & Moreno Batet (1991) and González Pérez (1995).

Size

Largest specimens in material examined of cl. 12.5-15 mm, tl. 53-57.5 mm; average size of cl. 6-15 mm, ovigerous ♀ of cl. 8-15 mm, tl. 60 mm (Balls 1926).

Body length up to 67 mm in the British Isles (Moyle & Smaldon 1990).

ECOLOGY AND BIOLOGY

Pestarella tyrrhena n. comb. occurs in intertidal and shallow subtidal zones (Dworschak 1998a), in fine sand (d'Udekem d'Acoz 1986; Dworschak 1992), in muddy sand with or without *Zostera* seagrass (d'Udekem d'Acoz 1989; Števíčič 1990) and in mud (Le Gall 1969), at 5-20 m or deeper (Moyle & Smaldon 1990). Picard & Pérès (1964) and Picard (1965) considered this species as characteristic of a relatively undisturbed muddy substrate.

Aspects of biology studied

Feeding behaviour (Dworschak 1987a); cadmium, mercury bioaccumulation and their effects (Thaker & Haritos 1989a, b); reproductive output (percentage of mother weight devoted to egg production) (Thessalou-Legaki & Kiortsis 1997); physiological aspects in relation to pollution (Thessalou-Legaki *et al.* 1997); biometric analysis (Dworschak 1998a); abundance of population in Corsica (de Vaugelas 1991); relation between burrow architecture, feeding mode and structure of the sediments (de Vaugelas 1998); burrow and burrow construction with role of tegumental glands (Dworschak 1998b, 2000).

REMARKS AND VARIATIONS

This is the most common callianassid species along the French Atlantic coast and the European coast of the Mediterranean, with much confusion in nomenclature.

It was described by Otto (1821, 1828) under the name *Callianassa laticauda* but was often confused with *C. subterranea* (Montagu, 1808). In 1893, Stebbing reported some *Callianassa* material from Jersey which he considered distinct from *subterranea* and which was named later *Callianassa Stebbingi* by Borradaile (1903). De Man (1928a) showed its identity with *C. laticauda*.

Giordani Soika (1943) stated that *Cancer candidus* Olivi, 1792 was identical with *Callianassa laticauda* Otto, 1821, and that Olivi's name, being the older of the two, should be employed. On the other hand, Holthuis (1947) considered that the three names *Astacus tyrrhenus* Petagna, 1792, *Cancer candidus* and *Callianassa laticauda* actually referred to the same species. He (Holthuis 1953) definitely settled the question and presented the main reason why Petagna's name should be preferred over Olivi's (Petagna's figure is far superior). The species name *tyrrhena* (Petagna, 1792) has been used thereafter.

Variations occur in: 1) the lower border of major P1 merus which is straight or slightly convex; 2) the length ratio of carpus/propodus/fingers in major P1, with fingers often shorter in male than in female; and 3) the Mxp3 ischium (Fig. 13G) is often, not always, narrower proximally than dis-

tally and narrower than the merus. The colour pattern is also variable: whilst most specimens are more or less tinged with pink, specimens with completely white pereopods are occasionally found (d'Udekem d'Acoz pers. comm.).

Characters given for this species in the key are reliable but its European congeners can also be differentiated by the dorsal plate of the uropodal exopod: its setal distal row is at short distance and indistinct from the posterior border in *P. tyrrhena* n. comb. and well apart from the posterior border in *P. candida* n. comb. and *P. whitei* n. comb.

Pestarella whitei (Sakai, 1999) n. comb.

(Fig. 15)

Callianassa Davyana White, 1847: 70. — de Man 1928a: 37.

Callianassa whitei Sakai, 1999a: 23, fig. 4C. — °Türkey 2001: 289. — Dworschak 2002: 64, fig. 1c, d, tabl. 1 (part).

Callianassa candida – Dworschak 1992: 194 (part).

TYPE MATERIAL. — Holotype: ♂, from Kap Monsena, S Val Salina, Istria near Rovinj, Croatia (SMF 14033); paratype: same locality, ♂ (SMF 24574).

MATERIAL EXAMINED. — Croatia. Rovinj, leg. U. Pettke, VII.1982, 1 ♂ holotype cl. 11 mm, tl. 49 mm (data given by Sakai; no data label accompanying specimen) (figured, SMF 14033). — S Palu, Rovinj, intertidal under stones, Dworschak coll., 2.VIII.1982, 1 ♀ (just moulted) (NHMW 6902). — Montauro, Rovinj, boulder field in 3 m, sand under stones, J. Ott coll., VII.1988, 1 ♂ cl. 12 mm (NHMW 6778).

DISTRIBUTION. — Currently known only from Croatia.

DIAGNOSIS

Rostrum (Fig. 15A) with blunt tip, no rostral spine. Telson (Fig. 15D) with proximal width about 1.5 times median length.

Eyestalk short, distal tip blunt or slightly pointed mesially; cornea disk-shaped, dorso-lateral or dorsal. Peduncle of A1 longer and stouter than that of A2. Mxp3 (Fig. 13F) operculiform, ischium-merus length about 1.5-1.6 times merus width, propodus slender, about twice as long as wide, lower border nearly straight, dactylus digitiform, 2.5-3 times as long as wide.

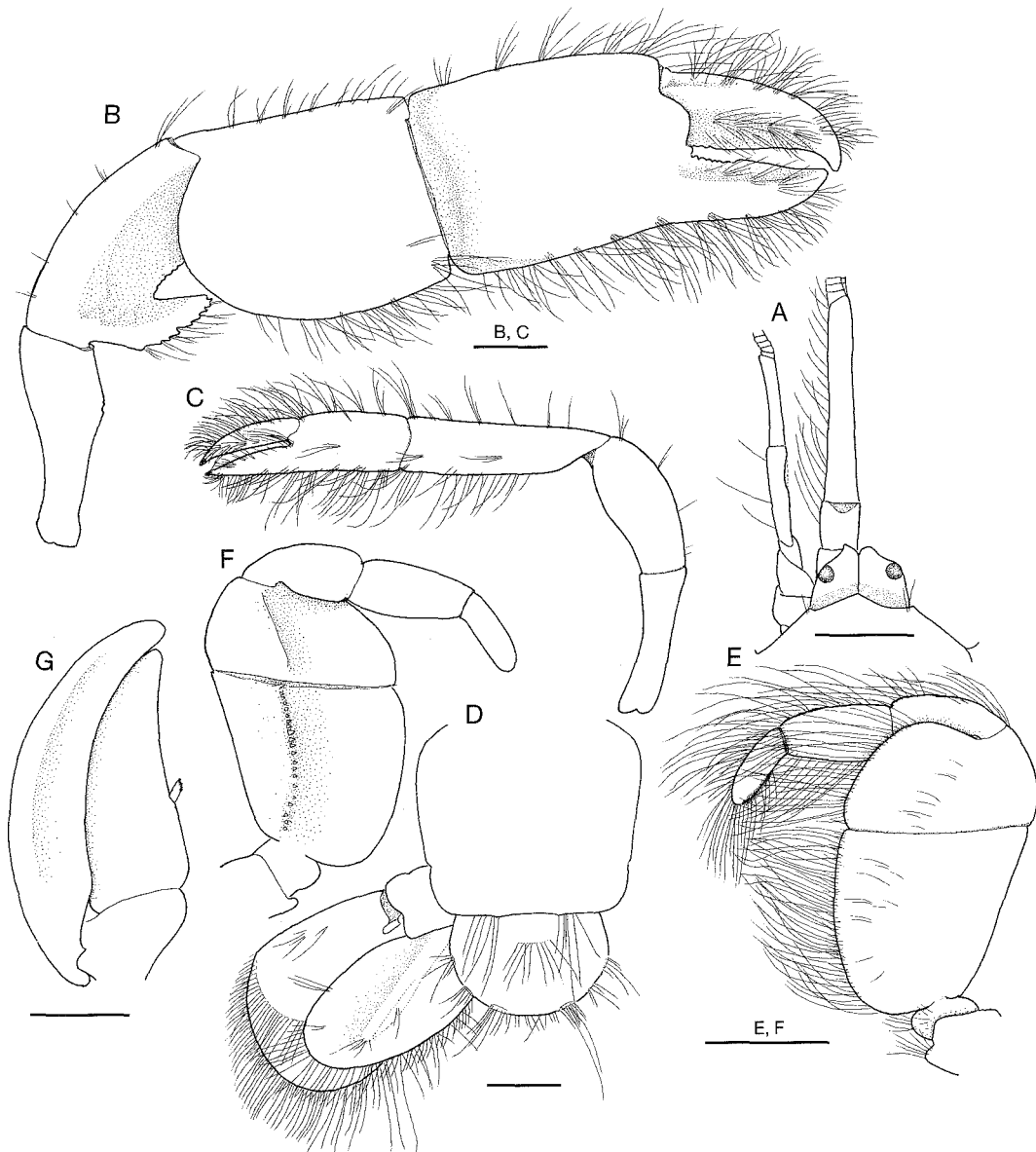


FIG. 15. — *Pestarella whitei* (Sakai, 1999) n. comb., holotype ♂ from Rovinj, Croatia (SMF 14033); A, D, after Sakai 1999a; A, anterior part of carapace; B, C, major and minor pereopod 1; D, telson and uropods; E, F, maxilliped 3, lateral and mesial view; G, pleopod 3. Scale bars: 2 mm.

Major P1 (Fig. 15B) merus with lower border straight or slightly convex, lower border of meral hook denticulated, pointed distally. Minor P1 unarmed (Fig. 15C), carpus with similar proximal and distal width, 2-2.5 times length of propodus.

Plp3-5 (Fig. 15G) with small *appendix interna*, projecting from inner border of endopod. Uropodal exopod (Fig. 15D) a little longer than distal width, dorsal plate with distal row of setae well apart from posterior border; endopod

elongated, nearly twice as long as telson, posterior border rounded.

Colour

Similar to *P. candida* n. comb. (Dworschak pers. comm.).

Size

Holotype: cl. 11-12 mm, tl. 49 mm.

ECOLOGY

Living in mud, under stones or in seagrass meadows, 0-4 m (Sakai 1999a; Dworschak 2002).

REMARKS

The chelipeds of the holotype (Sakai 1999a: fig. 4c, d) were probably figured *in situ* and certain features are inaccurate, e.g., the shape of the major P1 meral hook, or the length ratio of the carpus and propodus. The figures are also presented as mirror images, as if the major cheliped was on the left and the minor cheliped was on the right while it is actually the opposite. The two appendages are here detached from the body and laid flat for drawing (Fig. 15B, C). Their morphology is very similar to that of *P. candida* n. comb.

In his work on the fauna of the Adriatic, Pesta (1918: fig. 63, 63a, 63b) reported some material he assigned to *Callianassa stebbingi* (= *P. tyrrhena* n. comb.). Later, de Man (1928a: 34) and de Saint Laurent & Božić (1976: 24) placed it in *C. pestae* or *C. pontica* (= *P. candida* n. comb.), while Sakai (1999a: 23) considered it to belong to *P. whitei* n. comb.

The material examined by Pesta was probably a mixture of *P. candida* n. comb. and *P. tyrrhena* n. comb. (and also *P. whitei* n. comb.). Figure 63 of Pesta (1918) is likely to represent a specimen of the former species (meral hook of major P1 with pointed distal tip, uropodal exopod with setal row of dorsal plate well apart from posterior border). Figure 63a (an operculiform Mxp3) could be of either species, while figure 63b is clearly of *P. tyrrhena* n. comb. (telson about as long as wide, uropodal exopod with setal row of dorsal plate near posterior border). This material (or part of it) is still extant and housed at the Natur-

historisches Museum Vienna. It includes specimens of *P. candida* n. comb. (Dworschak pers. comm. and sketch) with an exception (NHMW 319) that could be a variation of *P. whitei* n. comb. (peduncle of A1 slightly longer than that of A2 in one side, about as long in the other; Mxp3 propodus slender).

Pestarella whitei n. comb. is similar to *P. candida* n. comb. in: 1) the eyestalk is short with the distal tip blunt or slightly pointed mesially; 2) the morphology of both P1; 3) the telson is wider than long; and 4) the uropodal exopod and endopod greatly exceed the telson. Distinguishing features are listed in the key and this species can be differentiated from its European congeners especially by the shape of its Mxp3 propodus (Fig. 15E, F). The latter is slender, approximately twice as long as wide, with the lower border nearly straight, while it is 1.5 times as long as wide, with the lower border convex in *P. candida* n. comb. and *P. tyrrhena* n. comb.

Pestarella whitei n. comb. is also similar to a non-European congener, but with a close distribution range, which is *P. convexa* n. comb. from Senegal (de Saint Laurent & Le Lœuff 1979: 73, fig. 10). It differs in: 1) the telson is about 1.5 times as wide as long in *P. whitei* n. comb. (1.3-1.4 times in *P. convexa* n. comb.); 2) uropods are more elongated, endopods nearly twice as long as telson in *P. whitei* n. comb. (uropodal endopod about 1.5 times as long as telson in *P. convexa* n. comb.); and 3) the uropodal exopod with the setal row of dorsal plate well apart from posterior border in *P. whitei* n. comb. (setal row of dorsal plate near posterior border in *P. convexa* n. comb.).

Subfamily CALLICHIRINAE Manning & Felder, 1991

TYPE GENUS. — *Callichirus* Stimpson, 1866, by original designation.

Genus *Calliapagurops* de Saint Laurent, 1973

TYPE SPECIES. — *Calliapagurops charcoti* de Saint Laurent, 1973, by original designation.

DIAGNOSIS. — Carapace with faint dorsal oval, long rostral and anterolateral spines; *linea thalassinica* complete. Abdominal somite 2 longest, longer than somite 6; telson wider than long, with rounded outline and transverse dorsal crest bearing spiniform setae.

Eyestalks cylindrical, length three to four times diameter of terminal corneas. A1 peduncle reaching approximately middle of much heavier A2 peduncle; antennal scale small. Epipod of Mxp1 with elongated anterior lobe. Epipod of Mxp2 small. Mxp3 operculiform, three or more meral spines on distal margin; propodus widened proximally, dactylus digitiform; exopod absent.

P1 unequal in males, subequal in females with numerous spines on lower border of ischium and merus. P4 chelate, with fixed finger approximately as long as dactylus; P5 chelate. Paired arthrobranch on Mxp3 and P1-4.

Plp1 uniramous, Plp2 biramous with small terminal *appendix interna* in both sexes, no *appendix masculina* in male. Plp2-5 foliaceous and biramous with *appendix interna* embedded in margin of endopod in both sexes. Uropodal endopod elongate ovate, longer than telson.

REMARKS

The genus *Calliapagurops* was established in 1973 for a new species, *Calliapagurops charcoti*, which was briefly diagnosed. The holotype and only known specimen was a damaged specimen, with the abdomen and pereopods 4 and 5 missing. The species was redescribed and partly figured by Sakai (1999a: 8, fig. 1) who erected a new subfamily, Calliapagropinae, for it. Recently, a new species, *Calliapagurops foresti* Ngoc-Ho, 2002, was described from the Philippines. The type material includes four specimens, three of them complete and in good condition. Their examination complements the diagnosis of the genus as given above. It also reveals that *Calliapagurops* is better placed in the subfamily Callichirinae *sensu* Tudge *et al.* (2000). The latter, which was synonymised with the Callianassinae by Sakai (1999a), is regarded as a valid subfamily (Ngoc-Ho 2002).

Calliapagurops charcoti de Saint Laurent, 1973 (Fig. 16)

Calliapagurops charcoti de Saint Laurent, 1973: 515. — Manning & Felder 1991: 771. — Sakai 1999a: 8, fig. 1. — Tudge *et al.* 2000: 141. — ?*Lindley *et al.* 2001: 46. — *Türkay 2001: 289. — Ngoc-Ho 2002: 540.

TYPE MATERIAL. — Holotype: ♀ from Azores, *Jean Charcot*, BIAÇORES, stn 109, 39°33'N, 31°17'W, 190-230 m, in shelly sand, 20.X.1971, cl. 9.5 mm without abdomen and P4, P5 (figured, MNHN Th 345).

DISTRIBUTION. — Only known from the type locality, at 190-230 m.

DIAGNOSIS

As for the genus, with details added: eyestalk reaching base of last article of A1 and not narrowing distally (Fig. 16A). Md (Fig. 16E), Mx1 (Fig. 16C), Mx2 (Fig. 16D), Mxp1 (Fig. 16B), Mxp2 (Fig. 16J) as figured. Mxp3 (Fig. 16K, L) with three or four spines on distal margin of merus. P1 (Fig. 16F, G) ischium with six or seven lower spines, merus with four to six lower spines, major P1 with both fixed finger and dactylus bearing low triangular tooth near midpoint of cutting edge. P4, P5, abdomen, telson, uropods and branchial formula unknown.

Colour

Unknown.

Size

Holotype and only known specimen of cl. 9.5 mm.

REMARKS

Although the holotype of this species was referred to by both de Saint Laurent (1973) and Sakai (1999a) as a male, it is a female. Differences between *C. charcoti* and its congener *C. foresti* are given in Ngoc-Ho (2002).

Subfamily EUCALLIACINAE Manning & Felder, 1991

TYPE GENUS. — *Eucalliax* Manning & Felder, 1991, by original designation.

REMARKS

This work considers the presence of an exopod on the Mxp3 an important taxonomic character. In the subfamily Eucalliicinae, it proposes to separate species having or lacking an exopod on the Mxp3.

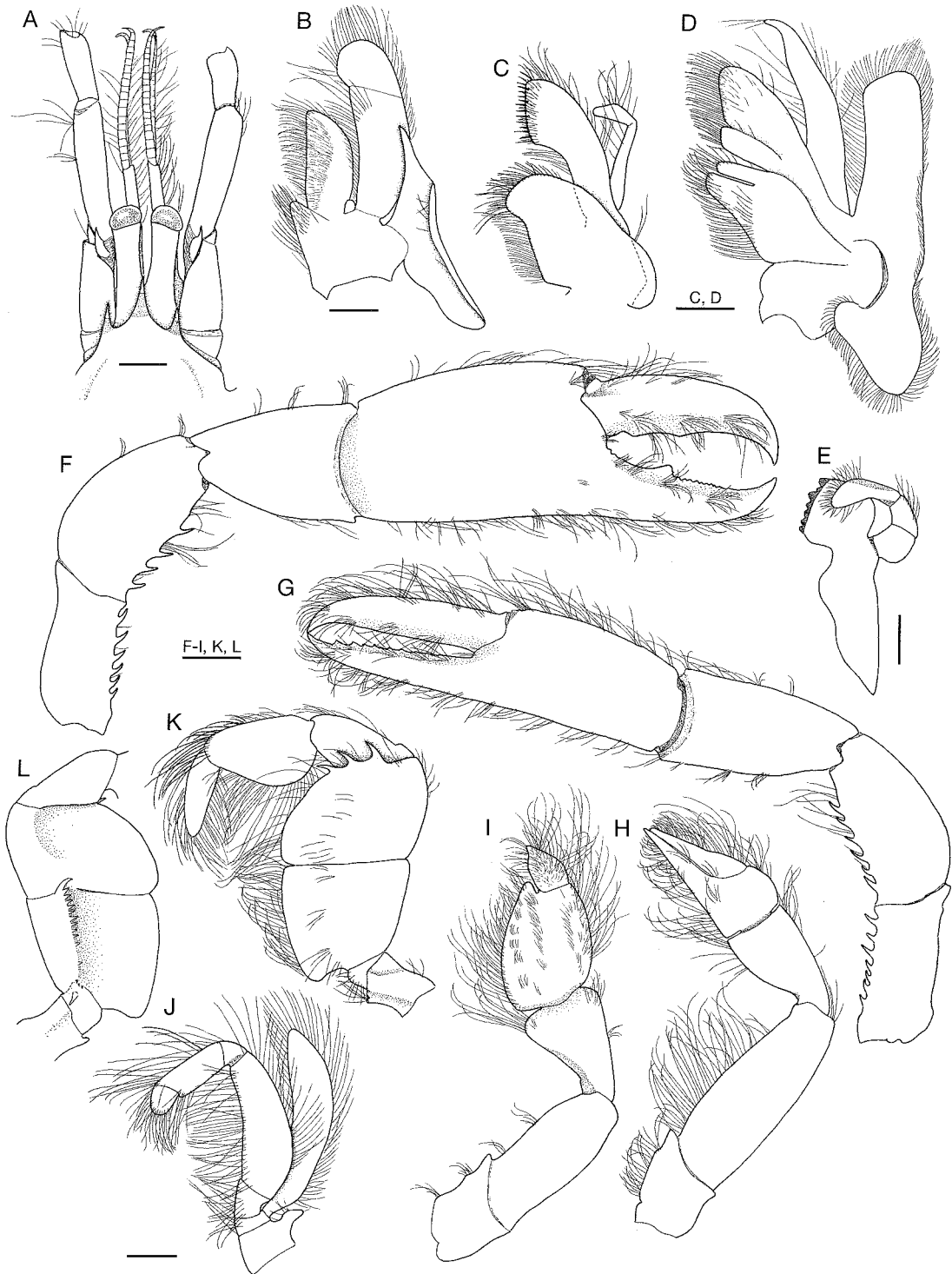


FIG. 16. — *Calliapagurops charcoti* de Saint Laurent, 1973, holotype, ♀ from Azores (MNHN Th 345); **A**, anterior part of carapace; **B**, maxilliped 1; **C**, **D**, maxillule and maxilla; **E**, mandible; **F**, **G**, major and minor pereopod 1; **H**, **I**, pereopod 2 and 3; **J**, maxilliped 2; **K**, **L**, maxilliped 3 and mesial view of ischium. Scale bars: A, F-I, K, L, 1 mm; B-E, J, 0.5 mm.

The genus *Eucalliax* erected by Manning & Felder (1991) as a distinct taxon from *Calliax* de Saint Laurent, 1973 is regarded as valid. Species lacking an exopod on the Mxp3 are placed either in *Calliax* s.s. or in *Eucalliax*.

Species having an exopod on the Mxp3 are assigned to either the genus *Paraglypturus* Türkay & Sakai, 1995 or *Calliaxina* n. gen.

Sakai (1999a) placed *Calliax punica* de Saint Laurent & Manning, 1982, *Calliax novaebritanniae* (Borradaile, 1899), *Calliax sakaii* de Saint Laurent, 1979 and *Calliax tooradin* Poore & Griffin, 1979 in the genus *Paraglypturus* with *Paraglypturus calderus* Türkay & Sakai, 1995 as the type species. The latter, nevertheless, differs from *Calliax punica* in significant features. It is proposed to exclude *Calliax punica* and its related species, *Calliax novaebritanniae*, *Calliax sakaii* from *Paraglypturus* and assign them to the new genus *Calliaxina* n. gen.

Genus *Calliax* de Saint Laurent, 1973

TYPE SPECIES. — *Callianassa (Callichirus) lobata* de Gaillande & Lagardère, 1966, by original designation.

DIAGNOSIS. — Carapace lacking dorsal oval; rostrum short, with blunt tip, rostral spine absent. Second abdominal segment 2 longest, longer than sixth, no lateral tufts of setae on segments 3-5. Telson about 1.2 times as wide as long, lateral border curved, posterior border straight or slightly convex.

Eyestalk about twice as long as wide, slightly flattened dorso-ventrally; cornea small, weakly pigmented. A1 peduncle shorter than that of A2. Mxp1 epipod large, tapering anteriorly. Mxp2 with small, leaf-like epipod. Mxp3 subpediform, propodus and dactylus rounded, exopod absent.

P1 unequal, dissimilar; fixed finger as long as dactylus and terminal in major P1, shorter than dactylus and subterminal in minor P1, with wide proximal gap and large triangular proximal tooth on cutting edge. P3 with small proximal heel on propodus, P5 subchelate. Paired arthrobranch on Mxp3 and P1-4.

Male and female Plp1 uniramous, male and female Plp2 biramous, all lacking *appendix interna*, male Plp2 with *appendix masculina* overreaching endopod. Plp3-5 biramous, foliaceous, *appendix interna* finger-like in both sexes. Uropodal endopod and exopod slightly longer than telson, with rounded posterior border; exopod with dorsal plate terminating in short distal setal row.

REMARKS

The genus *Calliax* was considered by Manning & Felder (1991: 781) as distinct from their newly established *Eucalliax*, but Sakai (1999a: 110) synonymised the two taxa. A number of *Calliax* and *Eucalliax* species have been described recently. Their examination confirms the validity of the latter genus and permits the former to be better defined.

Both *Calliax* and *Eucalliax* comprise species of Eucalliinae having no exopod on the Mxp3. It is proposed that two of these are assigned to *Calliax*: *Calliax lobata* (de Gaillande & Lagardère, 1966) (type species) and *Calliax doerjesti* Sakai, 1999.

A short diagnosis for the American species of *Eucalliax* was given by Manning & Felder (1991: 781). It is here amended after examination of new materials.

Rostrum triangular, rostral spine small or absent; cornea flattened, almost terminal. A1 peduncle shorter than that of A2. Mxp3 without exopod, operculiform. Chelipeds equal and similar, major without meral hook. Male and female Plp1 slender and uniramous, lacking *appendix interna*; male and female Plp2 slender and biramous, male Plp2 with *appendix interna* and *appendix masculina*, female Plp2 often with *appendix interna* (absent in *E. quadracuta*). Plp3-5 foliaceous and biramous in both sexes, with finger-like *appendix interna*. Telson over 1.5 times as wide as long, posterior border straight or slightly concave, often with dorsal transverse carina (absent in *E. bulimba*). Uropods longer than telson, endopod overreaching telson by at least half its length.

It can be noted that the Mxp3 figured by Manning & Felder (1991: fig. 3) and labeled as *Eucalliax* actually belongs to *Calliax lobata* as indicated in the legend.

The following species are placed in *Eucalliax*: *Eucalliax quadracuta* (Biffar, 1970) (type species), *Eucalliax aequimana* (Baker, 1907) n. comb., *Eucalliax bulimba* (Poore & Griffin, 1979) n. comb., *Eucalliax cearaensis* Rodriguez & Manning, 1992, *Eucalliax jonesi* (Heard, 1989), *Eucalliax mcilhennyi* Felder & Manning, 1994.

Differences between *Calliax* and *Eucalliax* (figures from Felder & Manning 1994 for *Eucalliax mcilhennyi*) species are: 1) A1 peduncle is distinctly shorter than that of A2, not overreaching the proximal border of the last article in *Calliax* (reaching mid-length of last article in *Eucalliax*); 2) Mxp3 is subpediform in *Calliax* (Fig. 17K, L) (operculiform in *Eucalliax* [Fig. 18P]); 3) P1 is unequal; the minor with the fixed finger shorter than and separated from the dactylus by a wide gap, bearing a large triangular proximal tooth in *Calliax* (Fig. 17D, E) (P1 is subequal and similar in *Eucalliax*, Fig. 18M, N); 4) male Plp2 has an *appendix masculina* (Fig. 18D), female Plp2 lacking an *appendix interna* in *Calliax* (Fig. 18B) (male Plp2 has both *appendix interna* and *appendix masculina* [Fig. 18L] female Plp2 often with *appendix interna* in *Eucalliax*, Fig. 18J); 5) the telson is less than 1.5 times as wide as long with the posterior border straight or slightly convex and no dorsal transverse carina in *Calliax* (Fig. 17J) (the telson is over 1.5 times as wide as long with the posterior border straight or slightly concave with the dorsal transverse carina often present in *Eucalliax* [Fig. 18O]); and 6) the uropods are about as long or slightly longer than the telson in *Calliax* (Fig. 17J) (uropods are longer with the endopod overreaching the telson by at least half of its length in *Eucalliax* [Fig. 18O]).

Calliax lobata (de Gaillande & Lagardère, 1966)
(Figs 17; 18)

Callianassa (Callichirus) lobata de Gaillande & Lagardère, 1966: 259, pls 1-4.

Calliax lobata – de Saint Laurent 1973: 514. — de Saint Laurent & Božić 1976: 28, figs 7, 15, 23, 27, 34. — Thessalou-Legaki & Zenetos 1985: 311. — °Thessalou-Legaki 1986: 183. — Manning 1987: 397. — Štević 1985: 313; 1990: 218. — Manning & Felder 1991: 783, figs 15f-j. — °Froglija 1995: 7. — Falciai & Minervini 1996: 145, 4 figs. — Sakai 1999a: 110, fig. 27a-c. — d'Udekem d'Acoz 1999: 155. — Tudge *et al.* 2000: 145, figs 3, 4 (cladogram). — °Türkyay 2001: 289.

TYPE MATERIAL. — Holotype: # ♂, Port-Miou, near Toulon, France, de Gaillande coll., X.1964 (MNHN Th 1296); paratypes: # 1 ♀ (MNHN Th 1298), 1 ♂, 1 ♀ (MNHN Th 84), 1 ♂, 1 ♀ (RMNH D 23011)

(# previously deposited in the Station marine d'Endoume, France).

MATERIAL EXAMINED. — France. Port-Miou, near Toulon, 5-10 m, de Gaillande coll., X.1964, ♂ holotype cl. 8 mm (figured) (dissected by the authors) (MNHN Th 1296); 1 ♀ paratype cl. 6 mm, tl. 21.5 mm, eyes and both Plp1, Plp2 lost (MNHN Th 1298), 1 ♂ paratype cl. 5 mm, tl. 20 mm, 1 broken ♀ paratype (figured) (MNHN Th 84), 1 ♂, 1 ♀ paratypes (RMNH D 23011); same data, 1 ♂ cl. 7 mm, poor condition (figured) (# MNHN Th 1297); same locality, de Gaillande coll., 1972, 3 ♂♂ tl. 21-25 mm, 1 ♀ tl. 25 mm (MNHN Th 674).

Croatia. Rovinj, Štević coll., 1983, 1 ♀ cl. 4.5 mm, tl. 18 mm approx., poor condition (MNHN Th 675).

OTHER MATERIAL EXAMINED. — *Eucalliax quadracuta* (Biffar, 1970), Venezuela, paratypes: 1 ovig. ♀ (MCZ 12872a), 1 ♂, 1 ♀ (MCZ 732). — *Eucalliax bulimba* (Poore & Griffin, 1979), Queensland, Australia, 1 ♀ (MVJ12184). — *Eucalliax aequimana* (Baker, 1907), King George Sound, 1 ♀ (MNHN Th 579).

DISTRIBUTION. — Mediterranean: Port-Miou (between Toulon and Marseille, France) (de Gaillande & Lagardère 1966; de Saint Laurent & Božić 1979); near Rovinj, Adriatic (Štević 1990), Aegean Sea (Thessalou-Legaki 1986).

DIAGNOSIS

As for the genus with details added: eyestalk (Fig. 17C) with cornea small, weakly pigmented, sometimes recognisable dorsodistally, according to de Saint Laurent & Božić (1976), indistinct at present in most material examined. Md (Fig. 18E) incisor process with triangular proximal and distal tooth separated by pectinate border. Mx1 (Fig. 18F) and Mx2 (Fig. 18G) as figured. Mxp3 (Fig. 17K, L) subpediform, ischium-merus length about 2.5 merus width, mesial ridge of ischium with eight or nine spinules; both propodus and dactylus rounded, propodus nearly as long as wide, dactylus more slender, about 1.3 as long as wide. P1 unequal (Fig. 17D, E), minor subchelate; both major and minor P1 with spines on lower border of ischium; lower border of merus with spines in major P1, unarmed in minor P1, carpus and propodus unarmed in both; fixed finger of major P1 with large median tooth on cutting edge, fixed finger of minor P1 shorter than dactylus with large triangular proximal tooth. P2-P5 (Fig. 17F-I) as figured. Telson (Fig. 17J) with

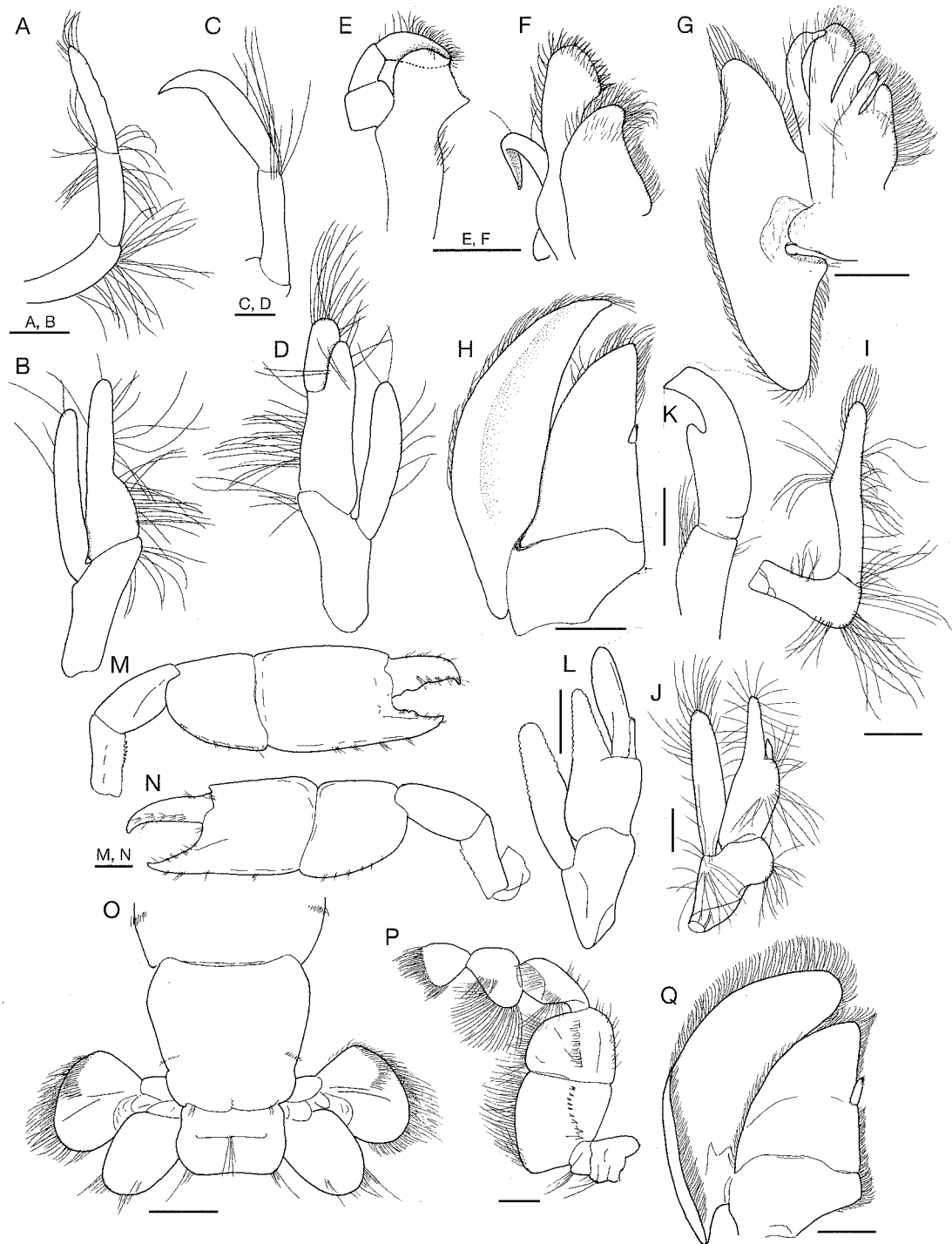


FIG. 18. — A-H, *Calliax lobata* (de Gaillande & Lagardère, 1966); A, B, paratype, ♀ from Toulon, France (MNHN Th 84); C, D, H, holotype from Port-Miou, France, ♂ (MNHN Th 1296); E-G, ♂ from Port-Miou (MNHN Th 1297); A, B, female pleopod 1 and 2; C, D, male pleopod 1 and 2; E, mandible; F, G, maxillule and maxilla; H, pleopod 3; I-Q, *Eucalliax mcilhennyi* Felder & Manning, 1994 (from Felder & Manning 1994); I, J, female pleopod 1 and 2; K, L, male pleopod 1 and 2; M, N, right and left pereopod 1; O, telson and uropods; P, maxilliped 3, mesial view; Q, pleopod 3. Scale bars: A-G, K, 0.5 mm; H-J, L-Q, 1 mm.

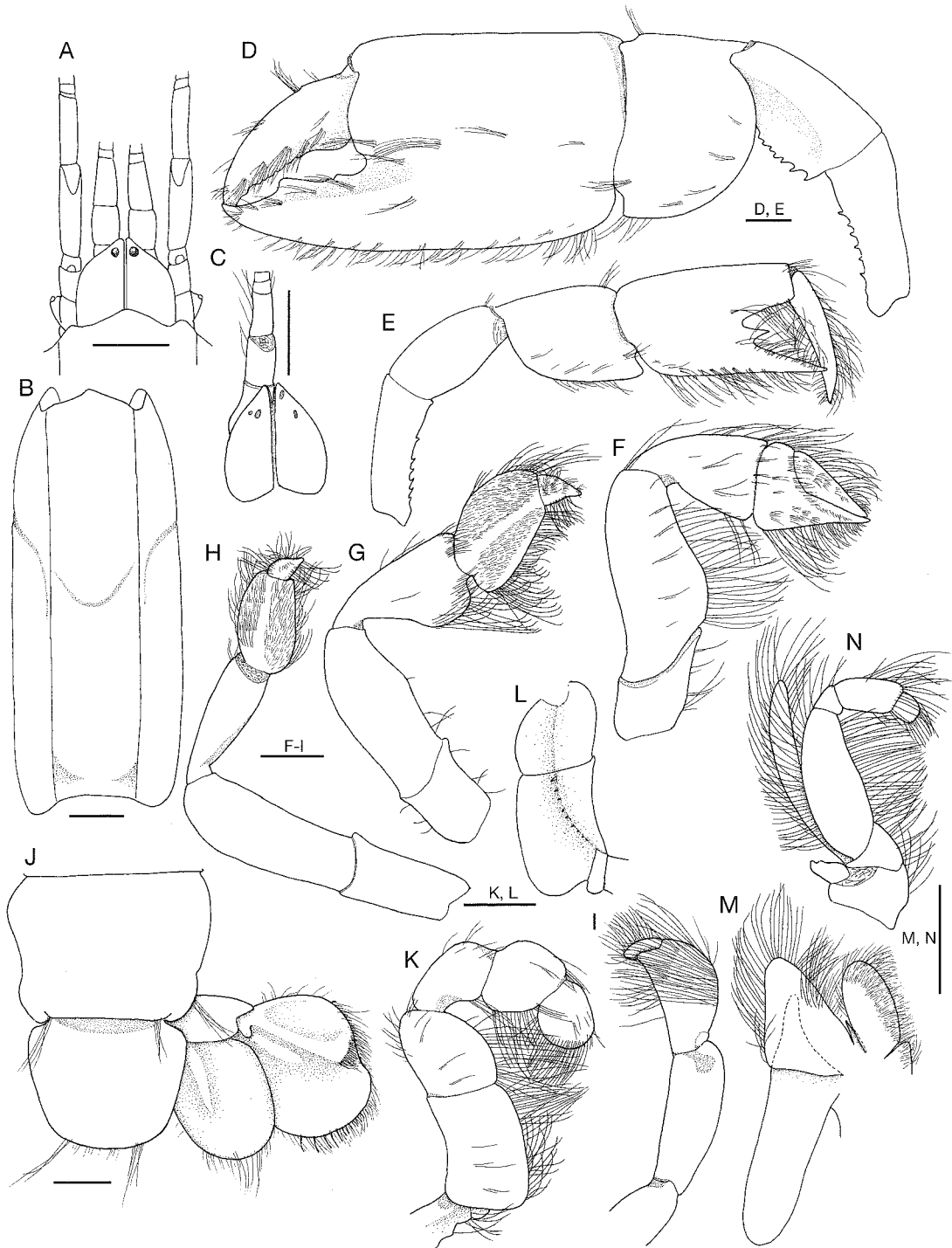


FIG. 17. — *Calliax lobata* (de Gaillande & Lagardère, 1966); **A**, ♀ from Toulon, France, anterior part of carapace (from de Saint Laurent & Božić 1976); **B-L**, holotype, ♂ from Port-Miou, France (MNHN Th 1296); **M, N**, ♂ from Port-Miou, France (MNHN Th 1297); **B**, carapace, dorsal view; **C**, eyestalk and left antennule; **D, E**, right and left pereopod 1; **F-I**, pereopod 2-4 and distal part of pereopod 5; **J**, telson and uropods; **K, L**, maxilliped 3 and mesial view of ischium; **M, N**, maxilliped 1 and 2. Scale bars: 1 mm.

posterior border weakly convex. Male and female Plp1, Plp2 (Fig. 18A, B and 18C, D) as figured. Plp3-5 (Fig. 18H) with finger-like *appendix interna*, sitting side by side with mesial border of endopod. Uropodal exopod (Fig. 17J) with lateral notch near upper third of posterior border.

Colour

Whitish (de Gaillande & Lagardère 1966).

Size

Small: cl. 4.5-8 mm, tl. 18-25 mm approximately.

ECOLOGY

Living in mud or silty mud, between 2 and 21 m (de Gaillande & Lagardère 1966; Štević 1990).

REMARKS

There is probably an error in the shape of the eyestalks presented by de Saint Laurent & Božić (1976) for this species and reproduced here (Fig. 17A). The female figured, from the type locality near Toulon, is at present in the collection of the MNHN (MNHN Th 674). The eyestalks are not as wide as depicted (about 0.7 time as wide as long) nor are they as wide in the holotype (Fig. 17C) or paratypes (see Sakai 1999a: fig. 27a) (about 0.45-0.5 time as wide as long).

Genus *Calliaxina* n. gen.

Calliax – de Saint Laurent & Manning 1982: 211.

TYPE SPECIES. — *Calliax punica* de Saint Laurent & Manning, 1982, by present designation.

SPECIES INCLUDED. — *Calliaxina novaebritanniae* (Borradaile, 1899) n. comb., *Calliaxina sakaii* (de Saint Laurent, 1979) n. comb.

ETYMOLOGY. — The species name refers to its relationship with *Calliax*. The gender is feminine.

DIAGNOSIS. — Carapace lacking dorsal oval, with transverse suture posterior to cervical groove. Rostrum broadly triangular with pointed tip or small rostral spine, pointed lateral projection on either side. Second abdominal segment largest, slightly larger than sixth, lateral tufts of setae present on segments 3-5. Telson approximately 1.2-1.6 times as wide as long, latero-

posterior angles rounded, posterior border straight or slightly concave in median part.

Eyestalk weakly flattened dorsoventrally; cornea disk-shaped. A1 peduncle shorter than that of A2. Mxp1 endopod elongate, epipod large, tapering distally. Mxp2 with bilobed epipod and single arthrobranch. Mxp3 operculiform, propodus with lower border strongly expanded proximally, dactylus rounded, exopod present.

P1 equal and similar; P3 with heel on proximal lower border. P4 propodus linear. P5 subchelate.

Single arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-4.

Male Plp1 uniramous with *appendix interna*. Male Plp2 biramous with *appendix interna* and *appendix masculina*. Female Plp1 uniramous, female Plp2 biramous with finger-like *appendix interna*. Plp3-5 biramous, foliaceous, *appendix interna* finger-like, sitting side by side with mesial border of endopod. Uropodal endopod overreaching telson by about half its length; dorsal plate on exopod with distal setal row well apart from rounded posterior border.

REMARKS

Differences between the genera *Calliax*, *Calliaxina* n. gen. and *Paraglypturus*, based on their type species *Calliax lobata*, *Calliaxina punica* n. comb. and *Paraglypturus calderus* Turkey & Sakai, 1995 are presented in Table 1.

De Saint Laurent & Manning (1982) stated that *Calliax lobata* and *Calliaxina punica* n. comb., both from the Mediterranean, were significantly different. They actually differ, as listed above, by many characters, the most important of which concern the morphology of the Mxp3, the P1, and also the male and female Plp1, Plp2.

Calliaxina n. gen. and *Paraglypturus* (Fig. 20K-O) (see also Turkey & Sakai 1995: figs 2-6) are similar in having an exopod on the Mxp3 but the ischium-merus shape differs (operculiform in *Calliaxina* n. gen., Fig. 19K, subpediform in *Paraglypturus*, Fig. 20K). Other discrepancies are: 1) the pointed rostrum and anterolateral projections are present in *Calliaxina* n. gen. (Fig. 19A, E) (absent in *Paraglypturus*); 2) Mxp2 is with arthrobranch in *Calliaxina* n. gen. (without in *Paraglypturus*); 3) P1 are subequal, similar, laterally compressed in *Calliaxina* n. gen. (Fig. 19C) (unequal, dissimilar, not compressed in *Paraglypturus*); 4) male Plp1 bears an *appendix interna* in *Calliaxina* n. gen. (Fig. 20C) (not in

TABLE 1. — Differences between the genera *Calliax* de Saint Laurent, 1973, *Calliixina* n. gen. and *Paraglypturus* Türkay & Sakai, 1995.

Characters	<i>Calliax</i>	<i>Calliixina</i> n. gen.	<i>Paraglypturus</i>
Pointed rostrum or rostral spine	absent	present	absent
Anterolateral projections on carapace	absent	present	absent
Suture line on carapace	absent	present	absent
Eye corneas	small, indistinct	small, disk-shaped	large, globulous
Mxp2 arthrobranch	absent	present	absent
Mxp3 ischium-merus	subpediform	operculiform	subpediform
Mxp3 exopod	absent	present	present
P1	unequal, dissimilar, laterally compressed	subequal, similar, laterally compressed	unequal, dissimilar, massive
P3 propod: lower proximal heel	<i>small</i> absent	present	present
Male Plp1: <i>appendix interna</i>	absent	present	absent
Male Plp2: <i>appendix interna</i>	absent	present	present
Male Plp2: <i>appendix masculina</i>	present	present	present
Female Plp2: <i>appendix interna</i>	absent	present	present
Plp3-5: <i>appendix interna</i>	finger-like	finger-like	stubby
Uropodal endopod/telson	overreaching about one-third length	overreaching about half length	overreaching about two-thirds length or more

Paraglypturus, Fig. 20M); 5) the *appendix interna* on Plp3-5 is digitiform in *Calliixina* n. gen. (Fig. 20G) (stubby in *Paraglypturus*, Fig. 20Q); and 6) the uropodal endopod overreaches the telson for at most half of its length in *Calliixina* n. gen. (Fig. 19D) (it is much longer in *Paraglypturus*).

Paraglypturus calderus material was taken from hydrothermally influenced sediments of the Mariana Arc. This is an environment of hot water (porewater temperature of over 50°C) and shallow depth (64-114 m) (Türkay & Sakai 1995). Besides characters shown above in comparison with *Calliixina* n. gen., this species displays a few others of unknown significance (Türkay & Sakai 1995: figs 3, 6): 1) eyestalks are weakly flattened dorso-ventrally with prominent, globulous, subterminal, well pigmented corneas; 2) the uropodal endopod in large males and females bears a yellow transparent circular structure on lower plate; and 3) eggs are small (0.2 mm in diameter) and attached to the Plp1 only in most females (seven/eight females), larger (0.5 mm in diameter) and attached to Plp1-5 in one female (Türkay & Sakai 1995: 29). Eggs are also few (less than 10 per female in sample SMF 22949 including three females).

Considering the morphological dissimilarities alone, differentiation between *Calliixina* n. gen. and *Paraglypturus* seems justified. *Paraglypturus*

calderus, nevertheless, shares with members of Callianassidae, and the Eucalliicinae in particular, many characteristics: 1) absence of a dorsal oval on the carapace; shape of eyestalks; 2) A1 peduncle shorter than that of A2; 3) Mxp3 propodus and dactylus ovate; 4) *appendix masculina* present on male Plp2; and 5) a dorsal plate present on the uropodal exopod. Its remote position in Tudge *et al.*'s (2000) cladogram as the sister taxon of all other callianassids is enigmatic.

Callianassa tooradin Poore & Griffin, 1979 was placed in *Paraglypturus* by Sakai (1999a). It shares similarities (see Poore & Griffin 1979: fig. 36) with *Paraglypturus calderus* in: 1) absence of a pointed rostrum and anterolateral projections on the carapace; 2) subpediform Mxp3 with exopod; 3) P1 unequal; 4) *appendix interna* absent from male Plp1; and 5) uropods much longer than the telson. There are differences: 1) small eye corneas instead of large, globulous; 2) minute Mxp1 endopod instead of elongate; 3) arthrobranch present on Mxp2; and 4) *appendix masculina* absent from male Plp2. Nevertheless, the similarities listed above, the morphology of Mxp3 especially, link the two species. It is proposed here that *Paraglypturus tooradin* (Poore & Griffin, 1979) provisionally remains in that genus as suggested by Sakai pending additional material for study in future.

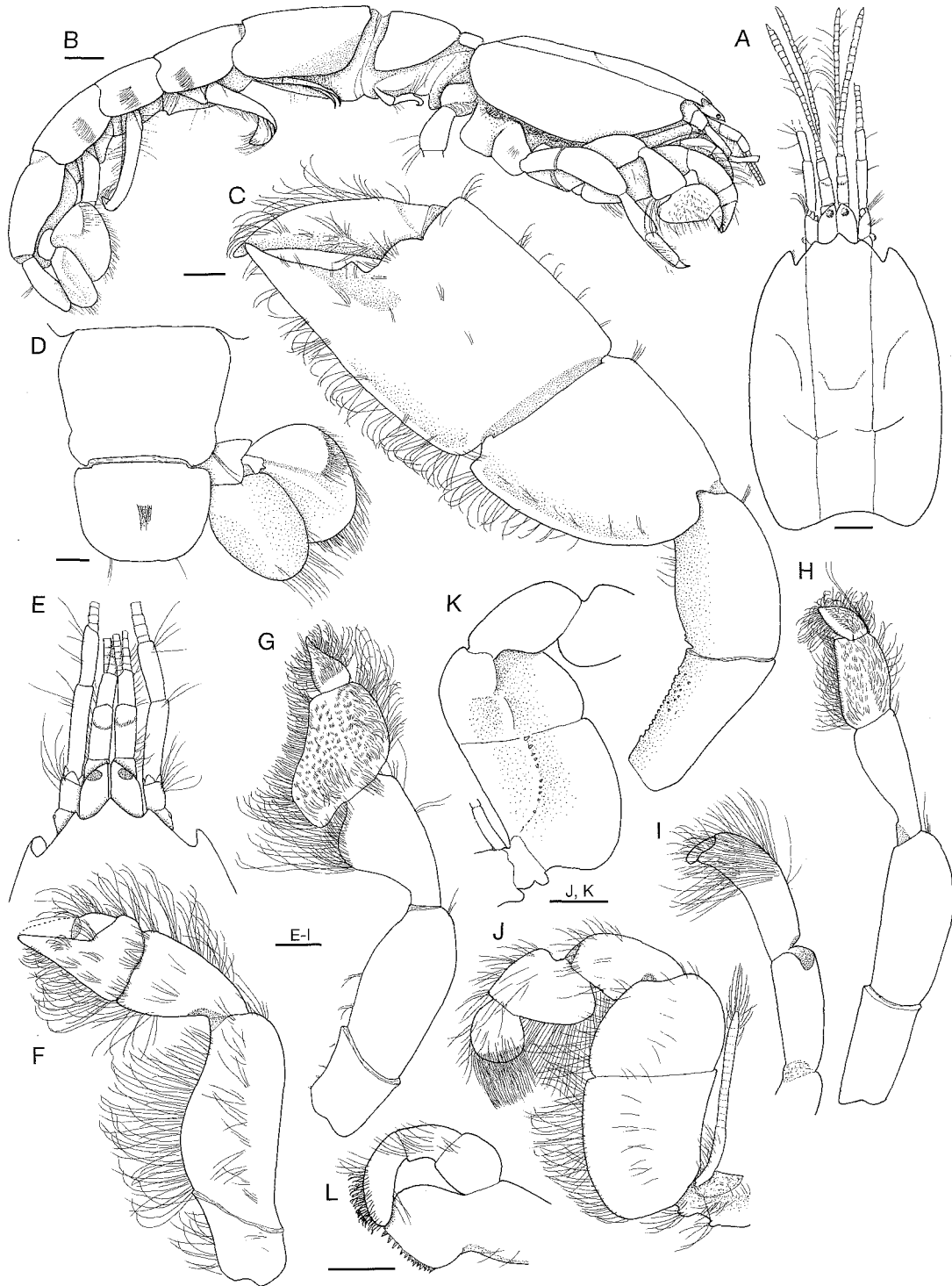


FIG. 19. — *Calliaxina punica* (de Saint Laurent & Manning, 1982) n. comb.; **A**, paratype, ♂ from Gulf of Tunis, Tunisia, carapace, dorsal view (from de Saint Laurent & Manning 1982); **B-L**, ♀ from Le Brusq, France (MNHN Th 1402); **B**, lateral view, pereopod 1 and 5 omitted; **C**, pereopod 1; **D**, telson and uropods; **E**, anterior part of carapace; **F-I**, pereopod 2-4 and distal part of pereopod 5; **J, K**, maxilliped 3 and mesial view of ischium, merus, carpus; **L**, mandible. Scale bars: A, C-K, 1 mm; B, 2 mm; L, 0.5 mm.

Calliuxina punica

(de Saint Laurent & Manning, 1982) n. comb.

(Figs 19; 20)

Calliux punica de Saint Laurent & Manning, 1982: 211, figs 1-6. — Thessalou-Legaki 1986: 183. — °Frogia 1995: 7. — Falciai & Minervini 1996: 145, 3 figs. — d'Udekem d'Acoz 1996: 58; 1999: 155. — Tudge *et al.* 2000: 156.

Paraglypturus punica – Sakai 1999a: 122. — °Türkyay 2001: 289. — Noël 2002: 240.

Calliux sp. – de Saint Laurent & Božić 1976: 29, figs 8, 16, 24, 35.

TYPE MATERIAL. — Holotype: ♂ from Gulf of Tunis, Tunisia, R. B. Manning coll., 27.I.1973 (USNM 172539); paratypes: same locality and collector, 26.IV.1973, 2 juv. (MNHN Th 563); R. B. Manning and M. L. Jones coll., 16.VIII.1973, 6 ♂♂, 4 ♀♀ poor condition (MNHN Th 565).

MATERIAL EXAMINED. — France. Le Brusuc, Var, muddy sand, 0.5 m, P. Noël coll., 14.XI.1997, 1 ♀ cl. 11 mm, tl. 40 mm (figured) (MNHN Th 1402).

Mediterranean (probably). Collection Sollaud ES 27, no date, 1 ♂ cl. 13 mm, tl. 42 mm approx. (abdomen broken) (figured) (MNHN Th 1355).

Greece. NW Kreta, northern part of Ormos Livadi, C. d'Udekem d'Acoz coll., 9.VII.1987, 1 ovig. ♀ cl. 9 mm, tl. 39 mm (MNHN Th 1403).

Tunisia. Gulf of Tunis, Salammbô, muddy sand, 0.5-1 m, R. B. Manning coll., 26.IV.1973, 2 juv. paratypes, cl. 3 and 3.5 mm, tl. 12 and 12.5 mm (MNHN Th 563). — Korbous, between Sidi Rais and Ain Kotor, in sea grass, about 0.5 m, R. B. Manning and M. L. Jones coll., 16.VIII.1973, 6 ♂♂, 4 ♀♀ paratypes tl. 12-26 mm poor condition (MNHN Th 565). — Gulf of Tunis, R. B. Manning coll., no date, 2 juv. cl. 3 and 4 mm (MNHN Th 562); 30.V.1973, 1 ♂ cl. 6.5 mm (MNHN Th 564).

OTHER MATERIAL EXAMINED. — *Calliuxina sakaii* (de Saint Laurent, 1979) n. comb., Japan, Tomioka, western Kyushu, 1 ♂ holotype (MNHN Th 312); 1 ♀ paratype (MNHN Th 311). — *Paraglypturus calderus* Türkay & Sakai, 1995, Marianas, N Rim of Esmeralda Caldera, 6 ♂♂, 5 ♀♀ (3 ovig.) paratypes (SMF 22950). — *Paraglypturus tooradin* (Poore & Griffin, 1979), Western Port, Victoria, Australia, 2 juv. paratypes (NMV J 302), 1 ♂ paratype (NMV J 303).

DISTRIBUTION. — Mediterranean: S of France; Tunis, Sardinia, Naples (de Saint Laurent & Manning 1982), Ionian and Aegean seas (Thessalou-Legaki 1986), W of Kreta (d'Udekem d'Acoz 1996).

DIAGNOSIS

Details added to diagnosis for the genus: rostrum broadly triangular with pointed tip, not reaching middle of eyestalks (Fig. 19A, E). Second abdo-

minal segment largest, lateral tufts of setae on segments 3-5 (Fig. 19B). Telson (Fig. 19D) approximately 1.2 times as wide as long, posterior border straight in median part.

Eyestalk larger and more prominent in juvenile than in adult. Mandible (Fig. 19L) incisor process with sharp teeth. Mx1 (Fig. 20A) and Mx2 (Fig. 20B) as figured. Mxp1 (Fig. 20C) endopod elongate, epipod large, tapering distally. Mxp2 (Fig. 20D) exopod overreaching merus of endopod; bilobed epipod and single arthrobranch present. Mxp3 (Fig. 19J, K) ischium-merus length less than twice merus width (more slender in small specimens of tl. < 20-25 mm), mesial ridge of ischium with nine or 10 spinules; dactylus rounded, slightly longer than wide; exopod present, reaching mid-length of merus in adult, smaller in juvenile.

P1 equal and similar (Fig. 19C), lower border of ischium and proximal lower border of merus with tubercles or denticles; carpus and propodus unarmed, lower border weakly heeled, propodus with elongate depression near base of fixed finger, cutting edge of latter bearing large triangular tooth near base or near mid length; dactylus approximately as long as palm, unarmed. P2 (Fig. 19F) merus with long setae on lateral surface. P3-P5 (Fig. 19G-I) and uropods (Fig. 19D) as diagnosed for the genus.

Colour

Orange-red on body and distal part of P1 from carpus onwards (specimen from Le Brusuc, Var; Noël pers. comm.) (de Saint Laurent & Manning 1982). The body is sometimes whitish and pereopods pure white (d'Udekem d'Acoz 1996).

Size

Specimens can reach large size, up to 65 mm in total length (ovigerous ♀ from Tunis, according to de Saint Laurent & Manning 1982). The types comprise however mostly juveniles or small specimens. Other material examined includes specimens of medium size: cl. 11 mm, tl. 40 mm.

ECOLOGY

This species lives in sand or muddy sand with or without seagrass, between 0.25-1 m depth (de Saint Laurent & Manning 1982 and present material).

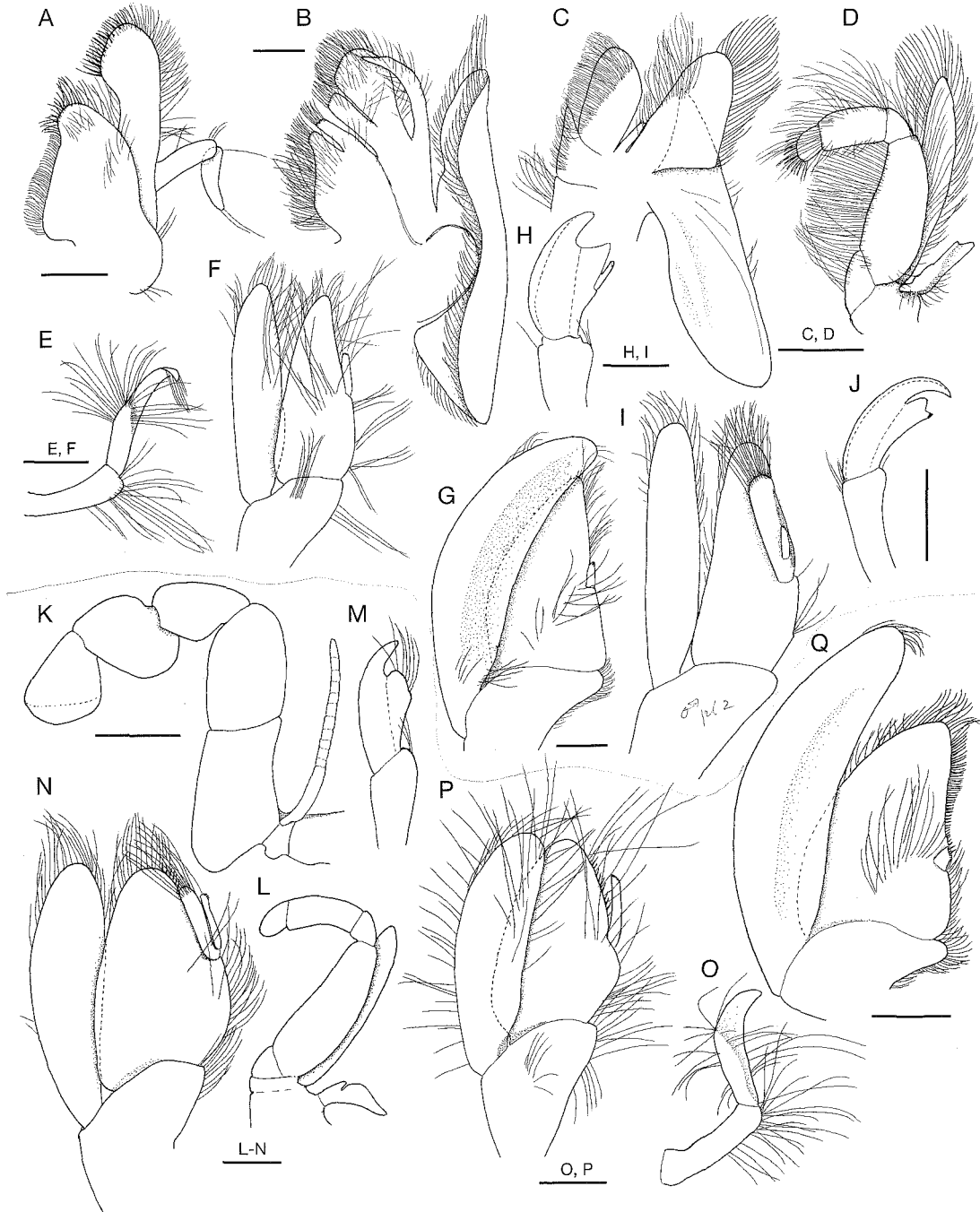


FIG. 20. — A-I, *Calliaxina punica* (de Saint Laurent & Manning, 1982) n. comb.; A-G, ♀ from Le Brusac, France (MNHN Th 1402); A, B, maxillule and maxilla; C, D, maxilliped 1 and 2; E, F, female pleopod 1 and 2; G, pleopod 3; H, I, ♂ from Mediterranean? (MNHN Th 1355), male pleopod 1 and 2; J, *Calliaxina sakaii* (de Saint Laurent, 1979) n. comb., holotype, ♂ from Tomioka, Japan (MNHN Th 312), male pleopod 1; K-Q, *Paraglypturus calderus* Türkay & Sakai, 1995, paratype, ♂ from Marianas (SMF 22950); K, L, maxilliped 3 and 2; M, N, male pleopod 1 and 2; O, P, female pleopod 1 and 2; Q, pleopod 3. Scale bars: A, B, L-P, 0.5 mm; C-K, Q, 1 mm.

REMARKS

Calliastina punica n. comb. often shares the same habitat with *Pestarella tyrrhena* n. comb. whose coloration is similar (de Saint Laurent & Manning 1982). In the field, separation between the two is only easy when the P1 are present: these are equal in the former species, distinctly unequal in the latter.

Family CTENOCHELIDAE Manning & Felder, 1991

Subfamily GOURRETINAE Sakai, 1999

TYPE GENUS. — *Gourretia* de Saint Laurent, 1973, by original designation.

Genus *Gourretia* de Saint Laurent, 1973

TYPE SPECIES. — *Callianassa denticulata* Lutze, 1937 (= *Callianassa subterranea* var. *minor* Gourret, 1887), by original designation.

DIAGNOSIS. — Carapace lacking dorsal oval and rostral carina; rostral spine usually present, small, straight or slightly upturned; lateral projection on either side small or absent. Telson about as long as proximal width; lateral borders parallel in proximal third, converging distally to straight or convex posterior border. A1 peduncle not overreaching that of A2. Mxp1 endopod elongate, epipod large, truncate anteriorly. Mxp2 with small epipod. Mxp3 pediform, with exopod; ischium with prominent toothed crest on mesial surface; lower distal margin of merus unarmed or with spines. Both major and minor P1 with proximal lower spine on merus; minor P1 with palm tapering distally. P2 fixed finger and dactylus with cutting edge unarmed or bearing teeth. P3 and P4 dactylus narrow, pointed distally. P5 subchelate.

Single arthrobranch on Mxp2, paired arthrobranch on Mxp3 and P1-4.

Male Plp1 uniramous, two-segmented, last segment bifurcate distally; male Plp2 biramous, foliaceous with *appendix interna* and *appendix masculina*. Female Plp1 uniramous, female Plp2 biramous, foliaceous with finger-like *appendix interna*. Plp3-5 biramous, foliaceous, with finger-like *appendix interna* sitting side by side with mesial border of endopod. Uropods about as long as telson; exopod without dorsal plate, posterior border with or without notch.

REMARKS

Gourretia currently includes eight species, as listed in Tudge *et al.* (2000):

– *G. barracuda* Le Lœuff & Intès, 1974;

– *G. biffari* Blanco Rambla & Linero Arana, 1994;

– *G. coolibah* Poore & Griffin, 1979;

– *G. crosnieri* Ngoc-Ho, 1991;

– *G. denticulata* (Lutze, 1937), type species;

– *G. labouensis* Le Lœuff & Intès, 1974;

– *G. laresi* Blanco Rambla & Linero Arana, 1994;

– *G. manihinae* Sakai, 1984.

Manning & Felder (1991) as well as Tudge *et al.* (2000) mentioned three differentiating characters for the above species: 1) rostrum straight or (slightly) upturned; 2) lower distal margin of Mxp3 merus unarmed or with spine; and 3) posterior border of uropodal exopod with or without notch. Two others can be added: 4) and 5) minor P1 and P2 with or without teeth on cutting edge of fixed finger and dactylus. None of them however permits a clear species grouping. Considering two examples, on basis of characters 1-3 only, for simplification, it can be noted that: 1) both *G. biffari* and *G. laresi* have an upturned rostral spine and a distal spine on the Mxp3 merus, but a notch on the uropodal exopod is present in the former, absent in the latter; and 2) like *G. laresi*, three other species, *G. barracuda*, *G. denticulata* and *G. manihinae*, bear a distal spine on the Mxp3 merus and no notch on the uropodal exopod, but they differ from *G. laresi* by having a straight rostral spine. These differences are regarded here as specific variations.

By contrast, the diagnostic characters cited above link members of the genus. The following are most significant: 1) Mxp1 bears an elongate endopod and a large epipod truncate anteriorly; 2) Mxp3 is pediform, with exopod and a prominent toothed crest on mesial surface of ischium; 3) both major and minor P1 have a lower proximal meral spine; 4) minor P1 with the palm tapering distally; 5) the morphology of male and female Plp1, Plp2; 6) the shape of telson with lateral borders parallel proximally and converging distally to the posterior border; and 7) uropods are about as long as the telson, the exopod without a dorsal plate. These clearly define the genus.

Several similarities exist between members of *Gourretia* and *Dawsonius latispina* (Dawson,

1967), type species of the genus *Dawsonius* Manning & Felder, 1991. The grouping of the genera *Gourretia* and *Dawsonius* in a subfamily Gourretinae, as proposed by Sakai (1999b), seems justified.

Gourretia denticulata (Lutze, 1937)
(Fig. 21)

Callianassa subterranea var. *minor* Gourret, 1887: 1034; 1888: 96, pl. 8, figs 1-15.

Callianassa denticulata Lutze, 1937: 6, figs 1-7; 1938: 170.

Gourretia serrata de Saint Laurent, 1979: 79. — Thessalou-Legaki & Zenetos 1985: 311. — °Thessalou-Legaki 1986: 184. — °Pancucci-Papadopoulou *et al.* 1999: 393.

Callianassa (Cheramus) subterranea var. *minor* – Pesta 1918: 205 (part).

Callianassa (Cheramus) minor – de Man 1928b: 26, 100.

Callianassa stebbingi – Gottlieb 1953: 440.

Callianassa minor – Holthuis & Gottlieb 1958: 56, figs 11, 12. — Harmelin 1964: 95. — Pérès & Picard 1964: 66. — Picard 1965: 59. — de Gaillande 1970: 377.

Gourretia denticulata – Lewinsohn & Holthuis 1986: 24. — Štević 1990: 218. — Manning & Felder 1991: 785. — Dworschak 1992: 210. — °Koukouras *et al.* 1992: 223. — Dounas *et al.* 1993: 48. — °Frogia 1995: 7. — Lopez de la Rosa *et al.* 1998: 393, fig. 1; 2002: 88. — d'Udekem d'Acoz 1999: 156. — Sakai 1999a: 128. — Tudge *et al.* 2000: 135. — ?Lindley *et al.* 2001: 46. — °Türkay 2001: 289.

Gourretia minor – de Saint Laurent 1973: 514. — Le Lœuff & Intès 1974: 26, figs 4a-k. — de Saint Laurent & Božić 1976: 27, figs 6, 14, 22, 37, 41, 48. — Manning & Štević 1982: 296. — Štević 1985: 127. — Ālciali & Minervini 1996: 145, figs.

TYPE MATERIAL. — Unknown.

MATERIAL EXAMINED. — **France.** Marseille, in sediments with *Posidonia*, A. Willsie coll., 1 ♀ (SMF 28336); Marseille, 1.8 m, 1 ♀ without abdomen (SMF 28785).

Adriatic. Parenzan coll., 1971, 1 ♂ cl. 9 mm, tl. 39 mm (figured) (MNHN Th 118), 1 ♂ cl. 9.5 mm approx. (damaged) (figured) (MNHN Th 119), 1 ♀ cl. 5.5 mm (MNHN Th 120), 1 ♂ cl. 4 mm, ♀ just moulted (poor condition) (MNHN Th 121).

Greece. Aegean Sea, Vourvourou Chalkidikis, 0.5-2 m, 10.V.1991, Siggitikos G., 1 ♂ (A.U.TH P 4528).

Israel. Haifa Bay, several spec., mostly juveniles, collected by bottomgrab or dredge, 34-82 m, between 1953-1956, leg. E. Gottlieb (RMNH D 13811-13830). — Athlit, bottomgrab, 54 m, 22.XI.1948, leg. A. Wirszubski, No. 710, 2 juv. (RMNH D 13831); bottomgrab, 46 m, 8.VIII.1951, leg. E. Gottlieb, No. 1002, 1 juv. (RMNH D 13832); 54 m, 28.XII.1952, leg. E. Gottlieb, No. 1069, 1 juv. (RMNH D 13833); bottomgrab, 54 m, 26.IX.1949, leg. A. Wirszubski, No. 809, 1 juv. (RMNH D 13834). — Gaza, dredge, 27 m, 21.VI.1947, leg. A. Wirszubski, No. 538, 1 juv. (RMNH D 13835); bottomgrab, 56 m, 31.IX.1947, leg. A. Wirszubski, No. 656, 1 juv. (RMNH D 13836). — Nahariya, bottomgrab, 55 m, 18.IX.1947, leg. A. Wirszubski, No. 637, 1 juv. (RMNH D 13837).

Tunisia. Gulf of Gabès, *Calypso*, 1965, stn SMF 1908, 27.IV.1965, 3 ♀♀ cl. 5.5-6mm (MNHN Th 918); stn SMF 1951, 2.V.1965, 1 ♀ cl. 6 mm (MNHN Th 919); stn SMF 1942, 2.V.1965, 2 ♂♂ cl. 4.5 and 5 mm, 1 ♀ cl. 5.5 mm and 1 ♀ cl. 6.5 mm, tl. 24 mm (figured) (MNHN Th 920).

OTHER MATERIAL EXAMINED. — *Gourretia barracuda* Le Lœuff & Intès, 1974, Ivory coast, off Abidjan, 1 ♂ holotype (MNHN Th 255). — *Gourretia biffari* Blanco Rambla & Linero Arana, 1994, Venezuela, NW Barcelona, 1 ♀ holotype (USNM 259410). — *Gourretia crosnieri* Ngoc-Ho, 1991, New Caledonia, Ouen Island, 1 ♀ holotype (MNHN Th 1202), near Nouméa, 1 ♀ paratype (MNHN Th 1203). — *Gourretia lahouensis* Le Lœuff & Intès, 1974, Ivory coast, "Grand Lahou", 1 ♂ holotype, 1 ♀ paratype (MNHN Th 253). — *Gourretia laresi* Blanco Rambla & Linero Arana, 1994, Venezuela, NW Chimana Islands, 1 ♂ holotype (USNM 259376).

DISTRIBUTION. — Eastern Atlantic: SW of Spain (Lopez de la Rosa *et al.* 1998, 2002). Mediterranean: Gulf of Marseille (de Saint Laurent & Božić 1976); Adriatic (Štević 1990); Aegean sea (Thessalou-Legaki 1986; Dounas *et al.* 1993); Gulf of Gabès, Tunisia (de Gaillande 1970); Cyprus (Lewinsohn & Holthuis 1986); Israel (Holthuis & Gottlieb 1958).

DIAGNOSIS

Details added to those given for the genus: carapace with small (Fig. 21A) or larger rostral spine overreaching middle of eyestalks (see Lopez de la Rosa *et al.* 1998). Telson (Fig. 21M) with convex posterior border.

Md (Fig. 21C) with small round teeth on cutting edge. Lower distal margin of Mxp3 merus (Fig. 21E) with one or two spines. Major P1 (Fig. 21I) ischium with spinules on lower border, merus with more or less pronounced lower rectangular

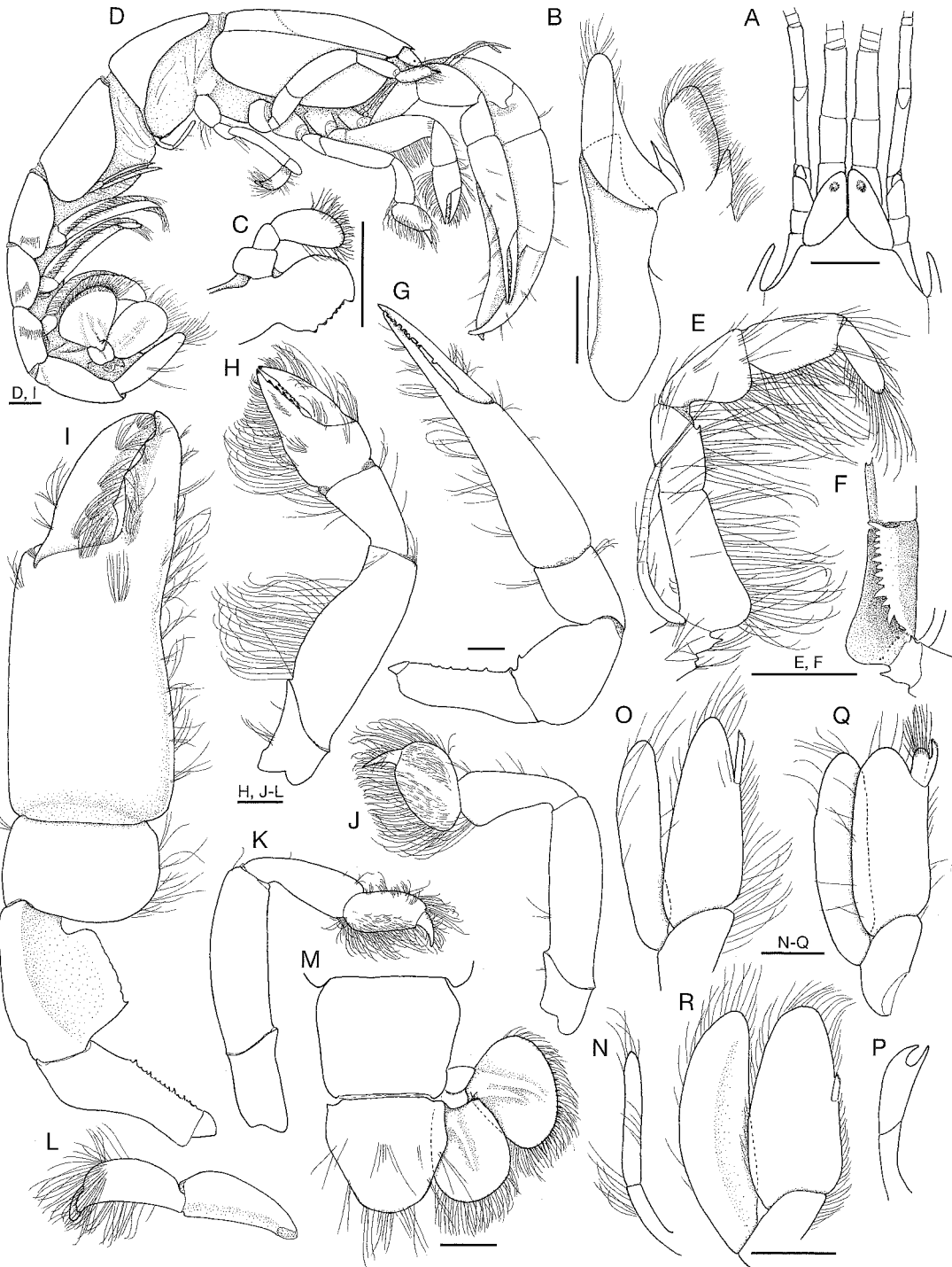


FIG. 21. — *Gourretia denticulata* (Lutze, 1937); **A**, ♂ from Kotor, Adriatic, anterior part of carapace (from de Saint Laurent & Božić 1976); **B**, **C**, ♂ from Adriatic (MNHN Th 119); **D-F**, **M-R**, from Gulf of Gabès, Tunisia (MNHN Th 920); **G-L**, ♂ from Adriatic (MNHN Th 118); **D-F**, **M-O**, ♀; **P-R**, ♂; **B**, maxilliped 1; **C**, mandible; **D**, lateral view; **E**, **F**, maxilliped 3 and mesial view of ischium; **G**, **I**, left and right pereopod 1; **H**, **J-L**, pereopod 2-4 and distal part of pereopod 5; **M**, telson and uropods; **N**, **O**, female pleopod 1 and 2; **P**, **Q**, male pleopod 1 and 2; **R**, pleopod 3. Scale bars: A-M, R, 1 mm; N-Q, 0.5 mm.

expansion bearing proximal spine, cutting edge of fixed finger with two triangular teeth. Minor P1 (Fig. 21G) with spinules on ischium, cutting edge of fixed finger and dactylus with seven or eight teeth on distal half. P2 (Fig. 21H) with teeth on cutting edge of both fixed finger and dactylus, larger on fixed finger. P3 (Fig. 21J) propodus oval in outline, P4 (Fig. 21K) propodus linear, P5 (Fig. 21L) subchelate. Male, female Plp1, Plp2 (Fig. 21N-Q) and Pl3 (Fig. 21R) as figured. No notch on posterior border of uropodal exopod (Fig. 21M).

Colour

Unknown.

Size

cl. 4.5-9.5 mm, tl. 18-40 mm.

ECOLOGY

This species lives among *Posidonia* seagrass (Harmelin 1964; Dworschak 1992), in sedimentary muddy bottoms, 2.5-100 m (Štević 1990) or 2.5-146 m depth (Dworschak 1992).

REMARKS (after Lewinsohn & Holthuis 1986)

This species was known in the past either under *Callianassa minor* or *Gourretia minor* or *Gourretia serrata*. It was first described by Gourret (1887) as *Callianassa subterranea* var. *minor*, and was later placed by de Saint Laurent (1973: 514) in a separate genus, *Gourretia*, for which it was made type species. In 1979, de Saint Laurent (1979: 79) reported that the name *Callianassa subterranea minor* Gourret, 1887 was a junior primary homonym of *Callianassa minor* Fischer, 1866, a fossil species from the Miocene of southern France. At the same time, a replacement name, *Gourretia serrata* nom. nov. was proposed for the species. De Saint Laurent overlooked however another available name that was *Callianassa denticulata* Lutze, 1937 which species de Saint Laurent & Božić (1976: 27) had previously synonymised with *Callianassa minor*.

This taxonomic question was settled by Lewinsohn & Holthuis (1986: 24) and the name *Gourretia denticulata* (Lutze, 1937) has been used thereafter.

Family LAOMEDIIDAE Borradaile, 1903

TYPE GENUS. — *Laomedea* de Haan, 1841, by original designation.

Genus *Jaxea* Nardo, 1847

TYPE SPECIES. — *Jaxea nocturna* Nardo, 1847, by original designation.

DIAGNOSIS. — Thalassinids with firm, white exoskeleton; *linea thalassinica* straight anteroposteriorly, distinct and well developed. Abdominal segments approximately of same length, abdominal pleura 2-6 with minute serrations. Telson longer than wide, longitudinal dorsal ridges present, posterior border convex, median spine absent.

Eye small, corneas with reduced pigmentation. Both A1 and A2 peduncle slender and greatly elongated; antennal scale moderately large. Mx2 scaphognathite with several long posterior setae. Mxp1 with large endopod, and large epipod; Mxp3 pediform with mesial spinous crest on ischium. P1 chelate, equal, greatly developed; P2-5 slender, simple.

Exopod on Mxp1-3; epipod on Mxp1-3 and P1-4; single podobranch on Mxp2-3 and P1-3; single arthrobranch on Mxp1, paired arthrobranch on Mxp2-3 and P1-4.

Plp1 absent in male, uniramous in female; male and female Plp2-5 slender, biramous. Uropod with suture on both rami.

Characteristic larvae with large eyes, long neck and slender body were named *Trachelifer* by Brook (1888).

Jaxea nocturna Nardo, 1847

(Figs 22; 23)

Cancer nocturnus Chiereghin, 1818: sp. 34, fig. 48 (MS name).

Jaxea nocturna Nardo, 1847: 4; 1869: 318, pl. 13, fig. 5. — Claus 1884: 302; 1885: 63. — *Brook 1888: 420. — Stebbing 1893: 187. — *Scott 1900: 405; 1902: 481; *1905: 214. — Norman & Scott 1906: 12. — Bouvier *1914: 194, figs 1-11; 1940: 98, fig. 66. — Selbie 1914: 96, pl. 15, figs 1-8. — *Southern 1915: 95. — *Williamson 1915: 452. — Pesta 1918: 193, fig. 60. — *Boraschi 1921: 6, tabl. 1, figs 8, 10. — *Caroli 1921b: 268, fig. 3; 1924: 153-197, figs 1-29, tabl. 8. — Balss 1926: 26; 1936: 14. — de Man 1928b: 16. — Miranda y Rivera 1933: 21. — *Tattersall 1938: 625, figs 1-3. — Chace 1939: 526. — Poulsen 1941: 235. — *Gurney 1942: 250, figs 101, 102. — Zariquiey Alvarez 1946: 105, fig. 133; 1968: 226, fig. 94b. — Gottlieb 1953: 441. — *Kurian 1956: 73. — Gordon 1957: 249. — Holthuis & Gottlieb 1958: 55. — *Bourdillon-

Casanova 1960: 107. — *Demirhindi 1961: 219, 3 figs, 1 tabl. — O'Ceidigh 1962: 163. — Picard 1965: 38. — Wear & Yaldwyn 1966: 4, *21. — Allen 1967: 18, 56, fig. p. 89. — Števcic °1969: 128; °1971: 529; 1979: 281; 1990: 215. — *Seridji 1971: 49. — Lagardère 1973: 84. — Le Lœuff & Intès 1974: 23. — *Thirirot 1976: 349, 367, tabl. 2, fig. 6. — Türkay 1976: 27. — Beaubrun 1979: 74, figs 47, 48. — Monchartmont 1979: 70. — Manning & Števcic 1982: 295. — García Raso 1983: 319. — Riedl 1983: 482, pl. 177, 2 figs. — Pervesler & Dworschak 1985: 33, figs 1-3, pls 1-4, tabs 1-4. — Thessalou-Legaki & Zenetos 1985: 311. — Campbell & Nicholls 1986: 218, 1 fig. — Thessalou-Legaki 1986: 182. — Müller 1986: 117. — Moyse & Smaldon 1990: 520, fig. 10.12 (part). — Dworschak 1992: 228. — °Koukouras *et al.* 1992: 223. — Noël 1992: 80. — °Diez *et al.* 1994: 47. — Hayward *et al.* 1995: 432, fig. 8.51 (part). — Nickell & Atkinson 1995: 181, fig. 2A-C, tabl. 2. — *Barnich 1996: 126, figs 6A, 6B, 67. — Falciai & Minervini 1996: 144, 1 fig. — Johns *et al.* 1997: 127. — Nickell *et al.* 1998: 741, 752, figs 4, 5. — Astall *et al.* 1997b: 669, 674, 675, fig. 1, tabs 1-5, pls 2, 4. — Hughes & Atkinson 1997: 640. — Pinn *et al.* 1998b: 243, fig. 1B; 1999a: 103, figs 1D-G, 4C, 5A-D; 1999b: 1461, fig. 1C, tabs 1-6. — d'Udekem d'Acoz 1999: 154. — Taylor *et al.* 2000: 265, figs 1, 2, tabs 1-3. — *González-Gordillo *et al.* 2001: 279. — *Martin 2001: 76, 1 fig. — °Türkay 2001: 289.

Calliaxis adriatica Heller, 1862: 440, pl. 3, figs 22-30; 1863: 208, pl. 6, figs 16-18. — Stalio 1877: 109. — Stossich 1880: 207. — Carus 1885: 491. — *Cano 1891: 16, pl. 4. — Scott 1899: 268, pl. 12, figs 18-20. — *Lo Bianco 1903: 187, 1909: 603. — Graeffe 1902: 69.

Jaxea cf. nocturna (fossils) – Della Cave 1988: 3, pls 1, 2. — Müller 1993: 5, fig. 3C, D.

TYPE MATERIAL. — No longer extant (Carlo Froggia pers. comm.).

MATERIAL EXAMINED. — **Great Britain.** Firth of Clyde, south Lady Isle, Ayrshire, muddy sand, 40 m, R. B. Pike coll., 30.X.1957, 1 ♂ (NHM 1962.7.5.10). **Ireland.** Skibbereen Co, Cork, W. M. Tattersall coll., 2 postlarvae (NHM 1937.10.27.1-2).

France. English Channel, Grande Vasière, 1 ♂ cl. 11.5 mm, tl. 27.5 mm (figured), 1 ♂, 1 ♀ cl. 10.5 and 11 mm, 1 juv. cl. 7.5 mm (MNHN Th 222). — Mediterranean, Banyuls, P. Noël coll., VI.1977, 1 ♀ cl. 11 mm, tl. 27 mm (figured) (MNHN Th 1342); dredge, A. Guille coll., 13.VIII.1976, 1 ♀ cl. 8.5 mm (MNHN Th 1343).

Spain. Vandellos, *Calypso*, stn 1, 74 m, mud, H. Zibrowius coll., 6.VIII.1977, 1 ♀ cl. 8.5 mm, poor condition (MNHN Th 732).

Adriatic. "Cotype"? of *Calliaxis adriatica*, coll. C. Heller 21163 94.65, Heller don., 1 ♂ broken, cl.

18 mm (MNHN Th 208). — Senigallia, 54 m, C. Froggia coll., 25.VIII.1978, 1 ♂ cl. 15.5 mm, tl. 40 mm (figured), 2 ♂ cl. 13 and 18 mm (MNHN Th 629). — Norman coll., 1 ♀ (NHML 1911.11.8.1054).

DISTRIBUTION. — East Atlantic: SW Scotland (Allen 1967), Ireland (Selbie 1914; O'Ceidigh 1962), SW England (Gordon 1957), English Channel, Bay of Biscay, France (Lagardère 1973), Canyon of Capbreton, France (Diez *et al.* 1994); Marseille (Picard 1965); Banyuls, France; southern Spain (Zariquiez Alvarez 1968; García Raso 1983); atlantic coast of Morocco (Türkay 1976). East Mediterranean: Adriatic (Bouvier, 1940; Manning & Števcic 1982; Pervesler & Dworschak 1985; Števcic 1990); Marmara sea (Müller 1986); Naples (Lo Bianco 1909), Greek seas (Thessalou-Legaki & Zenetos 1985; Thessalou-Legaki 1986; Koukouras *et al.* 1992); mediterranean coast of Israel (Holthuis & Gotlieb 1958).

Trachelifer larvae were reported from various areas including those with no adults so far captured: Turkey (Demirhindi 1961), Plogoff, Brittany, France (Martin 2001). Some larvae assigned to a species of *Jaxea* other than *J. nocturna* were collected in Banyuls, France (Thirirot 1976), also in the Adriatic (Kurian 1956).

Jaxea cf. nocturna fossils from the early Pliocene were found in Tuscany, Italy (Della Cave 1988), others from the Pliocene and Miocene were discovered in Catalonia, NE Spain (Müller 1993).

DIAGNOSIS

Rostrum (Fig. 22B) triangular, pointed anteriorly, slightly longer than wide at base with slight median longitudinal groove; lateral rostral border and antero-lateral border of carapace with spinules; eye small. *Linea thalassinica* and cervical groove well defined, the two do not cross. Pleura of abdominal somite 1 (Fig. 22A) pointed ventrally or with ventral spine; all abdominal pleura with ventral denticles. Telson (Fig. 22C) approximately 1.4 times as long as wide, posterior border convex, median longitudinal groove and two pairs of slight longitudinal ridges on dorsal surface, outer bearing spinules.

A1 and A2 peduncle (Fig. 22B) with elongate article 3 and 4 respectively; article 3 of A2 with three or four spinules on lateral external border; A2 scale large, with distal spinules. Md (Fig. 22G) with two-articulated palp. Mx1 (Fig. 22E) with two-articulated endopod. Mx2 (Fig. 22F) exopod bearing many long setae. Mxp1 (Fig. 23A) with distally spatulate endopod and large epipod. Mxp2 (Fig. 23B) epipod with large

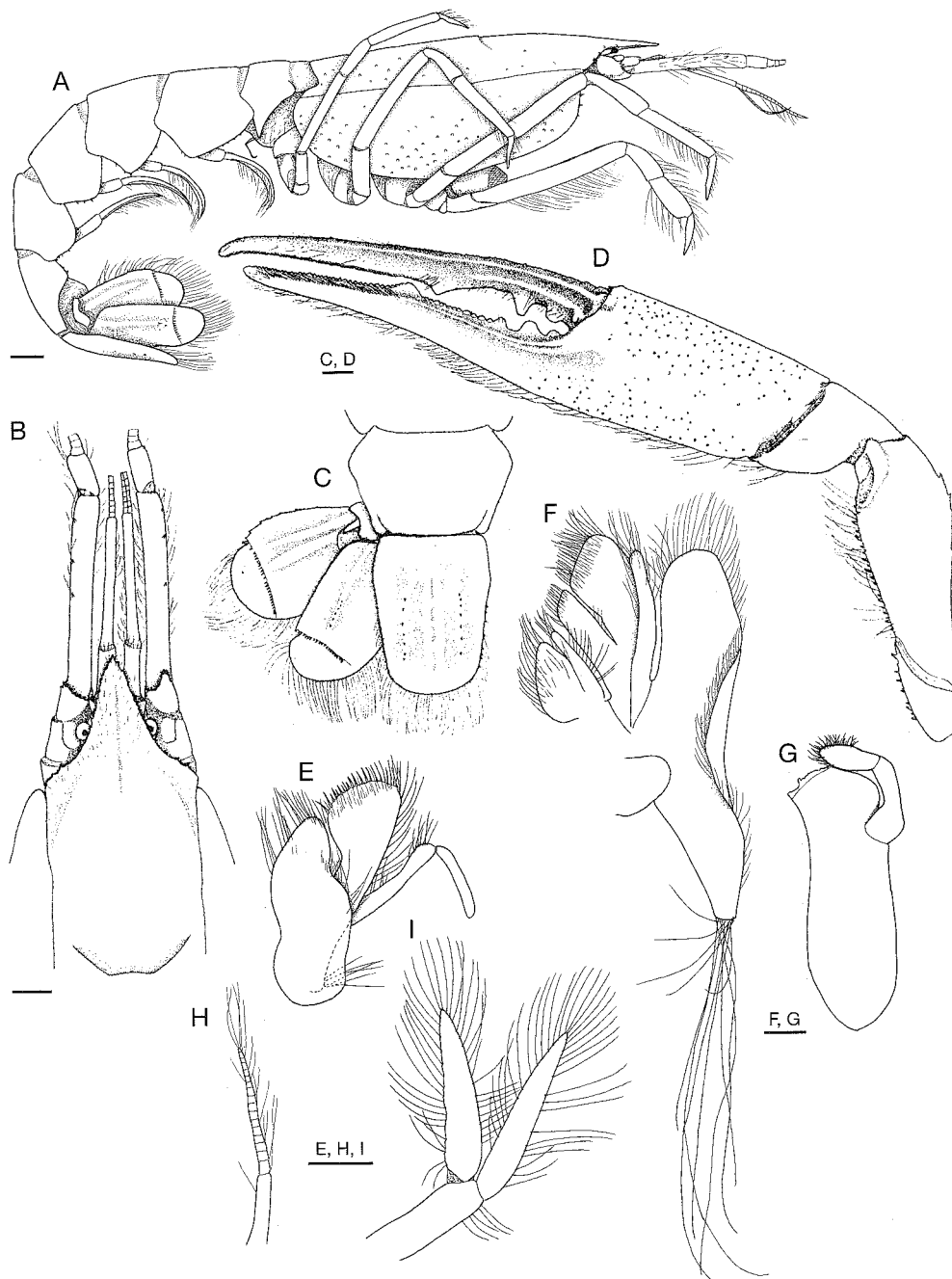


FIG. 22. — *Jaxea nocturna* Nardo, 1847; **A, H**, ♀ from Banyuls, France (MNHN Th 1342); **B-D, I**, ♂ from Adriatic (MNHN Th 629); **E-G**, ♂ from Grande Vasière, France (MNHN Th 222); **A**, lateral view, pereopod 1 omitted; **B**, anterior part of carapace; **C**, telson and uropods; **D**, pereopod 1; **E, F**, maxillule and maxilla; **G**, mandible; **H**, female pleopod 1; **I**, male pleopod 2. Scale bars: A-D, I, 1 mm; E-H, 0.5 mm.

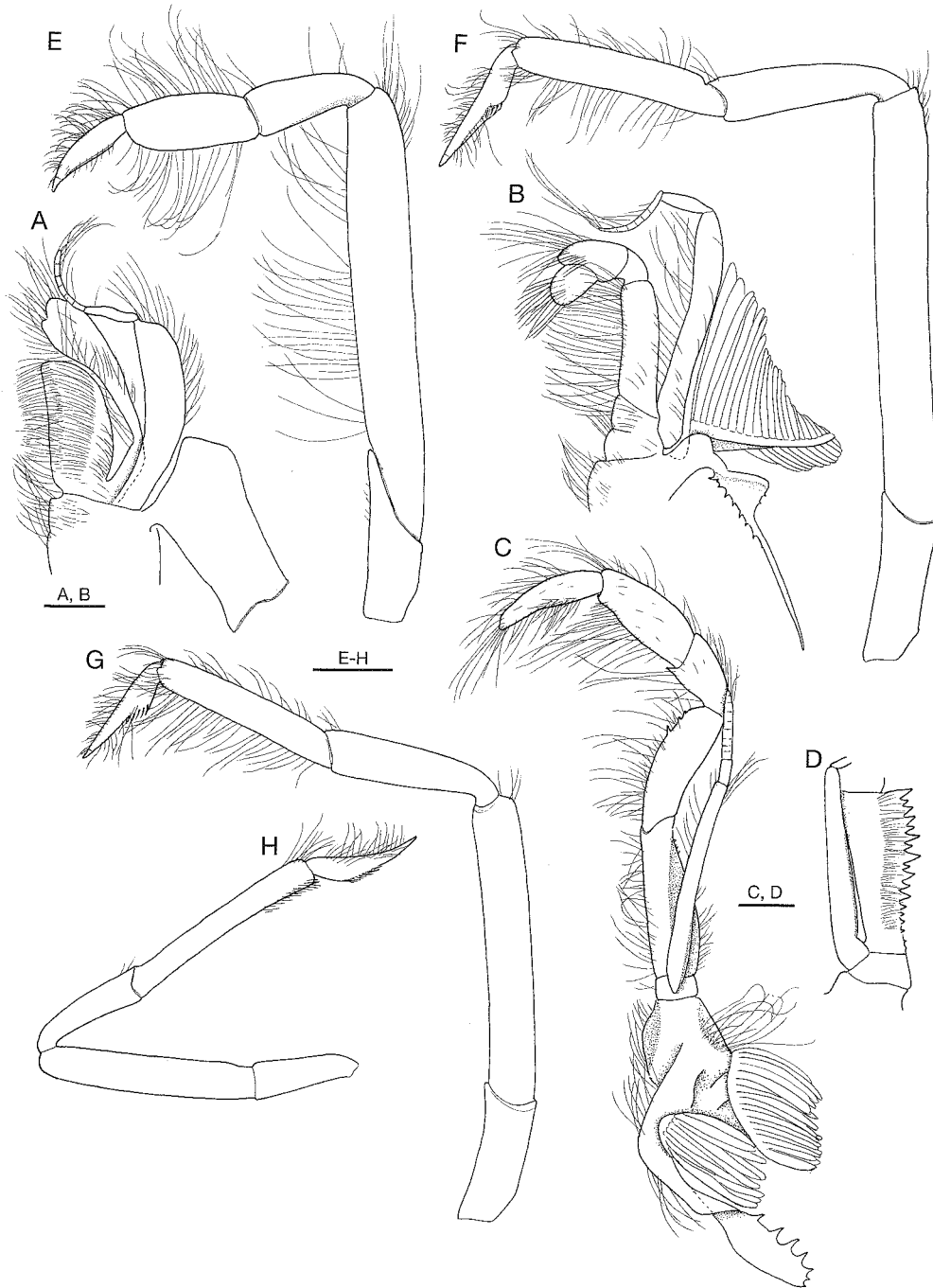


FIG. 23 — *Jaxea nocturna* Nardo, 1847; **A-D**, ♂ from Grande Vasière, France (MNHN Th 222); **A, B**, maxilliped 1 and maxilliped 2; **C, D**, maxilliped 3 and mesial crest on ischium; **E-H**, ♂ from Adriatic (MNHN Th 629), pereopod 2-5. Scale bars: A-D, 0.5 mm; E-H, 1 mm.

podobranch. Mxp3 (Figs 23C, D) with smaller podobranch and prominent mesial toothed crest on ischium.

P1 (Fig. 22D) chelate, equal, greatly developed, nearly as long as body; ischium and merus with spinules on whole lower border, meral upper spinules sometimes present; carpus with small lower distal spine; propodus granulate, fixed finger more than 1.5 times as long as palm; dactylus slightly longer than fixed finger, cutting edge of both with three or four large round teeth proximally, median triangular tooth and small round teeth in distal half.

P2-5 simple (Fig. 23E-H), P3-5 dactylus with lower spiniform setae.

Plp1 absent in male, uniramous in female (Fig. 22H), with basipod and faintly articulated flagellum. Male and female Plp2-5 (Fig. 22I) biramous, with slender exopod and endopod.

Uropod (Fig. 22C) with suture on both rami, lateral external border of exopod with spinules.

Trachelifer larvae recently reported in Barnich (1996: fig. 6A, B) and Martin (2001: 76).

Colour

White, pinkish or light brown (Campbell & Nicholls 1986); pinkish white with yellow or chesnut hairs (Moyses & Smaldon 1990); pinkish white (Falciai & Minervini 1996).

Size

Largest specimens in material examined: cl. 15.5-18 mm, tl. 40-47 mm. Largest size reported: tl. 40-60 mm (Moyses & Smaldon 1990).

ECOLOGY AND BIOLOGY

The species is rare in the Clyde sea area, living in mud or sandy mud, 18-80 m (Allen 1967), or in mud near the coast, in Marseille (Picard 1965). It is common in the Bay of Biscay, 0-100 m, in mud (Lagardère 1973), in soft mud or sandy mud, 15-100 m in the Adriatic (Bouvier 1940; Štević 1990); in mud, at 15 m depth or deeper, in the Ionian sea (Thessalou-Legaki & Zenetos 1985). It is scarce off the west coast of the British Isles, often as fragments in fish stomach (Moyses & Smaldon 1990) and was collected at 356-420 m

depth in Capbreton, France (Diez *et al.* 1994). The burrow, spiral shape with a horizontal extension, was studied by Pervesler & Dworschak (1985).

Trachelifer larvae are found in May to September, along the coasts of Ireland (Selbie 1914), in June-July in Cumbrae, SW of Scotland (Allen 1967), in March-October in Naples, Italy (Lo Bianco 1909), in May-June in Marseille, France (Bourdillon-Casanova 1960).

Aspects of biology studied

Burrow morphology and feeding behaviour (Nickell & Atkinson 1995); sulphide metabolism (Johns *et al.* 1997); branchial morphology, gill area and gill ultrastructure (Astall *et al.* 1997b); particle size selectivity and resource partitioning (Pinn *et al.* 1998b); morphology of mouthparts and pereopods in relation to feeding, ecology and grooming (Nickell *et al.* 1998); gut morphology and gut microflora (Pinn *et al.* 1999a); mouthpart morphology and mouthpart setal fringes (Pinn *et al.* 1999b); oxygen transporting properties of haemocyanin (Taylor *et al.* 2000).

Family UPOGEBIIDAE Borradaile, 1903

TYPE GENUS. — *Upogebia* Leach, 1814, by original designation.

Genus *Gebiacantha* Ngoc-Ho, 1989

TYPE SPECIES. — *Upogebia talismani* Bouvier, 1915, by original designation.

DIAGNOSIS. — Gastric region with lateral ridges, *linea thalassinica* depressed anteriorly, extending to posterior border of carapace. Rostrum approximately ovoid, bordered with teeth or spines, one or many infrarostral spines; antero-lateral border of carapace with two or more spinules. Posterior border of telson medially concave. Md without acute anterior tooth. Mxp1 without epipod; Mxp3 with small epipod or (rarely) without. P1 subchelate, carpus and propodus with numerous spines, lower border of propodus with one or two large spines posterior to fixed finger; fixed finger short, not exceeding half length of dactylus. Coxae of P1-3 or P1-4 with spines or spinules. Uropod exopod equal or longer than telson.

REMARKS

The genus *Gebiacantha* was established in 1989 to include 11 upogebiid species bearing infrarostral spines as well as numerous spines on pereopods. Its validity and comparison with the closely related genus, *Austinogebina* Ngoc-Ho, 2001, are discussed by Ngoc-Ho (2001b).

Gebiacantha talismani (Bouvier, 1915)
(Figs 24; 25)

Upogebia Talismani Bouvier, 1915: 184. — de Man 1927: 56; 1928b: 24, 47.

Gebicula Hupferi Balss, 1916: 35, figs 11-13.

Upogebia talismani — °Buchanan 1958: 24, 28. — de Saint Laurent 1971: 1259, figs 1-3. — Le Lœuff & Intès 1974: 52, fig. 15d-n. — Beaubrun 1979: 79, figs 50-52. — Števíčič 1979: 128. — de Saint Laurent & Le Lœuff 1979: 45, fig. 7. — Thessalou-Legaki 1986: 183. — °Koukouras *et al.* 1992: 223; 1993: 195. — Falciai & Minervini 1996: 149, 3 figs.

Gebiacantha talismani — Ngoc-Ho 1989: 118, 121. — Noël 1992: 82. — °Frogliá 1995: 8. — d'Udekem d'Acoz 1995: 61; 1999: 156. — García Raso 1996: 738. — °Pancucci-Papadopoulou *et al.* 1999: 393. — *González-Gordillo *et al.* 2001: 279. — Markham 2001: tabs 1, 2. — °Türkyay 2001: 289.

TYPE MATERIAL. — Holotype: Cap Blanc du Nord, Morocco, *Talisman*, stn 23, 15.VI.1883, 33°16'N, 08°53'W, 120 m, rocks, shells, 1 ♀ (MNHN Th 50).

MATERIAL EXAMINED. — Greece. SE Peloponnese, Monemvasia, brought ashore by fishermen, C. d'Udekem d'Acoz coll., 20.VII.1986, 1 ♂ cl. 11 mm (MNHN Th 1341). — Aegean Sea, *Calypso*, stn 1606, Sergisti Islet, North of Limnos I., 100 m, 3.VI.1960, 1 ♂, 1 ♀ (A.U.TH G1 2123).

Morocco. Cap Blanc du Nord, *Talisman*, stn 23, 15.VI.1883, 33°16'N, 08°53'W, 120 m, rocks, shells, 1 ♀ holotype, poor condition cl. 7.5 mm (MNHN Th 50). — Near Cap Blanc du Nord, 33°14'N, 8°49'W, 105 m, sand, Van Veen coll., 18.III.1976, RMNH don., 1 ♂ cl. 10 mm, tl. 28 mm (figured), 1 ♀ cl. 9.5 mm, tl. 27 mm (figured), 1 ♂ cl. 9 mm, 1 ♀ cl. 9 mm (MNHN Th 1352); same data, 5 ♂ cl. 6-10.5 mm, 16 ♀ cl. 9-10 mm (RMNH D 31566). — Sollaud coll., 1923-1926, 1 ♂ cl. 9.5 mm, 1 ♀ cl. 8 mm, 20 juv. cl. 4.5-5.5 mm (MNHN Th 1363).

Lybia. *Thalassa*, stn V 438, dredge, 120 m, 22.XI.1969, 1 ♂ cl. 8 mm, tl. 22 mm (figured by de Saint Laurent 1971), 1 ♂ cl. 10 mm, 1 ♀ cl. 7.5 mm (MNHN Th 51).

Sierra Leone. West Africa, 7°34'N, 13°31'W, 100 m, shells and mud, A. R. Longhurst, stn MB4/B4, 18.IV.1956, 1 ♂, 2 ♀, 3 juv. (RMNH D 32122). — 7°32'N, 14°07'W, 42 m, sand, A. R. Longhurst, stn MB1/A2, 22.II.1956, 3 ♂, 1 ♀ (RMNH D 32123). — 6°49'N, 11°45'W, 72 m, shells and mud, A. R. Longhurst, stn MB4/B3, 26.X.1956, 1 ♂, 1 ♀ (RMNH D 32124). — 7°39'N, 13°47'W, 80 m, shells and mud, A. R. Longhurst, stn MB4/B3, 18.IV.1956, 1 ♀ (RMNH D 32125).

Gulf of Guinea. *Calypso*, stn 94, mud and shells, 31 m, 27.VI.1956, 1 ♂ cl. 6 mm (MNHN Th 352). — Stn 90, 30 m, 26.VI.1956, 2 ♂ (1 without abdomen) cl. 5 mm (MNHN Th 285). — Stn 16, 100-109 m, 21.V.1956, 2 ♂ cl. 5 and 7 mm, 2 ♀ cl. 6.5 and 7 mm (MNHN Th 286).

Ivory Coast. Sassandra, *Reine Pokou*, 30 m, Le Lœuff & Intès coll., 9.XII.1967, 1 ovig. ♀ cl. 6.5 mm (MNHN Th 911). — Sassandra, *Reine Pokou*, 40 m, small dredge, P. Le Lœuff coll., 11.V.1966, 2 ♂ cl. 6 and 7 mm (broken), 2 ♀ cl. 6.5 mm approx. (poor condition) and 7 mm (without abdomen) (MNHN Th 590). — E of Jacquville, *Reine Pokou*, 200 m, small dredge, P. Le Lœuff coll., 20.I.1966, 1 ♂ cl. 5.5 mm (MNHN Th 591). — Sassandra, *Reine Pokou*, 200 m, small dredge, P. Le Lœuff coll., 11.II.1966, 1 ♂ cl. 5 mm and 1 ♀ cl. 6 mm (MNHN Th 592). — Grand Lahou, *Reine Pokou*, 70 m, small dredge, P. Le Lœuff coll., 9.III.1966, 1 ♂ cl. 7.5 mm (without abdomen, poor condition) (MNHN Th 593). — Cap de Palmes, *Reine Pokou*, 80 m, triangular dredge, P. Le Lœuff coll., 9.XII.1967, 1 ♀ cl. 7.5 mm and 1 juv. cl. 3 mm (MNHN Th 594). — Jacquville, *Reine Pokou*, 80 m, small dredge, P. Le Lœuff coll., 25.XI.1966, 2 ♀ (1 ovig.) cl. 6 and 7 mm (MNHN Th 595).

Ghana. R. Bassindale, stn 151, 2 ♂ (RMNH D 32126); R. Bassindale, stn 153, 1 juv. (RMNH D 32127); dredge, R. Bassindale, stn 153, 31.XII.1950, 3 juv. (RMNH D 32128).

Congo. Off Pointe Noire, 4°56'N, 4°27'E, *Ombango*, 140 m, dredge, A. Crosnier coll., 22.VIII.1969, 2 ♂ cl. 4 and 4.5 mm (MNHN Th 259).

Unknown locality. *Pourquoi pas*, stn 82, 1 ♂ cl. 12.5 mm (MNHN Th 912).

DISTRIBUTION. — Central Mediterranean: Malta; eastern Mediterranean: Lybia and Greece. Northwest coast of Africa, from Morocco to Congo.

DIAGNOSIS

Rostrum (Fig. 24A, B) ovoid, slightly longer than wide at base, six to eight teeth on lateral border, faint median groove on proximal half, three to five infrarostral spines; anterolateral border of carapace with four to six spines and spinules. Telson (Fig. 24H) approximately 1.1-1.2 times as wide as long, posterior border concave medially.

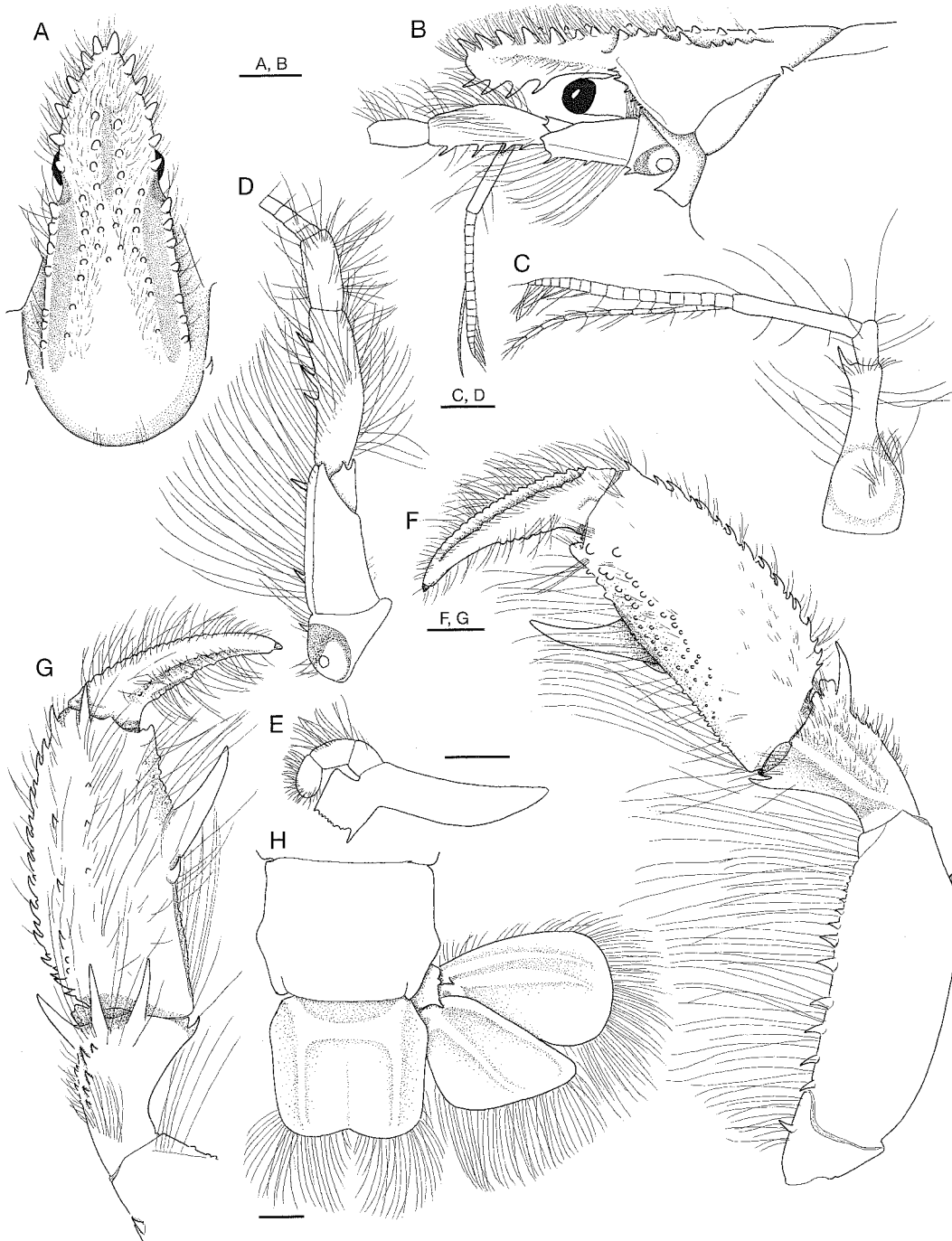


FIG. 24. — *Gebiacantha talismani* (Bouvier, 1915) from Cap Blanc du Nord, Morocco (MNHN Th 1352); **A, B, F-H, ♂**; **C-E, ♀**; **A, B**, anterior part of carapace, dorsal and lateral view; **C, D**, antennule and antenna; **E**, mandible; **F, G**, pereopod 1 and distal articles in mesial view; **H**, telson and uropods. Scale bars: A, B, F-H, 1 mm; C-E, 0.5 mm.

A1 peduncle (Fig. 24C) with lower spine on article 1; A2 peduncle (Fig. 24D) with two and three to five lower spines on article 3 and 4 respectively. Md (Fig. 24E) without mesio-anterior tooth.

P1 slender in young male and female, with small fixed finger (Fig. 25A-C), stouter and with much shortened fixed finger in large male (Fig. 24F, G). Ischium with spine on lower border. Merus with upper subdistal spine, eight to 10 spines and three to five spinules on lower border. Carpus with several spinules on upper border; three large upper mesial distal spines and lower distal spine. Propodus with three or four longitudinal rows of spines on mesial surface; large lower spine posterior to fixed finger followed by smaller one; fixed finger short or very short, unarmed. Dactylus with tubercles on upper border and a few others on mesial surface.

P2 (Fig. 25D) merus with upper subdistal spine, two to four lower spinules; carpus with four or five upper spines and lower subdistal spine, propodus with upper proximal spine. P3 (Fig. 25E) merus with upper distal spine and four or five lower spines, carpus with lower distal spine.

Uropod exopod (Fig. 24H) approximately 1.2 times as long as telson.

ECOLOGY

This species occurs among rocks and shells or in muddy sand (de Saint Laurent 1971), between 20-150 m.

REMARKS

Bouvier (1915), also de Saint Laurent (1971) and de Saint Laurent & Le Lœuff (1979) reported two type specimens for *U. talismani*, both female, of 20 and 30 mm in total length; only the smaller one (cl. 7.5 mm) is now present in the MNHN collection. It is in poor condition but clearly shows the species characteristics.

Young male of *Gebiacantha talismani* (Fig. 25A) (from de Saint Laurent & Le Lœuff 1979: fig. 7a) shows a slightly stouter P1 than the female but with a relatively long fixed finger. In large male from the type locality (RMNH-D 31566 and MNHN Th 1352) and elsewhere (MNHN Th 1341 and Th 912), P1 fixed finger is much shorter (Fig. 24F, G).

Genus *Upogebia* Leach, 1814

TYPE SPECIES. — *Cancer Astacus stellatus* Montagu, 1808, by original designation.

DIAGNOSIS. — Gastric region with lateral ridges, *linea thalassinica* depressed anteriorly, extending entirely or partly to posterior border of carapace; cervical groove well defined. Rostrum obtuse, bearing teeth or spines on lateral border, rarely unarmed. Anterolateral border of carapace unarmed or with spine. Telson often with faint inverted U-shaped carina dorsally, posterior border straight or slightly convex, unarmed.

Eye peduncle cylindrical, with pigmented terminal cornea. Antennal scale reduced. Mxp1-3 with exopod; Mxp1 and Mxp3 with or without epipod, Mxp2 with epipod bent mesially; no spinous crest (*crista dentata*) on Mxp3 ischium. P1 equal, chelate or subchelate; P2-4 simple, P5 subchelate. Plp1 absent in male, uniramous in female, Plp2-5 biramous, similar, lacking *appendix interna*. No suture on uropods.

Upogebia deltaura (Leach, 1815) (Figs 26; 27)

Gebia deltaura Leach, 1815: 342.

Gebia deltura Leach, 1816: pl. 31, figs 9, 10. — Desmarest 1825: 204. — H. Milne Edwards 1837a: 314. — Bell 1846: 225, 1 fig. — White 1857: 97. — Fischer 1872: 428. — Van Beneden 1884: 647. — Carus 1885: 490. — Lovett 1885: 14. — Kœhler 1886: 59. — Gourret 1888: 92, pl. 8, figs 16-29, pl. 9, figs 1-4. — Adensamer 1898: 621. — Sinel 1907: 217. — de Morgan 1910: 475, fig. 2. — Runnstrøm 1925: 33.

Gebia littoralis — *Sars 1884: 182, pls 3-5.

Gebia stellata — Lagerberg 1908: 54, pl. II fig. 10. — Schlegel 1912: 239. — Grieg 1927: 35 (part), 1 fig.

Gebiopsis deltaura — Balss 1926: 27, fig. 8.

Gebiopsis deltura — Stephensen 1910: 277.

Upogebia deltura — *Webb 1919: 85, pls 1-9, pl. 10, fig. 1, pl. 12 figs 1-4, 7, 8. — Gustafson 1934: 6. — Poulsen 1941: 216, 226, figs 6, 8.

Upogebia (Calliadne) deltaura — de Man 1927: 17, pl. 2, figs 8, 8b. — Balss 1936: 16.

Upogebia (Gebiopsis) deltaura — Borradaile 1903: 542. — Selbie 1914: 103. — Pesta 1918: 199, fig. 62. — Bouvier 1940: 106, fig. 70. — Gordon 1957: 249. — *Bourdillon-Casanova 1960: 109. — O'Ceidigh 1962: 164. — Noël 1992: 82.

Upogebia deltaura — Schellenberg 1928: 77, fig. 58. — Miranda y Rivera 1933: 21. — Bertrand 1940: 30. —

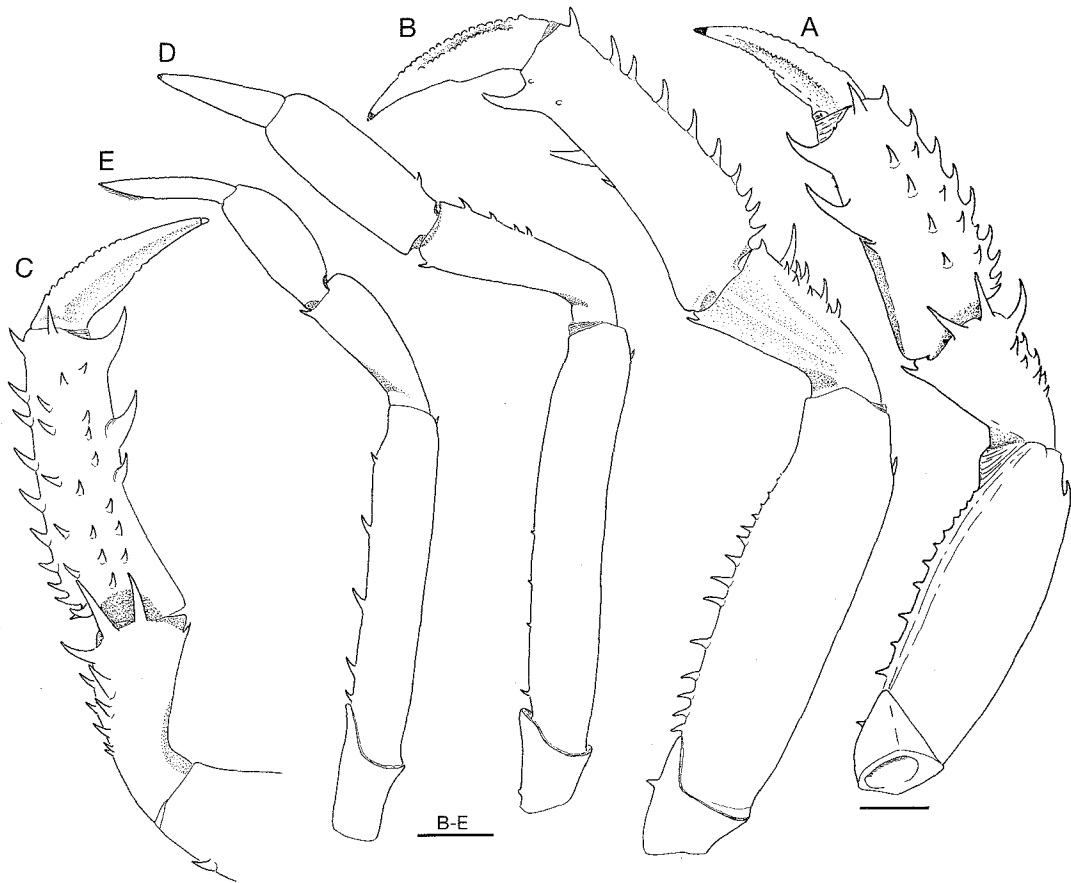


FIG. 25. — *Gebiakantha talismani* (Bouvier, 1915); **A**, ♂ from Lybia (MNHN Th 51), pereopod 1, mesial view (from de Saint Laurent 1971); **B-E**, ♀ from Cap Blanc du Nord, Morocco (MNHN Th 1352); **B, C**, pereopod 1 and distal articles in mesial view; **D, E**, pereopod 2 and 3. Scale bars: 1 mm.

*Gurney 1942: 246, fig. 99. — Zariquiey Alvarez 1946: 107, 108; 1968: 231. — Wilson 1951: pl. 31, 1 fig. — *Rees 1955: 74, fig. 4.5 (part). — *Kurian 1956: 76. — Tambs-Lyche 1958: 12, fig. 2. — *Heegaard 1963: 458, pl. 1, fig. 7, text figs 27-33. — ?Harmelin 1964: 94. — Picard 1965: 60. — Bourdon 1963: 429; 1965: 15. — Forest 1965: 347. — Holme 1966: 421, 452, fig. 14 (part). — Holthuis & Gottlieb 1958: 66. — de Gaillande 1970: 377. — de Saint Laurent 1971: 1261. — *Seridji 1971: 49. — Christiansen 1972: 41, fig. 48. — Naylor 1972: 69. — Lagardère 1973: 84. — Le Lœuff & Intès 1974: 56, figs 19, 19bis. — Neves 1974: 14. — Samuelsen 1974: 131. — °Pastore 1976: 107. — *Thiriou 1976: 350, 367. — Tebble 1976: 85 (association with the bivalve mollusc *Lepton squamosum* (Montagu, 1803)). — °Glaçon 1977: 36. — Beaubrun 1979: 76. — de Saint Laurent & Le Lœuff 1979: 40, 93, fig. 3. — Monchartmont 1979: 73. —

Domenech *et al.* 1981: 150. — Kocataş 1981: 162. — Ngoc-Ho 1981: 245; 1984: 511, fig. 6. — Adema *et al.* 1982: 28, fig. 8. — Manning & Froggia 1982: 324. — Cortiglia 1983: 78. — García Raso 1983: 318; 1990: 314. — Thessalou-Legaki & Zenetos 1985: 311. — Campbell & Nicholls 1986: 218, 1 fig. — Holthuis & Heerebout 1986: 62, fig. 81. — Lewinsohn & Holthuis 1986: 25. — Thessalou-Legaki 1986: 183. — Tunberg 1986: 753. — d'Udekem d'Acoz 1989: 176, fig. 5; 1995: 61, fig. 3; 1999: 156. — Moyses & Smaldon 1990: 520, fig. 10.13 (part). — Neves 1990: 670. — Števcic 1990: 215. — Dworschak 1992: 223. — °García Raso *et al.* 1992: 258. — °Koukouras *et al.* 1992: 223. — Noël 1992: 82. — °Froggia 1995: 8. — Hayward *et al.* 1995: 433, fig. 8.52 (part). — Eneman 1996: 159, fig. 1. — Falciai & Minervini 1996: 149, 1 fig. — °Brattegard & Christiansen 1997: 222. — Christiansen & Stene 1998: 76. — Astall *et al.* 1996:

821, tabs 1, 2; 1997a: 155, figs 1 (part), 3, 5, tabl. 1 (part); 1997b: 671, 675, fig. 1, tabs 1-5, pl. 2. — Hughes & Atkinson 1997: 640. — Lindahl & Baden 1997: 33. — Pinn *et al.* 1998a: 243, figs 2B, 2D; 1999a: 103, figs 2G, H, 3A, 4G, H; 1999b: 1461, figs 5, 6, tabs 1-6. — Hall-Spencer & Atkinson 1999: 871, figs 1-5. — Moen & Svensen 1999: 234, 2 figs. — Christiansen 2000: 233. — Taylor *et al.* 2000: 265, figs 1-3, tabs 1-3, 5, 6. — *González-Gordillo *et al.* 2001: 279. — Livory 2001: 33. — Markham 2001: tabs 1, 2. — *Martin 2001: 81, 1 fig. — °Türkey 2001: 289.

Uppogebia deltaura — ?Pères & Picard 1964: 66.

TYPE MATERIAL. — Holotype: Kingsbridge Estuary, Devon, UK, English Channel, North East Atlantic, Leach collection: ♀, posterior part of carapace damaged, left P1, P4, P5 present; left P2, right P1, P5 detached, merus missing (NHML 259 e).

MATERIAL EXAMINED. — North Sea. Doggerbank Ost, 54°49.14'N, 3°3.30'E, 27.2-29.7 m, F. K. Senckenberg, 1 ♀ cl. 10.5 mm (SMF 28334). — Spiekeroog, 27.VII.1959, 1 ♂ cl. 23 mm, 1 ovig. ♀ cl. 20 mm (SMF 28335). — Near Helgoland, 1877, 1 ♂ (RMNH D 4931). — NW Brandaris, in *Mustelus mustelus* (Linnaeus, 1758), Zool. Station Den Helder coll., 20.V.1950, 1 ♂ (RMNH D 7383). — Brown Banks, near Winterton Twenties, from stomach of *Solea solea* (Linnaeus, 1758), 20-27.VIII.1960, leg. J. Kruuk, 3 ♂♂, poor condition (RMNH D 16180). — 53°41'45"N, 3°55'E, 12.VIII.1971, leg. G. R. Heerebout, 2 ♂♂, 2 ♀♀ (RMNH D 27524). — 53°43.5'N, 4°27.2'E, 33 m, 1.VI.1971, leg. Rijks. Instituut voor Visserij Onderzoek, 2 ♂♂, 2 ♀♀ (RMNH D 27525). — 53°42'N, 3°55'E, 12.VIII.1971, *Tridens*, leg. G. R. Heerebout, 19 m, 7 ♀♀ (RMNH D 27526). — 54°02.5'N, 4°07.9'E, 42 m, 30.VI.1971, leg. Rijks. Instituut voor Visserij Onderzoek, 1 ♂ (RMNH D 28191). — 53°38'N, 4°31.6'E, 28-29 m, leg. Rijks. Instituut voor Visserij Onderzoek, 1 ♂ (RMNH D 28192). — 53°48.7'N 4°22.5'E, 37 m, 1.VI.1971, leg. Rijks Instituut voor Visserij Onderzoek, 1 ♂ (RMNH D 28193). — 53°38'N, 3°44'E, 34 m, 23.VI.1980, P. C. Goudswaard, stn 74, Rijks. Instituut voor Visserij Onderzoek, 4 ♂♂, 2 ♀♀ (RMNH D 32960). — 53°48'N, 04°13'E, 24.IV.1972, *Aurelia* cruise, don. Netherlands Institute for Sea Research, 17 ♂♂, 4 ♀♀ (RMNH D 33185). — 53°43'N, 04°17'E, 16.X-1.XI.1972, *Aurelia*, stn 180, leg. F. Creutzberg, v.s., don. NIOZ, 3 ♂♂, 1 ♀ (RMNH D 35738). — 53°38'N, 03°44'E, 34 m, 23.VI.1980, leg. P. C. Goudswaard, 2 ♂♂ (RMNH D 35739). — 53°40'N, 04°22'E, 26.VI-7.VII.1972, *Aurelia*, stn 117, leg. F. Creutzberg, c.s. don. NIOZ, 2 ♂♂ (RMNH D 35740). — North-Holland, 30 m, 21.VI.1958, don. NIOZ, 1 ovig. ♀ (RMNH D 35741). — 53°39'N, 5°42'E, 20 m, 26.X.1977, leg. P. I. Van Leeuwen,

don. R. Boddeke, RIVO, 2 ♀♀ (RMNH D 35742). — 53°48'N, 04°07'E, 24.IV-4.V.1972, *Aurelia* cruises, leg. F. Creutzberg, don. NIOZ, 3 ♂♂ (RMNH D 35744). — 53°39'N, 04°06'E, 29.IX.1975, *Aurelia*, stn 333, don. NIOZ, 1 ♂ (RMNH D 35745). — 53°52.5'N, 04°29.5'E, MS *Aurelia*, 2.II.1982, leg. P. C. Goudswaard, 1 ♀ (RMNH D 35746). — 54°03'N, 02°50'E, MS *Aurelia*, 20.X.1976, leg. F. Creutzberg, 1 cheliped (RMNH D 35747). — Surroundings Helgoland, 54°28'N, 06°13'E-54°42'N, 06°35'E, 3-12.V.1995, leg. J. Verkuil, 2 ♂♂ (RMNH D 46166).

Sweden. Prov. Goteborg och Bohus, Fiskebackskil, c. 120 km N Göteborg, Kristineberg Marine Research Station, Pettke coll., IX.1976, 44 ♂♂ cl. 7-20 mm, 41 ♀♀ cl. 7-17.5 mm (SMF 28331); 4 ♂♂ cl. 17-21 mm, 1 ♀ cl. 12 mm (SMF 28332); Kristineberg, IX.1975, 4 ♂♂ cl. 10.5-12.5 mm, 6 ♀♀ cl. 7.5-15 mm (SMF 28333). — Skagerrak, 20-30 m, exc. Leiden Biologists, stn 301, 3.VI.1971, 1 ♂ (RMNH D 28194). — E of Bonden Island, 58°12'N, 11°19'E, 20-30 m, *Amphioxus* sand, 3.VI.1971, Exc. Studens Leiden, 1 ex. (RMNH D 35734).

Netherlands. Teakettle Hole, 50 miles WNW of Den Helder, in stomach of *Egaleus galeus* (Linnaeus), 24.XI.1945, don. Zool. Station Den Helder, 1 damaged ♀ (RMNH D 6198). — NW of Brandaris, Texel, from stomach of *Mustelus mustelus* (Linnaeus, 1758), near oystergrounds, 25.X.1950, don. Zoological Station Den Helder, 1 ♂ (RMNH D 7382).

Great Britain. Firth of Clyde, off Lion Rock, R. B. Pike coll., 20.XII.1957, 3 ♂♂ (NHML 1962.7.5.5.7). — Devon, English Channel, Leach collection, 1 ♀ cl. 20 mm, tl. 65 mm approx. (figured) (holotype, NHML 259 e). — English Channel (see Holme 1961), 29 m, 3 ♂♂, 4 ♀♀ (2 ovig.) (NHML 1999.257-264); 35 m, 1 ♂, 3 ♀♀ (NHML 1999.247-256); 58 m, 4 ♀♀ (NHML 1999.242-245); 37 m, 1 ♀ (NHML 1999.241); 21 m, 1 ♂ carapace (NHML 1999.229); 34 m, 1 broken ♂ (NHML 1999.231); 18 m, 1 ♂ (NHML 1999.228); 37 m, 2 ♂♂, 1 ♀ (NHML 1999.239-249); 19 m, 1 ♂ (NHML 1999.226); 36 m, 1 ♀ (NHML 1999.233); 19 m, 1 ♀ abdomen (NHML 1999.227); 37 m, 1 ♂ abdomen (NHML 1999.232); 16 m, 1 ♂, 2 ♀♀ (NHML 1999.230); 35 m, 1 ovig. ♀ (NHML 1999.246) (see Holme 1966); 27 m, 3 ♂♂, 1 ♀ (NHML 1999.269-272); 33 m, 1 ♀ (NHML 1999.273); 36 m, 2 ♂♂, 3 ♀♀ (NHML 1999.234-238); 35 m, 9.XI.1961, 4 ♂♂, 1 ♀ (NHML 1999.306-310); 31 m, 1.II.1960, 4 ♂♂, 2 ♀♀ (NHML 1999.278-285); 57 m, 11.VII.1961, 4 ♂♂, 3 ♀♀ (NHML 1999.299-304); 22 m, 1.II.1960, 2 ♀♀ (NHML 1999.286-289); 68 m, 1 ♂ carapace (NHML 1999.321); 33 m, 2.II.1960, 1 ♂ exuvia (NHML 1999.297); 27 m, 1 ♂ abdomen (NHML 1999.294); 55 m, 31.I.1962, 5 ♂♂ (2 damaged)

(NHML 312-315); 38 m, 1.II.1960, 2 ♂♂ (NHML 1999.276-277); 37 m, 1 abdomen (NHML 1999.320); 52 m, 11.VII.1960, 1 ♂ (NHML 305); 29 m, 1.II.1960, 2 ♂♂, 1 ♀ (without abdomen) (NHML 1999.292-293); 46 m, 10.XI.1961, 1 ♂ (NHML 1999.319); 64 m, 31.I.1960, 1 ♀ (NHML 1999.275); 38 m, 1.II.1960, 2 ♂♂ (NHML 1999.290-291); 26 m, 2 ♂♂ (NHML 1999.295-296); 68 m, 3.II.1962, 1 ♂ (NHML 1999.322); 44 m, 10.XI.1961, 1 ♂ (NHML 1999.311); 51 m, 11.VII.1961, 1 ♂ (dried) (NHML 1999.298); 68 m, 3.II.1962, 2 ♂♂, 1 ♀ (NHML 1999.316-318); 31 m, 31.I.1960, 1 ♂ (NHML 1999.274); 27 m, 30.I.1960, 3 ♂♂ (damaged) (NHML 1999.265-268). — Plymouth, 1 ♂, 1 ♀ (NHML 1910.7.1-2); intertidal mud-flats, R. L. Rice coll., 8.IV.1971, 1 ♂ (NHML 1971.21); II.1945, 1 ♂ (NHML 1949.1.18.24); MBA purchased, VI.1950, 2 ♂♂ (NHML 1950.8.22.18-19); shell gravel, A. L. Rice coll., 18.III.1970, 1 ♂ (NHML 1972.20). — Plymouth Sound, Montagu coll., 3 ♂♂ (NHML 259 a, 259 b and 259 c). — Salcombe, Devon, 1 ♀ (NHML 1901.4.16.1). — Salcombe Harbour, 1 ♂, 1 ovig. ♀ (NHML 98.5.7.734). — Polperro, Cornwall, Norman collection, 1 ♂ (NHML 1911.11.8.1034). — Weymouth Bay, B. Horton coll., 10.V.1990, 1 ♀ cl. 16 mm (NHML 1999.995). — Plymouth, leg. Carlisle, V.1959, don. Zool. Station Napels, 1 ovig. ♀ (RMNH D 13012).

Belgium. Ostende, E. Van Beneden coll., 1 ♂ (NHML 98.5.7.731).

France. English Channel, Roscoff, collector unknown, 17.IX.1958, 1 ♀ cl. 18 mm, tl. 54 mm, 1 ♂ cl. 11 mm without abdomen (figured), 1 ♀ cl. 17.5 mm (MNHN Th 1316). — Briqueville, Normandy, low tides, B. Richer de Forges coll., III.1981, 1 ♂ cl. 21 mm, tl. 59 mm (MNHN Th 643). — Baie de Seine, 20-30 m, Gentil coll., 1 ♂ cl. 15 mm (MNHN Th 315). — Manche?, Baron of St-Joseph's collection, No. 20, 1911, 2 ♀♀ cl. 14.5 and 21 mm (MNHN Th 9), 2 ♀♀ cl. 8.5 and 11 mm (poor condition) (MNHN Th 487). — Atlantic, Bay of Concarneau, Glémarec coll., 1 ♂ cl. 6.5 mm (MNHN Th 8). — Coasts of France, 1 ovig. ♀ cl. 16.5 mm, 2 ♂♂ cl. 16-20 mm, 1 ♂ cl. 19 mm, tl. 58 mm (figured) (MNHN Th 38). — St-Vaast-la-Hougue, A. Malard coll., 1903, 1 ♀ cl. 23 mm approx. (poor condition) (MNHN Th 203). — Iroise sea, Brittany, Glémarec coll., 1 ♂ cl. 8 mm (MNHN Th 313), 1 ♂ cl. 5.5 mm, 1 ♀ cl. 6 mm (MNHN Th 314). — Bay of Morlaix, Brittany, J. H. Stock coll., 17.IX.1955, don. Zool. Museum Amsterdam, 1 ♀ (RMNH D 10991). — Island of Glénoan, near Concarneau, Brittany, 10-30 m, 14.IX.1958, 1 ♂, 1 ♀ (RMNH D 12533). — St-Servan, Brittany, IV.1924, 2 ♀♀ cl. 9 and 19 mm (MNHN Th 554). — You Bridge?, Y. Gruet coll., 26.VIII.1972, 1 ♂ cl. 22 mm (poor condition) (MNHN-Th 612). — Island of Chausey (Pierre aux Vras), low tides, A. Crosnier coll.,

VIII.1976, 1 ♂ cl. 7.5 mm (MNHN Th 440). — Mediterranean, Banyuls, sewage, P. Noël coll., 9.VI.1976, 3 ♂♂ cl. 4.5-8 mm (MNHN Th 1339). — Banyuls?, Thiriot coll., 1 ♀ cl. 7 mm (MNHN Th 666). — Monaco, 22.VIII.1960, leg. C. Carpine, 1 ♂, 1 ♀ (RMNH D 19889). — Fontaindreau, from the stomach of *Raja clavata* Linnaeus, 1758, 110-125 m, 3 ♂♂, 3 ovig. ♀♀ (RMNH D 28198).

Spain. Cadaqués, VIII.1950, leg. R. Zariquiey Álvarez, 1 ♀ (RMNH D 35743).

Italy. Porto Cesareo, Parenzan coll., 1 ♂ cl. 12 mm (MNHN Th 543).

Mediterranean. Balears, Ibiza, 5-6 m, 11.VIII.1954, 1 juv. cl. 3.5 mm (MNHN Th 1324).

Mauritania. Off Banc d'Arguin, 19°33'N, 16°55'W, depth 64 m, sticky grey mud, ophiurids, echinoids, bivalves, tubeworms, 1.2 m, Agassiz trawl, 15.VI.1988, 4 ♂♂, 3 ♀♀ (1 ovig.) (RMNH D 48000).

Sierra Leone. 7°15'N, 13°00'W, 100 m, bottom with sandy mud, 18.IV.1956, A. R. Longhurst coll., 1 ♂ broken (RMNH D 32139).

Ivory Coast (between Vridi and Jacquville). 60 m, Le Lœuff coll., 23.XI.1966, 2 ♂♂ cl. 4.5 and 6 mm (MNHN Th 283). — N Vridi, *Reine Pokou* Exped., 60 m, Le Lœuff coll., 22.VI.1966, 1 ♂ cl. 5 mm, 1 ♀ cl. 6 mm (MNHN Th 663). — Jacquville, *Reine Pokou* Exped., 60 m, Le Lœuff coll., 24.XI.1966, 1 ♀ cl. 8 mm (MNHN Th 668). — East of Grand Bassam, 37 m, Le Lœuff coll., 25.II.1967, 1 juv. cl. 5 mm (MNHN Th 670).

Togo. Togo coast, *Ombango* Exped., sandy mud, 59-60 m, A. Crosnier coll., 6.X.1963, 2 ♀♀ cl. 6 and 6.5 mm (MNHN Th 284).

DISTRIBUTION. — Eastern Atlantic: Sweden, Norway (Samuelsen 1974; Christiansen 2000) to Togo, including the English Channel; North Sea (Poulsen 1940; Adema *et al.* 1982); Mediterranean including Adriatic Sea (Pesta 1918; Štević 1990; Dworschak 1992), Aegean sea (Koukouras *et al.* 1992) and Cyprus (Lewinsohn & Holthuis 1986).

DIAGNOSIS

Rostrum (Fig. 26A, D) obtuse distally, slightly longer than wide at base, with two or three teeth on lateral border; antero-lateral border of carapace unarmed (Fig. 26B); pleura of first abdominal segment (Fig. 26G) pointed postero-ventrally; telson (Fig. 26C) approximately 1.2 times as wide as long.

A1 peduncle (Fig. 26B) with large spine on lower margin of article 1, A2 peduncle with smaller spine on lower margin of article 3. Md with large mesio-anterior pointed tooth. Mx1 and Mx2

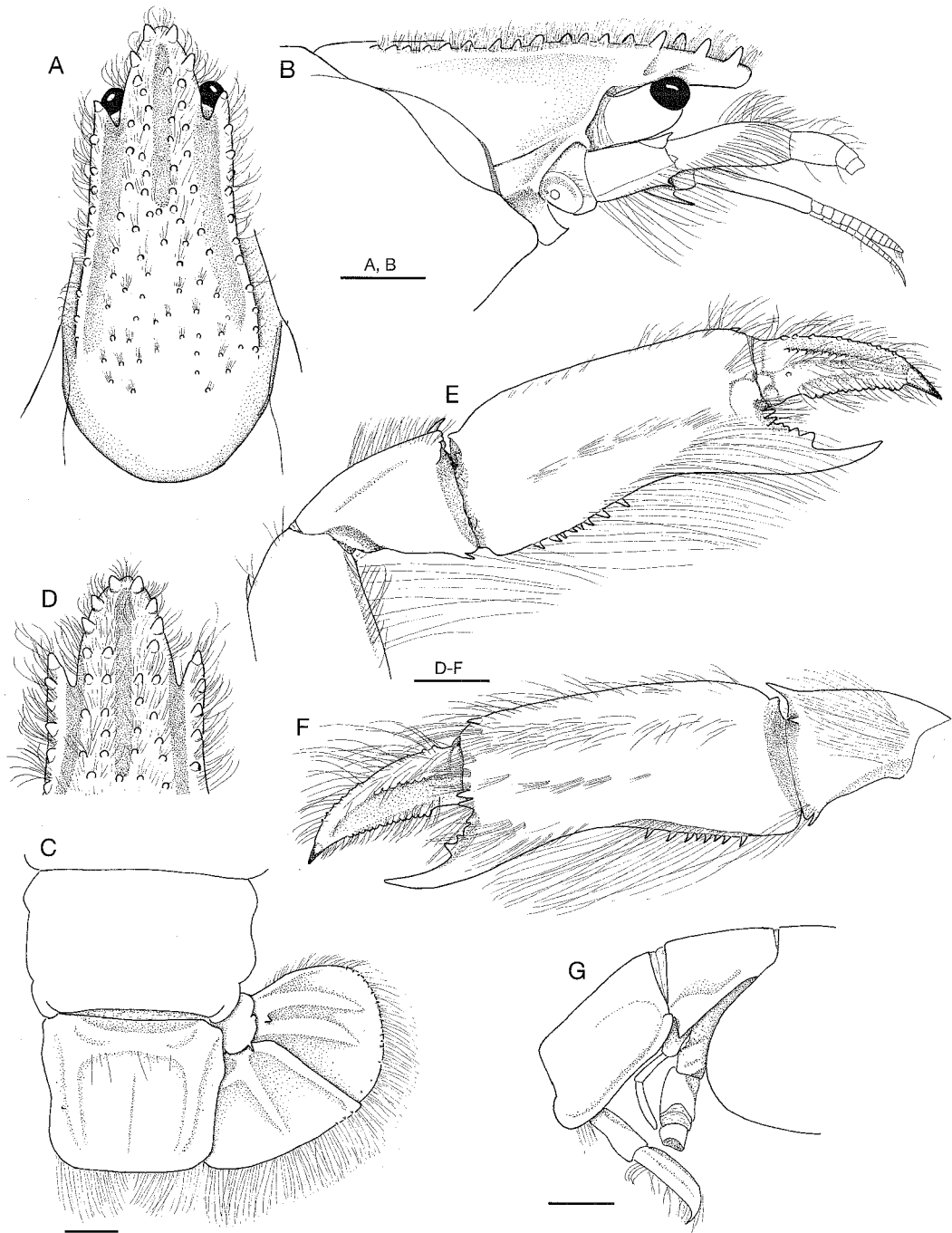


FIG. 26. — *Upogebia deltaura* (Leach, 1815); **A-C**, ♀ from Roscoff, France (MNHN Th 1316); **D-G**, holotype, ♀ from Devon, UK (NHML 259 e); **A, D**, anterior part of carapace and rostrum, dorsal view; **B**, anterior part of carapace, lateral view; **C**, telson and uropods; **E, F**, distal articles of pereopod 1, lateral and mesial view; **G**, abdominal segments 1 and 2, lateral view. Scale bars: A-F, 2 mm; G, 4 mm.

(Fig. 27D, E) as figured. Mxp1 (Fig. 27H) without epipod, Mxp3 (Fig. 27G) with epipod. P1 slightly stouter in male (Fig. 27A) than in female (Fig. 26E, F); merus with upper subdistal spine and two to five lower spines or spinules; carpus with large upper mesial distal spine, small lower distal spine and (sometimes) small median spines near mesial distal margin (Fig. 26F); propodus with small upper subdistal spine, both lateral and mesial surface with one or two distal spines near base of fixed finger; fixed finger as long as dactylus in young specimen, often shorter than dactylus in adult, with three to four triangular teeth on proximal half of cutting edge; dactylus with longitudinal row of round tubercles on external and mesial surface, small round teeth on cutting edge. P2 (Fig. 27B) with upper subdistal spine on merus and carpus. P3 (Fig. 27E) with spinules and tubercles on lower margin of merus. Large coxal spines on P1 and P2. Arthrobranch with double row of fine lamellae on either side of the rachis.

Plp1 absent in male, uniramous in female (Fig. 26G); Plp2-5, biramous, foliaceous. Exopod of uropod with proximal spinule, basipod also with spinule (Fig. 26C).

Colour

Bright orange, some specimens whitish (d'Udekem d'Acoz pers. comm.); grey yellow tinged green (Campbell & Nicholls 1986); dirty yellow, tinged white or red (Moyses & Smaldon 1990).

Size

Holotype of cl. 21 mm, tl. 65 mm approx. Largest specimens in material examined: cl. 18-21 mm, tl. 54-59 mm. Largest size reported: tl. up to 80 mm or exceptionally 150 mm (Moyses & Smaldon 1990).

ECOLOGY AND BIOLOGY

The population ecology of the species in western Sweden was studied by Tunberg (1986). In western Norway, it occurs in shell and mineral sand with some mud, at 3 m depth (Samuelsen 1974), in shallow water in southern part of the boreal

region (Christiansen 2000). It was found in muddy-gravel association off Plymouth, English Channel (Holme 1966), and was occasionally dredged from mud or muddy sand (Gordon 1957). It is common in Brittany, France, in coarse or muddy sand, with or without seagrass (d'Udekem d'Acoz 1989). Specimens were collected from shore, in Ireland (Selbie 1914), near the water edge on the beach (Southern 1915), between 20-40 m, in Portugal (Neves 1990), and were present in a variety of substrates from sand with high percentage of pebbles to muddy sand, in Patras Gulf, Greece, at 5-15 m depth (Thessalou-Legaki & Zenetos 1985).

Reproduction occurs in February-April in Roscoff, France (Bourdon 1965) in spring and summer in Plymouth, UK (Gordon 1957). Larvae are present in Roscoff during February-November, abundant in July-August, mainly near the bottom (i.e. at 15 m depth in a bottom of 20 m) during day time, in surface waters at night (Thiriot 1976), common in the Kilkieran Bay plankton, Ireland in April-October, plentiful in August (O'Céidigh 1962).

Aspects of biology studied

Functional anatomy of foregut (Ngoc-Ho 1984); branchial parasitic isopods (Astall *et al.* 1996); burrow morphology and burrow-dwelling lifestyle (Astall *et al.* 1997a); branchial morphology, gill area and gill ultrastructure (Astall *et al.* 1997b); particle size selectivity and resource partitioning (Pinn *et al.* 1998b); burrows in scottish mearl beds (Hall-Spencer & Atkinson 1999); gut morphology and gut microflora (Pinn *et al.* 1999a); mouthpart morphology and mouthpart setal fringes (Pinn *et al.* 1999b); functional response in filter feeding (Lindahl & Baden 1997); oxygen transporting properties of haemocyanin (Taylor *et al.* 2000).

VARIATIONS

There are variations in: 1) the rostrum often bears two, three or (rarely) four lateral rostral teeth; 2) the large upper distal spine on P1 carpus is sometimes accompanied mesially by one or two spinules (Fig. 26F); 3) the lower border of P1

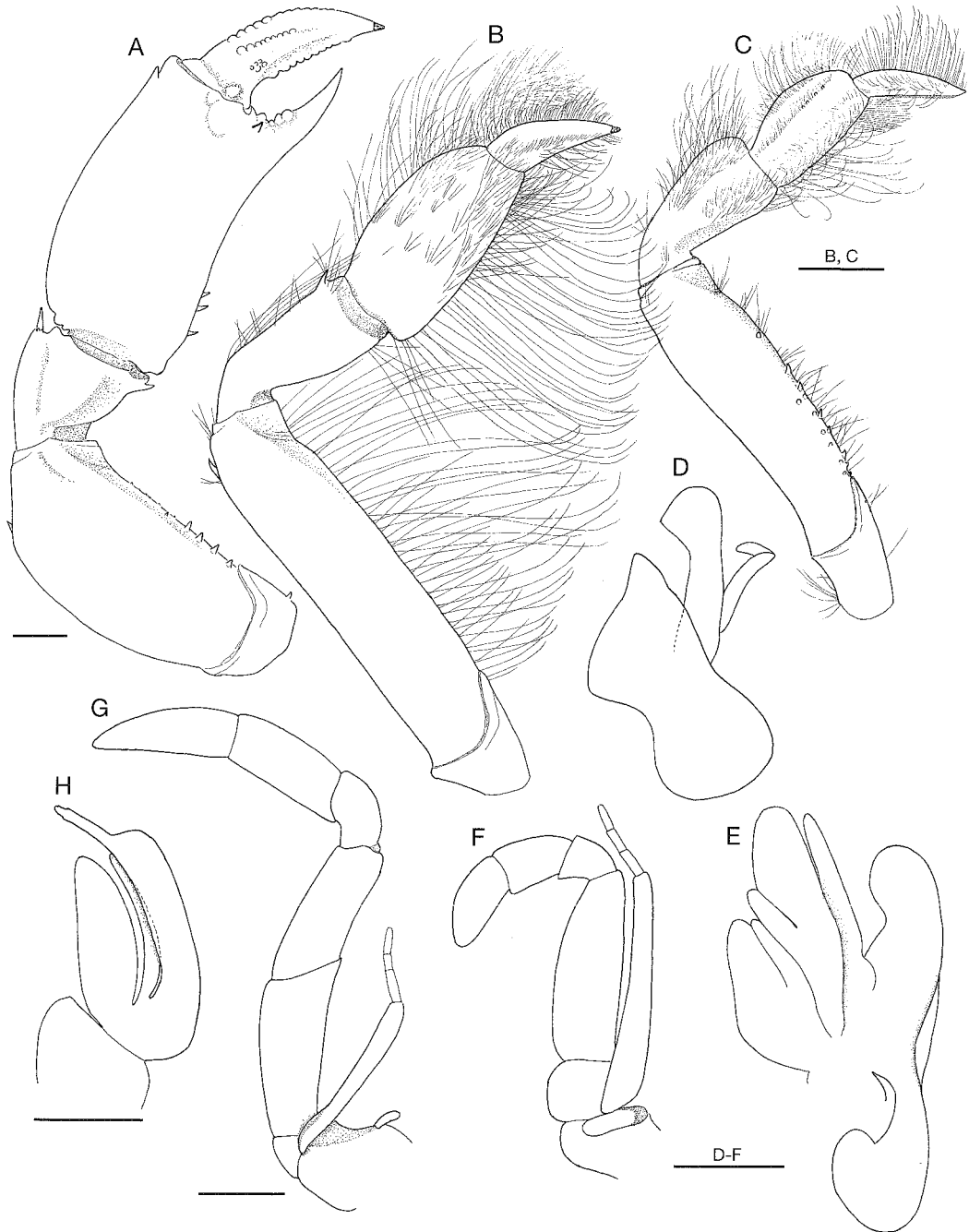


FIG. 27. — *Upogebia deltaura* (Leach, 1815); **A**, ♂ from coasts of France (MNHN Th 38); **B-H**, from Roscoff, France (MNHN Th 1316); **B, C**, ♀; **D-H**, ♂; **A-C**, pereopod 1-3; **D, E**, maxillule and maxilla; **F-H**, maxilliped 2, 3 and 1 respectively. Scale bars: A-C, 2 mm; D-H, 1 mm.

propodus has two to five spinules on the proximal half, three on the left and eight (rare) on the right in the holotype (Fig. 26E); 4) the distal lateral spine, as well as distal mesial spine near the base of P1 fixed finger, is larger in female than in male, and impaired, as on left P1 of holotype (rarely paired as on right P1 of holotype, Fig. 26E, F); 5) P1 fixed finger is about as long as the dactylus in small specimens (cl. 7-8 mm, tl. c. 20-22 mm), shorter than the dactylus in most large specimens, shortest in large males; and 6) P3 merus is sometimes unarmed.

REMARKS

Upogebia deltaura is close to *U. mediterranea* Noël, 1992 which is often associated with *Posidonia oceanica* seagrass. Some materials assigned to *U. deltaura* and reported as associated with *Posidonia* (Harmelin 1964; Pérès & Picard 1964) could actually belong to *U. mediterranea*. Differentiation of *U. deltaura* and *U. mediterranea* is discussed under the latter species.

U. deltaura is similar to *U. demani* de Saint Laurent & Le Lœuff, from the Gulf of Guinea, in the shape and spinulation of the rostrum (de Saint Laurent & Le Lœuff 1979: 41, fig. 4b), also in having a lower spine on article 3 of A2 peduncle. De Saint Laurent & Le Lœuff (1979: 42, fig. 4a) fail to mention and figure the latter character, but give in detail the differences between the two species.

The pointed postero-ventral pleura of abdominal segment 1 is the most important characteristic of *U. deltaura*. Along with the morphology of the rostrum and the unarmed antero-lateral border of the carapace, it permits a quick identification even of small specimens (e.g., MNHN Th 1324; cl. 3.5 mm). The carapace is thin and weakly calcified in some specimens.

Genital openings are visible in young male and female of cl. 5-5.5 mm (tl. c. 15-17 mm) but Plp1 appear at a later stage in female of cl. 6.5-8 mm (tl. c. 19-22 mm).

Upogebia deltaura, widely distributed in Europe, was also found in Western Africa (Ivory coast and Togo) by Le Lœuff and Crosnier (MNHN Th 283, 284, 663, 668, 670). Specimens from these

areas are apparently smaller than in Europe, but the adult size is not known as no ovigerous females were available for study.

Upogebia mediterranea Noël, 1992
(Figs 28; 29)

Upogebia n. sp. "*mediterranea*" Noël, 1992: 82.

Upogebia deltaura – ?Harmelin 1964: 94.

Upogebia deltaura – ?Pérès & Picard 1964: 66.

Upogebia cf. *deltaura* – Kocaraş 1981: 162. — Dworschak 1992: 223.

Upogebia mediterranea – Dworschak 1983: 40 (appendix) *nomen nudum*.

Upogebia mediterranea – °Frogli 1995: 8. — Asgaard *et al.* 1997: 23. — Abed-Navandi & Dworschak 1998: 609. — d'Udekem d'Acoz 1999: 157. — °Turkey 2001: 289.

Upogebia nitida – Le Lœuff & Intès 1974: 58 (part), fig. 20.

Upogebia cf. *nitida* – de Saint Laurent & Le Lœuff 1979: 93.

Upogebia nitida mediterranea – d'Udekem d'Acoz 1995: 60, 61, fig. 2.

Upogebia n. sp. – Thessalou-Legaki 1986: 184.

TYPE MATERIAL. — Lectotype: ♀ from Tamaris-sur-Mer, near Toulon, France (MNHN Th 1372) by present designation.

Paralectotypes: Tamaris-sur-Mer, same data as lectotype: 4 ♂♂, 3 ♀♀ (MNHN Th 1369); Banyuls, France, 1 ♂ (MNHN Th 665), 1 ♀ (posterior part of abdomen missing) (MNHN Th 667); Ibiza, Balears, Spain, 1 ♂ (MNHN Th 661); Gulf of Gabès, Tunisia, 1 ♀ (MNHN Th 921), 1 ♂ (MNHN Th 922), 1 ♂ (MNHN Th 923) and 1 ♂ (MNHN Th 924); Gulf of Oran, Algeria, 2 ♂♂, 2 ♀♀ (MNHN Th 486).

TYPE LOCALITY. — Tamaris-sur-Mer, France.

MATERIAL EXAMINED. — France. Tamaris-sur-Mer, near Toulon, collection Sollaud, No. ES 38, 25.XII.1932, ♀ lectotype cl. 15 mm, tl. 48 mm (figured) (MNHN Th 1372); same data, 1 ♂ paralectotype cl. 12 mm, tl. 36 mm (figured) and 3 ♂♂ paralectotypes cl. 13-14.5 mm, tl. 38-43 mm, 3 ♀♀ paralectotypes cl. 13-18 mm, tl. 42-56 mm (MNHN Th 1369). — Banyuls, France, in *Posidonia* rhizome, 7 m, P. Noël coll., 12.VIII.1976, 1 ♂ paralectotype cl. 6 mm, tl. 17 mm (MNHN Th 665); in Herbière de Racou, 5-7 m, P. Noël coll., 27.III.1979, 1 ♀

paralectotype (posterior part of abdomen missing) cl. 9 mm (MNHN Th 667). — Banyuls?, Thiriot coll., 1 ovig. ♀, broken rostrum, approx. cl. 8 mm (MNHN Th 1312); Banyuls, in bed of *Posidonia*, 5 m, P. Noël coll., 3.VI.1977, 1 ♂ (just moulted, poor condition) approx. cl. 11 mm (MNHN Th 664). — Cap d'Ail, near Villefranche-sur-Mer, night catch, C. Vadon coll., 28.V.1980, 1 ♀ cl. 11.5 mm (MNHN Th 1323). — Marseille, Port Cros Island, 1.8 m, A. Willsie coll., 18.V.1983, 1 ♂ cl. 10 mm (poor condition) (SMF 28328). — Marseille, in sediments with *Posidonia*, A. Willsie coll., 1982, 1 ♂ cl. 12.5 mm, tl. 38 mm, (MNHN Th 1325); 1988, 1 ♂ cl. 11 mm (SMF 28329). — Ponteau, W of Marseille, H. Zibrowius coll., 13.II.1978, 1 ♀ cl. 12 mm, tl. 37 mm (MNHN Th 1326), 1 ♀ cl. 11.5 mm (SMF 28330). — Villefranche-sur-Mer, Alpes-Maritimes, W. G. N. v. d. Sleen coll., 26.IV.1920, 1 ♂, 1 ovig. ♀ (RMNH D 16179). — Monaco, H. Nouvel coll., 15 m, 15.IV.1952, 4 ♂♂, cl. 9-11 mm, 3 ♀♀ cl. 10.5-11 mm (RMNH D 34028); 1974, 3 ♂♂ cl. 5.5-9.5 mm, 3 ♀♀ cl. 10-11 mm (RMNH D 34029); 10.V.1938, 1 ♀ cl. 10 mm (RMNH D 34030); 2.VII.1937, 2 ♀♀ cl. 6.5 and 9.5 mm (RMNH D 34031); IV.1938, 2 ♂♂ cl. 6.5 and 8.5 mm (RMNH D 34033); 15-25.VI.1937, 1 ♂ cl. 6 mm (RMNH D 34034); 1936, 10 ♂♂ cl. 5.5-7.5 mm, 7 ♀♀ (4 ovig.) cl. 7-11 mm (RMNH D 34035); 2.IV.1953, 1 ♂ cl. 7.5 mm (RMNH D 34036); VI.1937, 24 ♂♂ cl. 5.5-12 mm, 4 ♀♀ (3 ovig.) cl. 8-11 mm (RMNH D 34037). — Cap d'Ail, H. Nouvel coll., 9.IV.1953, 1 ♂ cl. 7 mm (RMNH D 34032).

Spain. Balears, Ibiza, 11.VIII.1954, 5-6 m, 1 ♂ paralectotype cl. 8 mm, tl. 23.5 mm (MNHN Th 661).

Italy. Ischia, Castello A., in *Posidonia* rhizome, W. Tertschnig coll., 14.V.1981, 4 ♂♂ cl. 8-13 mm and 1 ♀ cl. 13 mm (NHMW 6763). — Ischia, Lacco Ameno, in *Posidonia* rhizome, 2 m, K. Wittmann coll., 1.VI.1987, 1 ♂ cl. 12.5 mm, 2 ovig. ♀♀ cl. 13 and 14 mm (NHMW 6764). — Naples, Adensamer leg. 1898, 1 ♂ cl. 12 mm, 1 ♀ cl. 13.5 mm (NHMW 10959). — Naples, J. G. de Man, 1876, 1 ♂ cl. 10.5 mm (RMNH D 993); don. Zoöl. Station Naples, V.1959, 19 ♂♂ cl. 5-16 mm, 9 ♀♀ (3 ovig.) cl. 6-16 mm (RMNH D 13069).

Greece. Rhodos, R. Bromley coll., 2.VIII.1998, 1 ♂ cl. 11.5 mm (NHMW 17936). — Tavros, Chios Islands, G. Potts coll., 1 ♂ cl. 5 mm (NHML 1968: 607). — Kreta (Stavros), given by fishermen, C. d'Udekem d'Acoz coll., 15.VII.1987, 1 ♂ cl. 3.5 mm (d'Udekem d'Acoz). — Aegean Sea, 40 m, 18.VIII.1985, Strimonikos G., 1 ♀ (A.U.TH P 4529).

Malta. M'xiokk Bay, P. J. Schembri coll., 1 ♂ cl. 12.5 mm, 1 ♀ cl. 13 mm (NHML 1977: 158). — Market, Norman collection, 4 ♂♂ cl. 14-15.5 mm, 5 ♀♀ (3 ovig.) cl. 9-15 mm (NHML.1911.11.B.1024-1033).

Israel. Haifa Bay, 19 m, E. Gottlieb coll., 7.VI.1955, 1 juv. cl. 1.5 mm (RMNH D 13327); 18 m, 7.IX.1954, 1 ♀ cl. 5 mm (RMNH D 13328); 20 m, 18.X.1955, 1 juv. cl. 2 mm (RMNH D 13329).

Tunisia. Gulf of Gabès, *Calypso*, muddy sand with detritus, 25 m, 2.V.1965, 1 ♀ cl. 9 mm, tl. 27 mm (MNHN Th 921); 1 ♂ paralectotype cl. 11 mm, d. 31 mm (MNHN Th 922); muddy and chalky sand, 25 m, 19.IV.1965, 2 ♂♂ paralectotypes cl. 8 mm, tl. 24 mm (MNHN Th 923), cl. 9 mm, d. 26 mm (MNHN Th 924).

Algeria. Gulf of Oran, P. Pallary coll., 1900, 1 ♂ paralectotype cl. 9.5 mm, tl. 29 mm (figured), 1 ♂ paralectotype cl. 10 mm, tl. 30 mm and 2 ♀♀ paralectotypes, cl. 11 and 12 mm, tl. 32 and 34 mm (MNHN Th 486).

Morocco. Melilla, J. Ruttlant, 1 ♂ cl. 8 mm (RMNH D 5254).

Congo. Near Pointe Noire, trawling, 18 m, A. Crosnier coll., *Ombango*, 25.XI.1966, 1 ♀ cl. 5.5 mm (MNHN Th 231).

DISTRIBUTION. — Mediterranean and Congo (west African coast).

DIAGNOSIS. — Rostrum elongated triangular, slightly longer than wide at base, with two teeth on each lateral border; anterolateral border of carapace unarmed; pleura of first abdominal segment rounded posteroventrally; telson subquadrate. A1 peduncle with large lower spine on article 1; A2 peduncle unarmed. Md with large mesioanterior pointed tooth. P1 merus with upper subdistal spine and lower spinules or tubercles; carpus with large upper mesial distal spine and small lower distal spine; propodus with upper subdistal spine and lateral distal spinule near base of fixed finger, latter with three or four teeth on proximal half of cutting edge; dactylus as long as fixed finger with mesial proximal round tooth on cutting edge. P2 with upper subdistal spine on both merus and carpus. P3 merus unarmed. Large acute coxal spine on P1 and P2 in male and female. Uropods about as long as telson.

DESCRIPTION

Rostrum (Fig. 28A, B) elongated triangular, slightly longer than wide at base, projecting beyond eyes, with two large spiniform teeth on each lateral border. Faint median dorsal groove on rostrum and anterior part of gastric region. Lateral groove narrow and shallow, lateral ridge with 10 to 12 teeth, larger distally. *Linea thalassinica* distinct, extending to posterior border of carapace. Anterolateral border of carapace unarmed. Cervical groove deep, bearing minute denticles and tubercles on either side. Epistome rounded distally or with minute distal spinule.

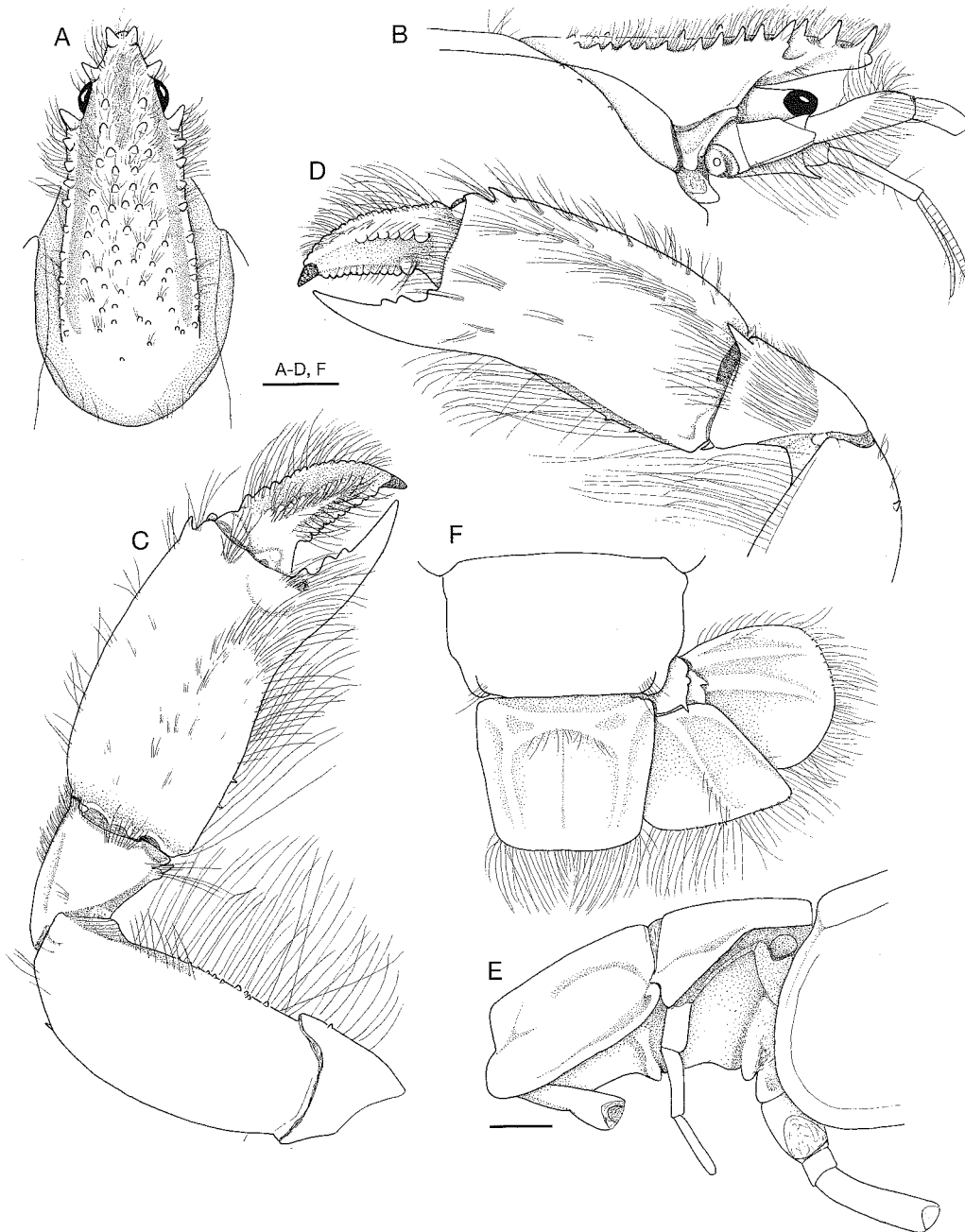


FIG. 28. — *Upogebia mediterranea* Noël, 1992; **A-E**, lectotype, ♀ from Tamaris-sur-Mer, France (MNHN Th 1372); **A, B**, anterior part of carapace, dorsal and lateral view; **C, D**, pereopod 1 and distal articles in mesial view; **E**, abdominal segments 1 and 2, lateral view; **F**, paralectotype, ♂, same locality (MNHN Th 1369), telson and uropods. Scale bars: 2 mm.

First abdominal segment slightly shorter than second, proximal part of pleura rounded ventrally (Fig. 28E). Telson (Fig. 28F, G) approximately quadrate, lateral and posterior borders weakly convex, an U-shaped carina and a faint median groove on upper surface.

Eyestalk (Fig. 28B) moderately long, cornea pigmented in preserved specimens. A1 (Fig. 29A) with large lower distal spine on peduncular article 1; peduncular article 3 about as long as second and first together; flagella not longer than peduncle. A2 peduncle unarmed (Fig. 29B), scale large, terminating in a spinule.

Md (Fig. 29C) with large mesio-anterior pointed tooth. Mxp1 without epipod, Mxp3 with small epipod. Arthrobranch with double or single (rare) row of fine lamellae on either side of rachis.

P1 (Figs 28C, D; 29F) cheliform, slightly stouter in male. Ischium with one or two lower spinules or tubercles. Merus over twice as long as wide, bearing upper subdistal spine and eight to 12 lower spinules and tubercles. Carpus with slight longitudinal groove on upper part of lateral surface, large mesial upper distal spine sometimes accompanied by one or two mesial distal spinules; smaller lower distal spine. Propodus about twice as long as wide in female, slightly stouter in male, with two to six spinules or denticles on proximal third of lower border, upper subdistal spine, and lateral distal spinule or tubercle near base of fixed finger; fixed finger with three or four teeth on proximal half of cutting edge. Dactylus approximately as long as fixed finger, with rounded tubercles on upper margin, proximal one largest and slightly pointed; longitudinal row of tubercles on both lateral and mesial surfaces, proximal mesial round tooth on cutting edge followed distally by faint teeth; corneous tip. P2 (Fig. 29D) merus over 4.5 times as long as wide with upper subdistal spine; carpus half as long as merus with small upper subdistal spine. P3 (Fig. 29E) and P4 unarmed, propodus and dactylus with lateral longitudinal row of corneous tubercles; dactylus pectinate on lower margin. Large coxal spine on P1 and P2.

Uropod (Figs 28F; 29G) exopod with proximal spinule and denticles on slightly convex posterior

margin; posterior margin of endopod almost straight; protopod with spinule hanging over endopod.

Coloration of a live specimen (MNHN Th 667) (Noël pers. comm.)

Gastric region with uniform orange colour on upper part, whitish laterally, with punctiform red chromatophores. Abdominal tergites and pleurites orange, with chromatophores, the latter a shade of light gray. Sternites transparent. Eye peduncle orange, with red chromatophores; cornea dark-wine. A1 peduncle transparent with a few red chromatophores. A2 peduncle with red chromatophores on articles 4 and 5; other articles whitish; flagella transparent.

P1: merus to dactylus orange, with a few red chromatophores on upper surface, lower surface lighter in color. Tip of dactylus dark brown and transparent. P2: distal part of merus to dactylus orange, lighter than on P1, with a few red chromatophores; proximal and lower part of merus opalescent white. P3-5 transparent, P3 and P4 with a few chromatophores from merus forwards. Pleopods transparent, with a few chromatophores on basis.

Size

Largest specimens in material examined: cl. 12-15 mm, tl. 36-48 mm.

ECOLOGY

Upogebia mediterranea occurs in muddy sand or sediments with *Posidonia*, 0-25 m. Burrows in firmground were studied by Asgaard *et al.* (1997).

VARIATIONS

1) The upper mesial distal spine of P1 carpus is accompanied laterally by one to three spinules; 2) the longitudinal row of tubercles on the lateral and mesial surfaces of the dactylus, as well as the proximal mesial round tooth on cutting edge is sometimes faint or absent (rare); and 3) arthrobranches are composed of a single row of lamellae on either side of the rachis in specimens from the Gulf of Gabès, Tunisia, and a double row of lamellae in the rest of the material examined.

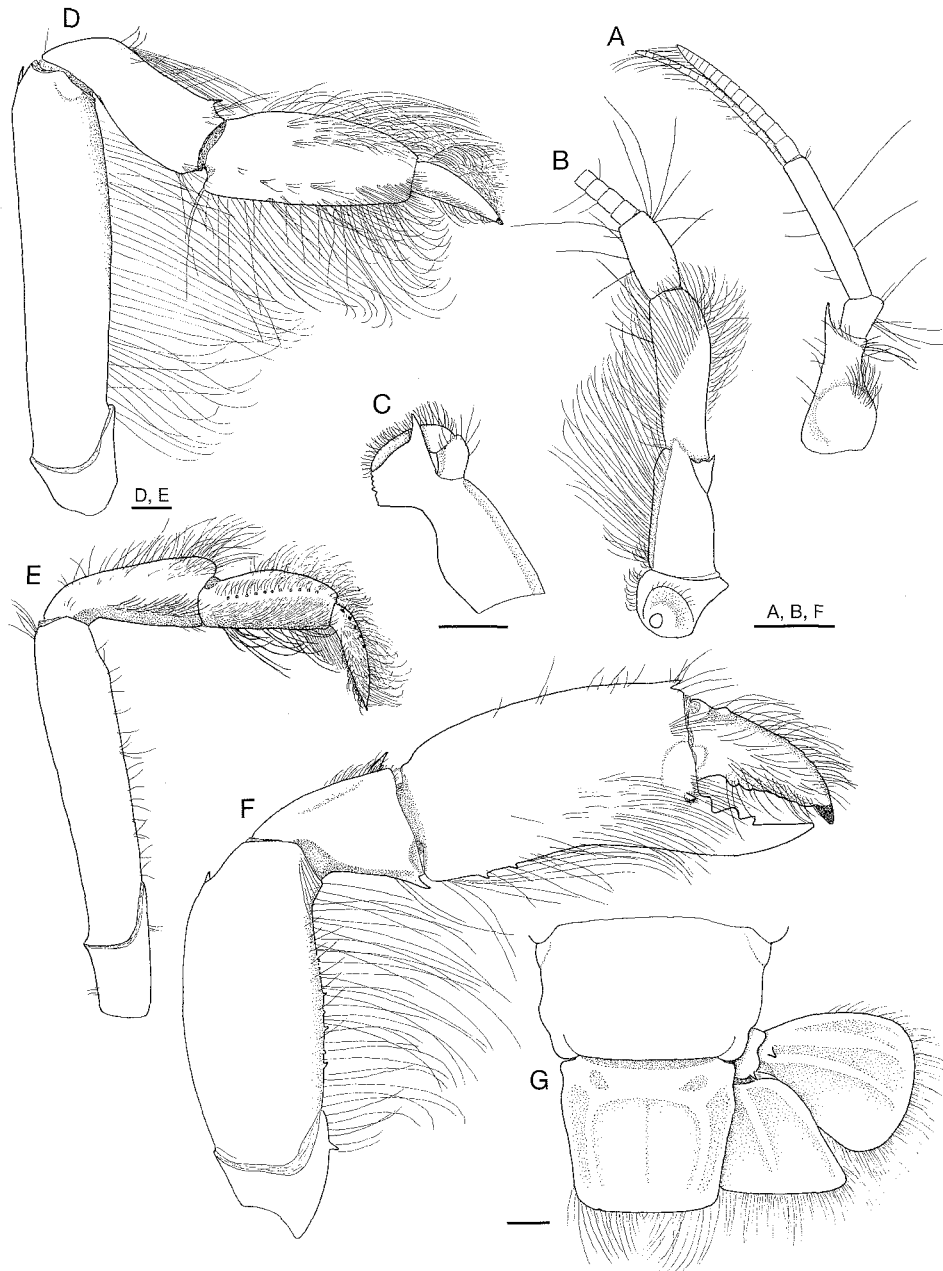


FIG. 29. — *Upogebia mediterranea* Noël, 1992; **A-C**, paralectotype, ♂ from Tamaris-sur-Mer, France (MNHN Th 1369); **D, E**, lectotype, ♀, same locality (MNHN Th 1372); **F**, paralectotype, ♂ from Balears (MNHN Th 661); **G**, paralectotype, ♂ from Gulf of Oran, Algeria (MNHN Th 486); **A, B**, antennule and antenna; **C**, mandible; **D-F**, pereopod 2, 3 and 1 respectively; **G**, telson and uropods. Scale bars: A, B, D-G, 1 mm; C, 0.5 mm.

REMARKS

This species, similar to both *U. deltaura* and *U. nitida*, was first mentioned by de Saint Laurent & Le Lœuff (1979: 93) as an undescribed species related to *U. nitida*.

According to Dworschak (1992: 223), it was cited again, under the present name *mediterranea*, as a taxon related to *U. deltaura*, by de Saint Laurent in a key to western Atlantic and Mediterranean species of *Upogebia* ("Tableau de détermination des *Upogebia* de l'Atlantique nord-oriental et de Méditerranée"). This key was given to participants of the IInd Colloquium Crustacea Mediterranea in Ancona, Italy (1979) but was never validly published. The species was subsequently recognized by Kocataş (1981), Thessalou-Legaki & Zenetos (1985) and Thessalou-Legaki (1986). It was mentioned by Noël (1992) in an identification key to decapod crustaceans from France and common European species ("Clé préliminaire d'identification des Crustacea Decapoda de France et des principales autres espèces d'Europe"). As Noël's key was published and contained diagnostic details, Noël is now the species' author according to the *International Code of Zoological Nomenclature* (ICZN 1999). The type series includes all specimens examined by him or de Saint Laurent before the species name was published. They were considered as syntypes and a lectotype was selected from them.

Upogebia mediterranea resembles *U. deltaura* in: 1) the shape and armature of the rostrum; and 2) the anterolateral border of carapace unarmed. It differs in the following characters: 1) the pleura of the first abdominal segment is rounded postero-ventrally in *U. mediterranea* (pointed in *U. deltaura*); 2) A2 peduncle is unarmed in *U. mediterranea* (with a lower distal spine on article 3 in *U. deltaura*); 3) P1 merus bears spinules and/or tubercles on its lower border in *U. mediterranea* (with spines and spinules in *U. deltaura*); 4) P1 propodus has no mesial distal spine near the base of the fixed finger in *U. mediterranea* (spine present in *U. deltaura*); 5) P1 dactylus bears a proximal mesial round tooth on the cutting edge in *U. mediterranea* (tooth often

absent in *U. deltaura*); 6) P1 dactylus and fixed finger are of about the same length in *U. mediterranea* (dactylus often longer than fixed finger in *U. deltaura*); 7) P3 merus is unarmed in *U. mediterranea* (with spinules and tubercles on the lower border in *U. deltaura*); and 8) the telson is approximately quadrate in *U. mediterranea* (about 1.2 times as wide as long in *U. deltaura*).

Upogebia mediterranea was considered closely related to *U. nitida* (A. Milne-Edwards, 1868) by de Saint Laurent & Le Lœuff (1979: 39, 93) and d'Udekem d'Acoz (1999: 157) or a subspecies of the latter (d'Udekem d'Acoz 1995). It was actually confused with the *U. nitida* in Le Lœuff & Intès (1974: 58, fig. 20). The small female these authors reported from Congo, of 5.5 mm in carapace length, and now deposited in the MNHN (MNHN Th 231), actually belongs to *U. mediterranea*. The excellent figures given agree perfectly with those of the latter species (Figs 28; 29), but with neither *U. nitida* (Figs 30; 31) nor *U. furcata* (Aurivillius, 1898) (see Le Lœuff & Intès 1974: fig. 18), a common species in the area. This female, bearing a large coxal spine on both P1 and P2, represents the only record of *U. mediterranea* outside the Mediterranean.

More likeness can be found between *U. mediterranea* and a newly established, non-European species, *U. senegalensis* Ngoc-Ho, 2001 from Senegal. The latter resembles both *U. mediterranea* and *U. nitida* and the three are sometimes hard to differentiate.

Similarities and differences between *U. mediterranea* and *U. senegalensis* are presented below with some details and summarized in Table 2. *U. mediterranea* and *U. senegalensis* are compared with *U. nitida* under the latter species and summarized in the same table.

U. mediterranea resembles *U. senegalensis* (see Ngoc-Ho 2001a: figs 1-3) in: 1) the shape of rostrum; 2) the shape and spinulation of P1 except for a subdistal tooth absent on dactylus cutting edge; and 3) an acute coxal spine on both P1 and P2.

It differs from *U. senegalensis* in: 1) the large A2 scale with pointed tip (small A2 scale with blunt tip in *U. senegalensis*); 2) absence of subdistal

tooth on the cutting edge of P1 dactylus (tooth present in *U. senegalensis*); 3) P2 bears a dorsal subdistal spine on both merus and carpus (P2 unarmed in *U. senegalensis*); and 4) the telson is subquadrate (telson slightly wider than long in *U. senegalensis*).

Upogebia nitida (A. Milne-Edwards, 1868)
(Figs 30; 31)

Gebiopsis nitidus A. Milne-Edwards, 1868: 63, pl. 18, figs 4-7. — Bouvier 1917: 118.

Gebia (*Gebiopsis*) *nitida* — Ortmann 1893: 50, pl. 4, fig. 2.

Upogebia (*Calliadne*) *nitida* — de Man 1928b: 24, 50 (key).

Upogebia nitida — de Saint Laurent & Le Lœuff 1979: 38, fig. 2. — d'Udekem d'Acoz 1999: 157.

Non *Upogebia nitida* — Le Lœuff & Intès 1974: 58 (part), fig. 20a-o (= *Upogebia mediterranea* Noël, 1992).

TYPE MATERIAL. — Lectotype: ♀; paralectotypes, 2 ♂♂, from Cape Verde Islands, Cape of St Vincent, Atlantic, subsequent designation by de Saint Laurent & Le Lœuff (1979) (MNHN Th 22).

MATERIAL EXAMINED. — **France.** Tamaris-sur-Mer, near Toulon, Sollaud coll., No. ES 38, 25.XII.1932, 2 ♀♀ cl. 16 and 16.5 mm, tl. 51 and 52 mm (figured) (MNHN Th 1393). — Banyuls, P. Noël coll., 4.VII.1975, 1 ovig. ♀ cl. 10 mm, tl. 31 mm, without P1 (MNHN Th 660).

Italy. Toscana, Livorno, G. Herweck leg., 1 ♀ cl. 15.5 mm, partly dried, without pereopods (SMF 28327).

Algeria. Gulf of Oran, P. Pallary coll., 1900, 1 ♀ cl. 13 mm, tl. 38 mm (MNHN Th 1392).

St Vincent. Cape Verde Islands, Atlantic, de Folin coll., ♀ lectotype cl. 8 mm, tl. 21 mm, 2 ♂♂ paralectotypes tl. 16 and 17 mm (specimens broken, poor condition, measurements by de Saint Laurent & Le Lœuff 1979) (figured) (MNHN Th 22). — Cape Verde Islands, *Talisman* Exp., dredge, 26.VII.1883, 1 ♂ cl. 6 mm, 1 ovig. ♀ cl. 8 mm, 4 juv. (MNHN Th 23).

Mauritanie. G. Bolloré coll., 1965, 2 ♂♂ broken, cl. 12 and 14 mm (measurements by de Saint Laurent & Le Lœuff 1979) (MNHN Th 383).

Senegal. Gorée, in lobsters net, Cadenat coll., 10.X.1950, 1 ovig. ♀ cl. 11.5 mm, tl. 35 mm (figured) (MNHN Th 278); Paraiso coll., 27.V.1948, 1 ♂ cl. 5 mm (MNHN Th 279). — Between Takona and Bel Air, 14-15 m, I. M. Marchad coll., 19.III.1954, 1 ♀ cl. 11 mm (MNHN Th 282); in

gallery of *Toredo* molluscs, 19.XI.1950, 1 ♂ cl. 2.75 mm (MNHN Th 281). — Dakar, R. Mauny coll., 25.IX.1949, 1 ♂ cl. 11 mm, 1 ♀ cl. 10 mm (MNHN Th 276); R. Mauny coll., 14.IX.1949, 1 ♂ cl. 11 mm (MNHN Th 277); 25.IX.1949, 3 ♂♂ cl. 6-11 mm, 1 ♀ cl. 6 mm (MNHN Th 273).

Gulf of Guinea. Sao Tomé, *Calypto*, stn 18, in front of Praia Lagarto, 11.VI.1956, 1 ovig. ♀ cl. 7 mm (MNHN Th 270); stn 19, 4-5 m, 12.VI.1956, 2 ovig. ♀♀ cl. 4 and 5.5 mm (MNHN Th 271). — Principe, stn 94, 31 m, 27.VI.1956, 1 ovig. ♀ cl. 5.5 mm (MNHN Th 272). — Annobon Island, *Ombango*, dredge, A. Crosnier coll., 11.XII.1965, 1 ♀ cl. 6 mm (MNHN Th 229), 50-60 m, 1 ♀ cl. 5 mm (MNHN Th 230).

DIAGNOSIS

Rostrum (Figs 30A, B; 31A, B) approximately triangular, slightly overreaching eyestalks, about as long as wide at base, with two teeth on either lateral border; anterolateral border of carapace unarmed; telson (Figs 30C; 31G) 1.1-1.2 times as wide as long. A1 (Figs 30B; 31B) peduncle with lower spine on article 1. P1 slightly stouter in male (Fig. 31D, E) than in female (Figs 30D, E; 31C) merus with lower border unarmed or denticulate; carpus with upper mesial distal spine; fixed finger with three or four round teeth on proximal half of cutting edge; dactylus about as long as fixed finger with proximal and (often) subdistal round tooth on cutting edge (Fig. 31E, J). P2 (Figs 30F; 31F) unarmed. Small coxal spine on either P1 or P2, seldom on both (and in male only).

Colour

Unknown.

Size

Types and material from northwest Africa: cl. 8-13 mm, tl. 21-38 mm.

Specimens examined from Europe: cl. 15-16.5 mm, tl. 51-52 mm.

VARIATIONS

1) rostral spines, often small, are larger in the lectotype (Fig. 31A); 2) P1 carpus bears a very small lower distal spine in a few specimens (Fig. 31I), likewise for lateral spinule near the base of the

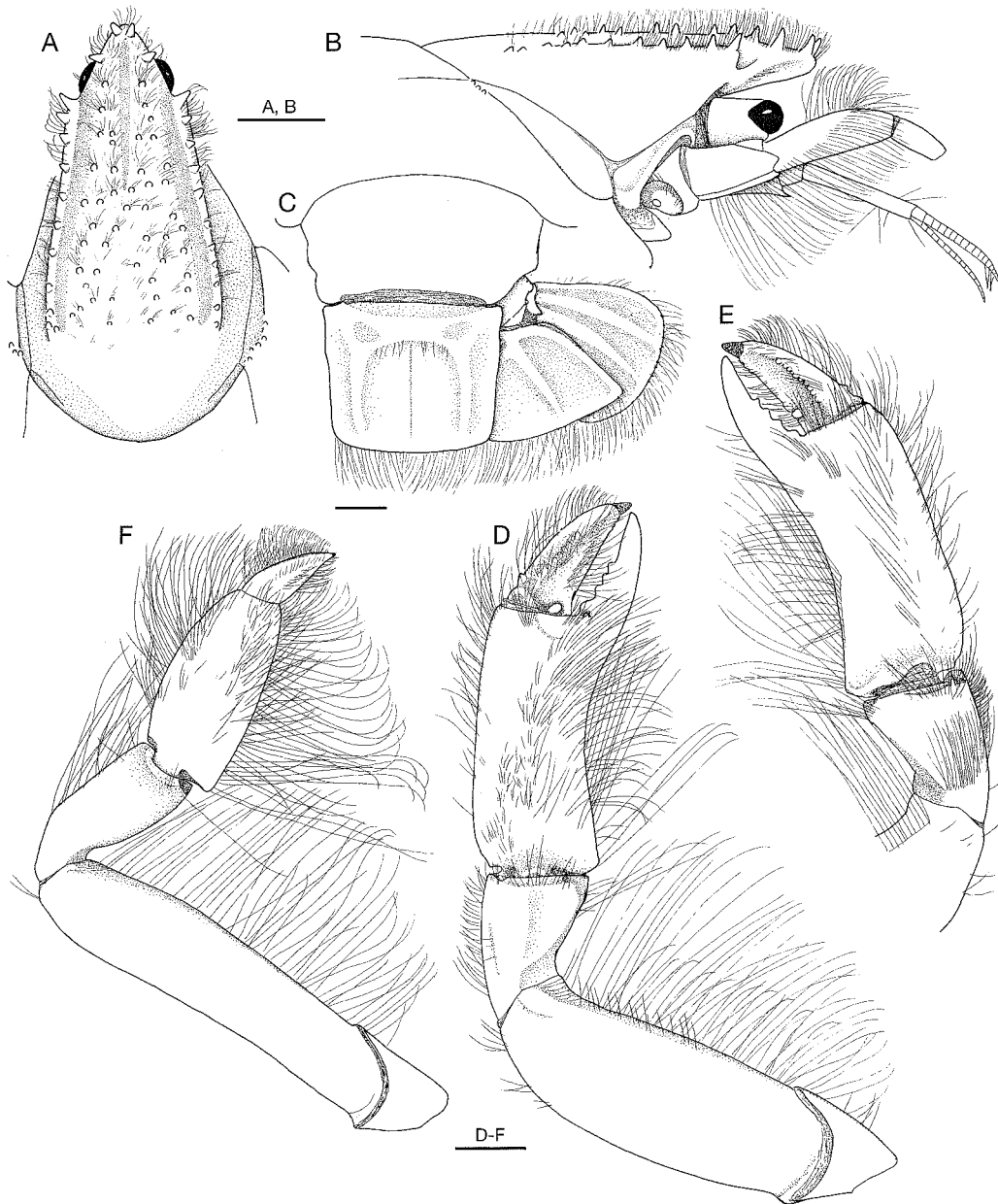


FIG. 30. — *Upogebia nitida* (A. Milne-Edwards, 1868), ♀ from Tamaris-sur-Mer, France (MNHN Th 1393); **A, B**, anterior part of carapace, dorsal and lateral view; **C**, telson and uropods; **D, E**, pereopod 1 and distal articles in mesial view; **F**, pereopod 2. Scale bars: 2 mm.

fixed finger (Fig. 30D); the proximal and/or subdistal tooth on the dactylus cutting edge is small or absent (Fig. 30D, E); and 3) the telson is subquadrate in small specimens of cl. < 6-6.5 mm.

REMARKS

Upogebia nitida differs from *U. mediterranea* in many features: 1) the rostrum is triangular in *U. nitida* (elongated triangular in *U. mediterranea*).

TABLE 2. — Distinguishing characters between *U. nitida* (A. Milne-Edwards, 1868), *U. mediterranea* Noël, 1992 and *U. senegalensis* Ngoc-Ho, 2001 (adapted from Ngoc-Ho 2001a).

Characters	<i>U. nitida</i>	<i>U. mediterranea</i>	<i>U. senegalensis</i>
Rostrum	triangular	triangular elongated	triangular elongated
Rostral teeth	often small	often large	often large
A2 scale	small	large, pointed at tip	small
Telson	wider than long	subquadrate	wider than long
P1 merus:			
upper subd. spine	absent	present	present
ventral border	unarmed or with denticles	with spinules and denticles	with spinules and denticles
P1 carpus: lower dist. spine	often absent	present	present, small
P1 propod:			
upper subd. spine	absent	present	present
P1 dactyl:			
teeth on cutting edge	1 prox., 1 subdistal	1 proximal	1 prox., 1 subdist.
P2 merus: upper subd. spine	absent	present	absent
P2 carpus:			
upper subd. spine	absent	present	absent
Coxal spine	small, on either P1 or P2	large, on both P1 and P2	small, on both P1 and P2

nea); 2) P1 merus has no upper subdistal spine, the lower border is unarmed or with denticles, P1 carpus bears a small upper mesial distal spine and no lower distal spine in *U. nitida* (P1 merus with upper subdistal spine, lower spinules and tubercles; P1 carpus with large upper mesial distal spine, small lower distal spine in *U. mediterranea*); 3) P1 propodus with the upper border unarmed and no lateral spinule near the base of fixed finger in *U. nitida* (P1 propodus with upper subdistal spine and a lateral spinule near the base of fixed finger in *U. mediterranea*); 4) P1 dactylus with a mesial proximal and subdistal tooth on the cutting edge in *U. nitida* (no subdistal tooth on the cutting edge in *U. mediterranea*); this character varies; 5) P2 is unarmed in *U. nitida* (both P2 merus and carpus bear an upper subdistal spine in *U. mediterranea*); and 6) small coxal spine on either P1 or P2, seldom on both in *U. nitida* (long and acute coxal spine on both P1 and P2 in *U. mediterranea*).

Similarities between *U. nitida* and *U. senegalensis* are (see Ngoc-Ho 2001a: figs 1-3): 1) A2 scale is small, not acute at tip; 2) a subdistal round tooth is present on the cutting edge of P1 dactylus; 3) P2 is unarmed; and 4) the similar shape of the telson.

Differences between *U. nitida* and *U. senegalensis* are: 1) the shape of the rostrum; 2) the spinulation of P1, the same as for *U. mediterranea*;

and 3) small coxal spine is present on either P1 or P2, seldom on both in *U. nitida* (coxal spine present on both P1 and P2 in *U. senegalensis*).

Distinguishing characters between *U. nitida*, *U. mediterranea* and *U. senegalensis* are presented in Table 2.

Upogebia pusilla (Petagna, 1792) (Figs 32; 33)

Astacus pusillus Petagna, 1792: 418, pl. 5, fig. 5.

Thalassina littoralis Risso, 1816: 76, pl. 3, fig. 2.

Gebia venetiarum Nardo, 1869: 314, pl. 13, fig. 3.

Gebia littoralis – Stalio 1877: 107. — Carus 1885: 490.

Gebia littoralis – Desmarest 1825: 234. — H. Milne Edwards 1837a: 313; 1837b: pl. 49, figs 1-11. — Lucas 1840: 475. — Heller 1863: 205, pl. 5, figs 12-15. — Czerniavsky 1868: 126. — Lafont 1868: 522. — °Fischer 1872: 429. — de Folin & Périer 1879: 211. — Stossich 1880: 206. — Sars 1883: 44. — Claus 1884: 746. — °Graeffe 1902: 69. — ?Gibert i Olivé 1920: 51, 1 fig.

Gebios littoralis – Risso 1827: 51.

Upogebia (*Upogebia*) *littoralis* – Borradaile 1903: 543. — de Man 1927: 29, figs 11-11b; 1928b: 23, 41 (key). — Monod 1937: 2.

Upogebia (*Upogebia*) *littoralis* – Pesta 1918: 197 (part), fig. 61a.



FIG. 31. — *Upogebia nitida* (A. Milne-Edwards, 1868); **A-C, F**, lectotype, ♀ from Cape Verde Islands (MNHN Th 22); **D, E**, paralectotype, ♂ from Cape Verde Islands (MNHN Th 22); **G-J**, ♀ from Gorée, Senegal (MNHN Th 278); **A, B**, anterior part of carapace, dorsal and lateral view; **C, D, I**, pereopod 1; **E, J**, distal articles of pereopod 1, mesial and lateral view; **F, P2**; **G**, telson and uropods; **H**, rostrum. Scale bars: 1 mm.

Upogebia littoralis - ?*Sars 1884: 182, pls 3-5. — Balss 1926: 26 (key). — Tucker 1930: 1. — Monod 1937: 2. — Makarov 1938: 52. — Bouvier 1940: 107, fig. 71. — Popovici 1940: 421, 485. — Zariquiey Alvarez 1946: 107, 108, pl. 5 fig. b, c. — °Gottlieb 1953: 441. — *Heegaard 1963: 460, figs 34-39. — ?Luther & Fiedler 1965: 50, 175, fig. on pl. 23. — Daguerre de Hureaux 1971: 67, pls 1-4. — Ngoc-Ho 1981: 245.

Upogebia litoralis — Ott *et al.* 1976: 62, figs 1-3, tabs 1, 2, pls 1, 2. — Balss 1936: 14.

Upogebia pusilla — Holthuis 1947: 321, fig. 1(5); 1956: 325; 1961: 32; 1977: 57. — *Bourdillon-Casanova 1960: 109. — Lewinsohn & Holthuis 1964: 54. — Pérès & Picard 1964: 55. — Picard 1965: 60. — Băcescu 1967: 220, figs 101-103. — de Gaillande 1968: 382; 1970: 377. — Zariquiey Alvarez 1968: 231, fig. 94a. — Le Gall 1969: 400. — Števičić 1969: 128; 1971: 529; Števičić 1990: 215. — Ktari-Chakroun & Azouz 1971: 21. — de Saint Laurent 1971: 1261 (key). — °Pastore 1976: 107. — Kartoulas & Koukouras 1974: 346. — Neves 1974: 15, fig. 5; 1987: 256. — *Thiriot 1976: 350. — Holthuis 1977: 57. — Merker Pocek 1977: 110. — Ngoc-Ho 1977: 313. — Beaubrun 1979: 77, fig. 49. — de Saint Laurent & Le Lœuff 1979: 43, fig. 5a. — Monchartmont 1979: 73. — Bourdon 1980: 1. — Domenech *et al.* 1981: 150, figs 37, 38. — Dworschak 1981: 25, figs 1-8; 1983: 20, figs 1-14; 1987a: 338, figs 1-7; 1987b: 421, fig. 1; 1988: 52, figs 1-10; 1992: 224, fig. 18a, c, g, h. — Manning & Števičić 1982: 296. — Cottiglia 1983: 74, figs 27b, 28, 29. — García Raso 1983: 320, fig. 1; 1985: 21. — Riedl 1983: 483, pl. 177, 2 figs. — Chaud 1984a: 1-176; 1984b: 194. — d'Udekem d'Acoz 1986: 103, figs 3-5; 1989: 176, fig. 6; 1995: 60; 1999: 157. — Thessalou-Legaki & Zenetos 1985: 311. — Müller 1986: 117. — Thessalou-Legaki 1986: 182. — Türkay *et al.* 1987: 92. — Geiss 1990: 208, 1 col. fig. — Moysse & Smaldon 1990: 520, fig. 10.13 (part). — Pérez Sánchez & Moreno Batet 1991: 140, 1 fig. — de Vaugelas 1991: 56, photo 2; 1998: 3, figs 1-3. — °García Raso *et al.* 1992: 258. — °Koukouras *et al.* 1992: 223. — Noël 1992: 82. — °Mayoral *et al.* 1994: 236. — Froglija 1995: 8. — Gonzalez Pérez 1995: 136. — Hayward *et al.* 1995: 434, fig. 8.52 (part). — Moosleitner & Patzner 1995: 120, 1 fig. — Falciai & Minervini 1996: 149, 4 figs. — Astell *et al.* 1997b: 671, fig. 1, tabs 1-5. — Ingle 1997: 80, fig. 7.4. — Kevrekidis *et al.* 1997: 799, figs 1-7, tabs 1-3. — Pinn *et al.* 1999a: 103, figs 2E, F; 1999b: 1461, figs 1F-H, 7, 8, tabs 1-6. — *González-Gordillo *et al.* 2001: 279. — Markham 2001: 197, tabs 1, 2. — *Martin 2001: 82, 1 fig. — °Türkay 2001: 289. — Lopez de Rosa *et al.* 2002: 88. — Noël 2002: 241.

Upogebia (Upogebia) pusilla — Noël 1992: 82 (key).

Upogebbia pusilla — Pérès & Picard 1964: 56.

TYPE MATERIAL. — Whereabouts unknown.

MATERIAL EXAMINED. — **Great Britain.** W English Channel, Holme's collection, stn 114, 50°19.1'N, 4°27.2'W, 35-37 m, 1 ♂ cl. 13 mm (NHML 2002.839).

France. Atlantic, Trébeurden, 1987, 4 ♂♂ cl. 10-16 mm, 2 ♀♀ cl. 15.5 and 16 mm (MNHN Th 1329); F. Meunier coll., III.1983, 1 ♂ cl. 7.5 mm, 1 ♀ cl. 14 mm (MNHN Th 1330). — Île Grande, clean sand, F. Meunier coll., 21.IX.1984, 3 ♂♂ cl. 10-17 mm (MNHN Th 1331); muddy sand, 2.X.1978, 1 ♂, 1 ♀, cl. 16 mm (MNHN Th 1340). — Brest, muddy sand, M.-N. Helleouet coll., 6.V.1997, 2 ♂♂ cl. 13.5 and 16 mm (MNHN Th 1332). — Bassin of Marennes-Oléron, in sediments of "Claire de Sendre", D. Fouché coll., II.1994, 1 ♂ cl. 18 mm, tl. 50 mm (figured) (MNHN Th 1317), 1 ♀ cl. 13 mm (MNHN Th 1410). — Bay of Chingoudy (western Pyrénées), A. Chaud coll., V.1982, 14 ♂♂ cl. 9-17 mm, 3 ♀♀ (1 ovig.) cl. 13-14.5 mm (MNHN Th 652). — Bassin of Arcachon, port de la Hume, intertidal (0.8-1.2 m), A. Chaud coll., 3 ♂♂ cl. 6.5-18 mm, 2 ♀♀ cl. 16 and 17 mm, tl. 46 and 48 mm (figured) and 3 ♀♀ cl. 9-16 mm (MNHN Th 645). — Auray, Brittany, R. Bourdon coll., 1 ♂ cl. 14 mm (MNHN Th 541). — Concarneau, Baron de St-Joseph's coll., VIII.1892, 1 ♀ cl. 15 mm (MNHN Th 39). — Carry-le-Rouet, A. Vayssié coll., 1912, 1 ♂ cl. 13 mm, 1 ♀ cl. 10 mm (MNHN Th 36). — Coast of France, 1939, 1 ♂ cl. 12 mm (MNHN Th 35). — Concarneau, in burrows of muddy sand, under rocks, excursion RMNH, 12.IX.1958, 1 ♂, 1 exuvia (RMNH D 12438). — Bay of Arcachon, R. Bourdon, III.1964, 2 ♂♂ (RMNH D 21559); A. W. Lacourt, VII.1976, 1 ♂ dry (RMNH D 45673). — Baie of Chingoudy, Hendaye, H. Nouvel coll., I.VIII.1953, 145 ♂♂, 128 ♀♀ (93 ovig.) (RMNH D 34027); A. Chaud coll., 2 ♂♂ cl. 13 and 15 mm, 1 ♀ cl. 14 mm (MNHN Th 646).

Mediterranean, Bay St-Trinité, 5 km from Porto Vecchio, Corsica, W. F. Roodenburg, 21.VII.1968, 1 ovig. ♀ (RMNH D 26474). — Banyuls, meadows of Grosse Island, P. Noël coll., 16.V.1978, 2 ♂♂ cl. 8 and 9 mm, 1 ovig. ♀ cl. 15.5 mm, tl. 47 mm (figured) and 2 ♀♀ cl. 12.5 and 14 mm (MNHN Th 621); 12.V.1978, 1 ♂ cl. 14 mm, tl. 45 mm (figured), 1 ♀ cl. 14 mm (MNHN Th 622); 22.V.1976, 1 ♀ cl. 6 mm (MNHN Th 673); Y. Bhaud coll., II.1976, 1 ♂ cl. 12 mm (MNHN Th 672); M. de Saint Laurent coll., V.1959, 2 ♀♀ cl. 7 and 13 mm, 1 juv. cl. 4 mm (MNHN Th 318); J. Forest coll., 14.VII.1950, 1 ♂ cl. 8.5 mm (MNHN Th 219); under a rock, J. M. Amouroux coll., 24.V.1976, 1 ♂ cl. 14 mm (MNHN Th 659); excursion Leiden Biologists, 25.IX.1937, 9 juv. (RMNH D 11728). — Nice, *Travailleur*, VII.1881, 1 ♂ cl. 11 mm (MNHN Th 37); 1 ♂ cl. 12 mm (MNHN Th 204). — Monaco, Prince de Monaco coll., 6.I.1905, 1 ♀ just moulted and exuvia,

approx. cl. 13 mm (MNHN Th 1328). — Marseille, Ponteau, 3 ♂♂ cl. 4.5-12 mm, 1 ♀ cl. 15 mm (poor condition) (SMF 28322). — Golfe de Fos, near Electricity plant at Ponteau, 2 m, H. Zibrowius coll., 5.IV.1977, 5 ♂♂ cl. 8-11 mm, 21 ♀♀ 9-11.5 mm (poor condition) (MNHN Th 598). — Anse des Laurons, near golfe de Fos, sand, 3 m, H. Zibrowius coll., 21.IV.1974, 1 ♀ cl. 10.5 mm (MNHN Th 366). — Le Brusuc, Var, muddy sand, 0.5 m, P. Noël coll., 14.XI.1997, 1 ♂ cl. 12.5 mm (MNHN Th 1334). — Languedoc, lagune de Manguis, J. L. Bouchereau coll., 1992, 1 ♀ cl. 14 mm (MNHN Th 1335). — Corsica, near Porto Vecchio, C. Monniot coll., VII.1997, exuviae only, 2 rostrums, several pereopods (MNHN Th 1333). — Cap Martin, Monaco, 10-15 m, dredge, 13.XII.1912, don. H. Nouvel, 11 ♂♂, 9 ♀♀ (RMNH D 34038). — Monaco, H. Nouvel, 2.VII.1937, 2 ♂♂, 3 ♀♀ (RMNH D 34039); 1936, 2 ♂♂, 1 ovig. ♀ (RMNH D 34040); 1 ♂ (RMNH D 34041); IV.1938, 1 ♂, 1 ♀ (RMNH D 34042); 19.IV.1912, Prince de Monaco coll., H. Nouvel don., 1 ♀ (RMNH D 34043); 1936, collection H. Nouvel, 1 ♀ (RMNH D 34044).

Portugal. Olhão, C. d'Udekem d'Acoz coll., 19.VII.1980, 5 ♂♂ cl. 10.5-17.5 mm, 2 ovig. ♀♀ cl. 14.5 mm (d'Udekem d'Acoz). — Cabo de Arnel, near Faro, excursion RMNH, 29.VII.1962, 1 ♂ exuvia (RMNH D 19026). — Praia do Faro, Algarve, excursion RMNH, 6.V.1971, 4 ♂♂, 2 ♀♀ (1 ovig.) (RMNH D 27490). — Caldeira do Mainho, Costado do Pedro José, Algarve, burrows in dry mud, at low tides, excursion RMNH, 5.V.1971, 3 ♂♂, 8 ♀♀ (4 ovig.) (RMNH D 27491). — Caldeira do Moinhoc Costado do Pedro José, Algarve, burrows in dry mud, at low tide, excursion RMNH, 3.V.1971, 1 ♂ (RMNH D 28197). — Praia de Faro, Algarve, mudflat at low tide, excursion RMNH, 2.XI.1974, 3 ♂♂, 3 ♀♀ (RMNH D 36259); 3.XI.1974, 9 ♂♂, 12 ♀♀ (RMNH D 36260). — SPMOPO1974, stn 080, Algarve, slightly W of Faro, mudflats near Praia de Faro, low tide, excursion RMNH 1974, 3.XI.1974, 2 ♀♀ (RMNH D 38477).

Spain. Port Lligat, 1-5 m, G. Fischer coll., 14 ♂♂ cl. 12.5-15 mm, 16 ♀♀ (6 ovig.) cl. 9-15 mm (SMF 28974). — Port Lligat, U. Pettke coll., 1.VIII.1985, 6 ♂♂ cl. 12.5-13.5 mm, 8 ♀♀ (3 ovig.) cl. 8.5-13.5 mm (SMF 28975). — Gerona, Cadaqués, M. Türkay coll., 30.III.1985, 8 spec. badly damaged, cl. c. 10-12 mm (SMF 28976). — Cadaqués, I. Gordon coll., 2 ♂♂ exuviae (NHML 1955.2.28.91); Zariquiey Alvarez pres., 1 ♂, 1 ♀ (NHML 1954.12.30.96-97). — Mouth of Ebre river, *Calypso* Exped., 1977, stn 4, 1 ♂ cl. 12 mm (MNHN Th 623). — Canary islands, Lanzarote, Santaella coll., IX.1973, 2 ♂♂ cl. 8 and 10 mm, 1 ovig. ♀ cl. 9 mm (MNHN Th 317); A. K. Totten coll., 10 ♂♂, 6 ♀♀ (3 ovig.) (NHML.1956.5.2.92-101). — Cadaqués near Barcelona, R. Zariquiey Alvarez, 1940, 2 broken spec.

(RMNH D 5253). — Playa Jonquet, N of Cadaqués, in c. 50 cm water, in holes in the ground, L. B. Holthuis, 13.VIII.1950, 3 ♂♂, 1 ♀, 1 juv. (RMNH D 6751). — Rio Fluvia, in front of mouth of Golfo de Rosas, brackish water, L. B. Holthuis, 16.VIII.1950, 1 ovig. ♀ (RMNH D 6752). — Cadaqués, sand and stones, in c. 75 cm water, in holes, L. B. Holthuis, 6.VIII.1950, 3 ♂♂, 2 ♀♀ (RMNH D 6753); from fishermen, 4-16.VIII.1949, 1 ♂ (RMNH D 6200); in c. 20 cm, 14.VIII.1959, 1 ♂ (RMNH D 15229). — Cala Junquet, N of Port Lligat, burrows in sand with stones, c. 20 cm, L. B. Holthuis, 20.VIII.1959, 1 ♂, 2 ♀♀ (1 ovig.), 6 juv. (RMNH D 15230). — Playa d'en Pere Fet, Cadaqués, sand, L. B. Holthuis, 23.VIII.1959, 1 ♂ (RMNH D 15231). — Cala Jugadora, S of Cabo de Creus, in sand, 0-0.2 m, L. B. Holthuis, 31.VII.1961, 7 ♂♂, 1 ♀ (RMNH D 16182). — Ria de Arosa, N of Cabo Cruz, excursion Leiden Biologists, 23.VII.1962, 7 ♂♂, 8 ovig. ♀♀ (RMNH D 17914). — Rio Unia, SE of Ria de Arosa, washed ashore, excursion RMNH, 17.VII.1962, 1 ♀ exuvia (RMNH D 19027). — Mouth of bay, SE of El Grove, from mud at low water mark, excursion RMNH, 24.VII.1962, 1 ♂ (RMNH D 19028). — Playa Barraña, Peninsula Chazo, in holes, sandy beach with some rocks, intertidal, excursion RMNH, 7.VII.1963, 22 ♂♂, 28 ovig. ♀♀ (RMNH D 19541). — Punta San Vicente, Peninsula del Grove, in sand, excursion RMNH, 1.VII.1963, 2 ♀♀ (RMNH D 19900). — Peninsula del Grove, Ria de Arosa, 0-0.5 m, excursion RMNH, 10.VII.1963, 1 ♀ exuvia (RMNH D 19901). — Playa de Barraña, Ria de Arosa, excursion RMNH, 10.VIII.1964, 6 ♀♀ (4 ovig.) (RMNH D 23797). — Playa Cerantes, Vigo, R. Margalef, II.1954, 1 ♂ (RMNH D 28185). — Playa Cerantes, Vigo, A. Figueras, 6.III.1954, 3 ♂♂ (RMNH D 28186). — Cabo de Creus, N of Cadaqués, 50 fms, J. Fortuny, VI.1947, 1 ovig. ♀ (RMNH D 28189); 27.VII.1945, 1 ♀ (RMNH D 28190). — Bahia de Cadiz, 5.5 m, sand, gravels and algae, large dredge, excursion RMNH, 13.V.1971, 1 ♂ exuvia (RMNH D 28196); 12-18 m, sand and algae, excursion RMNH, small dredge, 11.V.1971, exuviae of 3-4 spec. (RMNH D 28199). — Balears, Ibiza, San Antonia, R. Zariquiey Cenaarro, VII.1934, 3 ♂♂, 1 juv. (RMNH D 28200); 1 damaged spec. (RMNH D 35722). — SPMOPO1974, stn 049, Bay of Cadiz, coast of Punta de la Cruz, washed ashore, excursion RMNH, 26.X.1974, 1 ♂, 1 ♀ (RMNH D 38479). — East bank of Guadalquivir river near Bonanza, mud, H. O. von Hagen, summer 1960, 1 ♀ (RMNH D 23607).

Italy. Gulf of Gaeta, Licola, 1966/1968, Doerjes leg., 1 ♀ cl. 13 mm (SMF 28326). — Sicilia, K. Koltar coll., 2 ♂♂ (damaged), larger specimen cl. 12 mm (ZMUC 2706). — Grado, N Adriatic, intertidal, C. d'Udekem d'Acoz coll., IX.1997, 1 ♂ cl. 18 mm, tl. 50 mm (figured) and 2 ♂♂ cl. 15 and 16.5 mm, 3 ♀♀ (1 ovig.) cl. 15.5-17.5 mm (MNHN Th 1318). — Grado lagoon, 0.3-0.4 m, P. Dworschak leg., 1979,

- 6 ♂♂ cl. 16-20 mm, 3 ♀♀ (1 ovig.) cl. 11-18 mm (MNHN Th 630). — Lido di Starangano, 0.2-0.3 m, P. Dworschak leg., 1979, 5 ♂♂ cl. 7-15 mm, 3 ♀♀ cl. 8-15 mm (MNHN Th 631). — Entrance of Venice Lagoon, P. Sabbioni, in *Zostera noltii* meadow, intertidal, C. d'Udekem d'Acoz coll., 1.IX.1997, 1 ♂ cl. 6 mm, 1 ovig. ♀ cl. 17 mm (d'Udekem d'Acoz). — Naples, R. Gurney presented, 2 ♂♂, 2 ♀♀ (1 ovig.) (NHM.1947.3.18. 756-757). — Naples, 2 ♂♂, 1 ♀ (RMNH D 937); G. Stiasny coll., VIII.1924, 3 ♀♀ (RMNH D 2421). — Mergellina, Naples, 3-4 m, L. B. Holthuis coll., 29.IV.1950, 54 ♂♂, 44 ♀♀ (21 ovig.) (RMNH D 6516); E. Caroli coll., V.1959, 14 ♂♂, 16 ♀♀ (2 ovig.) (RMNH D 13014); J. H. Stock coll., V.1957, 1 ♂♂, 3 ♀♀ (RMNH D 15228). — Porto Cesaro, Strea Bay, in sand, 0.2-0.5 m, II.1967, 3 ♂♂ cl. 11-14 mm, 2 ♀♀ cl. 11 and 11.5 mm (MNHN Th 318). — Porto Cesaro, 1 ovig. ♀ cl. 15 mm (MNHN Th 319).
- Croatia.** Rovinj, Kuvi, seagrass, Excursion University Frankfurt, 18.VIII.1989, 2 ♂♂ cl. 8.5 and 14 mm, 3 ♀♀ cl. 9-15 mm (SMF 28323). — Rovinj, 1987, 2 ♂♂ cl. 8.5 and 10 mm, 2 ♀♀ cl. 11.5 and 12.5 mm (SMF 28324). — Istria, Rovinj, Val Salina, F. B. Burin coll., 21.VIII.1989, 3 ♂♂ cl. 10-14 mm (SMF 28325). — Rovinj, Števičić coll., 9.XI.1977, 2 ♀♀ cl. 11 and 13 mm (MNHN Th 613); P. Dworschak leg. 1979, 2 ♂♂ cl. 9 and 11.5 mm, 2 ♀♀ cl. 8 and 13 mm (MNHN Th 632).
- Romania.** Near Constantine, *Calypso* Exped. 1977, stn 3, 6.X.1977, 1 juv. cl. 4 mm (MNHN Th 628).
- Greece.** Thessalonique, 25.IX.1930, 1 ♀ cl. 19 mm (MNHN Th 209). — Lesbos Island, C. d'Udekem d'Acoz coll., 10.VII.1992, 5 ♂♂ cl. 5-7 mm (d'Udekem d'Acoz). — Aegean Sea, near harbour of Porto Lago, 0-2 m, excursion Leiden Biologists, 29.VI.1959, 16 ♂♂, 38 ♀♀ (RMNH D 13073); leg. Cardo Godo, don. R. Zariquiey Alvarez, 2 ♂♂, 1 ovig. ♀ (RMNH D 28195); Kolovrechtis, Evvoia I., 0-2 m, 2.VI.1971, 2 ♂♂, 2 ♀♀ (A.U.TH. G1 767). — Chalkidiki, Kassandra, Nea Fokia, G. Gorgiadis, 15.VIII.1971, 1 ♂ (RMNH D 28724). — S of Euboea Gulf, c. 38°30'N, 24°E, A. Koukouras, 3.II.1972, 3 ♂♂ (RMNH D 30380). — Chochlakos, Rhodes, SLM 4012, 16.X.1970, 26 m, 11 ♀♀ (all young specimens), 6 juv. (RMNH D 35724).
- Turkey.** Izmir, A. Kocataş coll., 2 ♂♂ cl. 13 and 14 mm, 2 ♀♀ cl. 13 and 15 mm (MNHN Th 619). — Tuzla near Izmir, A. Kocataş, 10.X.1966, 8 ♂♂, 1 ♀ (RMNH D 23345).
- Malta.** C. G. Thorogood pres., 14 ♂♂, 3 ovig. ♀♀ (NHML.1945.VI.15.1-15); 12 ♂♂, 10 ♀♀ (7 ovig.) (NHML.1945.VII.12.11-20).
- Mediterranean coast of Israel.** El Akhziv (= Geshet-Hasiv), N of Nahariya, together with *Synapta* spec., L. Fishelson, 25.II.1960, 1 ♀ (RMNH D 19217); 24.VI.1962, 1 ♂ (RMNH D 19218).
- Suez.** Suez Canal, A. Gruvel coll. 27.II.1904, 4 ♂♂ cl. 10-11.5 mm, 2 ♀♀ cl. 9 mm (MNHN Th 34).
- Algeria.** Bône, H. Lucas coll., 1849, 4 ♂♂ cl. 9-12.5 mm, 2 ♀♀ cl. 8 and 10 mm (MNHN Th 210). — Castiglione, R. Dieuzeide, VIII.1947, 3 ♂♂, 5 ♀♀ (RMNH D 6199).
- Morocco.** IV.1965, 2 ♂♂ cl. 10 mm (poor condition), 1 ♀ cl. 10 mm (MNHN Th 40); X.1964, 1 ♂ cl. 14.5 mm, 2 ♀♀ cl. 9 and 10 mm (MNHN Th 43). — Fedhala, J. Lionville coll., VIII.1923, 2 ♂♂ cl. 5.5 and 6 mm, 2 ♀♀ cl. 5.5 and 8 mm (MNHN Th 546); 1 ♂ cl. 10 mm (MNHN Th 544); Lionville, Lepiney & Bernaudot coll., 5.II.1935, 1 ♀ cl. 11 mm (MNHN Th 44); Lionville, Lepiney & Mineur coll., 5.III.1955, 1 ♂ cl. 11.5 mm (MNHN Th 41). — Bon Znina, Lepiney coll. 30.X.1940, 2 ♂♂ cl. 7 mm (MNHN Th 547). — Tanger, H. Charnier coll., 1 ♂, 1 ♀ cl. 10 mm (MNHN Th 545). — SPMOPO 1974, stn 34, S of Rabat, 1 km S of Oued Yquem, rocky shore with sandy lagoon, excursion RMNH, 19.X.1974, 1 ♂ (RMNH D 38476). — SPMOPO 1974, stn 38, atlantic coast, 23 km S of Rabat, 0-0.2 m, rock pools, excursion RMNH, 20.X.1974, 1 ♀ (RMNH D 38478). — SPMOPO 1974, stn 40, atlantic coast, 16 km S of Rabat, Temara, sandy beach with rocks, in rock pools, excursion RMNH 1974, 21.X.1974, 1 ♂ (RMNH D 38480).
- Tunisia.** Tunis, El Biban, Tidevandzonen, 17.V.1938, Nordisk Insulin-Lab's Exp., 1 ♀ cl. 10 mm (ZMUC 2707). — Gulf of Tunis, between Sidi Rais and A in Oktor, Manning, Forest, de Saint Laurent and Jones coll., 16.VIII.1973, 1 ♂ cl. 10.5 mm, tl. 30 mm, 10 ♂♂ cl. 8.5-16.5 mm, 16 ♀♀ (14 ovig.) cl. 8-16 mm (MNHN Th 713). — Salammbô, R. Manning & R. Ingle coll., 21.II.1974, 1 ♂, 1 ♀ (NHML.1974.182).
- Mauritania.** G. Bolloré coll., 1965, 1 ♀ cl. 13 mm (MNHN Th 384).
- ?**São Thomé** (West Africa). M. Nobre coll., 1889, 1 ♂ cl. 14 mm (MNHN Th 798).

DISTRIBUTION. — South of the British Isles, north-western Brittany, France in the North, Mediterranean including Corsica (de Vaugelas 1991, 1998) to Mauritania and São Thomé? in the South. According to Pesta (1918), Bouvier (1940), Zariquiey Alvarez (1968), *Upogebia pusilla* can be found as far north as Norway, the North Sea while according to Poulsen (1941), the species was absent from Norway. More recently, Moyse & Smaldon (1990) considered the distribution of *Upogebia pusilla* to include the British Isles, probably only the South. In this work, a male from the English coast of the English Channel has been found (NHML 2002.839).

The southernmost localities of the species distribution in Eastern Atlantic (Mauritania and Sao Thomé) were given by a single female of cl. 13 mm (tl. 43 mm) collected in 1965 and a male of cl. 14 mm (tl. 45 mm), collected in 1889. Both are in fair condition, but it is questionable whether the label accompanying the specimen from Sao Thomé is authentic.

The species is common around the Mediterranean and is also found in the Black Sea (Makarov 1938) and the Suez Canal (Monod 1937).

DIAGNOSIS

Rostrum (Fig. 32A, B) obtuse distally, about 1.2-1.3 times as long as wide at base, with four or five teeth on lateral border; anterolateral border of carapace with spine; telson (Fig. 32H) approximately 1.2-1.3 times as wide as long, distal margin narrower than proximal, posterior border straight or slightly concave medially.

A1 and A2 peduncle (Fig. 32B) with spine on lower margin of article 1 and 3 respectively; A2 scale with distal spine. Md with large mesio-anterior pointed tooth. Mxp1 without epipod, Mxp3 with epipod.

P1 stouter in male (Fig. 32C, D) than in female (Fig. 32F, G). Ischium with two to four spines on lower border. Merus with upper subdistal spine, three to six spines and spinules on proximal half of lower border and a double or single row of denticles distally. Carpus with large upper mesial distal spine and lower distal spine. Propodus more slender in female, dilated distally in large male (cl. > 11.5-12 mm); upper border with lateral longitudinal smooth crest and mesial crest bearing tubercles or denticles (Fig. 32E); small mesial upper subdistal spine, large mesial upper distal spine; both lateral and mesial surfaces with distal spine near cutting edge of dactylus; fixed finger shorter than dactylus, cutting edge smooth or with small teeth on proximal half. Dactylus 2.5-4 times as long as fixed finger, cutting edge with round teeth.

P2 (Fig. 33A) with upper subdistal spine and one to three lower spines on merus; carpus with upper and lower distal spine. P3 (Fig. 33B) with three or four lower spines on merus, carpus with lower distal spine. Small coxal spine on P1 and P2. Basipod of uropod with spinule hanging over endopod; exopod (Fig. 32G, H) triangular, about as long as distal width, with proximal spinule.

Colour

Usually dull green, sometimes brown (d'Udekem d'Acoz pers. comm.).

Variable, blueish to greenish-brownish (Dworschak pers. comm.); a coloured photograph is presented in Geiss (1990).

Size

Large specimens in material examined: cl. 15.5-18 mm, tl. 47-50 mm. In Northern Adriatic: males are of cl. 20-22 mm, tl. 55-61 mm, females of cl. 16-18 mm, tl. 46-52 mm, with a maximum size of 66 mm in males and 60 mm in females; males of tl. > 50 mm have a longer carapace than females of the same size (Dworschak 1988). Largest size reported, from North Aegean Sea: 82 mm for females, 106 mm for males (Kevrekidis *et al.* 1997).

BIOLOGY AND ECOLOGY

The biology of *U. pusilla* in the Bay of Chingoudy (Pays Basque), France was reported by Chaud (1984a, b). Its biology in Northern Adriatic, including burrow construction, environment, growth and production, feeding, pumping rate, was studied in detail by Dworschak (1981, 1983, 1987a, b, 1988).

In the Patra Gulf and Ionian Sea (Greece), this species was found living in a wide range of substrates with little or no mud, in shallow water; it was absent from *Posidonia* meadows (Thessalou-Legaki & Zenetos 1985). In Trébeurden, Brittany, many specimens were found at 20-25 cm depth, in an area with muddy sand and small *Zostera* (d'Udekem d'Acoz 1986), and also in coarse sand. They were dark green or brown coloured and may carry the parasitic isopod *Gyge branchialis* Cornalia & Panceri, 1861 (Tucker 1930; d'Udekem d'Acoz 1989). In Marseille, France, *U. pusilla* was regarded as the characteristic species of biocoenoses with muddy sand, in shallow and calm water (Pérès & Picard 1964; de Gaillande 1968).

Other aspects of biology studied

Branchial morphology, gill area and gill ultrastructure (Astall *et al.* 1997b); population dynamics, reproduction and growth (Kevrekidis *et al.* 1997); comparison of gut morphology and gut microflora (Pinn *et al.* 1999a); mouthpart

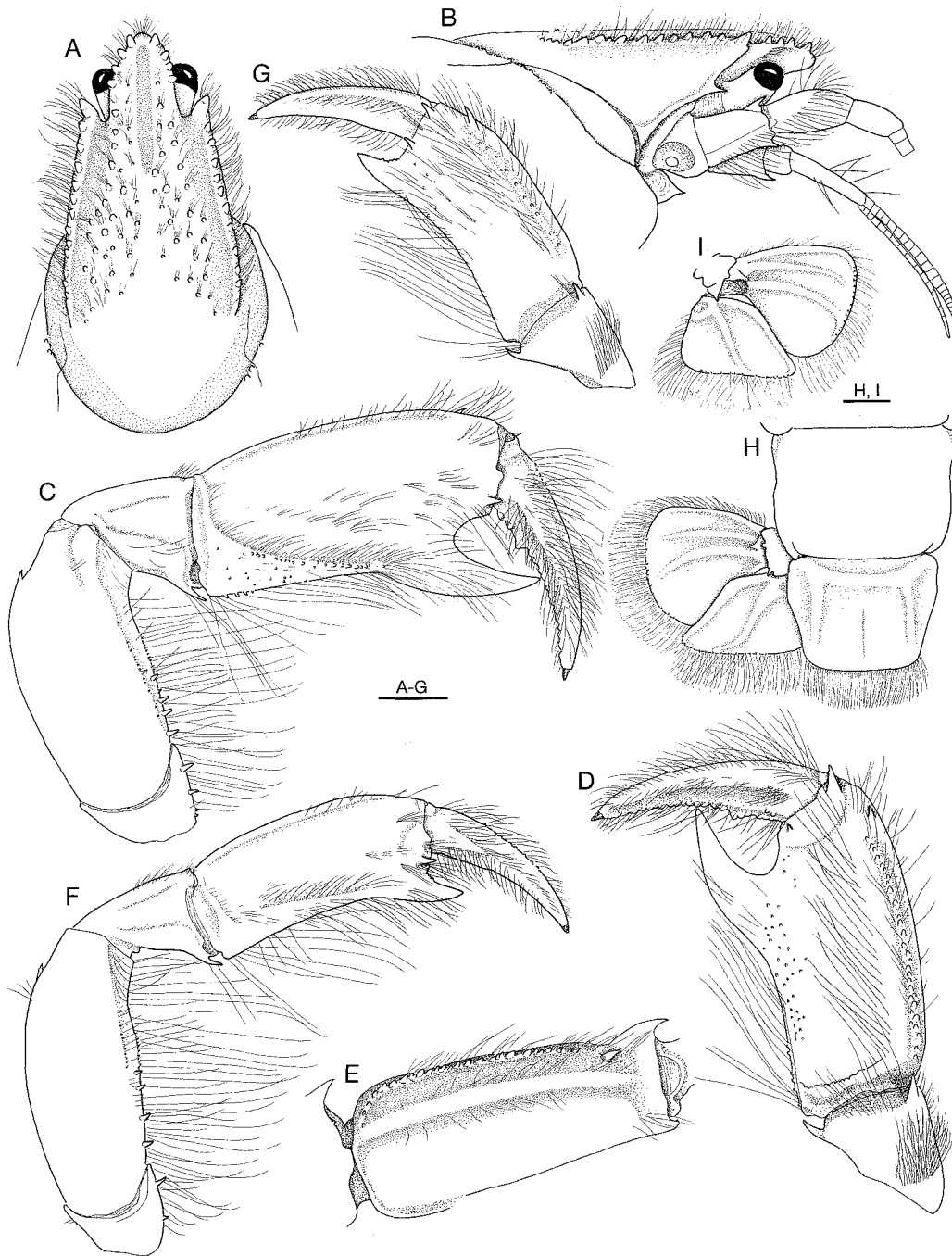


FIG. 32. — *Upogebia pusilla* (Petagna, 1792); **A-E**, ♂ from Oléron, France (MNHN Th 1317); **F-I**, ♀ from Arcachon, France (MNHN Th 645); **A, B**, anterior part of carapace, dorsal and lateral view; **C, F**, pereopod 1; **D, G**, distal articles of pereopod 1, mesial view; **E**, pereopod 1 propodus, upper view; **H**, telson and uropods; **I**, uropods. Scale bars: 2 mm.

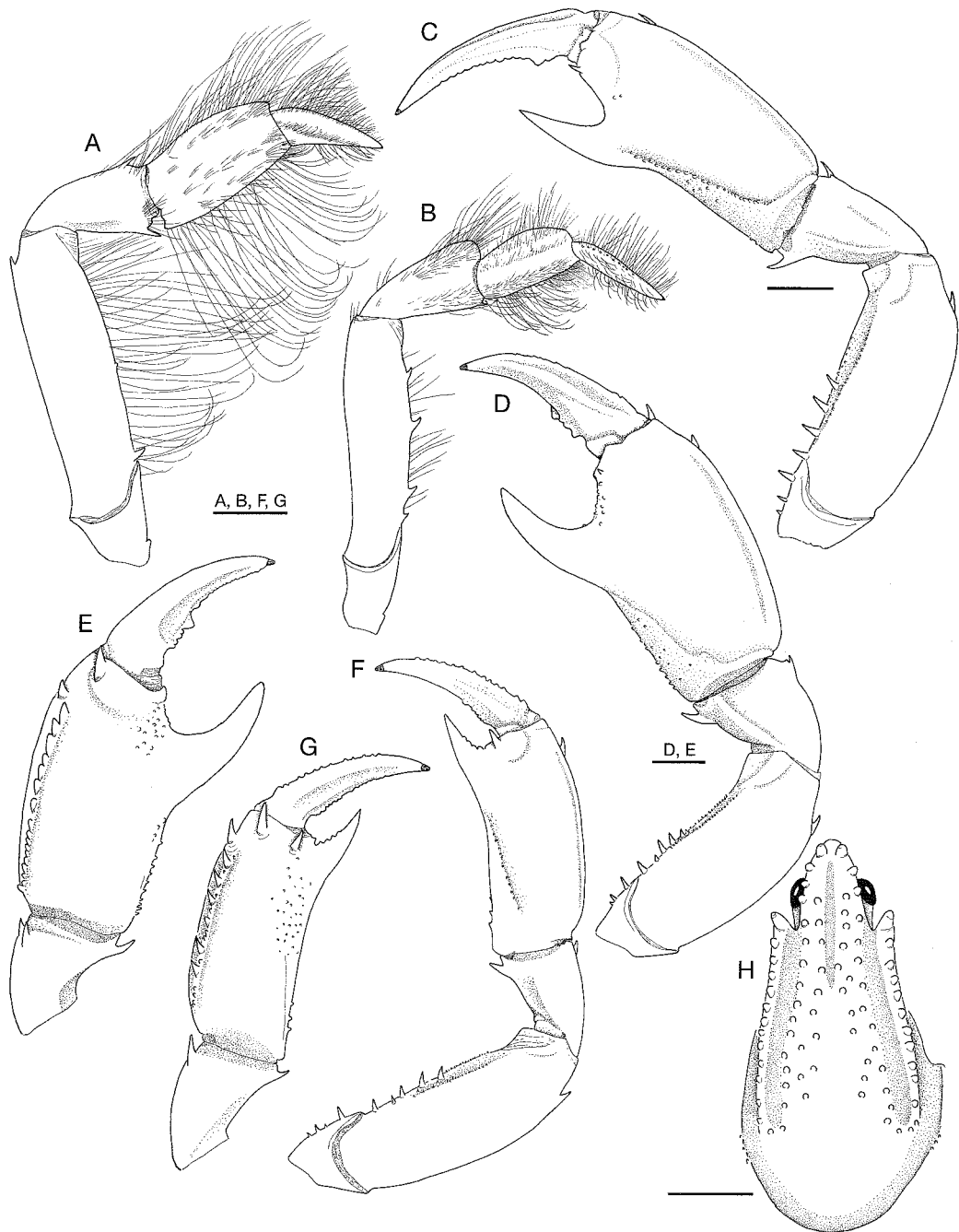


FIG. 33. — *Upogebia pusilla* (Petagna, 1792); **A, B**, ♂ from Oléron, France (MNHN Th 1317), pereopod 2 and 3; **C**, ♂ from Italy (MNHN Th 1318); **D, E, H**, ♂ from Banyuls, France (MNHN Th 622); **F, G**, ♀ from Banyuls (MNHN Th 621); **C, D, F**, pereopod 1; **E, G**, distal articles of pereopod 1, mesial view; **H**, anterior part of carapace. Scale bars: 2 mm.

morphology and mouthpart setal fringes (Pinn *et al.* 1999b); abundance of population in Corsica (de Vaugelas 1991); relation between burrow architecture, feeding mode and structure of the sediments (de Vaugelas 1998).

VARIATIONS AND REMARKS

Upogebia pusilla is the most common European upogebiid species but varies morphologically. Variation is greatest among Mediterranean populations and bring them near an allied species in the area, *U. tipica* (Nardo 1869). The two are sometimes so similar or hardly distinguishable that García Raso (1983), studying material from southern Spain, thought they might be identical. Examination of the present material reveals however that both species are valid, and their differentiation is discussed under *U. tipica*.

Most characteristics given to *U. pusilla* by authors such as de Man (1927), Bouvier (1940), de Saint Laurent (1971) concern P1 propodus, e.g., the distal dilation, the length/width ratio or the spinulation of its upper margin, but these are variable, as reported by García Raso (1983), and Dworschak (1992).

Characteristics of typical *U. pusilla* as listed in the diagnosis fit best specimens from the Atlantic, and some from the western Mediterranean.

Certain variations mentioned by García Raso (1983), affecting few specimens, can be considered as usual within large populations; they are: 1) paired or bifid postocular spine on anterolateral border of carapace (usually single); 2) bifid A2 scale (usually simple); and 3) lateral distal border of P1 carpus with two or three spinules (one usually).

Other variations occur more often, mainly in the rostrum and P1:

The rostrum is between 1.2-1.4 times as long as wide at base.

P1 propodus: 1) the length/width ratio varies between 1.7-2.65 in male, 2.15-2.8 in female, 2.8-3.7 in juvenile (García Raso 1983); 2) the mesial longitudinal crest on the upper margin is sometimes armed with spines (Fig. 33E, G); 3) both the lateral and mesial crests on the upper margin are sometimes very faint; 4) the distal

dilation at level of the fixed finger is nearly absent in female, weak in young male, pronounced in large male; 5) the median spine on the mesiodistal margin (near the cutting edge of the dactylus) is large in female (Fig. 32G), much smaller or absent in male (Fig. 32D); 6) the fixed finger is distal in female, slightly or strongly subdistal in male; 7) the fixed finger is about one-fourth to half as long as the dactylus; and 8) the dactylus and fixed finger cutting edge is unarmed or with small teeth.

The following characters which contrast with *U. tipica*, are more constant (the last one to a lesser extent): 1) the rostrum is less than 1.5 times as long as wide at base with four or five teeth on each lateral border; 2) P1 merus bears three to six spines and spinules on the proximal half of the lower margin, and denticles distally; 3) P1 propodus has a longitudinal upper smooth crest on the lateral surface, an upper longitudinal tuberculate or spinous crest on the mesial surface, an upper subdistal spine, an upper distal spine and a median distal spine near the cutting edge of dactylus (in females especially); and 4) the telson is wider than long, the uropodal exopod is triangular and about as long as its distal width, this appendage is slightly longer in juvenile.

Upogebia stellata (Montagu, 1808) (Figs 34; 35)

Cancer Astacus stellatus Montagu, 1808: 89, tabl. III, fig. 5.

Gebia stellata – Leach 1816: tabl. 31, figs 1-8. — Desmarest 1825: 204. — Bell 1846: 223, 1 fig. — White 1857: 97, pl. 7, fig. 3. — ?Bonnier 1887: 248. — Stephensen 1910: 277. — Lagerberg 1908: 55, pl. 2, fig. 10. — Schlegel 1912: 239, 250. — Runnström 1925: 28, pl. 3. — Grieg, 1927: 35 (part), not fig. — °Vilela 1936: 226.

Upogebia stellata – Stebbing 1893: 185. — Norman & Scott 1906: 12. — °Norman 1907: 357. — de Morgan 1910: 475, fig. 1. — Selbie 1914: 104. — *Webb 1919: 102, pl. 10, figs 2-11, pl. 11 figs 2-6, pl. 12 figs 5, 6, 9, 10. — Schellenberg 1928: 75, fig. 57. — Gustafson 1934: 12. — Bouvier 1940: 108, fig. 72. — Poulsen 1941: 216, 224, figs 5, 7, 9. — *Gurney 1942: 249, fig. 100. — Holthuis 1950: 111, fig. 39; 1958: 6, fig. 9. — Gordon 1957: 250. —

Tambs-Lyche 1958: 14. — Holme 1961: 415, 416; 1966: 433, 352. — Bourdon 1965: 16. — Allen 1967: 18. — Christiansen 1972: 41, fig. 47. — Naylor 1972: 73. — Samuelsen 1974: 132. — *Thiriou 1976: 350, 367. — Tebble 1976: 85 (association with the bivalve mollusc *Lepton squamosum* (Montagu)). — Lacourt 1977: 246. — Adema *et al.* 1982: 28, fig. 5, tabl. 6. — Holthuis & Heerebout 1986: 62, fig. 80. — Thessalou-Legaki 1986: 183. — Moysse & Smaldon 1990: 520, fig. 10.13 (part). — °Koukouras *et al.* 1992: 223. — °Froggia 1995: 8. — Hayward *et al.* 1995: 434, fig. 8.52 (part). — Nickell & Atkinson 1995: 181, fig. 2D, E, tabl. 3. — d'Udekem d'Acoz 1996: 60; 1999: 157. — Astall *et al.* 1996: 821, tabs 1, 2; 1997a: 155, fig. 1 (part), 2, 4, 6, tabl. 1 (part); 1997b: 669, fig. 1, tabs 1-5, pls 2, 3, 5. — °Brattegard & Christiansen 1997: 222. — Pinn *et al.* 1997: 1083, figs 1, 2, tabs 1-3. — Christiansen & Stene 1998: 76. — Nickell *et al.* 1998: 745, 752, figs 6, 7. — Pinn *et al.* 1998a: 243, fig. 2B, D; 1998b: 211, figs 1A, 2A; 1999a: 103, figs 3B-F, 5H; 1999b: 1461, tabs 1-6. — °Pancucci-Papadopoulou *et al.* 1999: 393. — Christiansen 2000: 233. — Taylor *et al.* 2000: 265, figs 1, 2, tabs 1-3, 5, 6. — Markham 2001: tabs 1, 2. — *Martin 2001: 83, 1 fig. — °Türkay 2001: 289.

Upogebia (Upogebia) stellata – Borradaile 1903: 543. — de Man 1927: 36, figs 14-14d. — Noël 1992: 83.

Non *Upogebia stellata* Grieg, 1927: 35 (part), fig. (= *U. deltaura* (Leach, 1815)). — Nobre 1931: 195, fig. 109; 1936: 122, fig. 102 (= *U. pusilla* (Petagna, 1792)).

TYPE MATERIAL. — Two specimens of this species from Plymouth Sound, previously belonging to Montagu's collection are in the Natural History Museum, London (NHML 258a and 258b) but the type, from the estuary of Kingsbridge, is missing, probably lost.

MATERIAL EXAMINED. — North Sea. NW of Texel, 53°36'N, 3°45'E, 34 m, P. C. Goudswaard, 23.IV.1980, 1 ovig. ♀ (RMNH D 35729); 53°52.5'N, 4°29.5'E, 42 m, MS *Aurelia*, leg. P. C. Goudswaard, 2.II.1982, 1 juv. (RMNH D 35730). — Off the English coast, 51°50'-52°20'N, 1°20'-2°00'E, NIOZ, leg. D. Eisma, 6-18.IX.1965, 1 spec. (RMNH D 35731). — C. 53°37'N, 3°35'E, *Aurelia* cruise, 6.X.1975, leg. F. Creutzberg, don. NIOZ, 1 ♂ (RMNH D 35732). — 53°43'N, 4°14'E, *Aurelia*, 24.IV-5.V.1972, leg. F. Creutzberg, don. NIOZ, 1 ovig. ♀ (RMNH D 35733).

Great Britain. Millport, Firth of Clyde, 20 m, R. B. Pike coll., 4 ♂♂, 2 ♀♀ (1 ovig.) (NHML 1962.7.5.1-4). — Port Erin, Isle of Man, Hartnoll coll., 1 ♂ (NHML 1960.VII.25:150). — Plymouth Sound, Montagu collection (dried, rehydrated), 1 ♀ cl. 11.5 mm (NHML 258 a), 1 broken ♀ (NHML 258 b). — Plymouth, 1 ♂, 1 ♀ (NHML 1910.7.1.3-

4); D. B. Carlisle, V.1959, 1 ♂, 1 ♀ (RMNH D 15227). — Salcombe Harbour, 1875, Norman coll., 1 ♀ (NHML.98.7.735). — English Channel, 55 m, 17.VII.1959 (see Holme 1966), 1 ♂ (NHML 325); 35 m, 1 ♂ (NHML 324); 37 m, 1 ♂ (NHML 323).

France. Roscoff, Brittany, R. Bourdon coll., 1 ♂ cl. 14 mm, tl. 41 mm (figured) and 2 ♂♂ cl. 11.5 and 13 mm; 2 ♀♀ (1 ovig.) cl. 12.5 mm (MNHN Th 324); a dozen of pereopods with 2 P1 (MNHN Th 322). — Meadow opposite Beuvan Bras, M. Cantacuzène coll., 20.XI.1957, 1 ♂ cl. 10 mm, 1 ♀ cl. 12 mm (MNHN Th 323). — Port de Primel, R. Bourdon coll., 18.II.1965, 1 ♂ cl. 12.5 mm; 1 ♀ cl. 16 mm, tl. 49 mm (figured) and 1 ovig. ♀ cl. 14 mm (MNHN Th 320); 16.II.1965, 1 ♀ cl. 14.5 mm (MNHN Th 321). — Callot island, near Roscoff, sandy beach at low tide, excursion RMNH, 17.IX.1958, 2 ♂♂ (RMNH D 12437). — Rade de Brest, Glémarec coll., 1 ♀ cl. 12 mm (MNHN Th 49); 1 ♀ cl. 7 mm (MNHN Th 420).

Greece. Orei Channel, stn DIO5, 21.XI.1991, 1 ♀ cl. 9 mm. — Rhodes, stn R. 48, XI.1983, 1 damaged spec. with 2 P1 (collection Thessalou-Legaki).

DISTRIBUTION. — European coasts of eastern Atlantic: Swedish west coast (Gustafson 1934), western Norway (Samuelson 1974), Denmark (Poulson 1941), Firth of Clyde, west Scotland (Allen 1967), Netherlands (Holthuis 1950), southern North Sea (Adema *et al.* 1982), coasts of Ireland (Selbie 1914), western English Channel (Holme 1961), Brittany, France; Greece (Thessalou-Legaki 1986).

DIAGNOSIS

Rostrum (Fig. 34A, B) obtuse distally, about twice as long as wide at base, six or seven lateral teeth on either border; antero-lateral border of carapace with one or two spines; lateral groove of gastric region well defined in anterior half, faint posteriorly. Telson (Fig. 34C) approximately 1.4-1.5 times as wide as long, lateral borders regularly curved, posterior border slightly concave medially.

A1 and A2 peduncle (Fig. 34B) with spine on lower margin of article 1 and 3 respectively. Md with large mesio-anterior pointed tooth. Mxp1 without epipod, Mxp3 with epipod.

P1 slightly stouter in male (Fig. 34D, F) than in female (Figs 34G; 35B). Ischium with one or two spines on lower margin. Merus with upper subdistal spine, five to eight spines on proximal two-thirds of lower margin and up to eight spinules distally. Carpus with upper, lower distal spine

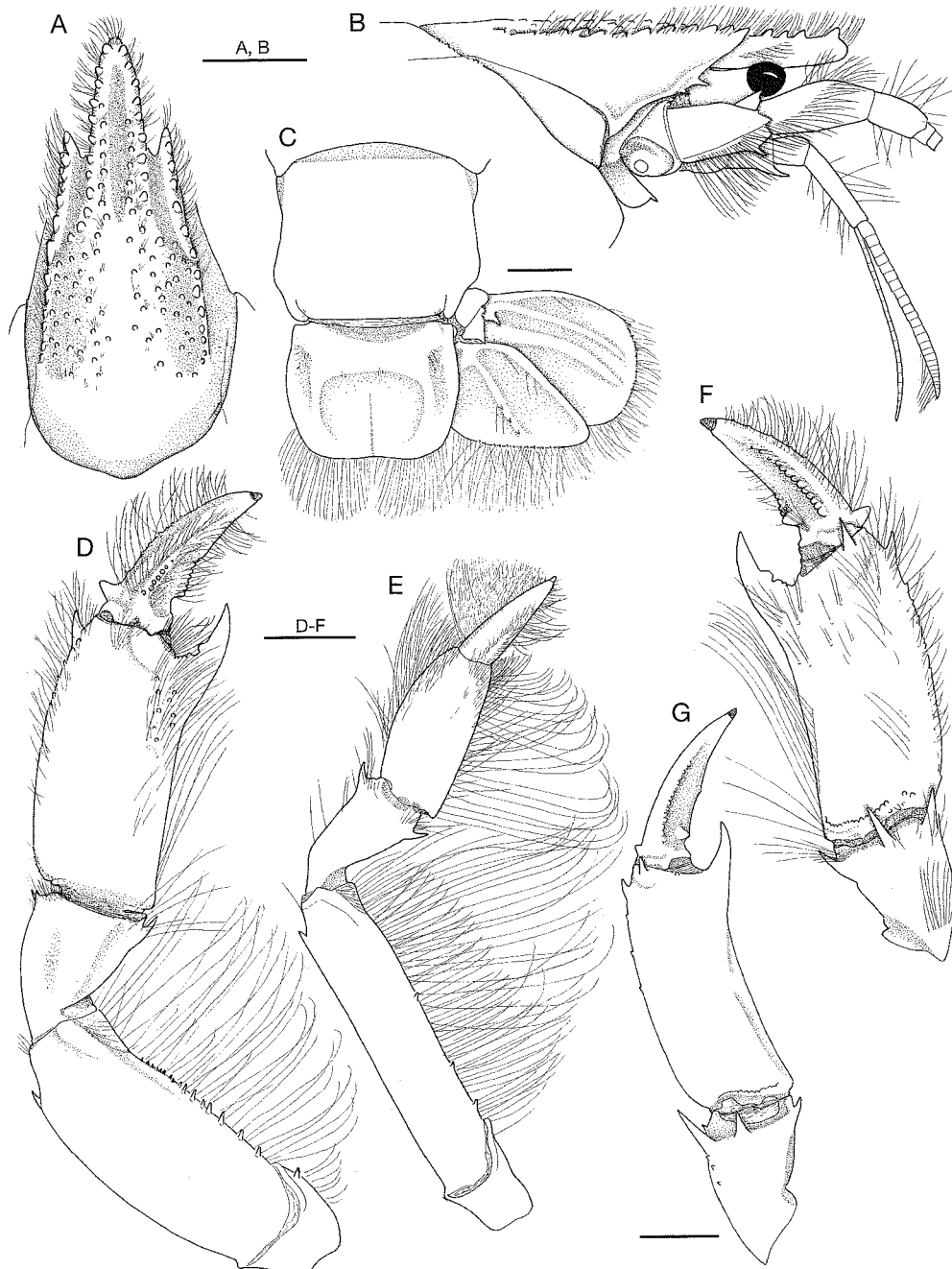


FIG. 34. — *Upogebia stellata* (Montagu, 1808); A-F, ♂ from Roscoff, France (MNHN Th 324); G, ♀ from Port de Primel, France (MNHN Th 320); A, B, anterior part of carapace, dorsal and lateral view; C, telson and uropods; D, pereopod 1; E, pereopod 2; F, G, distal articles of pereopod 1, mesial view. Scale bars: 2 mm.

and median distal spine on mesial surface. Propodus with upper subdistal spine followed posteriorly by one to four pointed tubercles; mesial surface with upper distal spine near articulation with dactylus; fixed finger about half as long as dactylus, cutting edge smooth or with round teeth proximally. Dactylus with proximal upper conical tooth often small in female, cutting edge with mesial proximal round tooth, small or absent in female.

P2 (Fig. 34E) with upper subdistal spine and two or three lower spinules on merus; carpus with upper and lower subdistal spine.

P3 (Fig. 35C) with two to four spines on lower margin of merus, carpus with lower subdistal spine.

Small coxal spine on P1 and P2, single pleurobranch on P5 (Fig. 35A) (absent in a young male of cl. 5.5 mm from North Sea (RMNH D 35730) and a female from Orei Channel of cl. 9 mm (collection Thessalou-Legaki).

Uropods (Fig. 34C) about as long as telson; basipod with spinule hanging over endopod; exopod about 1.5 as long as distal width, with proximal spinule.

Colour

Yellowish white, with minute stellated orange spots (Montagu 1808; White 1857; Moyse & Smaldon 1990).

Size

Type: nearly 2 inches long (tl. about 50 mm) (Montagu 1808). Largest specimens in material examined: cl. 14-16 mm, tl. 41-49 mm.

ECOLOGY AND BIOLOGY

In Gullmarfjord, Sweden, the species was found in a bottom of clay, sand and gravel, at 25-30 m depth (Gustafson 1934). It was less common in the North Sea than *U. deltaura* but was found in nearly the same localities (Adema *et al.* 1982). In western Norway, it was collected on the littoral, at low water, in mineral sand with some mud, or in shell sand, at 7-13 m; one specimen was found in mud at 120 m (Samuelsen 1974). It was recorded in shallow water in southern part of the

boreal region (Christiansen 2000), collected between 25-36 m in Danish waters (Poulsen 1941) and was rare in the Clyde sea area (Allen 1967). It is common on all coasts of the British Isles (Moyse & Smaldon 1990); fairly common around Roscoff, France, in the same intertidal areas as *U. deltaura*, but less abundant (Bourdon 1965). According to Holme (1966), it lives in a muddy-gravel substrate, off Plymouth, English Channel. Reproduction occurs in February-August in Roscoff (Bourdon 1965). Larvae are abundant in Roscoff from February to July, with the same distribution as *U. deltaura* (Thiriot 1976).

Aspects of biology studied

Burrow morphology and feeding behaviour (Nickell & Atkinson 1995); branchial parasitic isopods (Astell *et al.* 1996); burrow morphology and burrow-dwelling lifestyle (Astell *et al.* 1997a); branchial morphology, gill area and gill ultrastructure (Astell *et al.* 1997b); microbial flora associated with digestive system (Pinn *et al.* 1997); morphology of mouthparts and pereopods in relation to feeding, ecology and grooming (Nickell *et al.* 1998); diet (Pinn *et al.* 1998a); particle size selectivity and resource partitioning (Pinn *et al.* 1998b); gut morphology and gut microflora (Pinn *et al.* 1999a); mouthpart morphology and mouthpart setal fringes (Pinn *et al.* 1999b); oxygen transporting properties of haemocyanin (Taylor *et al.* 2000).

REMARKS

With an exception, the southernmost distribution of this species in the material examined, is Brittany, northwest France. Several samples collected in southwest France (Arcachon), Spain or Portugal and previously assigned to *U. stellata*, are actually *U. pusilla*. The possible exception is the material from Greece reported by Thessalou-Legaki (1986). It includes a small female (cl. 9 mm) from Orei Channel and two P1 of a very small and badly damaged specimen (not examined) from Rhodes. The female from Orei differs from typical *U. stellata* by having no pleurobranches on P5 of both sides, and by the uropods

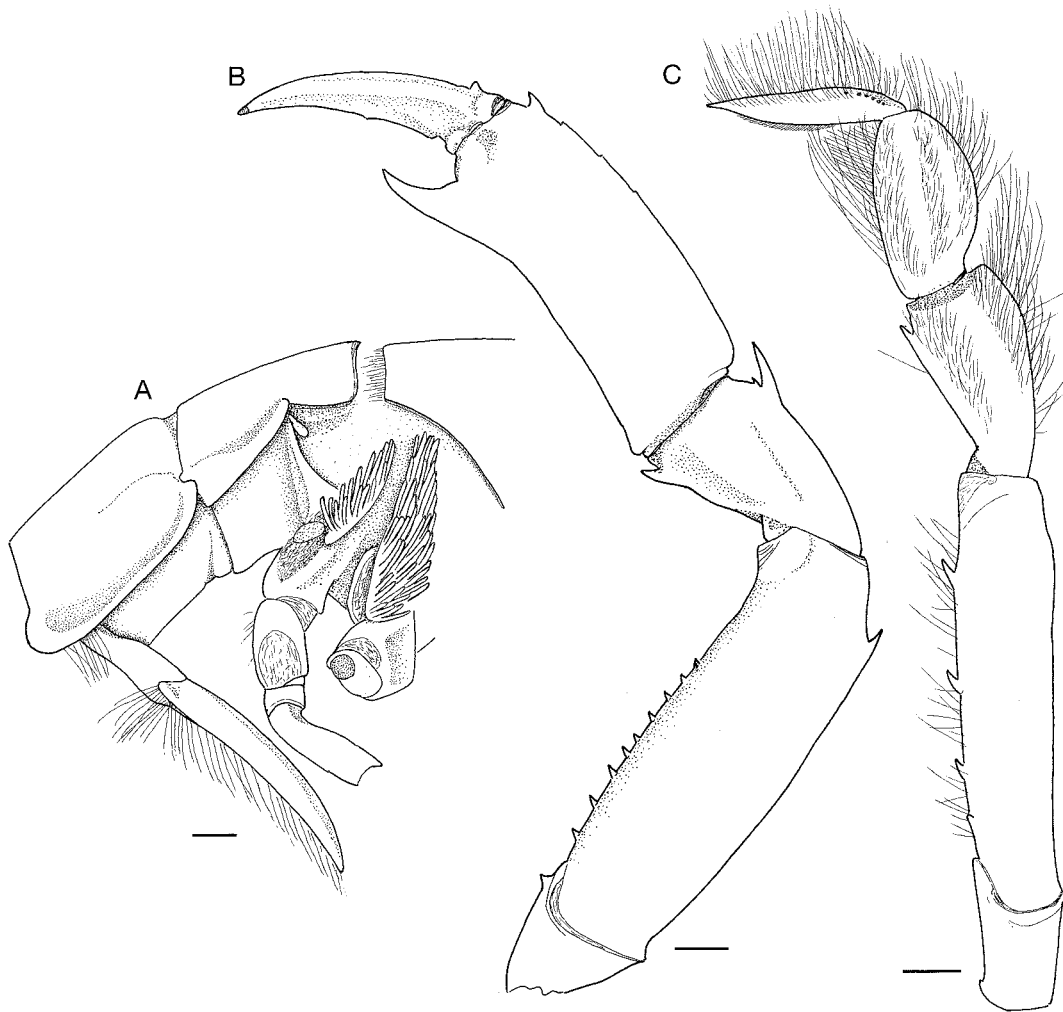


FIG. 35. — *Upogebia stellata* (Montagu, 1808); **A, C**, ♂ from Roscoff, France (MNHN Th 324); **B**, ♀ from Port de Primel, France (MNHN Th 320); **A**, abdominal segments 1, 2 and gills of pereopod 4 and 5 in lateral view, posterior arthrobranch of pereopod 4 omitted; **B, C**, pereopod 1 and 3. Scale bars: 1 mm.

distinctly longer than the telson. It could possibly belong to *U. stellata* in virtue of the shape of the rostrum, the posterior border of telson medially concave and a median distal spine on mesial surface of the P1 carpus. This is the only possibly correct record of this species (with variations) in the Mediterranean. Nobre (1931, 1936) reported *U. stellata* from Portugal, with a figure representing, with little doubt, a specimen of *U. pusilla*. Bonnier (1887) and Vilela (1936) reported *U. stellata* from the Bay of Concarneau, France

and from Faro, Portugal respectively; their materials have not been checked. More recently, Lacourt (1977) considered *U. stellata* as part of the marine fauna of the Bay of Concarneau. Specimens he studied were deposited (dried) in the Rijksmuseum of Natural History, Leiden, and one of these (RMNH D 45673) has been examined. It actually belongs to *U. pusilla*.

U. stellata was often confused with *U. deltaura* and a part of the material studied by Grieg as *U. stellata* (1927, with a figure) is likely *U. deltaura*.

De Morgan (1910) revealed the distinction between the two species in the anterolateral border of the carapace, with a spine in *U. stellata*, unarmed in *U. deltaura*. Also the P1 fixed finger is half as long as the dactylus in the former species, as long or nearly as long as the dactylus in the latter.

Upogebia stellata has also been confused with *U. pusilla* and *U. tipica*, for all three have a spine on the antero-lateral border of the carapace, a subcheliform P1 and like P2 and P3.

It can readily be differentiated from *U. pusilla* and *U. tipica*, as well as all other European *Upogebia*, in having a pleurobranch on the P5. Additional distinguishing features are: 1) P1 carpus has a median spine on its mesial distal border and the dactylus bears an upper proximal conical tooth (spine and tooth absent in *U. pusilla* and *U. tipica*); and 2) the telson is about 1.5 times as wide as long with lateral borders regularly curved and the posterior border slightly concave medially (it is 1.3 times as wide as long or approximately quadrate in *U. pusilla* and *U. tipica* respectively with lateral borders convex and the posterior border straight).

Upogebia tipica (Nardo, 1869)
(Figs 36; 37)

Bigea tipica Nardo, 1869: 317, pl. 13, fig. 4. — Borradaile 1903: 544.

Upogebia gracilipes de Man, 1927: 40, figs 15, 15a-d. — Balss 1936: 15. — Bouvier 1940: 110, fig. 73. — Zariquiey Alvarez 1946: 107, 108, pl. 5 figs a, d. — Bourdillon-Casanova 1960: 109.

Upogebia littoralis — °Gottlieb 1953: 440.

Upogebia tipica — Holthuis & Gottlieb 1958: 65. — Picard 1965: 114. — Zariquiey Alvarez 1968: 231. — Števičić °1969: 128; 1979: 282; 1985: 313; 1990: 216. — de Saint Laurent 1971: 1261. — Kattoulas & Koukouras 1974: 346. — *Thiriou 1976: 350. — Beaubrun 1979: 79, figs 53, 54. — Monchartmont 1979: 73. — Manning & Števičić 1982: 296. — Cottiglia 1983: 78. — García Raso 1983: 320. — Thessalou-Legaki & Zenetos 1985: 311. — Thessalou-Legaki 1986: 182. — Dworschak 1987c: pl. 3, fig. 11; 1992: 226, fig. 18b, d-f. — Lewinsohn & Holthuis 1986: 25. — °Koukouras *et al.* 1992: 223. — Noël 1992: 83. — °Frogliani 1995: 8. — Falciai

& Minervini 1996: 149, 1 fig. — d'Udekem d'Acoz 1996: 60; 1999: 158. — °Pancucci-Papadopoulou *et al.* 1999: 393. — Atkinson *et al.* 1998: 94, fig. 2. — *González-Gordillo *et al.* 2001: 279. — °Türkyay 2001: 289.

TYPE MATERIAL. — Whereabouts unknown.

MATERIAL EXAMINED. — France. Banyuls, 30 m, J.-M. Amouroux coll., 26.III.1998, 1 ♂ cl. 14 mm, tl. 38 mm (figured) and 4 ♂♂ cl. 11-14.5 mm; 1 ♀ cl. 11.5 mm, tl. 34 mm (figured) and 2 ♀♀ cl. 11 mm (MNHN Th 1319); 7.II.1996, 27.5 m, 6 juv. cl. 3.5-6 mm, 6 ♂♂ cl. 8-11 mm, 7 ♀♀ cl. 7.5-9 mm (MNHN Th 1336); P. Noël coll., 30 m, on coarse grit, VI.1976, 6 ♂♂ cl. 8-11.5 mm, 16 ♀♀ (15 ovig.) cl. 10-14 mm (MNHN Th 1337); sewage, 9.VI.1976, 15 ♂♂ cl. 8.5-14 mm, 14 ♀♀ (12 ovig.) cl. 9-14.5 mm (MNHN Th 641). — ?Banyuls, Thiriou coll., 7 ♂♂ cl. 9-12 mm, 1 ovig. ♀ cl. 10 mm (MNHN Th 1338). — ?Banyuls, 1 ♂ cl. 12.5 mm (MNHN Th 671). — Cap Béar, 60-70 m, J. Forest coll., 18.V.1955, 1 ♂ cl. 10.5 mm (MNHN Th 644). — N of Cap Béar, 42°31'22"N, 3°8'15"E, 5.IV.1951, don. Laboratoire Arago, 22 ♂♂, 16 ♀♀ (2 ovig.) (RMNH D 27236).

Spain. Near Massina, N of Cadaqués, leg. L. B. Holthuis, 28.VII.1955, 1 ♂ (RMNH D 28188).

Adriatic. Parenzan coll., 1 ♂ cl. 13.5 mm, tl. 37.5 mm (figured) and 5 ♂♂ cl. 11-12 mm, 1 ovig. ♀ cl. 12 mm, tl. 35 mm (figured) and 2 ovig. ♀♀ cl. 10 and 11.5 mm (MNHN Th 52).

Slovenia. Piran, Mus. Vindob. coll. (type specimen of *Upogebia gracilipes* de Man, 1927), 1 ♂ cl. 14.2 mm, tl. 41 mm (figured) (NHMW 304).

Croatia. W side of island Marjan at Split, 10-50 m, excursion Leiden Biologists, 15.VI.1962, 1 ♂ (RMNH D 19195).

Italy. Naples, J. Doerjes leg., 2 juv. cl. 3 and 5 mm (SMF 28321). — Trieste, Stp. 1860, tra studioamlingen, 10.XI.1917, 1 ♂, 1 ♀ cl. 11 mm (ZMUC 2705). — Thor, strn 27, 40°58'N, 13°49'W, 25 m, 1 ♂ cl. 7.5 mm (ZMUC 2709). — Golf of Taranto, 35 m, sand and mud, A. Varova, 3.VIII.1966, 1 juv. (RMNH D 23834); 23 m, sand, 7.VIII.1966, 1 ♂ (RMNH D 23835); 44 m, sand and mud, 15.IX.1966, 1 ♂ (RMNH D 23836).

Israel. Haifa Bay, dredge, 92 m, E. Gottlieb, 19.VIII.1955, 1 juv. (RMNH D 13596); bottomgrab, 55 m, 19.VIII.1955, 2 juv. (RMNH D 13597); dredge, 21.IX.1955, 1 ♂ (RMNH D 13598); bottomgrab, 42 m, 18.VIII.1955, 1 young ♀ (RMNH D 13599); 38 m, 18.VIII.1955, 1 juv. (RMNH D 13600); bottomgrab, 47 m, E. Gilat, 23.VII.1956, 1 juv. (RMNH D 19197). — Herzliya, bottomgrab, 90 m, A. Wirszubski, 24.VI.1947, 1 ovig. ♀ (RMNH D 13601); 58 m, 19.IX.1947, 1 ♀ (RMNH D 13602); dredge, 54 m, 24.VI.1947, 1 ♂, 1 ovig. ♀ (RMNH D 13603); 67 m, 14.XII.1949, 1 ♂ (RMNH D 13604); 45 m, 29.VIII.1947, 1 ovig. ♀ (RMNH D 13605). —

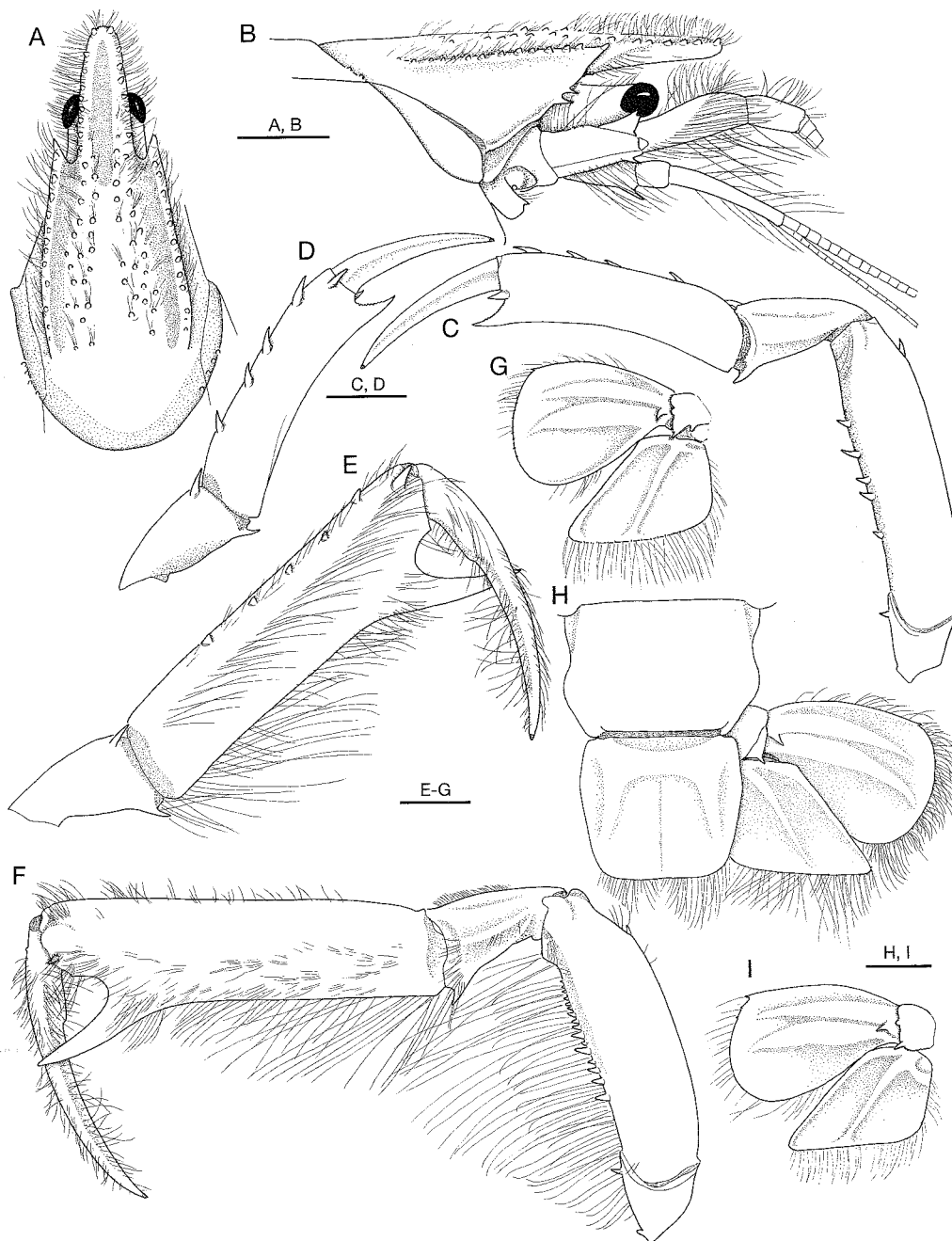


FIG. 36. — *Upogebia tipica* (Nardo, 1869) from Adriatic (MNHN Th 52); **A, B, E, F, δ** ; **C, D, G-I, f** ; **A, B**, anterior part of carapace, dorsal and lateral view; **C, F**, pereopod 1; **D, E**, distal articles of pereopod 1, mesial view; **G, I**, uropods; **H**, telson and uropods. Scale bars: 2 mm.

Gaza, dredge, 54 m, A. Wirszubski, 15.XI.1947, 1 ♂ (RMNH D 13607); bottomgrab, 56 m, 31.IX.1947, 1 juv. (RMNH D 13608). — Nabi Rubin, dredge, 138 m, A. Wirszubski, 24.V.1949, 1 spec. (RMNH D 13609); bottomgrab, 90 m, 30.IX.1947, 1 juv. (RMNH D 13610). — Nabi Junis, bottomgrab, 54 m, A. Wirszubski, 20.VI.1947, 1 ovig. ♀ (RMNH D 13611); 90 m, 14.XII.1949, 1 ♂ (RMNH D 13612). — Tel Aviv, dredge, 45 m, A. Wirszubski, 30.XI.1948, 1 juv. (RMNH D 13613); bottomgrab, 53 m, 14.XI.1947, 1 ♀ (RMNH D 13614). — Kefar Vitkin, bottomgrab, 54 m, A. Wirszubski, 13.XI.1947, 1 ♂, 2 juv. (RMNH D 13615); 235 m, 13.XI.1947, 1 ♂ (RMNH D 13616). — Rafah, dredge, 90 m, A. Wirszubski, 21.VI.1947, 1 ovig. ♀ cl. 6.5 mm (RMNH D 13617); 54 m, 22.VI.1947, 1 ♂ (RMNH D 13618). — Caesarea, dredge, 72 m, A. Wirszubski, 1.IX.1948, 1 ovig. ♀ (RMNH D 13619); bottomgrab, 54 m, 19.IX.1947, 1 ovig. ♀ (RMNH D 13620). — Athlit, bottomgrab, 137 m, E. Gottlieb, 13.IX.1951, 1 juv. (RMNH D 13621). — Nahariya, bottomgrab, 54 m, A. Wirszubski, 11.XI.1947, 1 spec. (RMNH D 13622). — Ascalon, bottomgrab, 46 m, E. Gottlieb, 10.IX.1951, 1 ♂ (RMNH D 13623). — Coast of Israel, S of Tel Aviv, 50 fms, dredge, E. Gilat, 2.XI.1961, 1 ♀ (RMNH D 19196).

DISTRIBUTION. — Mediterranean: Adriatic Sea (Nardo 1869; de Man 1927; Štević 1969; Manning & Štević 1982; Dworschak 1992); coast of Israel (Holthuis & Gottlieb 1958); Greek seas (Kattoulas & Koukouras 1974; Thessalou-Legaki & Zenetos 1985; Thessalou-Legaki 1986; Koukouras *et al.* 1992); Cyprus (Lewinsohn & Holthuis 1986); Italy: Naples, Trieste; France: Banyuls, Cap Béar.

DIAGNOSIS

Rostrum (Figs 36A; 37C) obtuse distally, 1.5-2.2 times as long as wide at base, with six to nine teeth on lateral border; anterolateral border of carapace with a spine (rarely two) (Fig. 36B); telson (Fig. 36H) approximately quadrate, lateral border convex, posterior border slightly concave medially.

A1 and A2 peduncle (Fig. 36B) with spine on lower margin of article 1 and 3 respectively. Md with large mesio-anterior pointed tooth. Mxp1 without epipod, Mxp3 with epipod.

P1 slightly stouter in male (Fig. 36E, F) than in female (Fig. 36C, D). Ischium with one or two spines on lower border. Merus with upper subdistal spine, seven to 12 spines on two-thirds or whole lower margin and spinules distally. Carpus with mesial upper distal spine and lower distal

spine. Propodus slender, about 2.5-4 times as long as wide; lateral surface with median distal spine near cutting edge of dactylus; mesial surface with row of two to five upper spines including subdistal one and upper distal spine near articulation with dactylus; cutting edge of fixed finger smooth or with small denticles. Dactylus 2.5-4 times as long as fixed finger, cutting edge smooth or with round teeth.

P2 (Fig. 37H) with upper subdistal spine, one or two lower spinules on merus; carpus with upper and lower distal spine. P3 (Fig. 37I) with one to three lower spines on merus; carpus with lower distal spine. Small coxal spine on P1 and P2. Basipod of uropod (Fig. 36G, H) with spinule hanging over endopod; exopod 1.3-1.5 times as long as distal width, with proximal spine.

Colour

Similar to *U. pusilla*, with small spots of brownish red (Dworschak pers. comm.).

Size

Largest specimens in material examined: cl. 12-14.5 mm, tl. 35-42 mm.

ECOLOGY

In the Adriatic, *U. tipica* prefers muddy bottoms below 9 m (Dworschak 1992). In the Patras Gulf, it was found in substrates with high percentages of mud and also in *Posidonia* meadows (Thessalou-Legaki & Zenetos 1985). It was collected from the infralittoral zone, in the Evvoia coast and Evvoia Gulf, at 5-50 m depth, in a bottom consisting of mud or mud mixed with sand (Kattoulas & Koukouras 1974). Abundant populations are found near Banyuls, at 25-30 m depth, in bottom with sand or grit (Amouroux pers. comm.).

Its burrow structure on *Squilla* grounds was reported by Atkinson *et al.* (1998), also by Dworschak (1987c: pl. 3, fig. 11).

VARIATIONS AND REMARKS

This species, so far reported from the Mediterranean only, presents certain variations and the first two are more pronounced between populations from

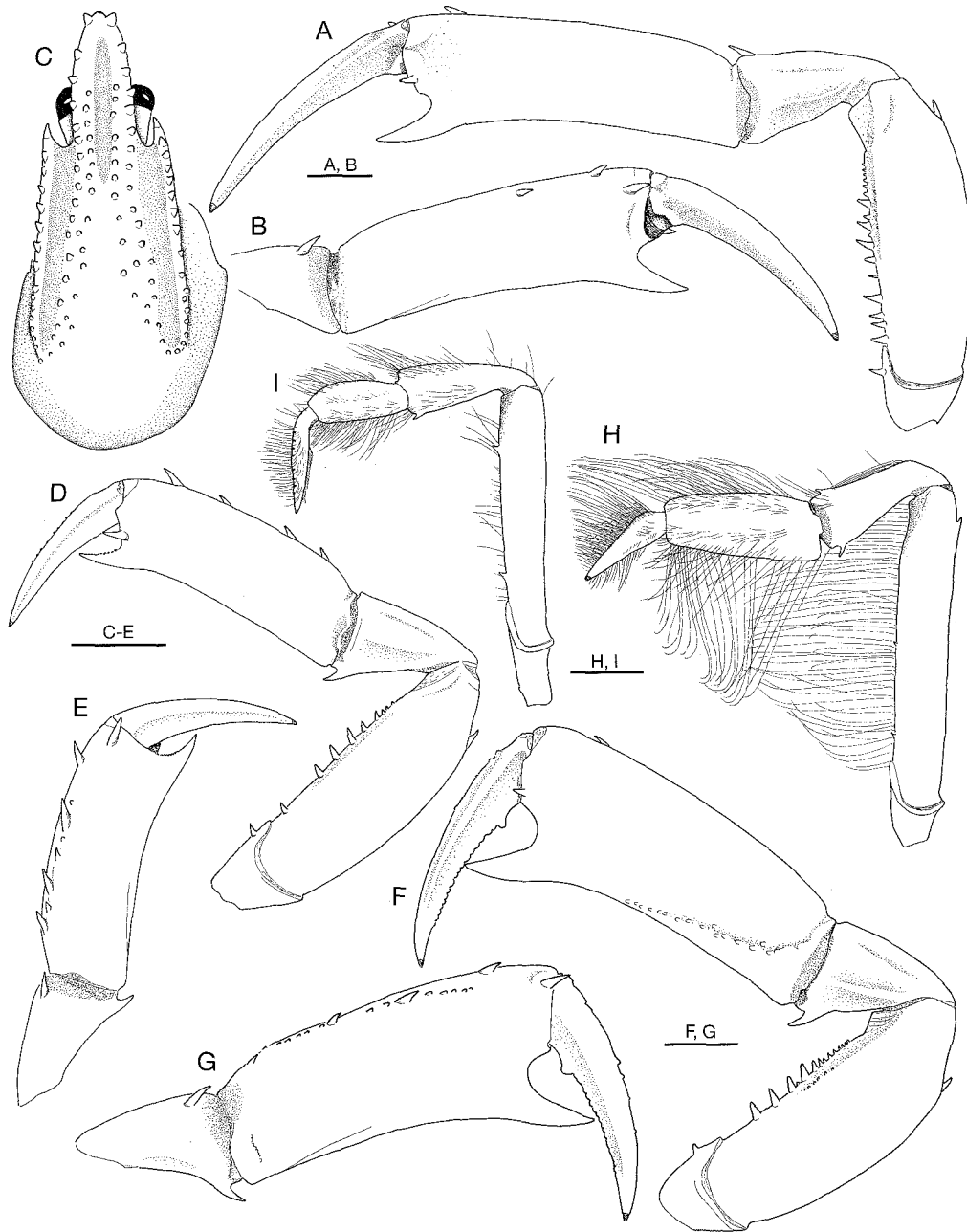


FIG. 37. — *Upogebia tipica* (Nardo, 1869); **A, B**, type specimen of *Upogebia gracilipes* de Man, 1927, ♂ from Slovenia (NHMW 304); **C-G**, from Banyuls, France (MNHN Th 1319); **C-E**, ♀; **F, G**, ♂; **H, I**, ♂ from Adriatic (MNHN Th 52); **A, D, F**, pereopod 1; **C**, anterior part of carapace; **B, E, G**, distal articles of pereopod 1, mesial view; **H, I**, pereopod 2 and 3. Scale bars: 2 mm.

the eastern and western part: 1) the length and spinulation of rostrum (it is longer and with more teeth in eastern specimens); 2) P1 slenderness (the ratio of the propodus length/width is 3-4 in the east, 2.5-3 in the west); 3) P1 propodus is sometimes with a lateral longitudinal smooth crest near the upper border; 4) or with spinules among the mesial upper spines (Fig. 37G); 5) the lower distal spine is exceptionally missing on the left P1 carpus of *U. gracilipes* type (MNW 304, Fig. 37A, B) and present on the right appendage; 6) the dactylus and fixed finger cutting edge is unarmed or bearing small teeth; and 7) the uropodal exopod has a lateral distal spinule or lacks it.

Upogebia tipica and *U. pusilla* are similar in having: 1) the antero-lateral border of carapace with a spine; 2) A1 and A2 peduncles bear a lower distal spine on article 1 and 3; and 3) the morphology and spinulation of P2 and P3.

Their differentiation, nevertheless, posed no problems to Dworschak (1992) who studied materials from the Adriatic. The two can be separated by the length of the rostrum, the morphology and spinulation of the P1. They are more similar in western Mediterranean and a great overlap exists in the length/width ratio of the P1 propodus. In areas where both are present, e.g., in Banyuls, France (comparing Fig. 33D-H with Fig. 37C-G), the following characters can help set them apart: 1) the rostrum is over 1.5 times as long as wide at base with six to eight teeth on each lateral border in *U. tipica* (less than 1.5 times as long as wide with four or five teeth on each lateral border in *U. pusilla*); 2) P1 merus bears spines and spinules on two-thirds or the whole lower margin in *U. tipica* (with three to six spines and spinules on proximal half of the lower margin in *U. pusilla*); 3) P1 propodus bears a longitudinal upper row of two to four spines on mesial surface and an upper mesial subdistal and distal spine; there is no mesial distal spine near the cutting edge of dactylus, no longitudinal upper smooth crest on the lateral surface in *U. tipica* (with upper longitudinal tuberculate or spinous crest on mesial surface, upper mesial subdistal, distal spine and median distal spine near cutting edge of dactylus; upper lateral longitudinal smooth crest often present in

U. pusilla); and 4) the telson is approximately quadrate, with the uropodal exopod longer than its distal width in *U. tipica* (telson is wider than long, with uropodal exopod about as long as its distal width in *U. pusilla*).

It can be added that *U. tipica* prefers deeper water than *U. pusilla* (Picard 1965; Thessalou-Legaki & Zenetos 1985; Dworschak 1992).

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