

**Northeastern Atlantic and Mediterranean hermit crabs (Crustacea:
Anomura: Paguroidea: Paguridae). I. The genus *Pagurus* Fabricius, 1775**

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A reappraisal of adult taxonomy of N.E. Atlantic and Mediterranean hermit crabs upholds the divisions A & B suggested for the species by MacDonald *et al.* (1957) from their studies of larval features. The nomenclature of three species is discussed. *Pagurus variabilis* (A. Milne Edwards and Bouvier, 1892) is relegated to the synonymy of *P. alatus* Fabricius, 1775 and *P. excavatus* (Herbst, 1791) is reinstated for Mediterranean and southern N. E. Atlantic material. A provisional check list is given of Paguroidean species occurring within the sea area 30°N-80°N: 30°W-30°E and the Mediterranean Sea. An illustrated identification key is provided to the *Pagurus* species within these regions.

Introduction

Knowledge of the hermit crab fauna of the temperate N.E. Atlantic Ocean and Mediterranean Sea is derived chiefly from the studies by Bell (1846, 1853), Henderson (1886), Bouvier (1896 a), A. Milne Edwards and Bouvier (1900), Lagerberg (1908), Pesta (1918), Selbie (1921), Bouvier (1940), Forest (1955), Zariquiey Alvarez (1968) and from various revisionary studies by De Saint Laurent-Dechancé (1966) and De Saint Laurent (1968 a, b, 1969, 1970). Additional literature references to papers dealing with the paguroidean crabs of these sea areas are given by Gordan (1956).

In some regions hermit crabs form a significant part of the total biomass (see Dyer *et al.* 1983) and their identification to species level is therefore of some importance when making comparative evaluations of marine communities. With this in mind, a revision of the N.E. Atlantic and Mediterranean Paguroidean crabs was begun by the author in 1983 with the aim of producing a suitable identification handbook for use by biologists engaged in general faunistic studies of these sea regions and who wish to identify their hermit crab collections.

This present paper summarizes studies completed to date on the taxonomy and nomenclature of the *Pagurus* species occurring in the N.E. Atlantic sea area (limited by co-ordinates 30°N-80°N, 30°W-30°E) and the Mediterranean Sea. A checklist is provided of all Paguroidean species reported from these areas and the opportunity is taken to include an illustrated key to the species of *Pagurus* examined during this study. Full references, bionomic information and distributions will be given in the proposed above mentioned handbook.

The genus *Pagurus* currently contains well over 100 species and is in need of a complete revisionary study. Several workers have recognized species groups, particularly while studying regional faunas. The most extensive review of these groups to date is by McLaughlin (1974) who recognized eight groups, two of which, the *bernhardus* and *trigonocheirus* groups respectively contain the two N.E. Atlantic species *P. bernhardus* (Linnaeus) and *P. pubescens* Krøyer (see p. 751). However,

McLaughlin remarked that 'Some species do not appear to adequately fit into existing groups nor into those proposed'.

Previously, two attempts have been made to establish groups for the N.E. Atlantic species of *Pagurus*. Milne Edwards and Bouvier (1892) and Bouvier (1940) proposed two divisions based upon the presence or absence in males, of a pleopod on the second abdominal somite. Those in which this pleopod is present were assigned to group I that included species with the current names of *P. forbesii* Bell, *P. cuanensis* Bell and *P. excavatus* (Herbst). Species in which this pleopod is absent, i.e. *P. alatus* (Fabricius), *P. bernhardus* (Linnaeus), *P. prideaux* Leach, *P. anachoretus* Risso, *P. carneus* Pocock and *P. chevreuxi* (Bouvier) were attributed to group II. A different arrangement was proposed by MacDonald *et al.* (1957) from studies of the larvae of five *Pagurus* species. They proposed that *P. bernhardus* and *P. pubescens* should be placed into group A and *P. prideaux*, *P. cuanensis* and *P. forbesii* into group B. They remarked that 'larval characters suggest that the two groups included in *Pagurus* are sufficiently distinct to merit separation into different genera' but added that such a revision must await examination of adult characters. Later, Pike and Williamson (1960) found that the larvae of *P. anachoretus* Risso, has features of both groups and also of a third—group C—into which they had placed the larvae of *Anapagurus*, *Spiropagurus* and *Cestopagurus*. The present study has shown that, using adult features, two groups can be recognized among the North eastern and Mediterranean *Pagurus* species that more or less correspond with the groups B & A as proposed by MacDonald *et al.* (1957). These 'groups' are respectively designated here as subdivisions I & II to avoid confusion in terminology with the species-groups (of lower ordinals) that also can be recognized within each of these two subdivisions. *P. anachoretus* is assigned here to subdivision II. Larval characters are included in the diagnosis of these two subdivisions but with reservation since these features are not known for all the species. Larval characters are also used to supplement the adult ones separating the species-groups in subdivision I but not for II since they are not known for two assigned species (*P. carneus* Pocock and *P. chevreuxi* (Bouvier)) whereas *P. anachoretus* shares larval features of both subdivisions.

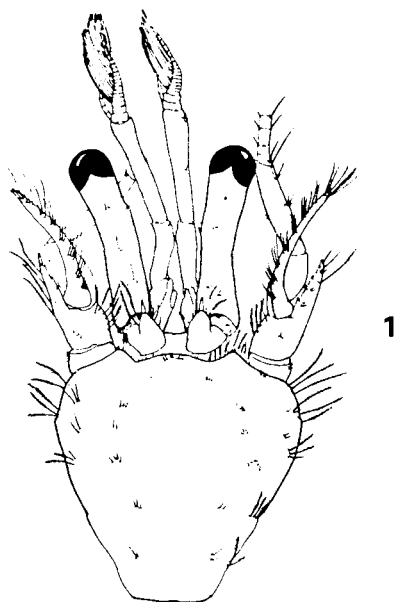
The adult features on which these two subdivisions can be recognized are: (1) anterior lobe of sternite configuration of the third pair of pereopods; (2) degree of development of the outer distal margin of the maxillule endopod; (3) presence or absence of spines or teeth on the lateral margins of the telson. Whether these combined features will prove to be of generic value can be determined only by examining the species currently attributed to *Pagurus* in which these characters are as yet undescribed.

The Subdivisions and species-groups of *Pagurus*

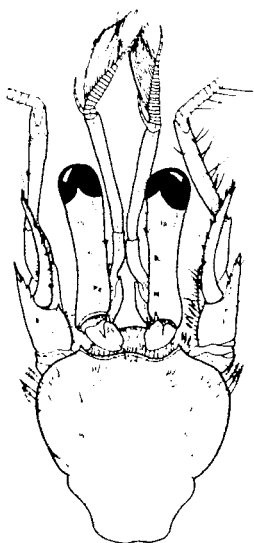
Subdivision I

Adult features: anterior lobe of sternite of third pair of pereopods triangular to sub-triangular and setose, with acute to subacute spines (figs. 45–50). Endopod of maxillule, outer distal margin rounded or obtusely produced (figs. 62–67). Posterior margin of telson armed with teeth or spines that extend on to lateral margins (figs. 56–61). ♂ with 0–4 unpaired pleopods.

Larval features: zoeae, telson broad, 4th spine not longer than $\frac{1}{2}$ maximum width of telson, 3rd spine reduced to acute process from third zoeal stage onwards. Antennal endopod with setae in first and second zoeae. Fourth zoea, endopods of uropods with setae. Megalopa, antennal flagellum not or hardly extending beyond chelae. Scaphognathite with 30–34 setae.

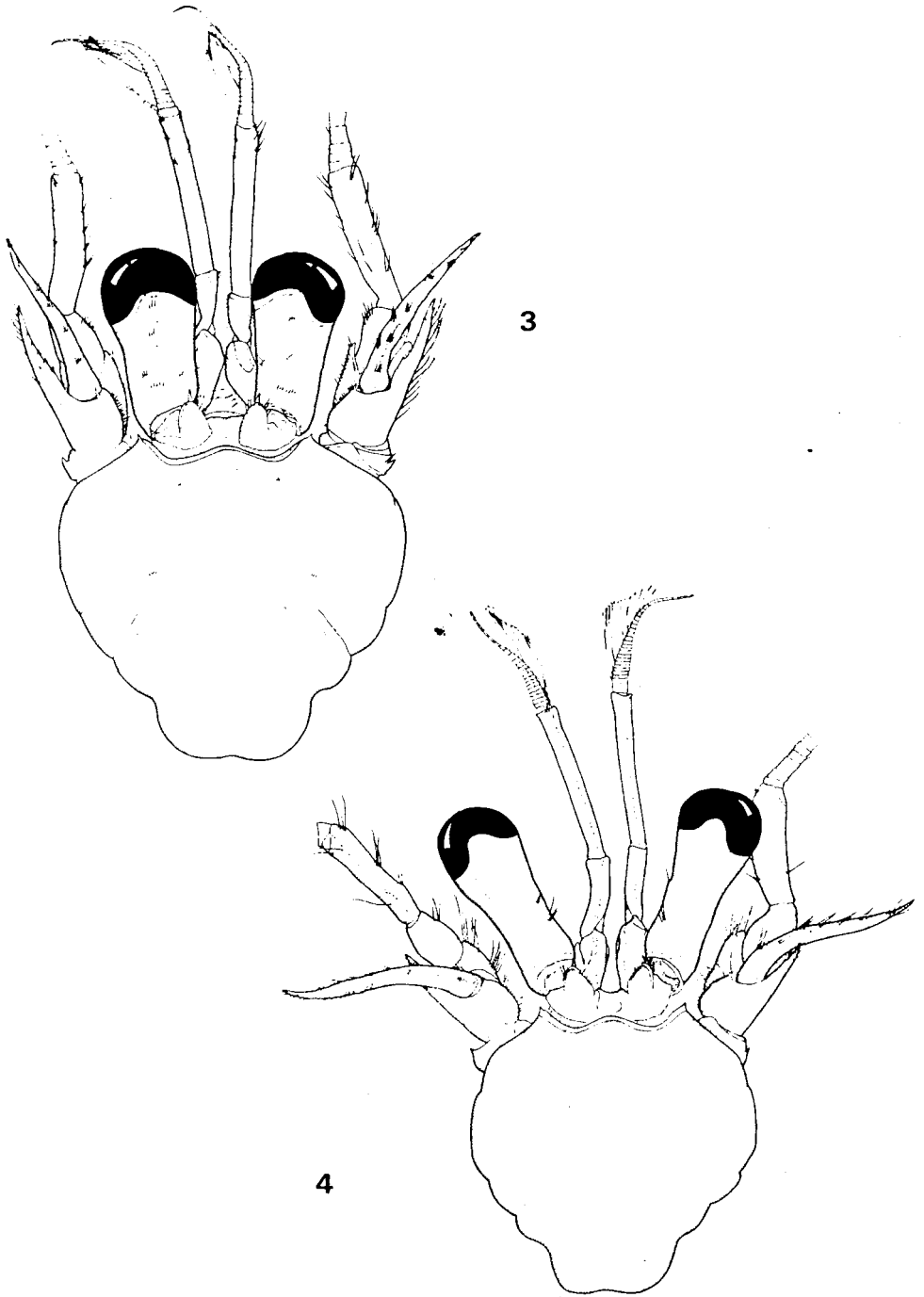


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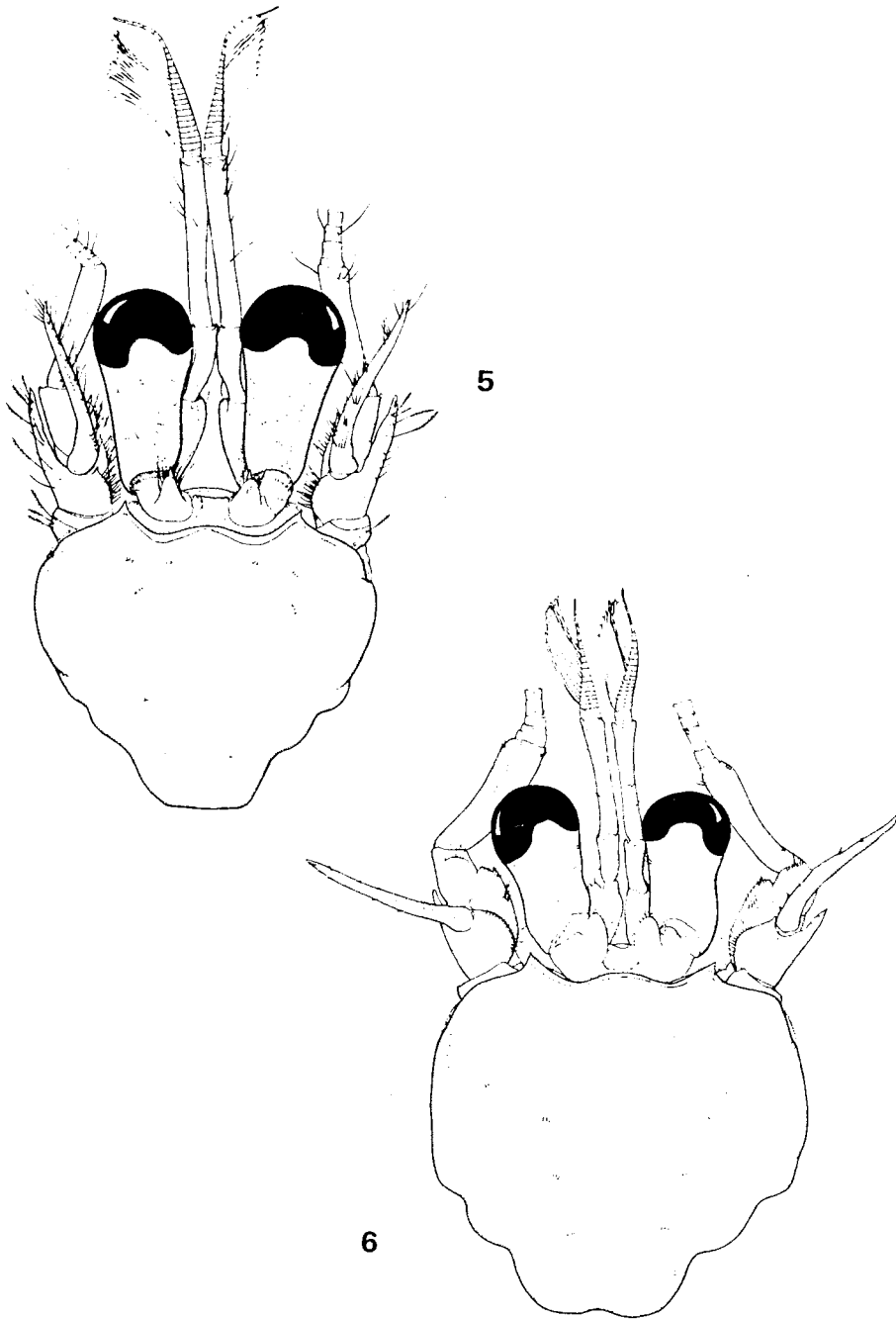


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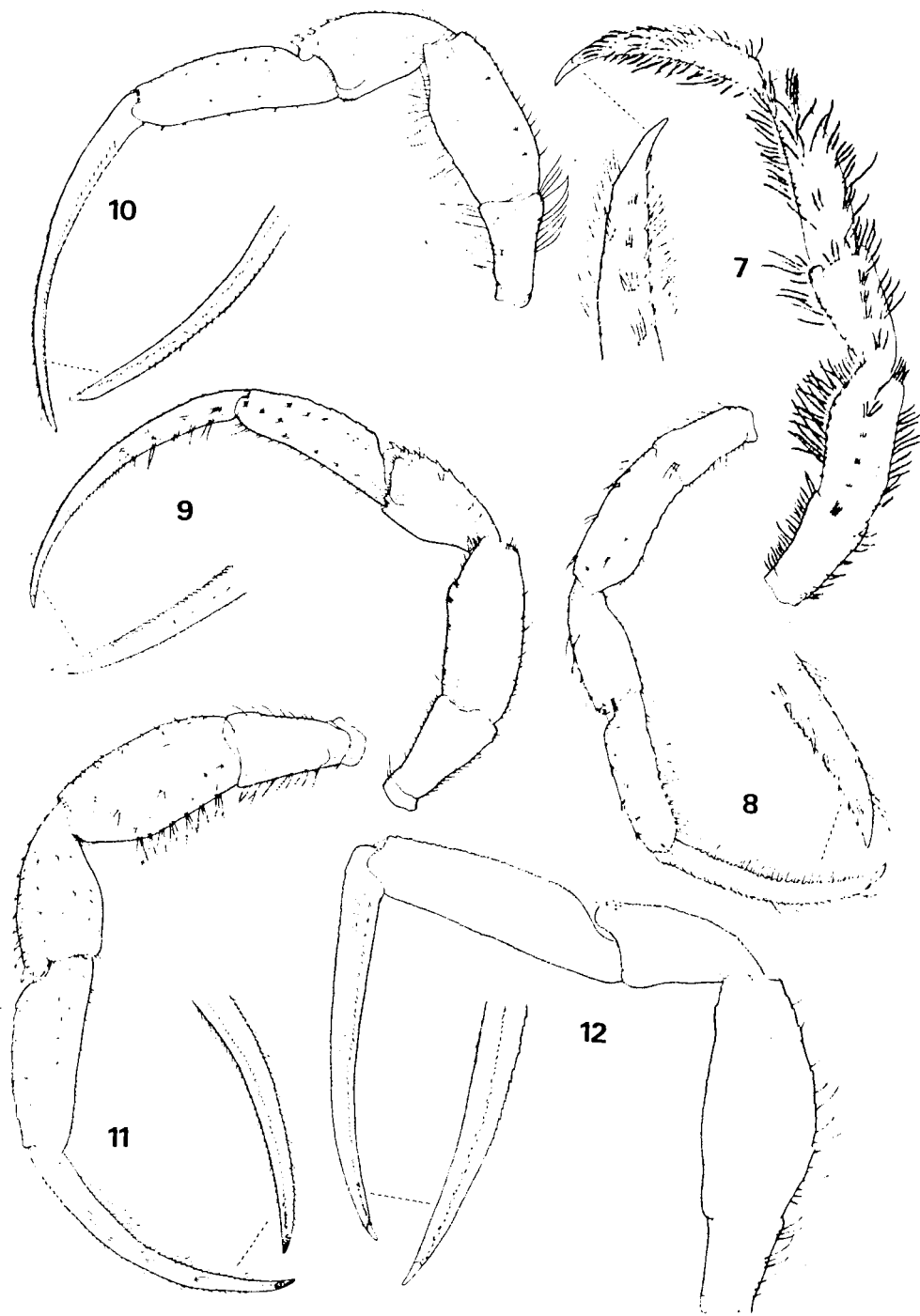
FIGS. 1 and 2. Dorsal aspects of shield and associated appendages of: 1 *Pagurus cuanensis* ♂, 6.5 mm s.l., Plymouth; 2 *P. forbesii* ♂, 5.0 mm s.l., Plymouth.



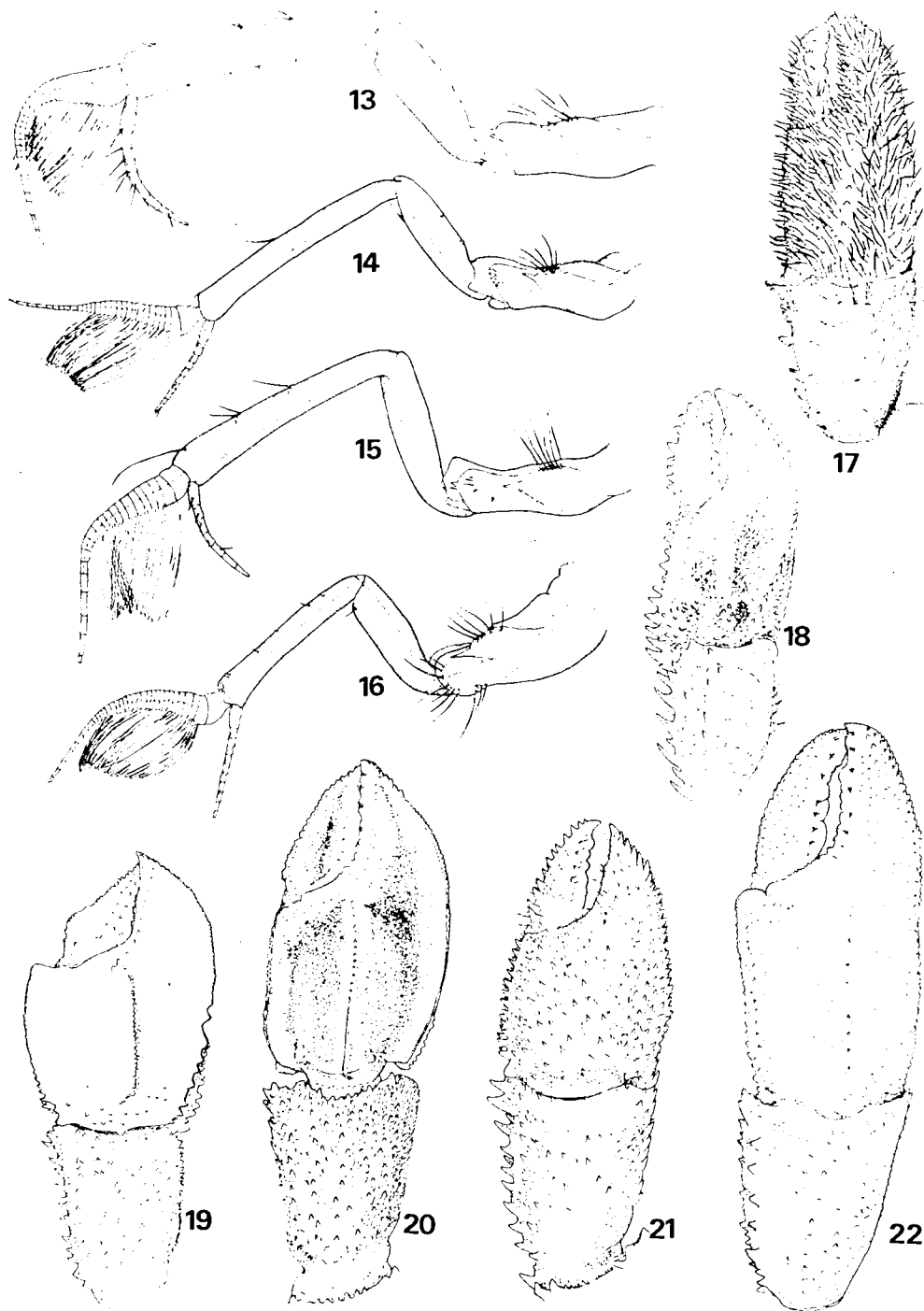
FIGS. 3 and 4. Dorsal aspects of shield and associated appendages of: 3 *Pagurus alatus* ♂, 8.6 mm s.l., S.W. Ireland; 4 *P. excavatus* ♂, 8.5 mm s.l., Naples.



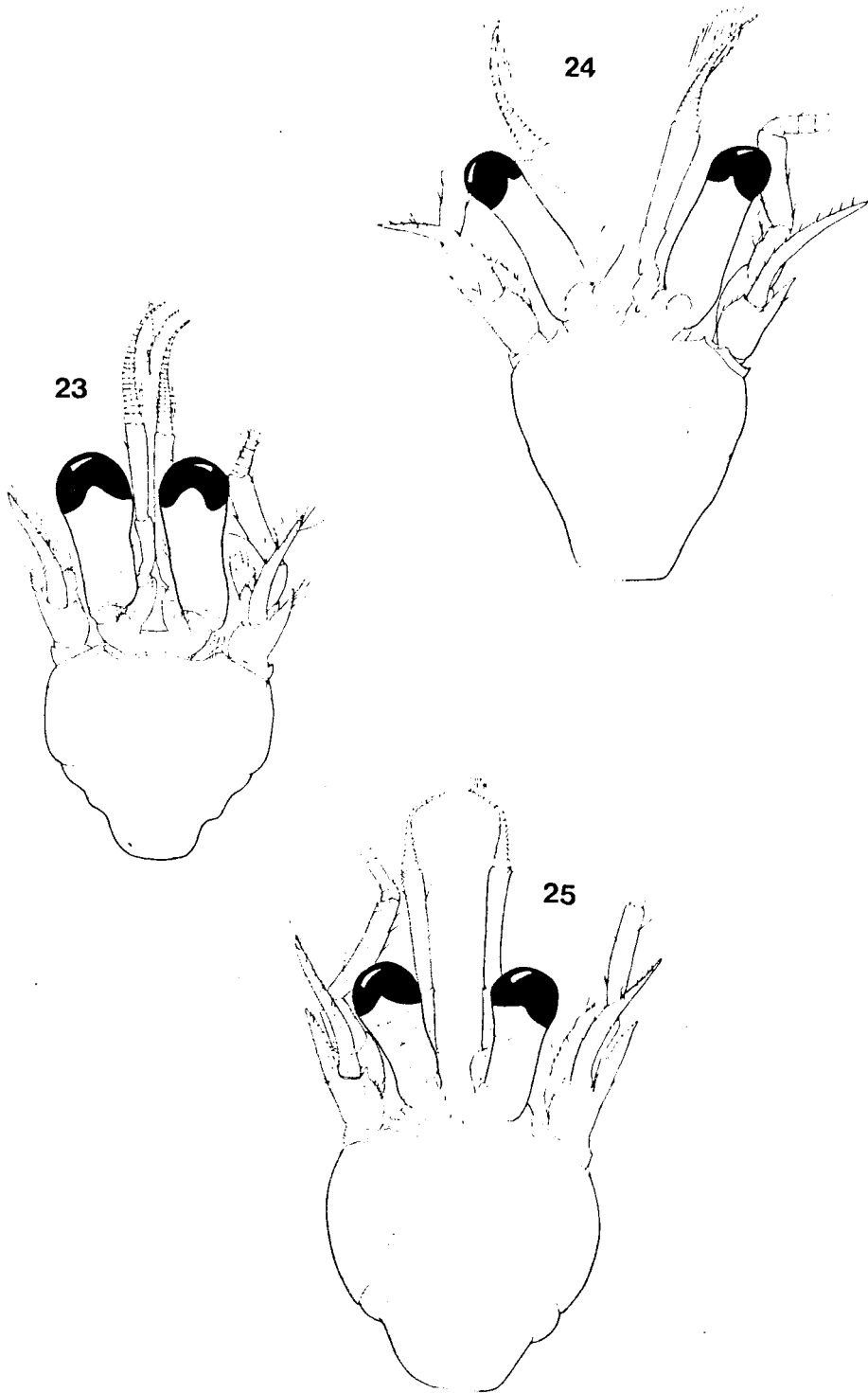
FIGS. 5 and 6. Dorsal aspects of shield and associated appendages of: 5 *Pagurus pubescentulus* ♀, 6.3 mm s.l., 4.39N:2.46W; 6 *P. prideaux* ♂, 11.5 mm s.l., near Eddystone, Plymouth.



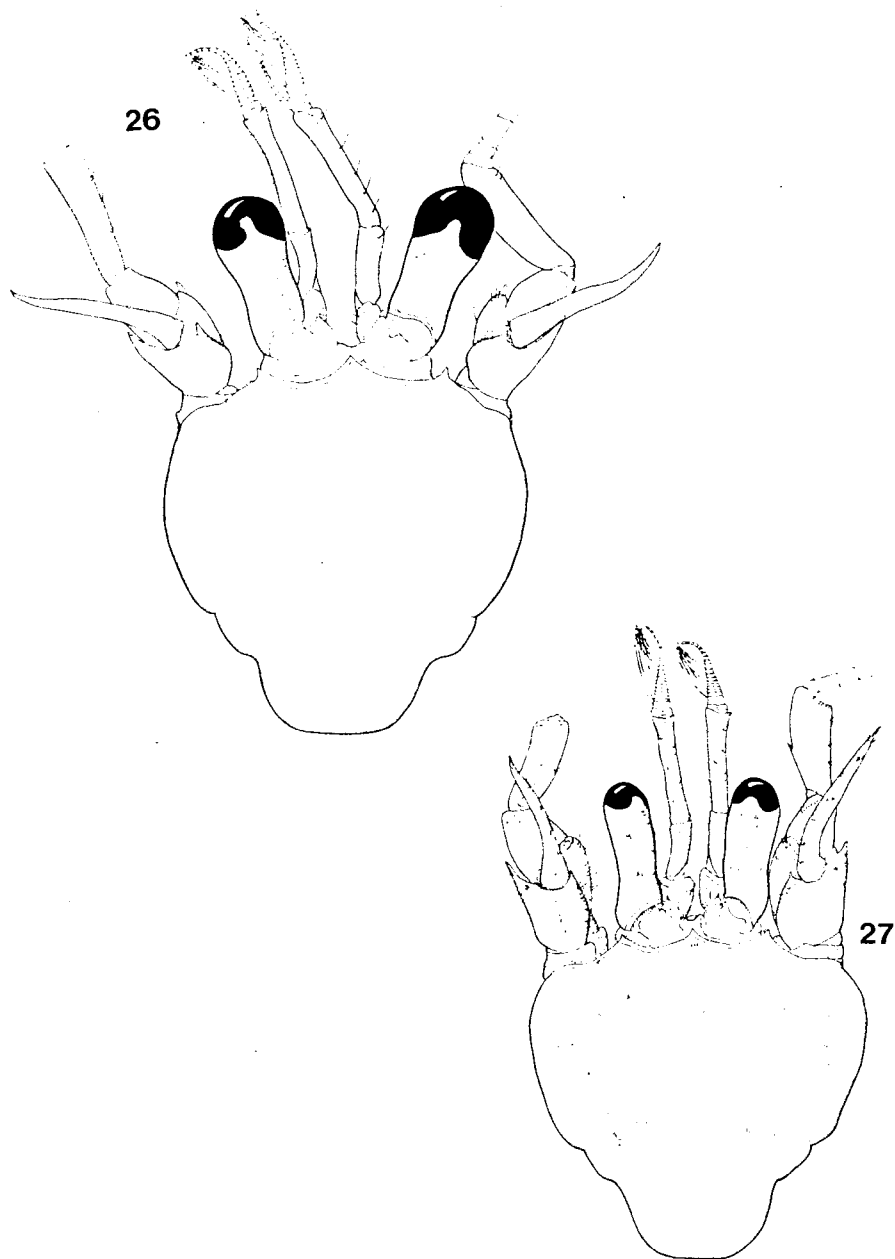
FIGS. 7-12. Left third pereiopod, outer aspects and inner aspects of distal parts of dactyls of: 7 *Pagurus cuanensis* ♂, 6.5 mm s.l., Plymouth; 8 *P. forbesii* ♂, 5.0 mm s.l., Plymouth; 9 *P. alatus* ♂, 8.6 mm s.l., S.W. Ireland; 10 *P. excavatus* ♂, 8.5 mm s.l., Naples; 11 *P. pubescentulus* ♀, 6.3 mm s.l., 4.39N:2.46W; 12 *P. prideaux* ♂, 11.5 mm s.l., near Eddystone, Plymouth.



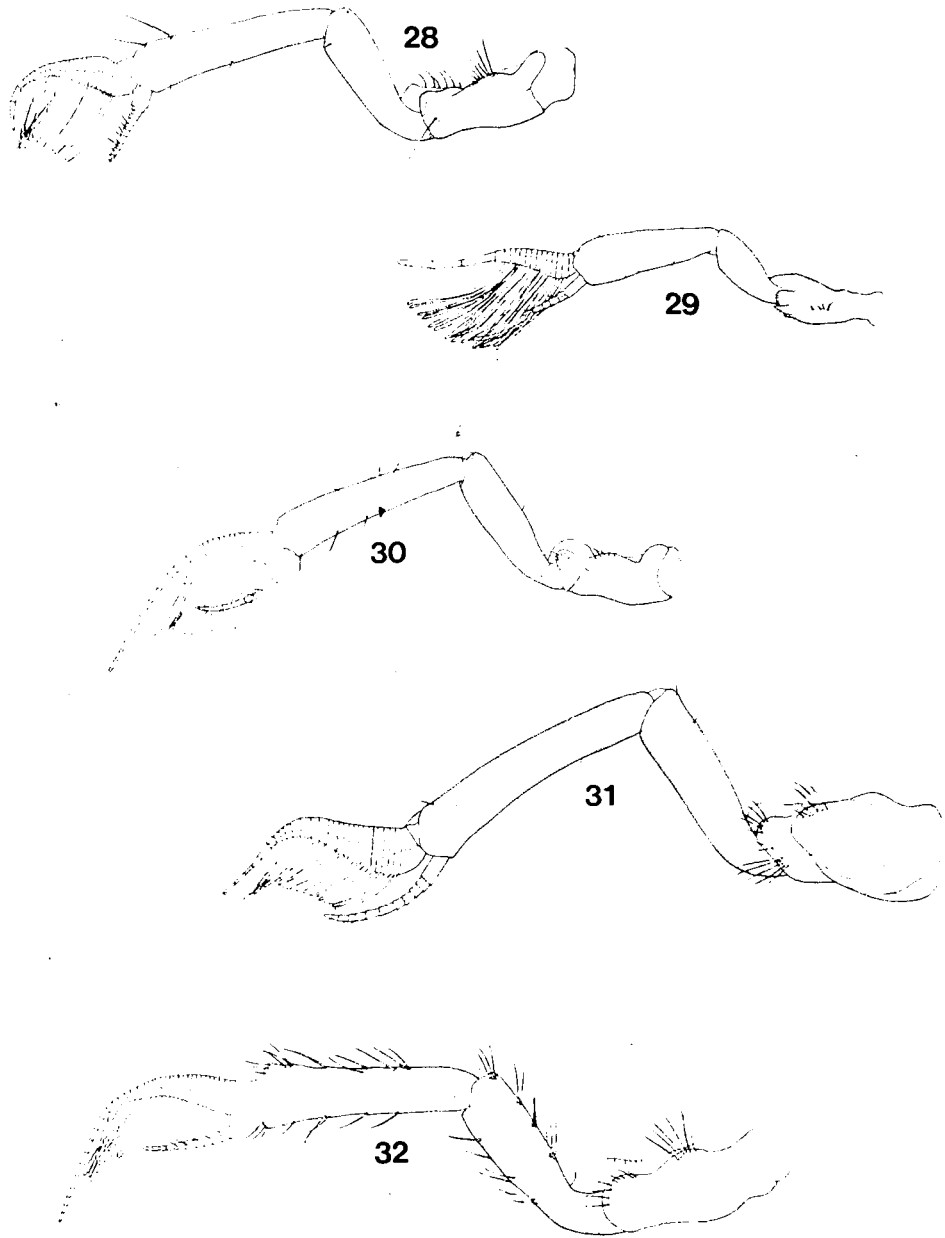
FIGS. 13-22. Left antennule: 13 *Pagurus alatus* ♂, 9.0 mm s.l., Shetland; 14 *P. excavatus* ♂, 8.5 mm s.l., Naples; 15 *P. pubescentulus* ♀, 6.3 mm s.l., 4-39N:2-46W; 16 *P. prideaux* ♂, 11.5 mm s.l., nr Eddystone, Plymouth; Right cheliped, outer aspects: 17 *P. cuanensis* ♂, 6.5 mm s.l., Plymouth; 18 *P. forbesii* ♂, 5.0 mm s.l., Plymouth; 19 *P. alatus* ♂, 9.0 mm s.l., Shetland; 20 *P. excavatus* ♂, 10.5 mm s.l., coast of Portugal; 21 *P. pubescentulus* ♀, 6.3 mm s.l., 4-39N:2-46W; 22 *P. prideaux* ♂, 13.0 mm s.l., near Eddystone, Plymouth.



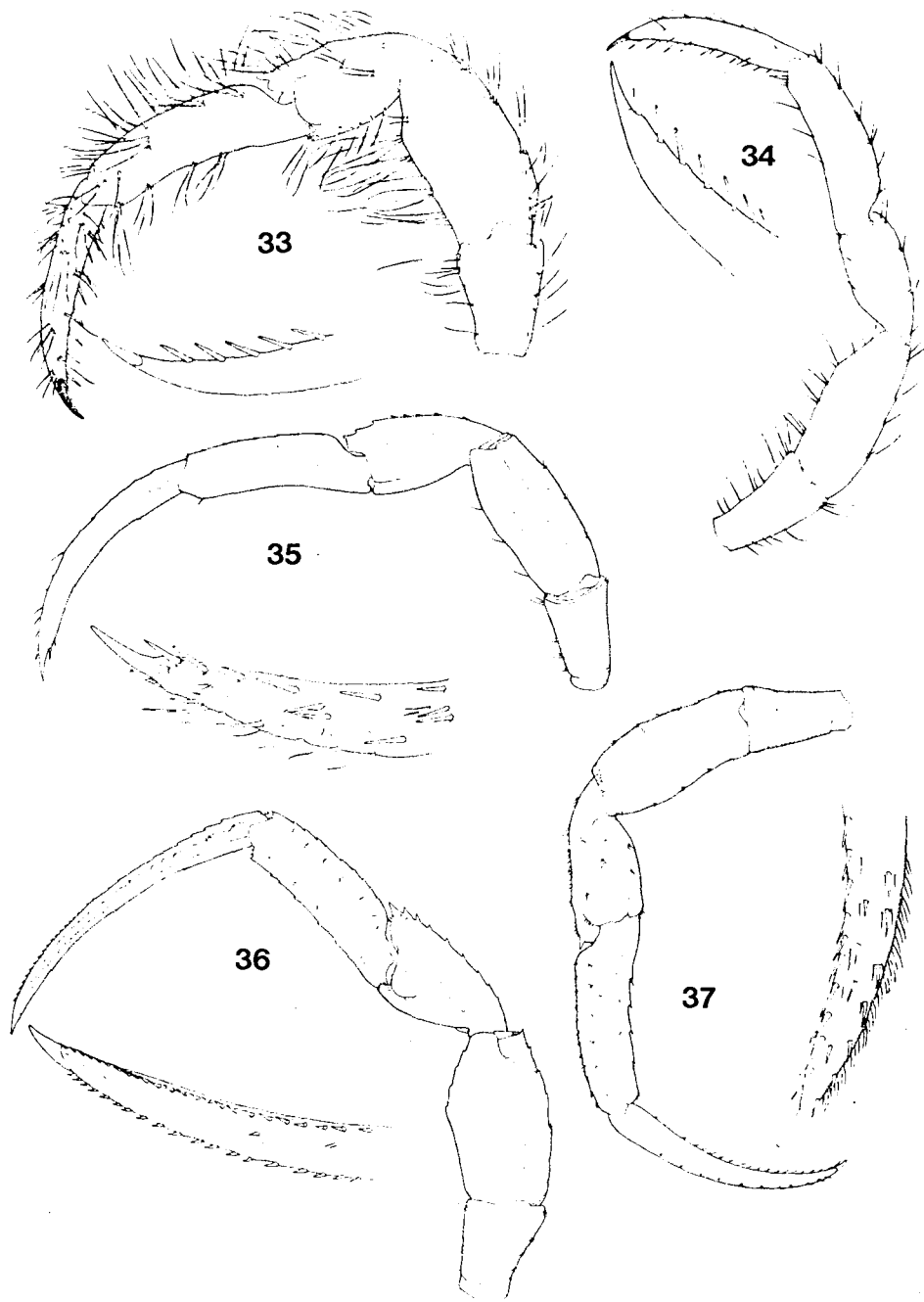
FIGS. 23-25. Dorsal aspects of shield and associated appendages of: 23 *Pagaurus anachoretus* ♂, 6.0 mm s.l., Naples; 24 *P. chevreuxi* ♂, 2.5 mm s.l., Naples; 25 *P. carneus* ♀, syntype, 9.0 mm s.l., off S.W. Ireland.



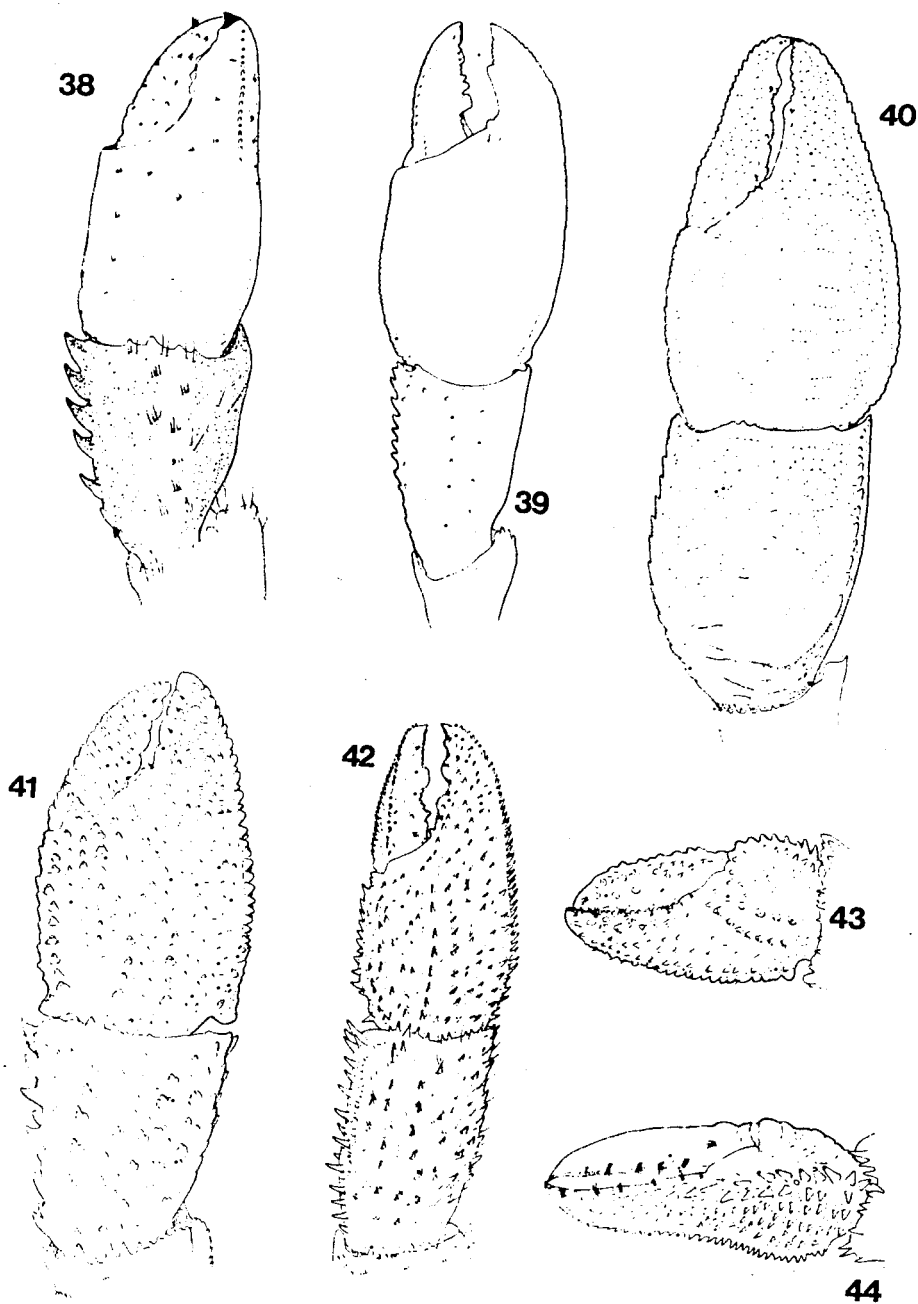
FIGS. 26-27. Dorsal aspects of shield and associated appendages of: 26 *Pagurus bernhardus* ♂, 15.5 mm s.l., Pembrokeshire, Wales; 27 *P. pubescens* ♂, 13.0 mm s.l., N.E. Atlantic 56°24N:09°12W.



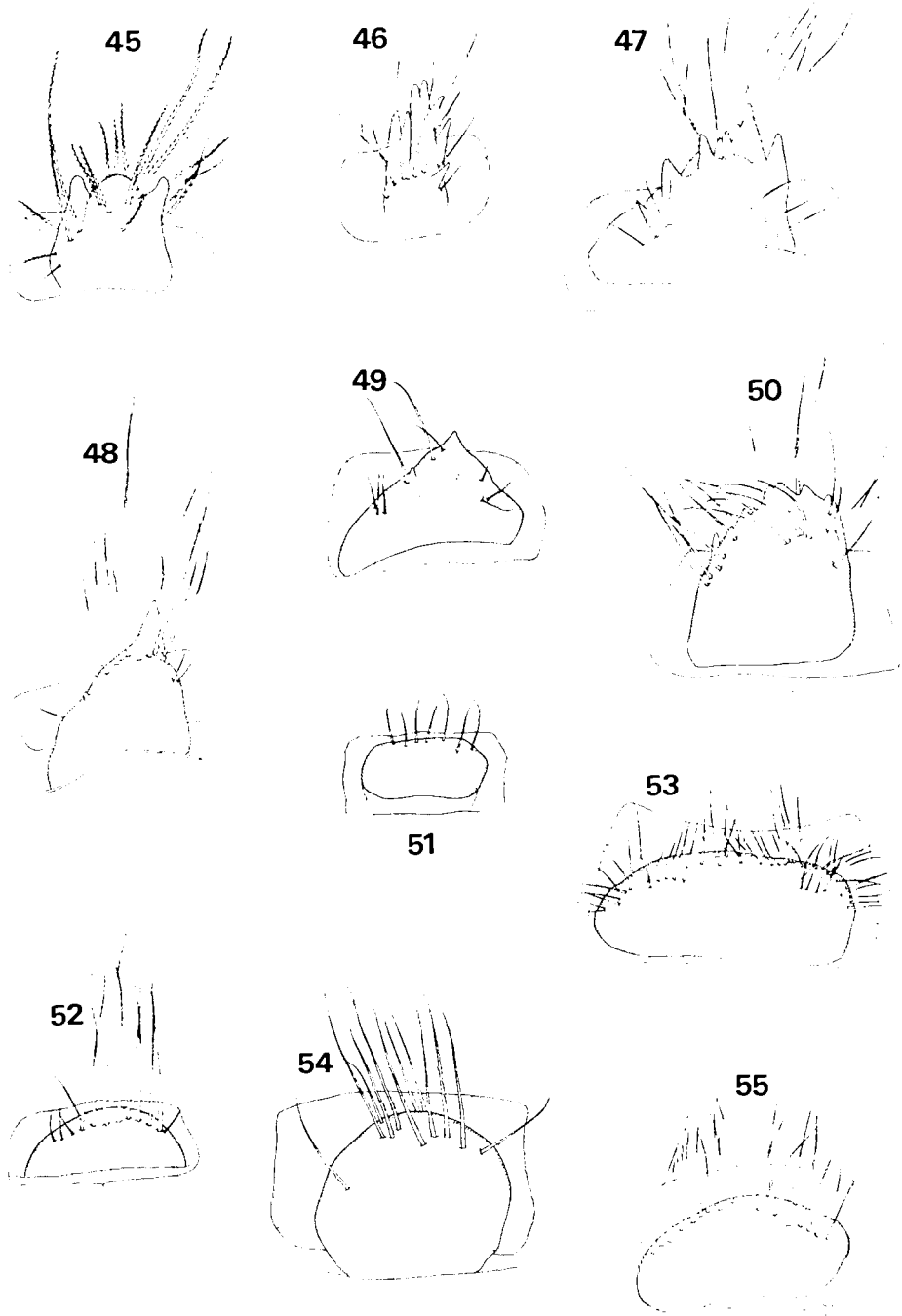
FIGS. 28-32. Left antennule: 28 *Pagurus anachoretus* ♂, 6.0 mm s.l., Naples; 29 *P. chevreuxi* ♂, 2.5 mm s.l., Naples; 30 *P. carneus* ♀, syntype, 9.0 mm s.l., off S.W. Ireland; 31 *P. bernhardus* ♂, 15.5 mm s.l., Pembrokeshire, Wales; 32 *P. pubescens* ♂, 13.0 mm s.l., N.E. Atlantic, 56°24N:09°12W.



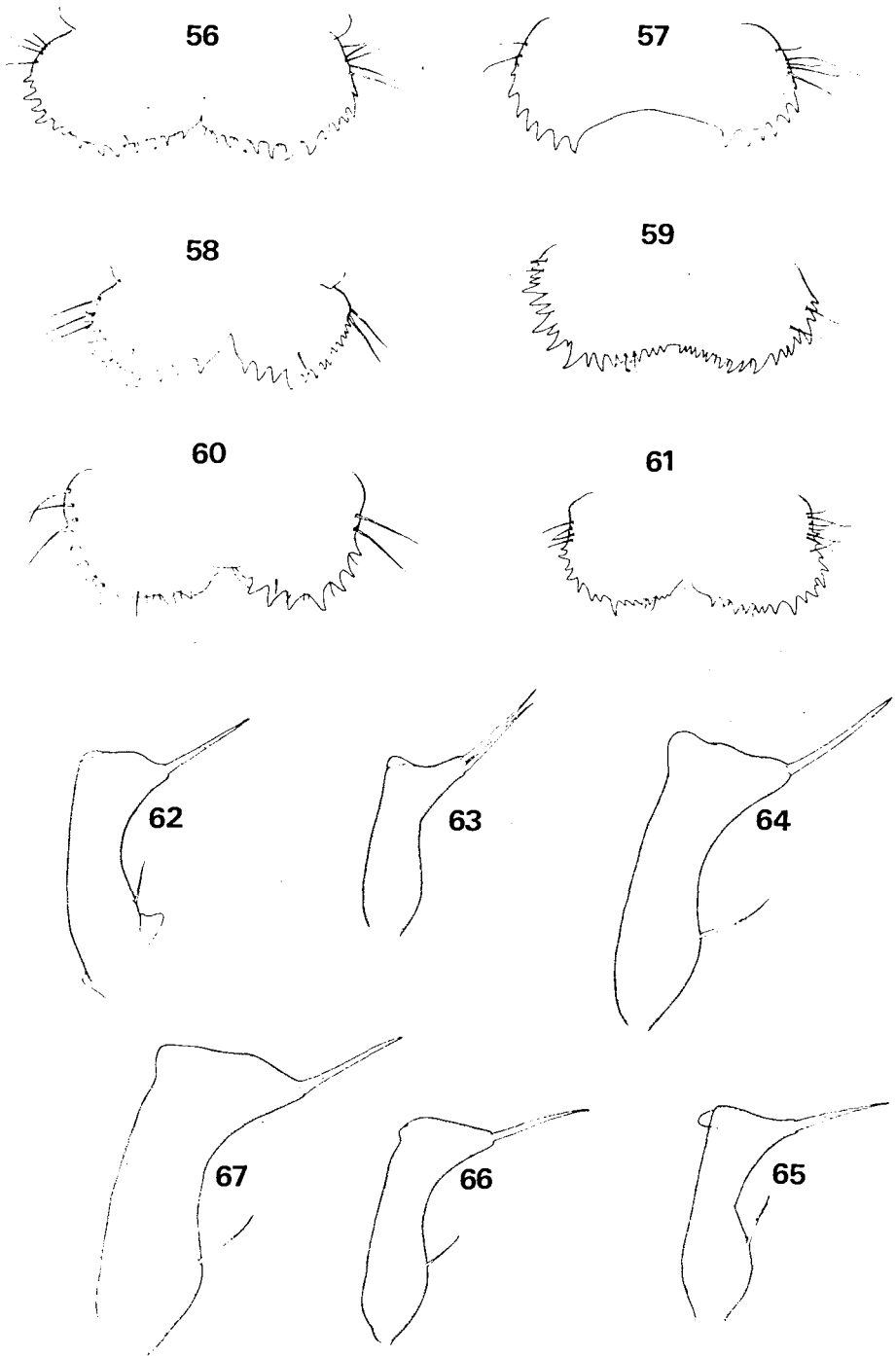
FIGS. 33-37. Left third pereiopod, outer aspects and inner aspects of distal parts of dactyls of: 33 *Pagurus anachoretus* ♂, 6.0 mm s.l., Naples; 34 *P. chevreuxi* ♂, 2.5 mm s.l., Naples; 35 *P. carneus* ♀, syntype, 9.0 mm s.l., off S.W. Ireland; 36 *P. bernhardus* ♂, 15 mm s.l., Kylesalia, Co. Galway, Ireland; 37 *P. pubescens* ♂, 13 mm s.l., N.E. Atlantic, 56°24'N:09°12'W.



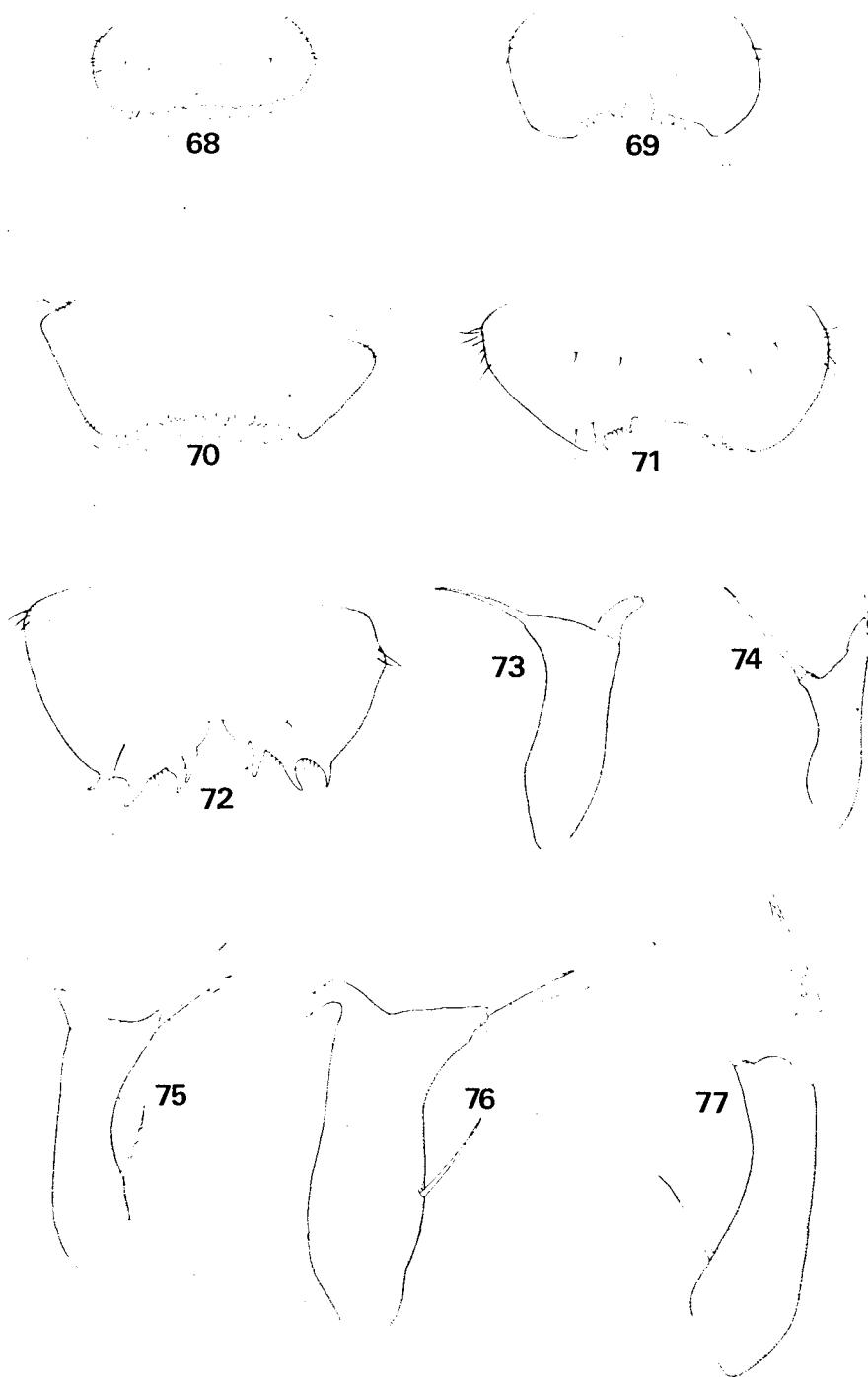
FIGS. 38-44. Right cheliped, outer aspects: 38 *Pagurus anachoretus* ♂, 6.0 mm s.l., Naples; 39 *P. chevreuxi* ♂, 2.5 mm s.l., Naples; 40 *P. carneus* ♀, syntype, 9.0 mm s.l., off S.W. Ireland; 41 *P. bernhardus* ♂, 15.5 mm s.l., Pembrokeshire, Wales; 42 *P. pubescens* ♂, 14.9 mm s.l., coast of Norway; Left cheliped, outer aspects: 43 *P. bernhardus* ♂; 44 *P. pubescens* ♂, from specimens in figs. 41, 42.



FIGS. 45-55. Anterior lobe of sternite of pereopod 3: 45 *Pagurus cuanensis* ♂, 7.5 mm s.l., Devon; 46 *P. forbesii* ♂, 5.0 mm s.l., Plymouth; 47 *P. alatus* ♂, 8.6 mm s.l., S.W. Ireland; 48 *P. excavatus* ♂, 8.5 mm s.l., Naples; 49 *P. pubescentulus* ♀, 6.3 mm s.l., 4-39N:2-46W; 50 *P. prideaux* ♂, 10.5 mm s.l., Holy Island, near Arran; 51 *P. chevreuxi* ♂, 2.5 mm s.l., Naples; 52 *P. anachoretus* ♂, 6.0 mm s.l., Naples; 53 *P. bernhardus* ♂, 15.5 mm s.l., Pembrokeshire, Wales; 54 *P. carneus* ♀, syntype, 9.0 mm s.l., off S.W. Ireland; 55 *P. pubescentulus* ♂, 13 mm s.l., N.E. Atlantic, 56-31N:09-13W.



FIGS. 56-67. Telson, dorsal aspects: 56 *Pagurus cuanensis* ♂, 7.5 mm s.l., Devon; 57 *P. forbesii* ♂, 5.0 mm s.l., Plymouth; 58 *P. alatus* ♂, 8.6 mm s.l., Naples; 59 *P. excavatus* ♂, 8.5 mm s.l., Naples; 60 *P. pubescentulus* ♀, 6.3 mm s.l., 43°39'N:2°46'W; 61 *P. prideaux* ♂, 10.5 mm s.l., Holy Island, near Arran; Endopod of right maxillule: 62 *P. cuanensis* ♂; 63 *P. forbesii* ♂; 64 *P. alatus* ♂; 65 *P. excavatus* ♂; 66 *P. pubescentulus* ♀; *P. prideaux* ♂, from specimens in figs 56-61.



FIGS. 68–77. Telson, dorsal aspects: 68 *Pagurus anachoretus* ♂, 6.0 mm s.l., Naples; 69 *P. chevreuxi* ♂, 2.5 mm s.l., Naples; 70 *P. carneus* ♀, syntype, 9.0 mm s.l., off S.W. Ireland; 71 *P. bernhardus* ♂, 15.5 mm s.l., Pembrokeshire, Wales; 72 *P. pubescens* ♂, 13 mm s.l., N.E. Atlantic, 56°31'N:09°13'W; Endopod of maxillule; 73 *P. anachoretus* ♂; 74 *P. chevreuxi* ♂ (both left); 75 *P. pubescens* ♂; 76 *P. bernhardus* ♂ (both right); 77 *P. carneus* ♀ (left), from specimens in figs. 68–72.

The following species are assigned to this subdivision. *Pagurus alatus* Fabricius, 1775; *Pagurus prideaux* Leach, 1815; † *Pagurus forbesii* Bell, 1845; *Pagurus cuanensis* Bell, 1845; *Pagurus excavatus* (Herbst, 1791); *Pagurus pubescentulus* (Milne Edwards and Bouvier, 1892) and within the N.E. Atlantic but outside of the study area, *Pagurus pycnacanthus* (Forest, 1955) and *Pagurus pulchellus* (Milne Edwards and Bouvier, 1892).

Three species-groups can be recognized in this subdivision on the following combined characters.

1. *alatus* group: ocular peduncles stout, noticeably subcylindrical, cornea strongly dilated; ocular acicles spatulate to subtriangular, dorsal surfaces concave. Left cheliped, outer propodal surface medially elevated and with prominent longitudinal row of acute tubercles; pereopods 2, 3 with dactyls usually slightly obliquely compressed distally. Maxilliped 1, peduncle of exopod moderately broadened proximally. Maxilliped 3, outer distal margin of carpus and of merus each with a spine; crista dentata with many acute teeth, one accessory tooth present. ♂ with 3 unpaired pleopods. Posterior margin of telson biconcave and with many teeth extending on to lateral margins.

Larval features (based upon *P. alatus*): first zoea—posterior margin of telson, length of 4th spine slightly longer than $\frac{1}{3}$ rd telson width; outer ramus of antennule with 7 setae/aesthetascs. Megalopa—1st segment of antennular peduncle without setae; endopod of pleopods with 3 hooks.

Species: *P. alatus* Fabricius, *P. excavatus* (Herbst), *P. pubescentulus* (Milne Edwards and Bouvier) and from outside the Area, *P. pulchellus* (Milne Edwards and Bouvier).

2. *prideaux* group: ocular peduncles stout, noticeably subcylindrical, cornea strongly dilated; ocular acicles spatulate, dorsal surfaces relatively flat. Left cheliped, outer propodal surface slightly elevated medially (more or less evenly convex) and with scattered tubercles; pereopods 2, 3 with dactyls obliquely compressed distally. Maxilliped 1, peduncle of exopod slightly broadened proximally. Maxilliped 3, outer distal margin of carpus and of merus each with a spine; crista dentata with moderate number of teeth, one accessory tooth present. ♂ without or with 4 unpaired pleopods. Posterior margin of telson concave, without median cleft and with numerous medium size to large teeth extending on to lateral margins.

Larval features (based upon *P. prideaux*): first zoea—posterior margin of telson, length of 4th spine noticeably shorter than $\frac{1}{3}$ rd telson width; outer ramus of antennule with 6 setae/aesthetascs. Megalopa—1st segment of antennular peduncle with setae; endopod of pleopods with 2 hooks.

Species: *P. prideaux* Leach, and from outside the area, *P. pycnacanthus* (Forest).

3. *cuanensis* group: ocular peduncles long and cylindrical; ocular acicles spatulate to subtriangular, dorsal surface slightly concave at the most. Left cheliped, outer propodal surface sometimes medially elevated and with acute to subacute tubercles; pereopods 2, 3 with dactyls slightly compressed distally but not obliquely so. Maxilliped 1, peduncle of exopod broadened proximally. Maxilliped 3, outer distal margin of carpus

† The precise month of publication for the name *sculptimanus* Lucas 1846, currently used for this species, is not known but must have been between January and March 1846. The work in which the name *forbesii* first appeared (Bell's Pt. IV of *A History of British Crustacea*) was actually on sale during the last week of December 1845 although dated 1846 (see Forest 1958, Gordon 1960, and personal correspondence between I. Gordon and H. O. Bull, 1959 in BMNH).

and of merus without spines; crista dentata with many teeth, one accessory tooth present. ♂ with 4 unpaired pleopods. Posterior margin of telson biconcave and with small to medium size teeth extending on to lateral margins.

Larval features (based upon *P. cuanensis* and *P. forbesii*): first zoea—posterior margin of telson, length of 4th spine exceeding $\frac{1}{3}$ rd of telson width; outer ramus of antennule with ? 4 setae/aesthetascs. Megalopal features not known.

Species: *P. cuanensis* Bell and *P. forbesii* Bell.

Subdivision II

Adult features: anterior lobe of sternite of third pair of pereopods broadly subquadrate to suboval, smooth and setose (figs. 51–55). Endopod of maxillule, outer distal margin produced as a conspicuous lobe or papilla, sometimes recurved, rarely segmented (figs. 73–77). Posterior margin of telson armed with teeth or spines that do not extend on to lateral margins (figs. 68–72). ♂ with 3 unpaired pleopods.

Larval features: zoeae-telson narrow, 4th spine longer than $\frac{1}{2}$ maximum width of telson, 3rd spine not reduced from third stage onwards and antennal endopod without setae (except in *P. anachoretus*). Fourth zoea, endopods of uropods without setae (except in *P. anachoretus*). Megalopa—antennal flagellum extending beyond chelae (except in *P. anachoretus* in which it extends to end of chelae); scaphognathite with 37 setae (*P. bernhardus*).

The following species are assigned to this subdivision. *Pagurus bernhardus* (Linnaeus, 1758); *Pagurus anachoretus* Risso, 1826; *Pagurus pubescens* Krøyer, 1838; *Pagurus carneus* Pocock, 1889; *Pagurus chevreuxi* Bouvier, 1896 a and within the N.E. Atlantic but outside of the study area, *Pagurus triangularis* Chevreux and Bouvier, 1892 and *Pagurus souriei* (Forest, 1952).

Five species groups can be recognized in this subdivision on the following combined characters; larval features are insufficiently known.

1. *bernhardus* group (after McLaughlin, 1974): rostrum acute; lateral projections marginal; ocular acicles spatulate, dorsal surfaces concave. Left cheliped, propodal outer surface gently convex and tuberculate; pereopods 2, 3 with dactyls noticeably obliquely compressed distally, marginal spines small and close together. Maxilliped 1, peduncle of exopod broadened proximally. Maxilliped 3 endopod, inner margin and outer distal margin of merus each with at least one spine; outer distal margin of carpus sometimes with a spine; crista dentata with moderate number of teeth, one accessory tooth present. Posterior margin of telson concave, sometimes medially incised, with a few small teeth.

McLaughlin (1974) assigned the following species to this group. *P. bernhardus* (Linnaeus) and the northwestern American species *P. armatus* (Dana, 1851); *P. ochotensis* Brandt, 1851 and *P. aleuticus* (Benedict, 1892).

2. *trigonocheirus* group (after McLaughlin, 1974): rostrum acute; lateral projections marginal; ocular acicles subtriangular, dorsal surfaces flat to slightly concave. Left cheliped, propodal outer surface medially elevated and with spiniform tubercles; pereopods 2, 3 with dactyls sometimes obliquely compressed distally, marginal spines stout and often widely spaced. Maxilliped 1, peduncle of exopod moderately broadened proximally. Maxilliped 3 endopod, inner margin and outer distal margin of merus each with at least one spine; outer distal margin of carpus sometimes with a spine; crista dentata with many teeth, one accessory tooth present. Posterior margin of telson biconcave, medially incised and with a few, large, recurved teeth.

McLaughlin (1974) assigned the following species to this group. *P. pubescens* Krøyer, and the northwestern American species *P. trigonocheirus* (Stimpson, 1858); *P. dalli* (Benedict, 1892); *P. undosus* (Benedict, 1892) and *P. stevensae* Hart, 1971.

3. *anachoretus* group: rostrum broad to subacute; lateral projections marginal; ocular acicles subtriangular, dorsal surfaces flat. Left cheliped, propodal outer surface convex and relatively smooth; pereopods 2, 3 with dactyls not obliquely compressed distally, marginal spines long and widely spaced. Maxilliped 1, peduncle of exopod slightly broadened proximally. Maxilliped 3 endopod, outer distal margin of merus without or with one spine; crista dentata with moderate number of teeth and with one or two accessory teeth. Posterior margin of telson biconcave and (sometimes slightly) medially incised, with many or few small teeth.

Species: *P. anachoretus* Risso, and from outside of the area, *P. triangularis* Chevreux and Bouvier and *P. souriei* (Forest).

4. *chevreuxi* group: rostrum narrow and elongate; lateral projections marginal; ocular acicles subtriangular, dorsal surfaces flat. Left cheliped, propodal outer surface relatively flat, sometimes with longitudinal median crest; pereopods 2, 3 with dactyls not obliquely compressed distally, marginal spines long and widely spaced. Endopod of maxillule with outer distal margin bearing incipiently segmented papilla. Maxilliped 3 endopod, inner and outer distal margins of merus with a spine (long and curved on inner margin); crista dentata with numerous small teeth, one accessory tooth present. Posterior margin of telson biconcave, medially incised and with numerous small teeth.

Species: †*P. chevreuxi* (Bouvier).

5. *carneus* group: rostrum acute; lateral projections submarginal; ocular acicles narrowly subtriangular, dorsal surface slightly concave. Left cheliped, propodal outer surface with a longitudinal median elevation bearing tubercles; pereopods 2, 3 dactyls slightly obliquely compressed distally, margins with spaced spines of moderate lengths. Endopod of maxillule with outer distal margin bearing a segmented papilla. Maxilliped 1, peduncle of exopod broadened proximally. Maxilliped 3, outer distal margin of merus with a spine; crista dentata with numerous small teeth and one large accessory tooth. Posterior margin of telson concave, slightly incised medially and with large subacute teeth alternating with groups of smaller teeth.

Species: *P. carneus* Pocock.

Remarks on the nomenclature of the names *Pagurus alatus*, *P. variabilis* and *P. excavatus*

Forest (1955: 110) considered *Pagurus excavatus* (Herbst, 1791) a synonym of *Pagurus alatus* Fabricius, 1775, maintaining that Fabricius' description of the chelipeds clearly identified this species as the *excavatus* of Herbst, (1791), the *angulatus* of Risso (1816), the *meticulosus* of Roux (1830) and the *tricarinatus* of Norman (1869). Fabricius' description of the chelipeds reads ... 'manibus laevibus, trialatis; dextra majore' ... and ... 'Chelae articulo penultimo scabro, ultimo sive manu laevi, alis tribus prominentibus, acutis' [with smooth hands, with three wings; right largest ... Penultimate segment of chelae rough, last segment (= chelae) smooth, with three prominent and sharp wings]. This description could equally apply to the N.E. Atlantic *P. variabilis* described by Milne Edwards and Bouvier (1892) a species not mentioned by Forest (1955) in his

† De Saint Laurent (1968 a) suggested that *P. chevreuxi* may need to be assigned to the genus *Cestopagurus* on account of the mouthparts and chelipeds that are morphologically very close to *C. timidus* (Roux) and to *C. coutieri* Bouvier, 1897. However, the absence of sexual tubes in the male of *P. chevreuxi* clearly excludes it from *Cestopagurus*.

discussion, but which Selbie (1921) considered distinct from *excavatus* Herbst. Selbie recognized both species and concluded '... that there is no genuine record of *E. excavatus* from a locality further north than the southern part of the Bay of Biscay, from which specimens have been recorded by Milne-Edwards and Bouvier'. The present study supports Selbie's opinion. Fabricius cited, as the type locality for *alatus* 'Habitat in Islandiae Bullis KOENIG'. This places the type locality far beyond the present accepted northern range of *excavatus* but within that of *variabilis*. The name *variabilis* A. Milne Edwards and Bouvier, 1892 is considered here a junior subjective synonym of *alatus* Fabricius, 1775 and the name *excavatus* Herbst, 1791 is reinstated for the N.E. Atlantic species distributed southward from the southern part of the Bay of Biscay and into the Mediterranean. In many southern regions of the area both species occur together.

Pagurus alatus (Fabricius) has been reported twice from Icelandic waters. Firstly by Olafsen and Povelsen, 1772 (as *Cancer diogenes*) and later by Fabricius, 1775 (as *Pagurus alatus*). The figure by Olafsen and Povelsen (tab. XI, fig. 1) show the crest on the outer propodal surface of the major cheliped, very typical of large specimens of this species. The true identity of their figure has been overlooked possibly because Stephensen (1939, 1, 7, 9) considered their *Cancer diogenes* to represent either *P. bernhardus* or *P. pubescens* both of which occur in Icelandic waters. It is likely that Olafsen and Povelsen did not intend to establish a new species but incorrectly identified their specimen with the *Cancer diogenes* Linnaeus, 1758 (= *Petrochirus diogenes* (Linnaeus, 1758)).

This confusion relating to the nomenclature of *Pagurus alatus* and *P. excavatus* may account for the discrepancies between larval descriptions of '*P. variabilis*' zoeae by Samuelson (1972) and that of '*P. alatus*' by Bookhout, 1972; the former was probably material of *P. alatus* and the latter perhaps of *P. excavatus*.

Provisional checklist of N.E. Atlantic species of Paguroidea within sea area 30°N–80°N; 30°W–30°E and Mediterranean Sea.

Superfamily PAGUROIDEA Latreille 1803: 136 (vide McLaughlin 1983)

Family DIOGENIDAE Ortmann 1892: 270

Genus *Calcinus* Dana 1851: 286

Calcinus ornatus (Roux 1830: Pl. 43)

Genus *Clibanarius* Dana 1852: 6

Clibanarius erythropus (Latreille 1818: 366)

Genus *Dardanus* Paulson 1875: 90

Dardanus arrosor (Herbst 1796: 170)

Dardanus calidus (Risso 1826: 39)

Genus *Diogenes* Dana 1851: 269

Diogenes pugilator pugilator (Roux 1829: Pl. 14)

Diogenes pugilator orientalis Codreanu and Balcesco 1968: 372

Genus *Paguristes* Dana 1851: 269

Paguristes eremita (Linnaeus 1767: 1049)*

Paguristes syrtensis de Saint Laurent 1971: 1099

Family PAGURIDAE Latreille 1803: 136

Genus *Acanthopagurus* de Saint Laurent 1968 b: 926

Acanthopagurus atlanticus (Bouvier 1922: 24)

* Synonym is *P. oculatus* (Fabricius 1775: 411), see Holthuis, 1977: 58.

- Acanthopagurus richardi* (Bouvier 1922: 22)
 Genus **Anapagurus** Henderson 1887: 321
Anapagurus bicorniger A. Milne Edwards and Bouvier 1892: 215
Anapagurus breviaculeatus Fenizia 1937: 25
Anapagurus brevicarpus A. Milne Edwards and Bouvier 1892: 215
Anapagurus chiroacanthus (Lilljeborg 1856: 118)
Anapagurus curvidactylus Chevreux and Bouvier 1892: 91
Anapagurus hyndmanni (Bell 1845: 182)
Anapagurus laevis (Bell 1845: 184)
Anapagurus longispina A. Milne Edwards and Bouvier 1900: 219
Anapagurus petiti Dechancé and Forest 1962: 297
 Genus **Catapaguroides** A. Milne Edwards and Bouvier 1892: 211
Catapaguroides iris Bouvier 1922: 29
Catapaguroides megalops A. Milne Edwards and Bouvier 1892: 213
Catapaguroides microps A. Milne Edwards and Bouvier 1892: 211
 Genus **Cestopagurus** Bouvier 1897: 229
Cestopagurus timidus (Roux 1830: Pl. 24)
 Genus **Nematopagurus** A. Milne Edwards and Bouvier 1892: 209
Nematopagurus longicornis A. Milne Edwards and Bouvier 1892: 210
 Genus **Pagurus** Fabricius 1775: 410
Pagurus alatus (Fabricius 1775: 411)
Pagurus anachoretus Risso 1826: 41
Pagurus bernhardus (Linnaeus 1758: 631)
Pagurus carneus Pocock 1889: 428
Pagurus chevreuxi (Bouvier 1896 b: 95)
Pagurus cuanensis Bell 1845: 178
Pagurus excavatus (Herbst 1791: 31)
Pagurus forbesii Bell 1845: 186
Pagurus prideaux Leach 1815: Tab. 26
Pagurus pubescentulus (A. Milne Edwards and Bouvier 1892: 219)
Pagurus pubescens Krøyer 1838: 314
 Genus **Spiropagurus** Stimpson 1858: 236
Spiropagurus elegans Miers 1881: 278
 Family **PARAPAGURIDAE** Smith 1882: 20
 Genus **Parapagurus** Smith 1879: 50
Parapagurus bicristatus bicristatus (A. Milne Edwards 1880: 43)
Parapagurus gracilipes (A. Milne Edwards 1891: 132)
Parapagurus pilosimanus pilosimanus Smith 1879: 51
Parapagurus ruticheles (A. Milne Edwards 1891: 133)

Key to the North eastern Atlantic and Mediterranean species of *Pagurus* Fabricius

- 1(2) Anterior lobe of sternite of pereopod 3 triangular to subtriangular (figs. 45–50) and with acute to subacute spines; lateral margins of telson armed with teeth or spines (figs. 56–61); outer distal margin of maxillule endopod rounded (fig. 62) or very slightly produced (figs. 63–67). 3
- 2(1) Anterior lobe of sternite of pereopod 3 broadly subquadrate (figs. 51, 53, 55), suboval (fig. 52) or almost rounded (fig. 54), smooth; lateral margins of telson without teeth or spines (figs. 68–72); outer distal margin of maxillule endopod strongly produced (fig. 75), usually as a papilla (figs. 73, 74) sometimes recurved (fig. 76) rarely segmented (fig. 77) 11

- 3(4) Breadth of cornea approximately $\frac{1}{4}$ length of eye (figs. 1 and 2). Small spinules on lower margins of dactyls (figs. 7, 8 insets) of pereopods 2, 3 5
- 4(3) Breadth of cornea approximately $\frac{1}{2}$ total length of eye (figs. 3-6). No spinules (but often stiff setae) on lower margins of dactyls (figs. 9-12) of pereopods 2, 3 7
- 5(6) Outer dorso-lateral process of antennal peduncular segment 2 extending well into distal $\frac{1}{2}$ of segment 4; acicle reaching to distal $\frac{1}{4}$ of segment 5 (fig. 1). Surfaces of chelipeds with long, often dense, setae. Palm of right cheliped (fig. 17) with outer surface evenly convex throughout; margins of propodus delineated by subacute to very acute (in large specimens *circa* 10 mm s.l.* from Mediterranean) tubercles. Lower margin of dactyl of pereopod 3 relatively smooth (fig. 7) *cuanensis*
- 6(5) Outer dorso-lateral process of antennal peduncular segment 2 not extending beyond proximal $\frac{1}{2}$ of segment 4; acicle not reaching beyond proximal $\frac{1}{3}$ rd of segment 5 (fig. 2). Surfaces of chelipeds generally sparsely setose. Palm of right cheliped (fig. 18) with two prominent depressions on outer surface; margins of propodus delineated by pronounced, acute (to almost spinose) teeth. Lower margin of dactyl of pereopod 3 with subacute teeth and spines (fig. 8) *forbesii*
- 7(8, 9, 10) Segment 1 of antennular peduncle, outer distal margin with one, two or sometimes three spines (fig. 13). Outer dorso-lateral process of antenna (of large *circa* 8.0 mm s.l., specimens) reaching just beyond distal margin of segment 4 and acicle reaching well beyond distal extremity of cornea (fig. 3); breadth of cornea slightly exceeding $\frac{1}{2}$ length of eye. Outer (particularly upper) surface of right cheliped palm† not strikingly concave (fig. 19). Larger pereopod 3, dactyl (of large specimens, *circa* 10 mm s.l.) as long as combined lengths of propodus + carpus and noticeably curved (fig. 9); ♂ with 3 unpaired pleopods *alatus*
- 8(7, 9, 10) Segment 1 of antennular peduncle, outer distal margin without or with small obtuse spines at the most (fig. 14). Outer dorso-lateral process of antenna (of large specimens *circa* 8.0 mm s.l.) not reaching to distal margin of segment 4 and acicle reaching only to extremity of cornea (fig. 4); breadth of cornea slightly less than $\frac{1}{2}$ length of eye. Outer upper (and sometimes lower) surface of right cheliped palm strikingly concave (fig. 20). Larger pereopod 3, dactyl (of large specimens, *circa* 9-10 mm s.l.) slightly longer than combined lengths of propodus + carpus and noticeably curved (fig. 10); ♂ with 4 unpaired pleopods *excavatus*
- 9(7, 8, 10) Segment 1 of antennular peduncle, outer distal margin with a bifurcate, acute spine (fig. 15). Outer dorso-lateral process of antenna reaching only just beyond distal margin of segment 4 and acicle reaching only to extremity of cornea (fig. 5); breadth of cornea slightly exceeding $\frac{1}{2}$ length of eye. Outer surface of right cheliped palm evenly convex throughout, never medially elevated, with conspicuous and acute teeth (fig. 21). Larger pereopod 3, dactyl less than combined lengths of propodus + carpus, noticeably curved (fig. 11); ♂ with 3 unpaired pleopods *pubescentulus*
- 10(7, 8, 9) Segment 1 of antennular peduncle, distal margin without spines (fig. 16). Outer dorso-lateral process of antenna (of specimens larger than *circa* 6.0 mm s.l.) not reaching to distal margin of segment 4 and acicle reaching beyond distal extremity of cornea (in specimens exceeding 9.0 mm s.l., fig. 6); breadth of cornea slightly exceeding $\frac{1}{2}$ length of eye. Outer surface of right cheliped palm evenly convex throughout and with small obtuse spines (fig. 22). Larger pereopod 3, dactyl as long as combined lengths of propodus + carpus and not noticeably curved (fig. 12); ♂ without pleopods *prideaux*
- 11(12) Rostrum absent (fig. 23). Peduncular segment 1 of antennule without medial or distal spine (fig. 28). Outer lower face (and sometimes upper margin) of right

* Shield length.

† The medial crest on the outer surface of the cheliped palm as shown in fig. 19 and present in large specimens (exceeding 9.0 mm s.l.) is often undeveloped in smaller specimens that have only a tuberculate longitudinal medial elevation on this part of the palm. This feature distinguishes juveniles of *alatus* from *pubescentulus* in which the palm is never elevated.

- cheliped propodus with longitudinal row of spaced tubercles grading to a conspicuous ridge posteriorly (fig. 38). Dactyl lower margin of pereopods 2-3 with one row of long spaced spines (fig. 33) *anachoretus*
- 12(11) Rostrum present. Peduncular segment 1 of antennule with an outer distal spine (fig. 29), medial spine (fig. 30) or without a spine (figs. 31, 32). Outer lower face of right cheliped propodus without row of spaced tubercles, these when present are confined to margin (figs. 41, 42). Dactyl lower margin of pereopods 2-3 with variably disposed spines (figs. 34-37) 13
- 13(14) Eyes narrow, breadth of cornea approximately $\frac{1}{3}$ rd length of eyestalk (fig. 24). A narrow triangular rostrum present that extends beyond ocular plate. Peduncular segment 1 of antennule with outer medial spine (fig. 29). Upper propodal margin of right cheliped compressed into crest defined by minute subacute teeth (fig. 39). Dactyl lower margin of pereopods 2-3 with one row of long spaced spines (fig. 34). Small species (*circa* 2.5 mm s.l.) *chevreuxi*
- 14(13) Eyes broad, breadth of cornea more than $\frac{1}{3}$ rd length of eyestalk. Rostrum broadly triangular, not extending beyond ocular plate (figs. 25-27). Upper propodal margin of right cheliped not compressed into a crest, variably tuberculate (figs. 40-42). Dactyl inner margin of pereopods 2-3 with variably disposed spines (figs. 35-37). Large species (*circa* 9-15 mm s.l.) 15
- 15(16) Peduncular segment 1 of antennule with outer medial spine (fig. 30). Outer dorso-lateral process of antennal peduncle segment 2 reaching to distal margin of segment 4 (fig. 25). Outer propodal surface of right cheliped very finely tuberculate (almost smooth to unaided eye, fig. 40). Dactyl inner surface of pereopods 2, 3 with long spines (fig. 35) *carneus*
- 16(15) Peduncular segment 1 of antennule without an outer medial spine (figs. 31, 32). Outer dorso-lateral process of antennal peduncle segment 2 not reaching to distal margin of segment 4 (figs. 26, 27). Outer propodal surface of right cheliped with subacute (fig. 41) or spinose tubercles (fig. 42). Dactyl inner surface of pereopods 2, 3 with small (fig. 36) or long (fig. 37) spines 17
- 17(18) Dactyls of pereopod 3 as long as combined lengths of propodus + carpus (fig. 36); spinules on inner surface relatively short and close together (fig. 36 inset). Propodal margins of right cheliped delineated by obtuse tubercles (fig. 41). Propodal outer surface of left cheliped relatively flat; longitudinal row of tubercles not placed on median elevation (fig. 43) *bernhardus*
- 18(17) Dactyls of pereopod 3 shorter than combined lengths of propodus + carpus (fig. 37); spinules on inner surface relatively long and noticeably spaced (particularly on upper inner surface, fig. 37 inset). Propodal margins of right cheliped delineated by very spinose tubercles (fig. 42). Propodal outer surface of left cheliped with longitudinal row of tubercles placed on medial elevation (fig. 44) *pubescens*

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