

## Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae

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### Abstract

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Keys, with illustrations of selected diagnostic characters, are provided for the seven families and 122 genera of the anomuran Superfamily Paguroidea, commonly known as hermit crabs and king crabs. In addition, abbreviated diagnoses are presented for the 69 genera presently assigned to the family Paguridae.

### Keywords

Crustacea, Anomura, Paguroidea, Paguridae, keys, diagnoses

### Introduction

The interest in, and attendance at, the symposium on *Biology of the Anomura* at the Fifth International Crustacean Congress, 2001, indicates the recent focus on this group of decapod crustaceans by researchers in several disciplines (e.g. Martin and Abele, 1986, 1988; Tudge and Jamieson, 1991; Cunningham et al., 1992; Elwood and Neil, 1992; Tudge, 1992, 1997a, b; Richter and Scholtz, 1994; Scholtz and Richter, 1995; d'Amato and Corach, 1997; McLaughlin and Lemaitre, 1997, 2001a; Tudge et al., 1998; Morrison and Cunningham, 1999; Förster and Baeza, 2001; Macpherson and Machordom, 2001; Tudge et al., 2001). Much of this attention has been directed to the morphologically very diverse assemblage commonly known as hermit crabs and king crabs (Fig. 1). It is not surprising that perusal of some of these references demonstrates the lack of agreement among carcinologists on changes in the classification of this group from 1987 to 2001. Specifically, because of endophragmal differences, Forest (1987) reinstated the superfamily Coenobitoidea Dana, 1851, that had been suppressed by McLaughlin (1983), combining it with the superfamily Paguroidea Latreille, 1802, under the Section Paguridea. Forest's (1987) and Forest et al.'s (2000) information, based on unpublished observations of Mme M. de Saint Laurent, Muséum national d'Histoire naturelle, Paris, apparently was not sufficiently convincing to Martin and Davis (2001), who in their *Updated classification of Recent Crustacea*, once again suppressed the Coenobitoidea and grouped all hermit crab families under the Superfamily Paguroidea. As pointed out by

Holthuis (1993), the category, section, was defined by the third edition of International Code of Zoological Nomenclature (1985) as a subdivision of a genus. The fourth edition (1999), article 10.4, reaffirms that definition. Although the Code does not deal with taxonomic levels above the family group, the use of the term, section, in other hierarchical levels does not seem appropriate. Therefore, I have adopted the classification of the Anomura proposed by Martin and Davis (2001).

To complicate matters even further, there has been an explosion of new genera over the past two decades, as well as additions to and other changes in the hierarchy. Thus it appeared that the presentation of an illustrated set of keys to the families and genera of the Superfamily Paguroidea, would benefit not only new-comers to the field of paguroid systematics, but to specialists in other disciplines as well. The user of the keys contained herein will not be hampered, whether he or she concurs with the Martin and Davis (2001) classification or the classification of Forest (1987) and Forest et al. (2000).

Although within the Diogenidae, several of the larger genera have been reported on in considerable detail (e.g. Forest, 1984, 1995; Morgan, 1991; Poupin, 1997; Rahayu and Forest, 1993, 1995), as have the Lithodidae (Dawson and Yaldwyn, 1985; Macpherson, 1988), Pylochelidae (Forest, 1987), Coenobitidae (Nakasone, 1988), and Parapaguridae (Lemaitre, 1989, 1996, 1997, 1999), such is not the case for the family Paguridae. The few comprehensive studies of this family have been, for the most part, regional and/or not easily accessed (e.g. McLaughlin and Haig, 1984, 1989; McLaughlin, 1997; Asakura, 2000, 2001). Therefore, while keys to all of the genera are

presented, the key to the family Paguridae is supplemented with an overview of the morphology of the family itself, and abbreviated diagnoses of the 69 genera (including two subgenera) currently recognised.

The key to families is an adaptation of that presented by McLaughlin and Lemaitre (2001c) when they introduced the new family Pylojacquesidae. Portions of the keys to the genera have been adapted from Forest (1984, 1987), Macpherson (1988), Lemaitre (1996), McLaughlin (1997), Forest and McLaughlin (2000), de Saint Laurent and McLaughlin (2000), McLaughlin and Lemaitre (2001b), Asakura (2001), and Lemaitre and McLaughlin (in press). In some instances, intrageneric variability has made it necessary, either to key individual species that do not conform entirely with particular diagnostic characters of the genus, or to key the genus more than once. In these instances, the notation (in part) follows the generic name and author.

Terminology, for the most part, follows that of Forest and McLaughlin (2000) for Coenobitidae and Diogenidae, de Saint Laurent and McLaughlin (2000) for the Paguridae, and Lemaitre (2000) for the Parapaguridae; however, the interpretation of quadriserial gills employed by Lemaitre (in press) has been used in preference to the more general terminology of McLaughlin and de Saint Laurent (1998). Enumeration of body somites follows that of Pilgrim (1973), while that of thoracomeres follows that of Forest et al. (2000). Terminology for the Lithodidae follows that of Sandberg and McLaughlin (1998) for the cephalothorax and its appendages, and that of McLaughlin and Paul (2002) for the abdominal tergites. The illustrations of key characters provided throughout should preclude any necessity to refer to these earlier works to utilise the keys; however, it must be emphasised that the illustrations are of characters and not necessarily of those of particular genera.

As was noted by Forest et al. (2000), the ocular peduncles are thought to be two or three-segmented. The references to the ultimate and penultimate segments of the ocular peduncles refer to the distal-most and median segments, respectively. The first segments are believed to be represented by a fused segment most frequently reported as the "ocular lobe(s)", which usually is unarmed, but may be provided with a pair of small spines. Sandberg and McLaughlin (1998: 11, fig. 3A) and Forest et al. (2000: 24, figs 1b, 1c) have defined the ocular acicle as a small calcified plate basally on the penultimate peduncular segment. In contrast, Boyko and Harvey (1999: 383, fig. 2A) have contended that the ocular acicle is not part of the plate, but only an anterodorsal spine or plate-like extension of the "proximal" peduncular segment. Unfortunately, Boyko and Harvey's definition applies only to those species where some type of projection is produced from the plate itself, which is not the case in all hermit crabs. The "ocular plate" of some Pylochelidae is nothing more than the plate itself. To say then that these species lack ocular acicles does not seem justified, as there is no evidence to suggest a lack of homology between the simple ocular plate and the ocular plate that has developed a projection of one form or another. In the keys presented herein, the term ocular acicle refers to the entire calcified plate whose projected portion, if present, may be simple (represented by a single spinose process) bifid, (with two distal spines) or

multispinose (having three or more spines on the distal margin).

Certain species of the Coenobitidae possess calcified, tubular elongations of one or both coxae of pereopod 5 in males; however, only in males of a number of genera of the Paguridae are membranous, chitinous, or weakly calcified sexual tubes developed. When present, these structures provide diagnostic characters of significant importance. Although most descriptions have included the orientation of the sexual tube (e.g. across the ventral body surface, toward the exterior, etc.), heretofore, these tubes have been described only in very generalised terms, such as long, short, coiled, or with a terminal filament. For the purposes of the key to the Paguridae, four more precisely defined descriptive terms pertaining to tube length, have been adopted herein, i.e., very short ( $\leq$  length of coxa measured on its ventral surface), short, (1–2 coxal lengths), medium ( $>2$ –5 coxal lengths), long ( $>5$  coxal lengths). Additionally, a very slight protuberance is referred to in the key as a papilla. Keys to the genera are arranged according to the key to the families, and do not imply any phylogenetic relationships. The family Pylojacquesidae McLaughlin and Lemaitre, 2001c is represented only by the monotypic genus *Pylojacquesia*.

#### Keys to the families of Paguroidea

1. Antennules with upper rami of flagella terminating bluntly, somewhat "stick-like" (Figs 1a, b, 2h) (semiterrestrial) ..... Coenobitidae
- Antennules with upper rami of flagella terminating in tapered filament, not "stick-like" (Figs 1c–g, k–q, 2i, j, 3a, c–j, m) (marine, estuarine) ..... 2
2. Paired pleopods on abdominal somites 2–5; abdominal tergites 1–5 well defined, well calcified (Fig. 1c) ..... Pylochelidae
- No paired pleopods on abdominal somites 4 and 5; abdominal tergites variable, but most frequently not well calcified (Figs 1d–g, i, l–p, 3a) ..... 3
3. Maxilliped 3 generally approximate basally (Figs 2a–c); chelipeds equal, subequal or unequal, left frequently largest (Figs 1d–g) ..... Diogenidae
- Maxilliped 3 generally widely separated basally (Figs 2d–f); chelipeds unequal or less frequently subequal, right usually largest (Figs 1i–q) ..... 4
4. Mandible with incisor process mostly corneous, armed with prominent, acute teeth (Fig. 4i); sternite XI distinctly separated from sternite XII by membranous area (Fig. 2l) ..... Pylojacquesidae
- Mandible with incisor process calcareous (Fig. 4j) or with only mesial edge corneous, lacking acute teeth; sternite XI not distinctly separated from sternite XII, usually fused (Fig. 2m) ..... 5
5. Pereopod 4 developed as normal walking leg (Figs 1i–k; 3b, 8h); body crab-like; abdomen recurved and carried under cephalothorax (Figs 1j, k) ..... Lithodidae
- Pereopod 4 not developed as normal walking leg (Figs 1l–q, 3a); body not crab-like; abdomen usually not recurved and carried under cephalothorax ..... 6

- 6. Exopod of maxilliped 1 with flagellum (Fig. 4m) . . . . . Paguridae
- Exopod of maxilliped 1 without flagellum (Fig. 4n) . . . . . Parapaguridae

**Key to genera of Coenobitidae**

- 1. Pereopod 4 elongate, chelate; abdomen somewhat flexed (Fig 1a); rostrum well developed . . . *Birgus* Leach, 1815
- Pereopod 4 short, not chelate; abdomen spirally twisted (Fig 1b); rostrum obsolete . . . *Coenobita* Latreille, 1829

**Key to genera of Pylochelidae**

- 1. Shield incompletely separated from posterior carapace, linea transversalis not apparent medially (Figs 3c, e); telson divided into anterior and posterior articulating plates (Fig. 5a) . . . . . 2
- Shield completely separated from posterior carapace, linea transversalis clearly apparent medially (Figs 3d, f–h); telson not divided into anterior and posterior articulating plates (Fig. 5b) . . . . . 3
- 2. Shield approximately as long as broad; anterior margin with median concavity and rarely rostral spinule (Fig. 3c); corneas always hemispherical . . . . . *Pylocheles* A. Milne-Edwards, 1880
- Shield distinctly broader than long; anterior margin with rounded rostral lobe (Fig. 3e) or with short rostral spine; corneas reduced or absent (Fig. 3e) . . . . . *Cheiroplatea* Bate, 1888
- 3. Penultimate segments of ocular peduncles without ocular acicles developing squamiform or spiniform anterior projections (Figs 3f, h) . . . . . 4
- Penultimate segments of ocular peduncles with ocular acicles each developing triangular or squamiform anterior projection (Figs 3d, i, j, m) . . . . . 6
- 4. Penultimate segments of ocular peduncles each with well developed, rounded or subrectangular plate (Fig. 3f); telson with pair of oblique lateral incisions, terminal margin with prominent median cleft; maxilliped 2 without epipod . . . . . *Pomatocheles* Miers, 1879
- Penultimate segments of ocular peduncles each with reduced, narrow, calcified plate (Fig. 3g, h); telson with or without pair of oblique lateral incisions, but never prominent, terminal margin with or without median cleft; maxilliped 2 with epipod (Fig. 4o) . . . . . 5
- 5. Shield as long as broad; rostral spine short, without accessory ventral spine; ultimate segments of ocular peduncles spinose, conical and tapered (Fig. 3g); telson rectangular, longer than broad, with pair of faint, oblique, lateral grooves, terminal margin with slight median notch . . . . . *Parapylocheles* Alcock, 1901
- Shield broader than long; rostrum very prominent, with accessory ventral subdistal spine; ultimate segments of ocular peduncles unarmed, basally swollen (Fig. 3h); telson subquadrate, slightly broader than long, without pair of faint, oblique, lateral grooves, terminal margin entire . . . . . *Cancelllocheles* Forest, 1987

- 6. Abdominal somites, pleopods 3–5, and uropods symmetrical; telson subrectangular, longer than broad, usually with transverse line of flexion delimiting rounded posterior lobes (Fig. 5b); maxilliped 3 without epipod (Fig. 4q) . . . . . *Trizocheles* Forest, 1987
- Abdominal somites, pleopods 3–5, and uropods asymmetrical; telson variable; maxilliped 3 with epipod (Fig. 4p) . . . . . *Mixtopagurus* A. Milne-Edwards, 1880

**Key to genera of Diogenidae**

- 1. Well developed arthrobranches present on arthrodistal membranes at bases of cheliped and maxilliped 3; pleurobranch present on somite XI (thoracomere 5, above pereopod 2) (Fig. 4a) . . . . . 2
- Reduced or vestigial arthrobranches present on arthrodistal membranes at bases of cheliped and maxilliped 3; no pleurobranch present on somite XI (thoracomere 5, above pereopod 2) (Fig. 4c) . . . . . *Pseudopaguristes* McLaughlin, 2002
- 2. 14 pairs of gills; pleurobranch present on somite XIV (thoracomere 8, above pereopod 5) (Fig. 4a) . . . . . 3
- 13 pairs of gills; no pleurobranch present on somite XIV (thoracomere 8, above pereopod 5) (Fig. 4b) . . . . . 14
- 3. Endopod of maxillule with well developed external lobe (Fig. 4k) . . . . . 4
- Endopod of maxillule without well developed external lobe (Fig. 4l) . . . . . 8
- 4. Ischium of maxilliped 3 with well developed crista dentata (Figs 2b–f) . . . . . 5
- Ischium of maxilliped 3 without well developed crista dentata (Fig. 2a) . . . . . 12
- 5. Chelipeds equal or unequal, each with stridulatory mechanism developed on mesial face of palm (Fig. 6a) . . . . . 6
- Chelipeds markedly unequal, left largest; neither with stridulatory mechanism developed on mesial face of palm (Fig. 6b) . . . . . *Allodardanus* Haig and Provenzano, 1965
- 6. Chelipeds with acute, corneous-tipped spines on carpi and chelae; males often with pleopod 2 paired, endopod well developed, reduced or absent (Fig. 7g) . . . . . *Strigopagurus* Forest, 1995
- Chelipeds with tubercles or transverse striate on carpi and chelae; males without pleopod 2 paired . . . . . 7
- 7. Chelipeds equal or left larger; carpus and palm with transverse striae bordered with fine setae (Fig. 6c); dactyls of ambulatory legs equal to or longer than propodi; females with unpaired pleopods 2–5 egg-carrying . . . . . *Ciliopagurus* Forest, 1995
- Chelipeds equal, carpus and palm covered with generally blunt tubercles; dactyls of ambulatory legs much shorter than propodi; females with unpaired pleopod 5 non egg-carrying . . . . . *Trizopagurus* Forest, 1952
- 8. Chelae symmetrical, together forming operculum (Fig. 6d); uropods symmetrical (Fig. 8j) . . . . . *Cancellus* H. Milne Edwards, 1836
- Chelae symmetrical or asymmetrical, together not forming operculum; uropods generally asymmetrical . . . . . 9

9. Chelipeds unequal, right distinctly larger ..... *Petrochirus* Stimpson, 1858  
 — Chelipeds subequal or unequal, left usually at least slightly larger ..... 10
10. Shield with prominent Y-shaped linea in posterior half (Figs 8a, c); posterior carapace primarily membranous; left cheliped slightly to considerably larger than right ... 11  
 — Shield without prominent Y-shaped linea (Fig. 8b, l); posterior carapace well calcified; chelipeds subequal ... *Tisea* Morgan and Forest, 1991
11. Rostrum triangular; ocular acicles each with prominent triangular or subtriangular acicular projection (Figs 8a, b); chelipeds and ambulatory legs with ring-like transverse striae (Fig. 6e); females with well-developed brood pouch (Fig. 7d) ..... *Aniculus* Dana, 1852  
 — Rostrum broadly rounded or obsolete (Fig. 8c, l); ocular acicles each with subrectangular or subquadrate acicular projection (Fig. 8c); chelipeds and ambulatory legs most often without ring-like transverse striae; females without brood pouch ..... *Dardanus* Paul'son, 1875
12. Antennal flagella with microscopic setae ..... *Pseudopagurus* Forest, 1952  
 — Antennal flagella with paired, moderate to long setae (Fig. 2k) ..... 13
13. Chelipeds equal or slightly subequal, similar, dactyls opening in generally horizontal plane (Fig. 6f) ..... *Isocheles* Stimpson, 1858  
 — Chelipeds unequal and dissimilar; dactyls opening in almost vertical plane (Fig. 6g) *Loxopagurus* Forest, 1964
14. Males with pleopods 1 and/or 2 paired, modified as gonopods (Figs 7a, e, f); females with (Figs 2m, 7b, c) or without pleopod 1 paired, modified ..... 15  
 — No paired pleopods in either sex ..... 16
15. Pereopod 4 chelate (Fig. 5t); unpaired pleopods 3–5 occurring on either right or left side of abdomen ..... *Paguroopsis* Henderson, 1888  
 — Pereopod 4 not chelate; unpaired pleopods 3–5 occurring on left side of abdomen only ... *Paguristes* Dana, 1851
16. Chelipeds subequal (Fig. 1f) ..... 17  
 — Chelipeds unequal, left appreciably larger (Figs 1d, e, g)... ..... 18
17. Ocular acicles bi or multispinose, contiguous or closely set (Fig. 1f, 8b); posterior margin of abdominal somite 6 unarmed ..... *Clibanarius* Dana, 1852  
 — Ocular acicles simple, widely separated (Figs 3a, d); posterior margin of abdominal somite 6 spinulose ..... *Bathynarius* Forest, 1989
18. Rostrum obsolete, roundly subtriangular or broadly rounded, intercalary rostral process present, well developed, reduced or vestigial (Fig. 3i) ..... *Diogenes* Dana, 1851  
 — Rostrum moderate to well developed, triangular, intercalary rostral process absent ... *Calcinus* Dana, 1851
- process short, broad, triangular, not usually overreaching distal margins of corneas ..... 2
- Abdomen generally firm, at least partially calcified, not sac-like; abdominal tergites 3–5 usually well calcified (Figs 9f–k), sometimes with median areas membranous; rostral process well-developed, prominent, truncate or spiniform (Fig. 8f, h), overreaching distal margins of corneas (Fig. 3b) ..... 6
2. Tergite of abdominal somite 2 divided into median, paired lateral and paired marginal plates (Figs 9a, b, d, e, h) . 3  
 — Tergite of abdominal somite 2 divided into paired lateral and marginal plates, median plate virtually nonexistent (Fig. 9c) ..... *Placetrion* Schalfew, 1892
3. Median plate of abdominal somite 2 well calcified or with cluster of calcified granules (Figs 9a, b) ..... 4  
 — Median plate of abdominal somite 2 membranous (Fig. 9d) ..... 5
4. Carapace well calcified, dorsal surface and margins armed with numerous subequal spines; rostral process with dorsal and lateral spines ..... *Acantholithodes* Holmes, 1895  
 — Carapace weakly calcified, dorsal surface lacking spines but setose or pubescent; rostral process simple, lacking dorsal and lateral spines (Fig. 1i) ..... *Hapalogaster* Brandt, 1850
5. Surface of carapace covered with squamose prominences, chelipeds tuberculate (Fig. 6p) ..... *Oedignathus* Benedict, 1895  
 — Surface of carapace and chelipeds covered with transverse ridges or crests (Fig. 6q) ..... *Dermaturus* Brandt, 1850
6. Carapace nearly smooth, unarmed, broader than long and completely covering ambulatory legs when legs are drawn in against body (Figs 1h, 8h); rostral process broad, compressed, distally truncate (Fig. 1h, 8h) ..... *Cryptolithodes* Brandt, 1848  
 — Carapace armed with granules, tubercles or spines, not broader than long and not completely covering ambulatory legs when legs are drawn in against body; rostral process variable in shape, but not compressed and distally truncate ..... 7
7. Sternite of somite XI (pereopods 2) with deep longitudinal medial groove or pit (Fig. 2n) ..... 8  
 — Sternite of somite XI (pereopods 2) without deep longitudinal medial groove or pit ..... 10
8. Tergite of abdominal somite 2 subdivided into median and paired lateral and marginal plates (Figs 9a, b, d, e, h) . 9  
 — Tergite of abdominal somite 2 usually subdivided into median and paired marginal plates (Fig. 9i), rarely undivided ..... *Lithodes* Latreille, 1806
9. Tergites of abdominal somites 3–5 with only spinulose or spiniform nodules calcified (Fig. 9e) in males; females with lateral plates of left side well delineated; antennal acicle usually absent ..... *Neolithodes* A. Milne-Edwards and Bouvier, 1894  
 — Tergites of abdominal somites 3–5 with lateral plates clearly delineated in both sexes, median plate with nodular calcification, accessory marginal plates well developed (Figs 9h, i); antennal acicle present ..... *Paralithodes* Brandt, 1848

### Key to genera of Lithodidae

1. Abdomen usually soft, membranous, sac-like; abdominal tergites 3–5 not fully calcified (Figs 1i, 9a–d) rostral

- 10. Tergite of abdominal somite 2 subdivided into 3–5 well calcified plates (Figs 9 e, f, h, i) . . . . . 11
  - Tergite of abdominal somite 2 undivided (Figs 9g, j, k) . . . . . 12
- 11. Tergite of abdominal somite 2 subdivided into 3 plates (median and paired laterals) (Fig. 9f) . . . . . *Phyllolithodes* Brandt, 1848
  - Tergite of abdominal somite 2 subdivided into 5 plates (median, paired lateral and marginal) (Figs 9e, h) . . . . . *Rhinolithodes* Brandt, 1848
- 12. Rostral process thick, non-spiniform, hammer-shaped (Fig. 1j); antennal acicle small, rudimentary; tergites of abdominal somites 4 and 5 with median plates irregularly calcified . . . . . *Sculptolithodes* Makarov, 1934
  - Rostral process more or less spiniform; antennal acicle well-developed; tergites of abdominal somites 4 and 5 with median plates regularly and entirely calcified (Figs 9f, g, j, k) . . . . . 13
- 13. Rostral process formed by anterior process (basal spine) and dorsal spine or granule (Fig. 8g) . . . . . *Glytholithodes* Faxon, 1895
  - Rostral process formed by anterior process (basal spine) and at least 1 pair of dorsal spines (Fig. 8f) . . . . . 14
- 14. Lateral tergal plates of abdominal somite 3 entire (Figs 9f, j); antennal acicle moderately spinulose; walking leg 3 always equal to or longer than carapace width . . . . . *Paralomis* White, 1856
  - Lateral tergal plates of abdominal somite 3 each with small accessory plates sundered anteromedially (Figs 9g, k); antennal acicle extremely spinulose; walking leg 3 never equal to or longer than carapace width . . . . . *Lopholithodes* Brandt, 1848

**Pylojacquesidae**

*Pylojacquesia* McLaughlin and Lemaitre, 2001c  
See figs 2d, l, 3j, 5w, 7i.

**Key to genera of Paguridae**

- 1. Gill formula includes 3 well developed or reduced pleuro-branches, 1 each on somites XI–XIII (thoracomeres 5–7, above pereopods 2–4) (Fig. 4b) . . . . . 2
  - Gill formula includes fewer than 3 pleurobranches (Figs 4c, d) . . . . . 10
- 2. Pleurobranches on somites XI and XII (thoracomeres 5 and 6, above pereopods 2 and 3) reduced, rudimentary or vestigial . . . . . 3
  - Pleurobranches on somites XI and XII (thoracomeres 5 and 6, above pereopods 2 and 3) well developed . . . . . 4
- 3. Chelipeds markedly unequal; female with paired gonopores on coxae of pereopod 3 (Fig. 2m) . . . . . *Propagurus* McLaughlin and de Saint Laurent, 1998
  - Chelipeds subequal; female with single gonopore on coxa of left pereopod 3 . . . . . *Chanopagurus* Lemaitre, 2003
- 4. No unpaired pleopods in males; tergite of abdominal somite 6 strongly calcified . . . . . 5
  - Some unpaired pleopods in males; tergite of abdominal

- somite 6 not strongly calcified . . . . . 6
- 5. Chela of right cheliped with large spine at base of dactyl (Fig. 6j); males with paired, modified pleopods 1 and 2; abdominal tergite 6 operculate (Fig. 8d) . . . . . *Xylopagurus* A. Milne-Edwards, 1880
  - Chela of right cheliped without large spine at base of dactyl; males without paired, modified pleopod 1; abdominal tergite 6 not operculate . . . . . *Lithopagurus* Provenzano, 1968
- 6. Males with (Fig. 7a) or without at least 1 pair of modified pleopods; females with or without pleopod 1 paired, modified . . . . . 7
  - Males with no pleopods paired, modified; females with pleopod 1 paired, modified (Figs 7b, c) . . . . . 9
- 7. Males with pleopod 2 paired, modified . . . . . *Tomopaguroides* Balss, 1912
  - Males without pleopod 2 paired, modified . . . . . 8
- 8. Right cheliped much larger than left, with massive chela (Fig. 6k) . . . . . *Bathypaguroopsis* McLaughlin, 1994
  - Right cheliped only slightly larger than left, chela not massive . . . . . *Tomopaguroopsis* Alcock, 1905
- 9. Right cheliped with dactyl opening obliquely (Fig. 6h); pereopod 4 semichelate (Figs 5n, p, r, s, v); protopods of uropods without elongate spine . . . . . *Pylopaguroopsis* Alcock, 1905
  - Right cheliped with dactyl opening horizontally (Fig. 6f); pereopod 4 not semichelate; protopods of uropods each with elongate spine (Fig. 5j) . . . . . *Munidopagurus* A. Milne-Edwards, 1880
- 10. Pleurobranch present on somite XII (thoracomere 7, above pereopod 4) (Fig. 4d) . . . . . 11
  - No pleurobranch present above pereopod 4 . . . . . 70
- 11. Arthrobranches well developed on maxilliped 3 (Figs 4a, b, d) . . . . . 12
  - Arthrobranches rudimentary, vestigial or absent on maxilliped 3 (Fig. 4c) . . . . . 74
- 12. Gill structure distally or deeply quadriserial (Figs 4g, h) . . . . . 13
  - Gill structure biserial (Fig. 4f) . . . . . 21
- 13. Crista dentata of maxilliped 3 with 1 or more accessory teeth (Figs 2c, f) . . . . . 14
  - Crista dentata of maxilliped 3 without accessory tooth (Figs 2b, d, e) . . . . . 19
- 14. Chelipeds subequal (Fig. 1f, q) . . . . . 15
  - Chelipeds distinctly unequal, right largest (Figs 1i–p) . . . . . 17
- 15. Females with paired, modified pleopod 1 (Figs 7b, c) . . . . . *Michelopagurus* McLaughlin, 1997
  - Females without paired, modified pleopod 1 . . . . . 16
- 16. Rostrum triangular; ventral margins of dactyls of ambulatory legs each with row of corneous spinules . . . . . *Pagurodes* Henderson, 1888
  - Rostrum broadly rounded; ventral margins of dactyls of ambulatory legs each with row of long stiff bristles . . . . . *Pseudopagurodes* McLaughlin, 1997
- 17. Males with short (1–2 coxal lengths) left sexual tube (Figs 7m–o, q); females with paired, modified pleopod 1 (Figs 7b, c) . . . . . *Tarrasopagurus* McLaughlin, 1997

- Males with medium (>2–5 coxal lengths) to long (>5 coxal lengths) right sexual tube (Figs 7h, j–m); females without paired, modified pleopod 1 . . . . . 18
- 18. Male right sexual tube directed across body ventrally from right to left (Figs 7j, k, m); female with paired gonopores (Fig. 2m) . . . . . *Cestopagurus* Bouvier, 1897
- Male right sexual tube directed toward exterior (Figs 7h, i, l); female with single left gonopore . . . . . *Trichopagurus* de Saint Laurent, 1968
- 19. Chelipeds subequal, right stronger, but not appreciable longer . . . . . *Iridopagurus* de Saint Laurent-Dechancé, 1966a
- Chelipeds distinctly unequal; right usually appreciably longer . . . . . 20
- 20. Male with very short (<1 coxal length) to short (1–2 coxal lengths) left sexual tube (Figs 7h–o, q); female with paired, modified pleopod 1 (Figs 7b, c) . . . . . *Pagurojacksia* de Saint Laurent and McLaughlin, 2000
- Male with moderate (>2–5 coxal lengths) to long (>5 coxal lengths) left sexual tube (Fig. 7p); female without paired, modified pleopod 1 . . . . . *Turleania* McLaughlin, 1997
- 21. Lateral margins of shield each developed into pair of blunt or spiniform, wing-like processes (Fig. 3k) . . . . . *Porcellanopagurus* Filhol, 1885a
- Lateral margins of shield not developed into pair of blunt or spiniform, wing-like projections . . . . . 22
- 22. Males with very short (<1 coxal length) to long sexual tube(s) (>5 coxal lengths) (Figs 7h–q) . . . . . 23
- Males without sexual tube(s) (Figs 7r, s) . . . . . 45
- 23. Females with paired, modified pleopod 1 (Figs 7b, c) . . . . . 24
- Females without paired, modified pleopod 1 . . . . . 25
- 24. Carpus of right cheliped strongly produced ventrally (Fig. 6o); uropods asymmetrical . . . . . *Goreopagurus* McLaughlin, 1988
- Carpus of right cheliped not strongly produced ventrally; uropods symmetrical or nearly so (Fig. 8j) . . . . . *Pylopagurus* A. Milne-Edwards and Bouvier, 1891 (part)
- 25. Distinct male sexual tube produced from gonopore on only 1 coxa (Fig. 7o, p), papilla present or absent from opposite gonopore . . . . . 26
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- 27. Right chela markedly larger than left . . . . . 28
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- 28. Telson with transverse indentation (Figs 5b, c, f–i); male with paired gonopores (Figs 2l, m) . . . . . 29
- Telson without transverse indentation (Figs 5d, e, j, k); male sometimes without right gonopore (Fig. 7p) . . . . . *Micropagurus* McLaughlin, 1986
- 29. Telson with terminal margin(s) unarmed (Figs 5e, i, j) . . . . . 30
- Telson with terminal margin(s) armed with spines (Figs 5d, f, g, k) . . . . . *Anapagurus* Henderson, 1886
- 30. Telson with terminal margin entire (Figs 5d, e); ocular peduncles with corneas strongly dilated (Fig. 3m) . . . . . *Forestopagurus* García-Gómez, 1994
- Telson with terminal margin marked by prominent median cleft (Figs 5b, c, f–i); ocular peduncles with corneas reduced . . . . . *Pygmaeopagurus* McLaughlin, 1986
- 31. Females with paired gonopores . . . . . 32
- Females with single gonopore on coxa of left pereopod 3 *Anapagrides* de Saint Laurent-Dechancé, 1966b (part)
- 32. Males with 3 or fewer unpaired pleopods . . . . . 33
- Males with 4 unpaired pleopods . . . . . *Acanthopagurus* de Saint Laurent, 1968 (part)
- 33. Sexual tube very short (<1 coxal length) to moderate (>2–5 coxal lengths) . . . . . 34
- Sexual tube long (>5 coxal lengths) . . . . . 35
- 34. Rostral lobe broadly rounded; pereopod 4 with single row of corneous scales in propodal rasp (Figs 5p, q, u); sexual tube of moderate length, directed toward exterior . . . . . *Catapagurus* A. Milne-Edwards, 1880
- Rostral lobe triangular; pereopod 4 with 2 or more rows of corneous scales in propodal rasp (Figs 5n, r, s, v); sexual tube short or very short, directed anteriorly or posteriorly . . . . . *Parapagurodes* McLaughlin and Haig, 1973 (part)
- 35. Right sexual tube directed toward exterior and upward across dorsal body surface . . . . . *Hemipagurus* Smith, 1881
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- 36. Sexual tube terminating in elongate filament (Fig. 7h) . . . . . *Nematopaguroides* Forest and de Saint Laurent, 1968 (part)
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- 37. Abdomen reduced (Figs 1i, l, n–p); males without paired or unpaired pleopods; females only with unpaired uniramous pleopods 2–4 . . . . . 38
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- Left chela not triangular or subtriangular in cross-section, dactyl and fixed finger dorsoventrally flattened ..... *Manucomplanus* McLaughlin, 1981
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54. Telson with lateral indentations suggesting division into anterior and posterior portions (Figs 5b, f-i) ..... 55
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64. Males with both coxae of pereopod 5 produced, gonopores each masked by tuft of long, stiff setae; telson with

- markedly concave terminal margin, outer angles acute, with extremely prominent pair of spines adjacent to median cleft (Fig. 5h) . . . . . *Diacanthurus* McLaughlin and Forest, 1997
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- Telson without distinct transverse indentation (Figs 5d, e, j) . . . . . *Discorsopagurus* McLaughlin, 1974
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- Uropods generally symmetrical; abdomen not spirally flexed . . . . . 69
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70. Crista dentata with 3 or 4 very large, widely-spaced spine-like teeth (Fig. 2g) . . . . . *Scopaeopagurus* McLaughlin and Hogarth, 1998
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73. Males with 3 unpaired pleopods; left sexual tube partially obscured by tufts of setae . . . . . *Catapaguroides* A. Milne-Edwards and Bouvier, 1892
- Males with 4 unpaired pleopods . . . . . *Decaphyllus* de Saint Laurent, 1968
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- Rostrum not strongly deflected downward, without prominent epirostral spine . . . . . 75
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- Male sexual tube without terminal fringe of dense curved setae; preungual process developed at base of claw of pereopod 4 . . . . . *Enneobranchus* García-Gómez, 1988

#### Key to genera of Parapaguridae

1. Corneas present . . . . . 2
- Corneas absent (Fig. 8l) . . . . . *Typhlopagurus* de Saint Laurent, 1972
2. Rostrum short, not exceeding ocular peduncles . . . . . 3
- Rostrum long, often exceeding ocular peduncles (Fig. 1q) . . . . . *Probeebei* Boone, 1926
3. Ocular acicles distinctly developed (Figs 8a–c, e, l) . . . 4
- Ocular acicles weakly developed or obsolete (Fig. 1p) . . . . . *Tylaspis* Henderson, 1885
4. Posterior carapace mostly membranous; unpaired left pleopods 3–5 . . . . . 5
- Posterior carapace calcified; asymmetrically paired pleopods 3–5 . . . . . *Bivalvopagurus* Lemaitre, 1993
5. Shield about as broad or broader than long; rostrum bluntly triangular or broadly rounded; abdomen flexed . 6
- Shield distinctly longer than broad; rostrum acutely triangular; abdomen straight . . . . . *Tsunogaipagurus* Osawa, 1995
6. Shield distinctly broader than long; dactyls of ambulatory legs straight or nearly so; corneas strongly dilated (Fig. 3m); pleopod 2 of male with short exopod and strongly twisted distal segment (Fig. 7e) . . . . . *Strobopagurus* Lemaitre, 1989
- Shield about as broad as long; dactyls of ambulatory legs curved; corneas moderately or weakly dilated; pleopod 2 of male lacking exopod and distal segment not twisted (Fig. 7f) (rarely absent) . . . . . 7
7. Vestigial pleurobranch present on each side of somite XIV (thoracomere 8, above pereopod 5) (Fig. 4e) . . . . . *Sympagurus* Smith, 1883
- Vestigial pleurobranch absent on each side of somite XIV (thoracomere 8, above pereopod 5) . . . . . 8
8. Epistomial spine straight (Fig. 8m) or absent . . . . . 9
- Epistomial spine strongly curved upward . . . . . *Oncopagurus* Lemaitre, 1996
9. Gill structure bi- or quadriserial (Figs 4f–h); segment 4 of antennal peduncle armed with dorsodistal spine; length of ocular peduncles, including corneas, at least half length of shield . . . . . *Paragiopagurus* Lemaitre, 1996
- Gill structure quadriserial (Figs 4g, h); segment 4 of antennal peduncle unarmed; length of ocular peduncles, including corneas, less than half length of shield (except *Parapagurus bowieri* Stebbing, 1910) . . . . . *Parapagurus* Smith, 1879



**Paguridae** Latreille, 1802

In the abbreviated generic diagnoses presented, characters common to the family are not repeated. Statements simply of pleopod number refer to the unpaired left pleopods. The expression “distally divided” (formerly “intermediate”) is used to indicate gill lamellae (Fig. 4g) that while not deeply or completely subdivided, do show partial distal cleavage or distinct indentations. Genera are arranged in alphabetical order.

*Diagnosis.* Cephalothorax usually with only shield weakly to strongly calcified; rostrum produced as median projection or rounded lobe; lateral projections usually well developed. Gills bi- or quadriserial phyllobranchia, 8–13 pairs. Ocular peduncles with penultimate segments each provided with acicle. Antennal acicles most commonly with only terminal spine. Maxillipeds 3 separated by moderate to broad sternal plate; ischium usually with well developed crista dentata, sometimes reduced, with or without 1 or more accessory teeth. Chelipeds unequal or subequal, right generally larger. Ambulatory legs with dactyls and propodi usually similar from right to left, occasionally dissimilar; dactyls usually with ventral row of corneous spines; carpi usually armed with at least dorsodistal spine. Pereopod 4 usually semichelate, sometimes subchelate, infrequently chelate or simple; preungual process present or absent at base of claw; rarely circular sensory structure (type A P4 structure, cf. McLaughlin, 1974) on lateral face of dactyl. Fifth pereopods usually chelate, occasionally subchelate. Males usually with paired gonopores on coxae of pereopod 5, occasionally only with single left gonopore; membranous, chitinous, or very weakly calcified sexual tube frequently developed in conjunction with gonopore on one or both coxae; usually without, but occasionally with pleopods 1 and/or 2 paired and modified; with or without unpaired left pleopods on abdominal somites 3–5 or 2–5. Females usually with paired gonopores on coxae of pereopod 3, occasionally only single left gonopore; often without, but frequently with, pleopod 1 paired and modified; with unpaired left pleopods on somites 2–5, or less frequently, 2–4. Uropods usually asymmetrical, occasionally symmetrical. Telson usually with lateral indentations separating anterior and posterior portions; posterior lobes usually separated by median cleft. Type genus: *Pagurus* Fabricius, 1775.

***Acanthopagurus*** de Saint Laurent, 1968

*Diagnosis.* Gills biserial, 11 pairs. Rostrum obtusely and roundly triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped much stronger than left. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short, massive sexual tube on right coxa of pereopod 5, directed obliquely toward midline; left coxa without sexual tube, or possibly with small papilla protruding from gonopore; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Anapagurus ?dubius* A. Milne-Edwards and Bouvier, 1900.

***Agaricochirus*** McLaughlin, 1981

*Diagnosis.* Gills biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela generally ovate, armature usually as mushroom-shaped tubercles. Carpi of ambulatory legs lacking dorsodistal spine. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe absent, reduced and styliform, or small and subquadrate. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; preungual process small. Coxae of male pereopods 5 occasionally with slight papilla protruding from one or both gonopores; pleopods 3–5. Female with paired, modified pleopod 1; pleopods 2–5. Uropods symmetrical or nearly so, protopods produced posteriorly. Telson with median cleft usually broadly U-shaped, posterior lobes usually symmetrical, terminal margins unarmed. Type species: *Pylopagurus boletifer* A. Milne-Edwards and Bouvier, 1893.

***Alainopaguroides*** McLaughlin, 1997

*Diagnosis.* Gills biserial, 11 pairs. Anterior carapace vaulted and generally well calcified, with anterolateral regions slightly depressed. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata somewhat reduced, 1 accessory tooth. Chelipeds subequal; right stronger, but not necessarily longer. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow, transverse anterior lobe. Pereopod 4 weakly semichelate, propodal rasp rudimentary; prominent tubular preungual process. Abdomen reduced; tergal plates of somites 2–5 sometimes very faintly delineated. Male with moderate, stout sexual tube on coxa of right pereopod 5, left often with very short tube; no unpaired pleopods. Female pleopods 2–4. Uropods generally symmetrical. Telson with terminal margins narrowly to broadly oblique. Type species: *Alainopaguroides lemaitrei* McLaughlin, 1997.

***Alainopagurus*** Lemaitre and McLaughlin, 1995

*Diagnosis.* Gills biserial, 11 pairs. Anterior carapace vaulted and generally well calcified, with anterolateral regions distinctly globular. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Right cheliped stronger, but not markedly longer. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow, transverse anterior lobe. Pereopod 4 subchelate, propodal rasp with 1 row of corneous spines; no preungual process. Pereopod 5 subchelate. Male with stout, moderate sexual tubes of approximately equal length on coxae of both pereopods 5, each with long setae mesially and terminally; no unpaired pleopods. Female with single gonopore opening posteriorly on coxa of left pereopod 3; pleopods 2–4 only. Abdomen reduced; tergal plate of somite 2 weakly delineated; tergal plates of somites 3–5 clearly defined, chitinous or very weakly calcified. Uropods symmetrical. Telson with terminal margin entire. Type species: *Alainopagurus crosnieri* Lemaitre and McLaughlin, 1995.

***Alloeopagurodes*** Komai, 1998

*Diagnosis.* Gills biserial, 11 pairs. Ocular acicles simple. Rostrum prominent, lateral projections reduced. Antennal

acicles each with row of spines on mesial surface. Crista dentata with 1 accessory tooth. Right cheliped elongate in large males. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe, margin spinose. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Right coxa of pereopod 5 in male with short, mesially directed sexual tube; coxa of left with very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins rounded. Type species: *Alloeopagurodes spiniacacula* Komai, 1998.

**Anapagrides** de Saint Laurent-Dechancé, 1966

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe subrectangular to subcircular. Pereopod 4 semichelate, propodal rasp with 1 row of corneous scales. Male with short, posteriorly directed sexual tube on right coxa of pereopod 5; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins straight to oblique. Type species: *Eupagurus (Spiropagurus) facetus* Melin, 1939.

**Anapagurus** Henderson, 1886

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as rounded lobe. Ocular acicles simple; ocular lobes unarmed or with pair of spines. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal, right much larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of left pereopod 5 in male with short to moderate sexual tube directed toward exterior and often curved over abdomen dorsally; coxa of right sometimes with short sexual tube; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins generally oblique. Type species: *Pagurus laevis* Bell, 1846.

**Anisopagurus** McLaughlin, 1981

*Diagnosis.* Gills biserial, 11 pairs. Rostrum well developed or reduced to rounded lobe. Ocular acicles simple or multispinose. Crista dentata with 1 accessory tooth. Right chela usually suboperculate. Left cheliped with propodal-carpal articulation rotated 0–45° from perpendicular. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular to subtriangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 3 or 4 rows of corneous scales; preungual process usually moderately well developed. Males with pleopods 3–5. Females with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins rounded, sometimes somewhat excavated. Type species: *Pylopagurus bartletti* A. Milne-Edwards, 1880

**Bathypaguropsis** McLaughlin, 1994

*Diagnosis.* Gills quadriserial, 13 pairs. Rostrum well developed. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped massive, chela operculate or nearly so;

propodal-carpal articulation approximately 30° from perpendicular; left cheliped with propodal-carpal articulation with 30–60° counterclockwise rotation. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp of 1 or more, sometimes incomplete, rows of corneous scales; no preungual process. Male with pleopods 2–5. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Bathypaguropsis yaldwyni* McLaughlin, 1994.

**Catapaguroides** A. Milne-Edwards and Bouvier, 1892

*Diagnosis.* Gills biserial, 10 pairs, no pleurobranch on somite XIII (thoracomere 7, above arthrobranchs of pereopod 4). Rostrum as rounded lobe. Ocular acicles simple. Crista dentata more or less reduced, no accessory tooth. Chelipeds unequal, right appreciably stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 semichelate. Male with moderate to long sexual tube on coxa of right pereopod 5, directed from right to left under thorax and recurved anteriorly; coxa of left with very short or short tube concealed between 2 thick tufts of sternal setae; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins straight or oblique. Type species: *Catapaguroides microps* A. Milne-Edwards and Bouvier, 1892.

**Catapagurus** A. Milne-Edwards, 1880

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata somewhat reduced, with 1 accessory tooth. Chelipeds elongate, unequal, right stouter than left. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process prominent. Coxa of right pereopod 5 of male with moderate sexual tube, curving toward exterior over lateral side of abdomen, left coxa occasionally with very slightly protruded papilla; pleopods 3–5. Female with pleopods 2–4 or 2–5. Telson with terminal margins oblique. Type species: *Catapagurus sharreri* A. Milne-Edwards, 1880. (Generic diagnosis restricted by Asakura, 2001)

**Ceratopagurus** Yokoya, 1933

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, similar, moderately long and slender. Sternite of somite XII (thoracomere 6, pereopods 3) not known. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson unknown. Type species: *Ceratopagurus pilosimanus* Yokoya, 1933.

**Cestopagurus** Bouvier, 1897

*Diagnosis.* Gills distally quadriserial, 11 pairs. Rostrum prominent, acutely triangular. Ocular acicles simple. Crista dentata

with 1 accessory tooth. Chelipeds very unequal; right much stronger and distinctly sexually dimorphic. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with long sexual tube on right coxa of pereopod 5, orientated toward left across ventral body surface; left coxa without gonopore, or with gonopore and very short sexual tube directed toward right; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins horizontal to oblique. Type species: *Cestopagurus coutieri* Bouvier, 1897.

***Chanopagurus*** Lemaitre, 2003

*Diagnosis.* Gills quadriserial, 13 pairs (11 pairs presumably functional), pleurobranches of somites XI and XII (thoracomeres 5 and 6, above pereopods 2 and 3) reduced or rudimentary. Rostrum broadly rounded. Corneas reduced, located ventrolaterally on ultimate peduncular segments. Ocular acicles simple, basally contiguous. Crista dentata well developed, and 1 accessory tooth. Chelipeds subequal Sternite of somite XII (thoracomere 6, pereopod 3) divided into anterior and posterior lobes by distinct, membranous hinge. Pereopod 4 semichelate, propodal rasp with 1–2 rows of corneous scales, no preungual process. Male unknown. Female with single gonopore on coxa of left pereopod 3; pleopod 1 paired, modified; pleopods 2–5. Uropods asymmetrical. Telson symmetrical, with distinct lateral indentations, posterior lobes each with “half-moon” contour and blade-like lateral margin. Type species: *Chanopagurus atopos* Lemaitre, 2003.

***Decaphyllus*** de Saint Laurent, 1968

*Diagnosis.* Gills biserial, 8–10 pairs, no pleurobranches on somites XI, XII, XIII (thoracomeres 5–7, above pereopods 2–4), arthrobranches of maxilliped 3 small, vestigial or absent. Ocular acicles simple. Crista dentata reduced, no accessory tooth. Chelipeds subequal in length, but right appreciably stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular or subovate anterior lobe. Pereopod 4 simple, without propodal rasp; no preungual process. Pereopod 5 semichelate. Male with long sexual tube developed on coxa of right pereopod 5, directed from right to left across ventral body surface and curved anteriorly; left with short sexual tube directed from left to right; pleopods 2–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson without lateral indentations; terminal margin entire or with minute median cleft. Type species: *Decaphyllus spinicornis* de Saint Laurent, 1968.

***Diacanthurus*** McLaughlin and Forest, 1997

*Diagnosis.* Gills biserial, 11 pairs. Rostrum obsolete or as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; left cheliped with some degree of clockwise rotation of propodal-carpal articulation, dorsolateral margin of chela weakly to strongly inflated proximally. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular anterior lobe. Pereopod 4 semichelate;

propodal rasp with several rows of corneous scales; no preungual process. Male with pleopods 3–5. Females with pleopods 2–5. Telson with posterior lobes each contoured as “half-moon”; blade-like lateral margin and acute terminal angle broadly separated by U-shaped median cleft, inner margins each with 1 prominent spine in basal half. Type species: *Eupagurus spinulimanus* Miers, 1876.

***Discorsopagurus*** McLaughlin, 1974

*Diagnosis.* Gills biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right larger. Sternite of somite XII (thoracomere 6, pereopods 3) with semicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with multiple rows of corneous scales; no preungual process. Male with or without slight papilla protruding from gonopores on one or both coxae of pereopods 5; pleopods 3–5 or 2–5. Female with pleopods 2–5. Abdomen straight or slightly flexed, not twisted; tergites of somites 3–4 paired, incompletely fused chitinous plates; tergite 6 strongly calcified. Uropods symmetrical. Telson with or without slight lateral indentations; terminal margin entire, straight or concave. Type species: *Pylopagurus schmitti* Stevens, 1925.

***Elassochirus*** Benedict, 1892

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right considerably larger, carpus often with wing-like expansions; left with propodal-carpal rotation approximately 90° counterclockwise. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular to subsemiovate anterior lobe. Pereopod 4 weakly semichelate; dactyl with circular sensory structure on lateral face (Fig. 3v); propodal rasp with several rows of corneous scales; no preungual process. Male with pleopods 3–5, rarely only 3–4. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Bernhardus tenuimanus* Dana, 1851.

***Enallopaguropsis*** McLaughlin, 1981

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela suboperculate; left cheliped with propodal -carpal rotation of approximately 60° from perpendicular. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe as single capsulate seta. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; preungual process small to moderately large. Male usually without sexual tubes, occasionally with very short tube or papilla from one or both gonopores; with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen straight or slightly flexed. Telson without lateral indentations, terminal margin convex, entire or with shallow median concavity. Type species: *Pylopagurus guatemoci* Glassell, 1937.

***Enallopagurus* McLaughlin, 1981**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela subovate; left cheliped with propodal-carpal rotation of 15–30° from perpendicular. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe subcircular to subquadrate. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process moderately small. Male usually without sexual tubes, occasionally with very short tube or papilla, most frequently on right coxa; with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen straight or slightly flexed. Telson without lateral indentations, terminal margin convex, entire or with inconspicuous median indentation. Type species: *Pylopagurus spinicarpus* Glassell, 1938.

***Enneobranchus* García-Gómez, 1988**

*Diagnosis.* Gills distally quadriserial, 9 pairs, pleurobranch on somite XIII (thoracomere 7, above arthrobranches of pereopod 4) but arthrobranches absent from arthrobranchial membrane of maxilliped 3. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal, right stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with marginally armed, subrectangular anterior lobe. Pereopod 4 simple; propodal rasp with 1 row of corneous scales; preungual process prominent. Male with moderate to long, coiled sexual tube on coxa of left pereopod 5; right coxa sometimes with papilla or very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminals straight or oblique. Type species: *Enneobranchus flavioculatus* García-Gómez, 1988.

***Enneopagurus* McLaughlin, 1997**

*Diagnosis.* Gills quadriserial; 9 pairs, pleurobranch on somite XIII (thoracomere 7, above arthrobranches of pereopod 4) but arthrobranches absent from arthrobranchial membranes of maxilliped 3. Rostrum triangular, not deflected. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal, right more robust. Sternite of somite XII (thoracomere 6, pereopods 3) with subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of scales; no preungual process. Pereopod 5 semichelate. Coxa of left pereopod 5 of male with moderate, rather stout sexual tube directed exteriorly and dorsally, terminally somewhat spatulate and with fringe of dense curved setae; right occasionally with protruded papilla; pleopods 3–5. Female with pleopods 2–5. Telson with lateral indentations weakly indicated; terminal margins oblique. Type species: *Enneopagurus garciagomezi* McLaughlin, 1997.

***Enneophyllus* McLaughlin, 1997**

*Diagnosis.* Biserial gills, 9 pairs, pleurobranch on somite XIII (thoracomere 7, above arthrobranches of pereopod 4) but arthrobranches absent from arthrobranchial membrane of maxilliped 3. Rostrum well developed, strongly depressed. Ocular acicles

simple. Crista dentata somewhat reduced, without accessory tooth. Chelipeds unequal, right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with small anterior lobe. Pereopod 4 semichelate, propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 weakly semichelate. Coxa of left pereopod 5 of male with long, basally stout sexual tube directed exteriorly and curved dorsally across abdomen from left to right; coxa of right without sexual tube; pleopods 3–5. Female unknown. Abdomen straight. Telson with very weak transverse indentations; terminal margins oblique. Type species: *Enneophyllus spinirostris* McLaughlin, 1997.

***Forestopagurus* García-Gómez, 1994**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds markedly unequal, right elongate in large males. Sternite of somite XII (thoracomere 6, pereopod 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with moderate sexual tube on coxa of left pereopod 5; right without sexual tube; no unpaired pleopods. Female with pleopods 2–4. Telson with terminal margin entire. Type species: *Anapagurus drachi* Forest, 1966.

***Goreopagurus* McLaughlin, 1988**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal, right very elongate, with prominently produced ventral carpal margin. Sternite of somite XII (thoracomere 6, pereopods 3) with subovate to subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process present or absent. Male with short, posteriorly or laterally directed sexual tube on coxa of right pereopod 5; left coxa often with papilla or very short sexual tube; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight or oblique. Type species: *Pagurus piercei* Wass, 1963.

***Haigia* McLaughlin, 1981**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum narrowly triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right cheliped with chela subquadrate to subrectangular. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with pleopods 3–5. Female with pleopod 1 paired, modified, pleopods 2–5. Abdomen flexed or straight. Telson with terminal margins straight or slightly excavated. Type species: *Pylopagurus diegensis* Scanland and Hopkins, 1969.

***Hemipagurus* Smith, 1881**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata somewhat reduced,

with 1 accessory tooth. Chelipeds elongate, unequal, right stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with rectangular, sometimes armed, anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scale; preungual process prominent. Right coxa of pereopod 5 of male with long sexual tube directed toward exterior and curved over dorsal surface of abdomen toward left; left coxa sometimes with papilla or very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins oblique. Type species: *Hemipagurus gracilis* Smith, 1881. (Genus reinstated by Asakura, 2001)

***Icelopagurus* McLaughlin, 1997**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata somewhat reduced, with 1 accessory tooth. Chelipeds elongate, subequal, right stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of spiniform scales; preungual process tubular. Coxa of right pereopod 5 of male with stout, short sexual tube directed posteriorly and externally; left usually with very short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins rounded. Type species: *Icelopagurus crosnieri* McLaughlin, 1997.

***Iridopagurus* de Saint Laurent-Dechancé, 1966**

*Diagnosis.* Gills quadriseriate, 11 pairs. Rostrum as broadly rounded or very obtusely triangular lobe. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subrectangular anterior lobe. Pereopod 4 simple; propodal rasp with 1 row of corneous scales; preungual process present or absent. Male with long, coiled sexual tube on coxa of left pereopod 5; tube development on right coxa varying from simple papilla to short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins usually straight. Type species: *Spiropagurus iris* A. Milne-Edwards and Bouvier, 1893.

***Labidochirus* Benedict, 1892**

*Diagnosis.* Gills biserial, 11 pairs. Carapace, exclusive of branchiostegites, generally heavily calcified throughout; posterior carapace broader than shield. Rostrum prominent. Ocular acicles simple, obscured basally by anterior margin of shield. Crista dentata with 1 accessory tooth. Chelipeds subequal or unequal, right larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe, usually armed with spines medianly. Pereopod 4 simple; propodal rasp with 1 or 2 rows of corneous scales; no preungual process. Male without unpaired pleopods. Female with pleopods 2–5. Abdomen reduced. Telson with terminal margins straight. Type species: *Pagurus splendescens* Owen, 1839.

***Lithopagurus* Provenzano, 1968**

*Diagnosis.* Gills biserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal; right chela operculate. Sternite of somite XII (thoracomere 6, pereopods 3) with subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; apparently no preungual process. Pereopod 5 minutely chelate. Male with pleopod 2 paired, modified; no unpaired pleopods. Female with pleopods 2–4. Abdomen reduced. Uropods generally symmetrical. Telson without lateral indentations; terminal margin entire. Type species: *Lithopagurus yucatanicus* Provenzano, 1968.

***Lophopagurus (Australeremus)* McLaughlin, 1981**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right chela subrectangular to subtriangular; dorsal surface of palm usually circumscribed by row of dorsomesial, dorsoproximal and dorsolateral marginal spines; left chela with dorsolateral margin elevated, at least proximally, and frequently expanded; propodal-carpal rotation variable. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular, subovate or slender rod-like anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process minute. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen frequently straight or only weakly flexed. Uropods symmetrical or asymmetrical. Telson with terminal margins straight, oblique or rounded. Type species: *Eupagurus cookii* Filhol, 1883.

***Lophopagurus (Lophopagurus)* McLaughlin, 1981**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right chela with dorsomesial margin depressed, dorsal surface with sloping or concave dorsomesial component; left chela with dorsal midline elevated into prominent keel or crest. Ambulatory legs with dactyl and propodus of left pereopod 3 sometimes dissimilar. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subrectangular anterior lobe, occasionally armed. Pereopod 4 semichelate; propodal rasp with 1 row of scales; usually no preungual process. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight, oblique or rounded. Type species: *Eupagurus thompsoni* Filhol, 1885b.

***Manucomplanus* McLaughlin, 1981**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum broadly triangular or rounded. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right cheliped exhibiting considerable sexual dimorphism; left cheliped with propodal-carpal articulation rotated 15–45°. Sternite of somite XII (thoracomere 6, pereopod 3) with elongate, slender or acutely triangular, usually spinulose, anterior lobe. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; preungual process usually well developed. Male with pleopods

3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique or rounded. Type species: *Eupagurus (Elassochirus) corallinus* Benedict, 1892 (= *Eupagurus unguatus* Stüder, 1883).

***Michelopagurus*** McLaughlin, 1997

*Diagnosis.* Gills quadriserial, 11 pairs. Rostrum as broadly rounded or obtusely and bluntly triangular lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right appreciably stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row, or rarely incomplete double of scales; no distinctive preungual process. Right, left, or both coxae of pereopods 5 of male with short sexual tube partially masked by tuft of setae; pleopods 3–5. Female with paired, modified pleopod 1; pleopods 2–5. Telson with terminal margins rounded. Type species: *Pagurodes limatulus* Henderson, 1888.

***Micropagurus*** McLaughlin, 1986

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as rounded lobe or obsolete. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Chelipeds unequal, right largest. Sternite of somite XII (thoracomere 6, pereopods 3) with broad, subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1–3 rows of corneous scales; no preungual process. Coxa of left pereopod 5 of male with moderate to long sexual tube; right with or without gonopore; pleopods 3–5. Female with pleopods 2–5. Telson without lateral indentations; terminal margin entire. Type species: *Micropagurus devaneyi* McLaughlin, 1986.

***Munidopagurus*** A. Milne-Edwards, 1880

*Diagnosis.* Gills biserial, 13 pairs. Rostrum acute. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds elongate, unequal, right longer and somewhat stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with bluntly subtriangular anterior lobe. Pereopod 4 unusually elongate, simple; propodal rasp replaced by row of setae; no preungual process. Male without unpaired pleopods. Female with pleopod 1 paired, modified; pleopods 2–4. Uropods symmetrical, propods each with prominent, posteriorly directed spine. Telson without lateral indentations, terminal margin entire. Type species: *Eupagurus macrocheles* A. Milne-Edwards, 1880.

***Nematopaguroides*** Forest and de Saint Laurent, 1968

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as broadly rounded or obtusely triangular lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal or somewhat unequal, right usually largest. Sternite of somite XII (thoracomere 6, pereopods 3) with irregularly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp of 1 row of corneous scales; preungual process usually present. Male with moderate to long sexual tube on coxa of right pereopod 5, usually directed obliquely toward exterior and with terminal

filament; left coxa with or without short to moderate sexual tube; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins oblique. Type species: *Nematopaguroides fagei* Forest and de Saint Laurent, 1968.

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

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as weakly and obtusely subtriangular, broadly rounded or obsolete lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds moderately long and slender; subequal, with right generally slightly longer and/or more robust. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemiovalate to roundly rectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of scales; no preungual process. Male with moderate to long, often distally filamentous, sexual tube on coxa of right pereopod 5, orientated from right to left across ventral body surface; coxa of left with papilla, very short or short sexual tube; pleopods 3–5. Females with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight, rounded, somewhat oblique, or prominently oblique. Type species: *Nematopagurus longicornis* A. Milne-Edwards and Bouvier, 1892.

***Orthopagurus*** Stevens, 1927

*Diagnosis.* Gills biserial, 11 pairs. Rostrum prominent. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right considerably larger, suboperculate. Sternite of somite XII (thoracomere 6, pereopods 3) with subovate anterior lobe. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; no preungual process. Male with pleopods 3–5. Female with pleopods 2–5. Abdomen straight or slightly flexed; tergites chitinous, usually in form of lateral plates, tergite of somite 5 entire; tergite of somite 6 strongly calcified. Telson with terminal margins straight. Type species: *Pagurus minimus* Holmes, 1900.

***Ostraconotus*** A. Milne-Edwards, 1880

*Diagnosis.* Gills biserial, 10 pairs, no pleurobranch on somite XIII (thoracomere 7, above pereopod 4). Cephalothorax nearly completely calcified. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata reduced, without accessory tooth. Chelipeds unequal, right largest. Pereopods 2 and 3 with paddle-shaped dactyls. Sternite of somite XII (thoracomere 6, pereopods 3) with elongate, slender, subrectangular anterior lobe. Pereopod 4 with broadly expanded and flattened propodus, no propodal rasp; dactyl elongate, simple. Pereopod 5 subchelate. Male with long sexual tube on coxa of right pereopod 5; coxa of left without sexual tube or with papilla; no unpaired pleopods. Female with pleopods 2–4. Abdomen reduced. Uropods symmetrical. Telson with terminal margin entire. Type species: *Ostraconotus spatulipes* A. Milne-Edwards, 1880.

***Paguridium*** Forest, 1961

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory

tooth. Chelipeds unequal, right largest. Sternite of somite XII (thoracomere 6, pereopod 3) not described. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales. Male with coxae of pereopod 5 markedly asymmetrical; gonopore on coxa of left masked by tuft of long, stiff setae directed from left to right and extending across ventral body surface, usually also with papilla or very short sexual tube; no unpaired pleopods. Female with pleopods 2–5. Telson with terminal margins straight. Type species: *Eupagurus ?minus* Chevreux and Bouvier, 1892.

***Paguritta* Melin, 1939**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicle simple or bifid. Antennal flagella with paired very long setae armed with prominent setules on each article. Crista dentata with 1 accessory tooth. Chelipeds unequal; right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular or subquadrate anterior lobe, anterior margin usually with few blunt spines. Pereopod 4 semichelate, propodal rasp with 1 row of corneous scales; no preungual process. Male usually with papilla or very short sexual tube one or both coxae of pereopods 5; no unpaired pleopods. Female with pleopods 2–4. Uropods symmetrical. Telson with terminal margins straight. Type species: *Paguritta gracilipes* Melin, 1939.

***Pagurixus* Melin, 1939**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds markedly unequal; right chela exhibiting considerable sexual dimorphism, often greatly swollen or extremely elongate in large males. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe subrectangular or subquadrate. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with coxae of pereopod 5 asymmetrical, right largest; gonopore of right coxa of pereopod 5 obscured by tuft of moderate to long, stiff setae directed toward left; pleopods 3–5. Female with paired gonopores or single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins straight, rounded or oblique. Type species: *Eupagurus (Pagurixus) boninensis* Melin, 1939.

***Pagurodes* Henderson, 1888**

*Diagnosis.* Gills quadriserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds elongate, subequal, right stouter. Sternite of somite XII (thoracomere 6, pereopods 3) with marginal spinules on subrectangular anterior lobe. Pereopods 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of right pereopod 5 of male with stout, short to moderate sexual tube directed posteriorly, coxa of left sometimes with papilla or very short sexual tube; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins oblique or nearly perpendicular. Type species: *Pagurodes inarmatus* Henderson, 1888.

***Pagurus* Fabricius, 1775**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum variable. Ocular acicles simple, bifid or multispinous. Crista dentata with 1 or more accessory teeth. Chelipeds generally very unequal, right usually appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with variably-shaped anterior lobe. Pereopod 4 usually semichelate; propodal rasp with 1 to several rows of corneous scales; with or without preungual process. Male usually without, rarely with slight papilla protruded from gonopore on one or both coxae of pereopod 5; with no paired, modified pleopods, usually with unpaired pleopods 2–5 or 3–5, rarely without unpaired pleopods. Female usually with paired, rarely with single left gonopore on coxa(e) of pereopods 3; without paired pleopod 1, usually with unpaired pleopods 2–5, rarely 2–4. Abdomen usually spirally twisted, occasionally straight. Uropods asymmetrical, infrequently symmetrical. Telson with terminal margins rounded, straight or oblique, usually with median cleft. Type species: *Cancer bernhardus* Linnaeus, 1758 [as defined by lectotype selection by Forest and Holthuis (1955: 312); specimen figured by Swammerdam (1737: pl. 2 fig. 1)]

***Pagurojacquesia* de Saint Laurent and McLaughlin, 2000**

*Diagnosis.* Gills quadriserial, 11 pairs. Rostrum as rounded lobe. Ocular acicles simple. Crista dentata without accessory tooth. Chelipeds subequal, right stronger, but not always longer. Sternite of somite XII (thoracomere 6, pereopods 3) with armed or unarmed, subovate to subquadrate anterior lobe. Pereopod 4 subchelate or very weakly semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 subchelate. Coxa of left pereopod 5 of male with club-like, stout, very short to moderate left sexual tube directed toward exterior and provided with terminal tufts of very long setae, coxa of right with small gonopore; pleopods 3–5. Females with paired, modified pleopod 1, pleopods 2–5. Telson with terminal margins very oblique. Type species: *Jacquesia polymorpha* de Saint Laurent and McLaughlin, 1999.

***Parapagurodes* McLaughlin and Haig, 1973**

*Diagnosis.* Gills biserial, or occasionally distally quadriserial; 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right largest. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 2 or more rows of corneous scales; usually with small preungual process. Coxa of right pereopod 5 of male with very short to short sexual tube, left with or without similarly very short to short sexual tube; pleopods 3–5. Female with pleopods 2–5. Telson with terminal margins rounded or oblique. Type species: *Parapagurodes makarovi* McLaughlin and Haig, 1973.

***Phimochirus* McLaughlin, 1981**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum usually triangular, occasionally only as rounded lobe. Ocular acicles simple.

Crista dentata with 1 to several accessory teeth. Chelipeds markedly unequal; right chela subovate to subcircular. Sternite of somite XII (thoracopod 6, pereopods 3) with subsemiovalate to subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process prominent. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique. Type species: *Eupagurus operculatus* Stimpson, 1859.

***Porcellanopagurus* Filhol, 1885a**

*Diagnosis.* Gills biserial, 11 pairs. Anterior carapace vaulted and well calcified; lateral margins of shield each developed into 2 blunt or spiniform, wing-like projections. Rostrum triangular or truncated. Ocular acicles simple, obscured from dorsal view by broad rostrum. Posterior carapace well calcified anteriorly and usually drawn out into projecting lobes. Crista dentata with 1 accessory tooth. Chelipeds unequal, right appreciably larger. Sternite of somite XII (thoracomere 6, pereopod 3) with broad, subrectangular lobe. Pereopod 4 usually semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with coxae of pereopods 5 sometimes expanded posteroventrally, but usually without very short sexual tube developed; without unpaired pleopods. Female with paired gonopores located posteriorly on coxae of pereopods 3; pleopods 2–4. Abdomen reduced, usually globular, with tergites at least faintly delineated. Uropods generally symmetrical. Telson often carried ventrally; terminal margin rounded, entire or with slight median cleft. Type species: *Porcellanopagurus edwardsi* Filhol, 1885a.

***Propagurus* McLaughlin and de Saint Laurent, 1998**

*Diagnosis.* Gills generally quadriserial, 13 pairs (11 or 12 pairs presumably functional), with pleurobranch on somite XI (thoracomere 5, above pereopod 2) rudimentary or well-developed, pleurobranch on somite XII (thoracomere 6, above pereopod 3) always rudimentary. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal; right longer and stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 2 to several rows of corneous scales; no preungual process. Male with pleopods usually 3–5, occasionally 2–5. Females with pleopods 2–5. Telson with terminal margins generally oblique. Type species: *Pagurus gaudichaudii* H. Milne Edwards, 1836.

***Protoniopagurus* Lemaitre and McLaughlin, 1996**

*Diagnosis.* Gill biserial, 11 pairs. Rostrum obtusely triangular. Ocular acicles simple or bifid. Crista dentata with 1 accessory tooth. Chelipeds subequal; right slightly larger, both suboperculate. Sternite of somite XII (thoracomere 6, pereopods 3) with small subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 10–12 rows of corneous scales; no preungual process. Male without unpaired pleopods. Female with pleopod 1 paired, modified; pleopods 2–4. Abdomen reduced.

Uropods symmetrical. Telson with terminal margin entire. Type species: *Protoniopagurus bioperculatus* Lemaitre and McLaughlin, 1996.

***Pseudopagurodes* McLaughlin, 1997**

*Diagnosis.* Gills distally quadriserial, 11 pairs. Rostrum reduced and rounded. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right somewhat stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of right pereopod 5 of male with long sexual tube, stout proximally and drawn out into filament distally. Female with pleopods 2–5. Telson with oblique terminal margins. Type species: *Pagurodes piliferus* Henderson, 1888.

***Pygmaeopagurus* McLaughlin, 1986**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal; right exceptionally large. Sternite of somite XII (thoracomere 6, pereopods 3) with semicircular anterior lobe. Pereopod 4 simple or weakly semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short to moderate, rod-like sexual tube on coxa of left pereopod 5, no gonopore on coxa of right; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins oblique. Type species: *Pygmaeopagurus hadrochirus* McLaughlin, 1986.

***Pylopaguridium* McLaughlin and Lemaitre, 2001**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Right cheliped markedly larger than left, subrectangular, operculate. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular or subovate anterior lobe, usually armed with few small spines. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with paired gonopores, but coxae of pleopods 5 asymmetrical, left produced posteriorly; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins straight. Type species: *Pylopaguridium markhami* McLaughlin and Lemaitre, 2001b.

***Pylopaguropsis* Alcock, 1905**

*Diagnosis.* Gills biserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped usually massive, chela operculate or semioperculate; dactyl frequently articulating obliquely with palm. Ambulatory legs with dactyls and propodi of pereopods 3 frequently dissimilar. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 to 4 rows of corneous scales, with or without preungual process. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique, concave or straight. Type species: *Pylopagurus magnimanus* Henderson, 1896.



***Pylopagurus*** A. Milne-Edwards and Bouvier, 1891

*Diagnosis.* Gills biserial, 11 pairs. Rostrum acute. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right cheliped markedly larger than left; chela subcircular to subrectangular, operculate. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow subovate, subquadrate, or subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process small to very prominent. Male usually without, but occasionally with papilla or very short sexual on one or both coxae of pereopod 5; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Abdomen straight or rarely flexed. Uropods symmetrical or nearly so. Telson with terminal margins concave or oblique. Type species: *Eupagurus discoidalis* A. Milne-Edwards, 1880

***Rhodochirus*** McLaughlin, 1981

*Diagnosis.* Gills biserial, 11 pairs. Rostrum obtusely triangular or as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Right chela subovate to subquadrate; at least some spines or tubercles with basal rosettes. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process well developed. Male with pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique. Type species: *Pylopagurus rosaceus* A. Milne-Edwards and Bouvier, 1893.

***Scopaeopagurus*** McLaughlin and Hogarth, 1998

*Diagnosis.* Gills biserial, 10 pairs, no pleurobranch on somite XIII (on thoracomere 7, above arthrobranches of pereopod 4). Rostrum triangular. Ocular acicles simple. Crista dentata consisting of 2 or 3 strong curved, spine-like teeth; no accessory tooth. Chelipeds grossly unequal, right massive. Sternite of somite XII (thoracomere 6, pereopods 3) with roundly rectangular anterior lobe. Pereopod 4 weakly semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short sexual tube on coxa of left pereopod 5, coxa of right with only small papilla; pleopods 2–5. Females with single gonopore on coxa of left pereopod 3; pleopods 2–5. Telson with terminal margins oblique. Type species: *Scopaeopagurus megalochirus* McLaughlin and Hogarth, 1998.

***Solenopagurus*** de Saint Laurent, 1968

*Diagnosis.* Gills distally quadriserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right somewhat longer and stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with subsemicircular to subquadrate anterior lobe. Propodus and dactyl of left pereopod 3 dissimilar in having numerous plumose setae on lateral faces. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process usually present. Male with long sexual tube on coxa of right pereopod 5, directed toward exterior and curved dorsally, coxa of left usually with small papilla; pleopods 3–5. Female

with pleopods 2–5. Telson with terminal margins straight or oblique. Type species: *Cestopagurus lineatus* Wass, 1963.

***Solitariopagurus*** Türkay, 1986

*Diagnosis.* Gills biserial, 10 pairs, no pleurobranch on somite XIII (thoracomere 7, above arthrobranches of pereopod 4). Anterior carapace vaulted and strongly calcified; lateral margins of shield each developed into 3 blunt or spiniform lobes; posterior carapace lobe consisting of elongate median and small lateral elements. Rostrum prominent. Ocular acicles reduced, simple; hidden from dorsal view by anterior margin of shield. Crista dentata with 1 accessory tooth. Right cheliped much stronger, but not appreciably longer than left. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 subchelate; propodal rasp with 1 row of corneous scales; no preungual process. Pereopod 5 subchelate. Male with stout, short to moderate, equal or unequal sexual tubes developed on coxae of both pereopods 5, right frequently longer; each with long setae subterminally and terminally; no unpaired pleopods. Female with single gonopore posteriorly on coxa of left pereopod 3; pleopods 2–4. Abdomen reduced; tergal plate of abdominal somite 2 weakly delineated; tergal plates of somites 3–5 clearly defined. Uropods symmetrical; protopods each with very prominent, posteriorly directed spine. Telson with terminal margin entire. Type species: *Solitariopagurus profundus* Türkay, 1986.

***Spiropagurus*** Stimpson, 1858

*Diagnosis.* Gills biserial, 11 pairs. Rostrum as broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal, right usually slightly stronger, but not necessarily longer. Sternite of somite XII (thoracomere 6, pereopods 3) with anterior lobe narrowly subrectangular, occasionally obsolete. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with long, usually coiled, terminally blunt sexual tube on coxa of left pereopod 5, right without sexual tube but sometimes with small papilla; pleopods 3–5. Female with pleopods 2–5. Telson with characteristic, acutely triangular posterior lobes (Fig. 3c), terminal margins very oblique. Type species: *Pagurus spiriger* De Haan, 1849.

***Tarrasopagurus*** McLaughlin, 1997

*Diagnosis.* Gills distally quadriserial, 11 pairs. Rostrum obtusely triangular or broadly rounded, with 1 or more marginal spinules. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds markedly unequal, right considerably longer and stronger. Sternite of somite XII (thoracomere 6, pereopods 3) with semicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Male with short sexual tube on coxa of left pereopod 5, directed anteriorly or posteriorly, right sometimes also with short or very short tube developed, sometimes with only papilla; pleopods 3–5. Female with pleopod 1 paired, modified; pleopods 2–5. Telson with terminal margins oblique. Type species: *Tarrasopagurus rostrodenticulatus* McLaughlin, 1997.

***Tomopaguroides* Balss, 1912**

*Diagnosis.* Gills quadriserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata not described. Chelipeds grossly unequal, right largest. Sternite of somite XII (thoracomere 6, pereopods 3) with small, triangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1, possibly 2, rows of corneous scales; apparently no preungual process. Male with pleopod 2 paired, modified; pleopods 3–5. Female unknown. Abdomen straight, tergite of somite 5 as thickened, possibly calcified plate; uropods symmetrical. Telson terminal margin not described. Type species: *Parapagurus valdiviae* Balss, 1911.

***Tomopaguopsis* Alcock, 1905**

*Diagnosis.* Gills quadriserial, 13 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds subequal; right usually somewhat more robust. Subquadrate anterior lobe of sternite of somite XII (thoracomere 6, pereopod 3) with convex median, marginally setose, elevation. Pereopod 4 semichelate; propodal rasp with several rows of corneous scales; no preungual process. Male with or without pleopod 1 paired, modified; pleopods 2–5. Female with pleopods 2–5. Telson with terminal margins rounded. Type species: *Tomopaguopsis lantana* Alcock, 1905.

***Tomopagurus* A. Milne-Edwards and Bouvier, 1893**

*Diagnosis.* Gills biserial, 11 pairs. Rostrum triangular or sometimes only broadly rounded lobe. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, right appreciably larger. Sternite of somite XII (thoracomere 6, pereopods 3) with subovate to subsemicircular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; preungual process prominent. Male usually without, rarely with pleopod 1 paired but reduced or vestigial; pleopods 3–5. Female usually with pleopod 1 paired, modified, rarely without pleopod 1; pleopods 2–5. Telson with terminal margins oblique. Type species: *Tomopagurus rubropunctatus* A. Milne-Edwards and Bouvier, 1893.

***Trichopagurus* de Saint Laurent, 1968**

*Diagnosis.* Gills distally quadriserial, 11 pairs. Rostrum triangular. Ocular acicles simple. Crista dentata with 1 accessory tooth. Chelipeds unequal, some degree of sexual dimorphism. Sternite of somite XII (thoracomere 6, pereopods 3) with subrectangular anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of corneous scales; no preungual process. Coxa of male right pereopod 5 with moderate sexual tube directed toward the exterior; left with very short tube; pleopods 3–5. Female with single gonopore on coxa of left pereopod 3; pleopods 2–5. Type species: *Catapaguroides ?trichophthalmus* Forest, 1954.

***Turleania* McLaughlin, 1997**

*Diagnosis.* Gills quadriserial, 11 pairs. Rostrum narrowly triangular. Ocular acicles simple or multispinous. Crista dentata

without accessory tooth. Chelipeds unequal or subequal, right appreciably stouter, but not necessarily longer. Sternite of somite XII (thoracomere 6, pereopods 3) with generally subquadrate anterior lobe. Pereopod 4 semichelate; propodal rasp with 1 row of scales corneous scales; no preungual process. Coxa of left pereopod 5 of male with moderate to long, often weakly spiraled sexual tube provided with sparse terminal tuft of stiff setae; right occasionally with papilla; pleopods 3–5. Females with pleopods 2–5. Telson with terminal margins oblique. Type species: *Laurentia albatrossae* McLaughlin and Haig, 1996a.

***Xylopagurus* A. Milne Edwards, 1880**

*Diagnosis.* Gills biserial or distally quadriserial, 13 pairs. Rostrum obtusely triangular. Ocular acicles multispinose. Crista dentata with 1 accessory tooth. Chelipeds grossly unequal; palm of right with prominent spine or protuberance at mesial dorsodistal angle. Sternite of somite XII (thoracomere 6, pereopods 3) with narrow or subtriangular anterior lobe. Pereopod 4 semichelate; propodal rasp with numerous rows of small, corneous scales; no preungual process. Pereopod 5 subchelate, sometimes sexual dimorphic. Male with pleopods 1 and 2 paired, modified; no unpaired pleopods. Female with pleopods 2–4. Tergites of abdominal somites 2–5 as narrow calcified plates, tergite 6 heavily calcified and operculate; uropods symmetrical. Telson without lateral indentations, broader than long, terminal margin entire. Type species: *Xylopagurus rectus* A. Milne-Edwards, 1880.

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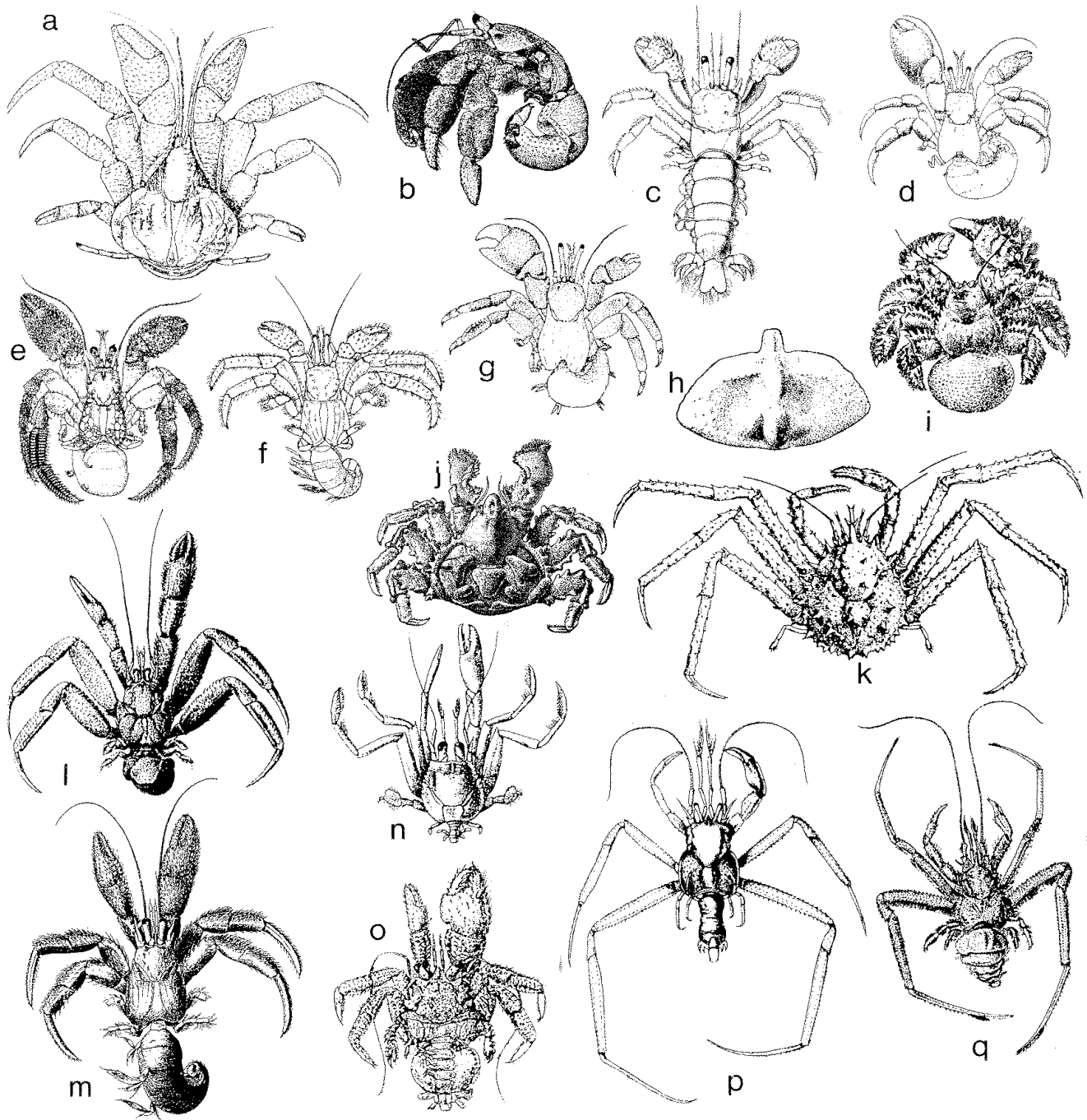


Figure 1. Morphological diversity among members of the Paguroidea. a, b, Coenobitidae, c, Pylochelidae; d–g, Diogenidae; h–k, Lithodidae, l–o, Paguridae, p, q, Parapaguridae: a, *Birgus latro* Leach; b, *Coenobita clypeatus* (Fabricius); c, *Trizocheles spinosus* (Henderson); d, *Allodardanus bredini* Haig and Provenzano; e, *Dardanus venosus* (H. Milne Edwards); f, *Clibanarius arethusa* De Man; g, *Calcinus tibicen* (Herbst); h, *Cryptolithodes sitchensis* Brandt; i, *Hapalogaster dentata* (De Haan); j, *Sculptolithodes derjugini* Makarov; k, *Lithodes murrayi* Henderson; l, *Labidochirus splendescens* (Owen); m, *Propagurus gaudichaudi* (H. Milne Edwards); n, *Ostraconotus spatulipes* A. Milne-Edwards; o, *Porcellanopagurus edwardsi* Filhol; p, *Tylaspis anomala* Henderson; q, *Probeebeei mirabilis* Boone. [a, f after Alcock, 1905; b, from Chace and Hobbs, 1969; c, k, p, from Henderson, 1888; d, e, g, after Chace et al. 1985; h, from Makarov, 1938; i, j, from Vinogradov, 1950; l from McLaughlin, 1974; m, from Benedict, 1901 as *Eupagurus patagonensis* Benedict; n, after A. Milne-Edwards and Bouvier, 1893; o, after Forest, 1951; q, from Wolff, 1961; not to scale.]

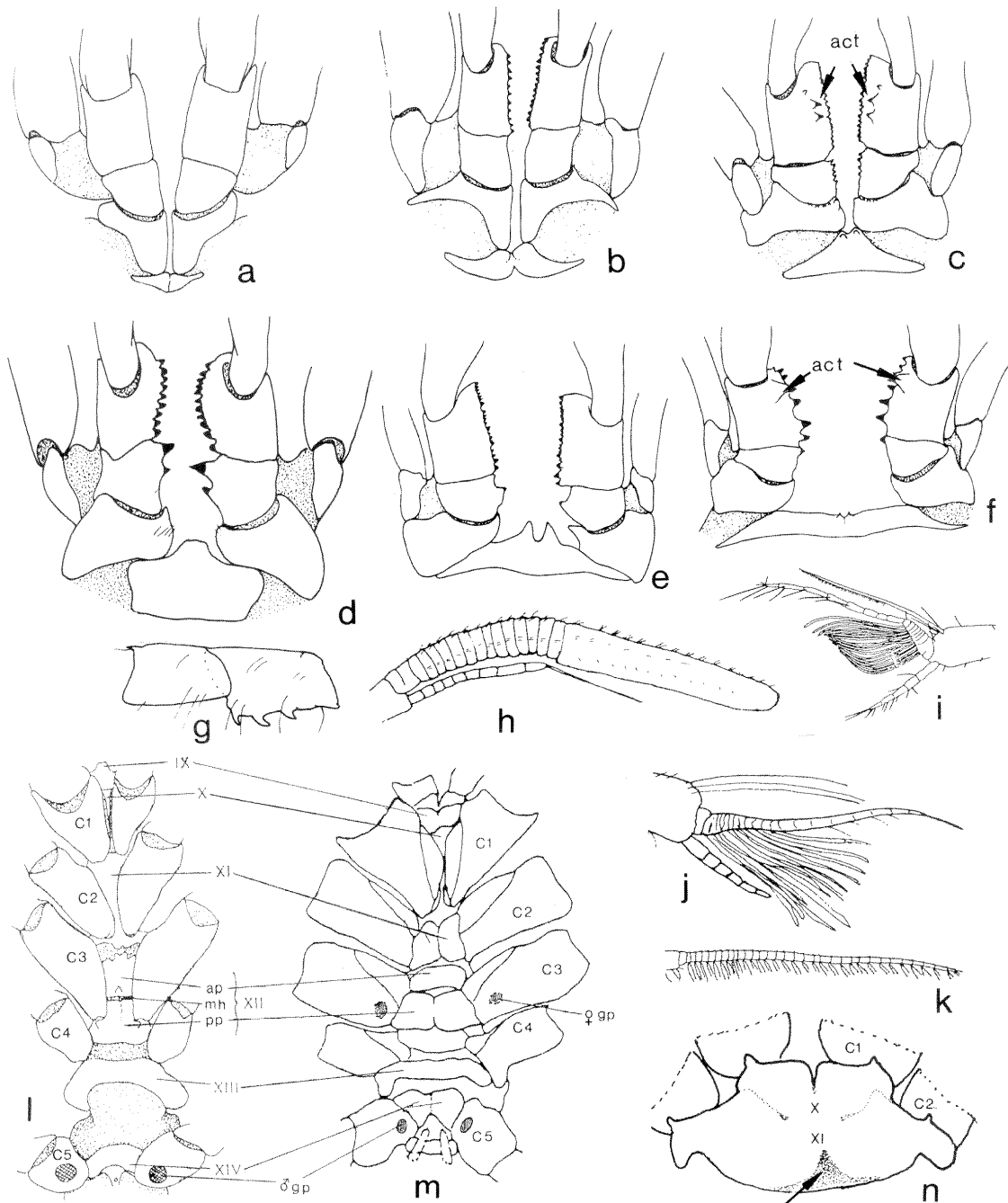


Figure 2. Bases and paired basis-ischium of maxilliped 3: a, Coenobitidae – *Coenobita clypeatus* (Fabricius); b, Diogenidae – *Clibanarius vittatus* (Bosc); c, Pylochelidae – *Mixtopagurus paradoxus* A. Milne-Edwards; d, Pylojacquesidae – *Pylojacquesia colemani* McLaughlin and Lemaitre; e, Parapaguridae – *Parapagurus pilosimanus* Smith; f, Paguridae – *Pagurus pollicaris* Say; g, reduced teeth on crista dentata of ischium, *Scopaeopagurus megalochirus* McLaughlin and Hogarth.

Antennular and antennal flagella. h–j, antennular flagella: h, Coenobitidae; i, *Pagurus imafukui* McLaughlin and Konishi; j, generalised flagella of Diogenidae, Paguridae and Parapaguridae; k, antennal flagellum with paired ventral setae.

Thoracic sternites and coxae of pereopods: l, *Pylojacquesia colemani* McLaughlin and Lemaitre; m, generalised Paguridae; n, *Lithodes aequispinus* Benedict (sternites X and XI only; groove and pit of sternite XI indicate by arrow). Abbreviations: act = accessory tooth (teeth) indicated by arrows; ap = anterior portion; C 1–5 = coxae of pereopods 1–5; gp = gonopore; mh = membranous hinge; pp = posterior portion. [a–f, l, from McLaughlin and Lemaitre, 2001c; g, from McLaughlin and Hogarth, 1998; h, from McLaughlin and Dworschak, 2001; i from McLaughlin and Konishi, 1994; j, from Forest et al. 2000; k, from McLaughlin and Haig, 1996b, m, adapted from McLaughlin, 1974; not to scale]

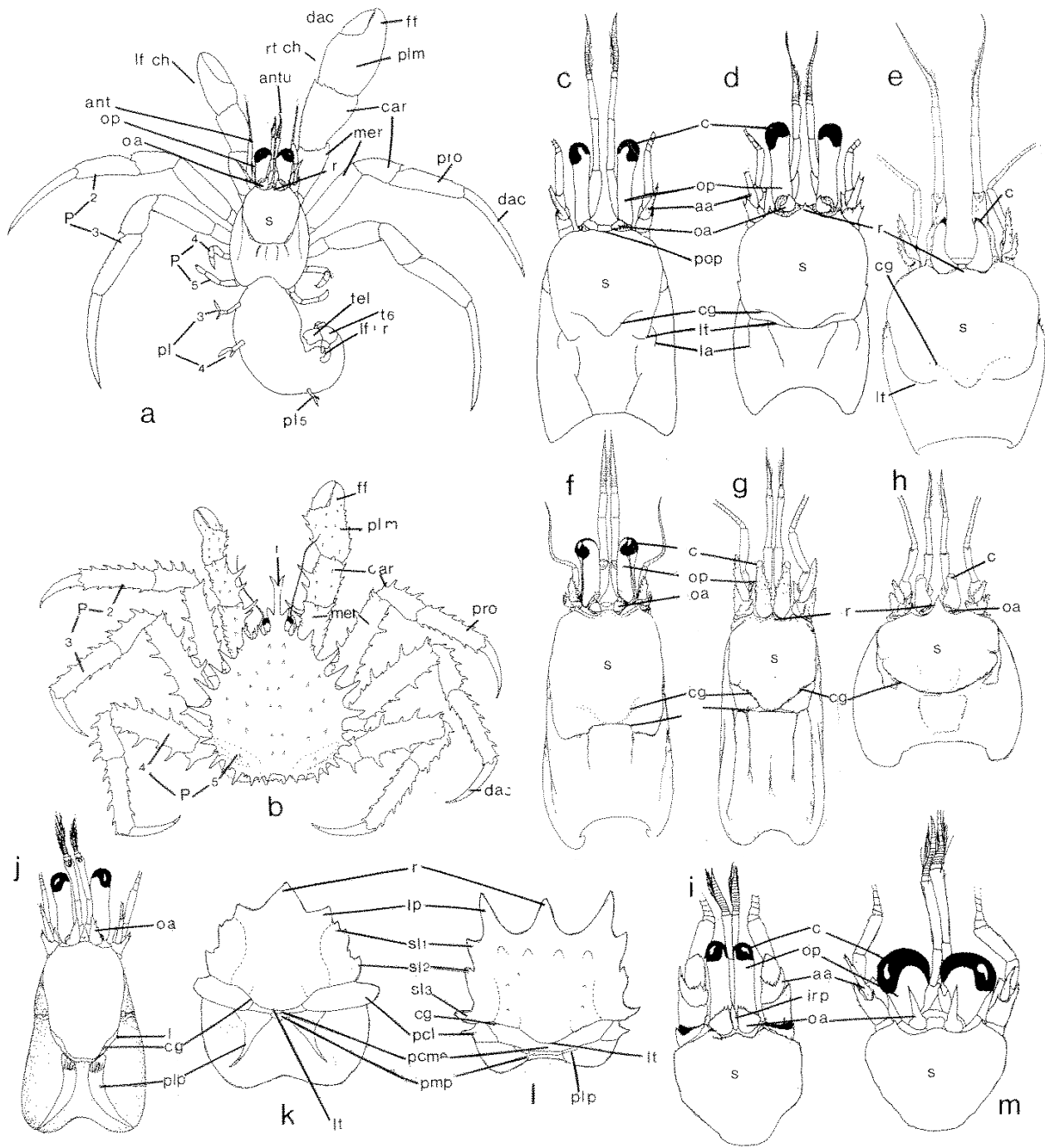


Figure 3. Basic morphology: a, diagrammatic pagurid (whole animal, dorsal view); b, diagrammatic lithodid (whole animal, dorsal view). Cephalothorax or shield, with or without cephalic appendages: c–h Pylochelidae; i, Diogenidae; j, Pylojacquesidae; k–m Paguridae. c, *Pylocheles*; d, *Trizocheles*; e, *Cheiroplatea*; f, *Pomatocheles*; g, *Parapylocheles*; h, *Cancelllocheles*; i, *Diogenes*; j, *Pylojacquesia*; k, *Porcellanopagurus*; l, *Solitariopagurus*; m, *Hemipagurus*. Abbreviations: aa = antennal acicle; ant. = antenna; antu = antennule; c, cornea; car = carpus; cg = cervical groove; dac = dactyl; ff = fixed finger; irp = intercalary rostral process; la = linea anomurica; lf ch = left cheliped; lf ur = left uropod; lp = lateral projection; lt = linea transversalis; mer = merus; oa = ocular acicle; op = ocular peduncle; P2–5 = pereopods 2–5; pcl = posterior carapace lobe; pcme = posterior carapace median element; pl3–5 = pleopods 3–5; plm = palm; pmp = posterior median plate; pop = post-ocular projection; pro = propodus; r = rostrum or rostral lobe; rt ch = right cheliped; s = shield; sl1–3 = shield lobes 1–3; t6 = abdominal tergite 6; tel = telson. [a, b, adapted from Sandberg and McLaughlin, 1998; c, d from Forest et al. 2000; e–h, from Forest, 1987; i, from McLaughlin and Clark, 1997; j, from McLaughlin and Lemaitre, 2001c; k, l, from McLaughlin, 2000; m, from McLaughlin, 1997 (as *Catapagurus*); not to scale.]

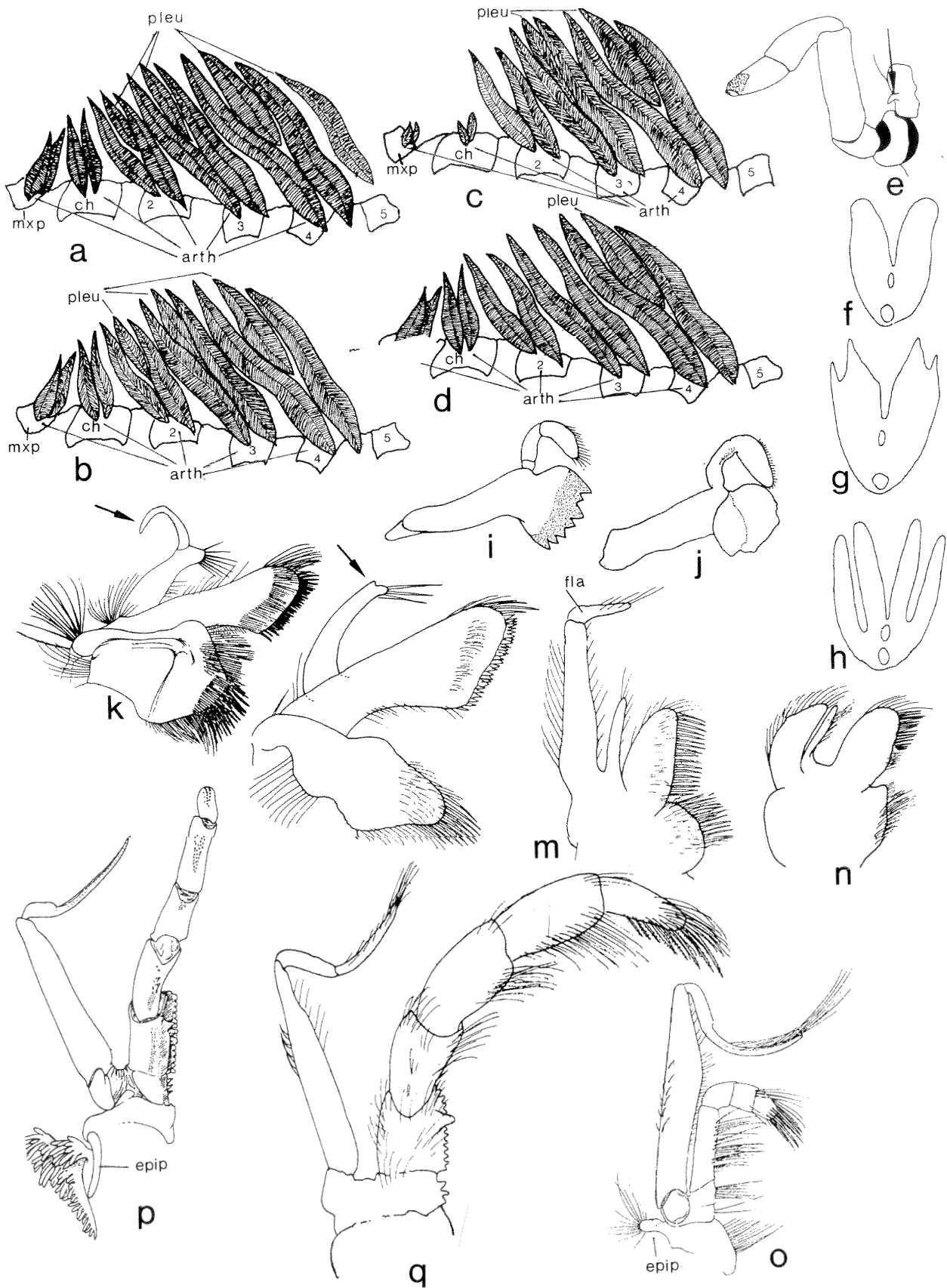


Figure 4. Gills: a, left gill series of 14 pairs (paired arthrobranches on arthrodistal membranes of maxilliped 3, chela, and pereopods 2–4; single pleurobranches on somites XI, XII, XIII, and XIV (thoracomeres 5–8, above pereopods 2–5)); b, left gill series of 13 pairs (paired arthrobranches on arthrodistal membranes of maxilliped 3, chela, and pereopods 2–4; single pleurobranches on somites XI, XII, and XIII (thoracomeres 5–7, above pereopods 2–4)); c, left gill series with paired arthrobranches reduced or vestigial on arthrodistal membranes of maxilliped 3 and cheliped; pleurobranches absent from somites XI and XIV (thoracomeres 5 and 8, above pereopods 2 and 5); left gill series of 11 pairs (paired arthrobranches on arthrodistal membranes of maxilliped 3, chela, and pereopods 2–4; single pleurobranch on somite XIII (thoracomere 7, above pereopod 4); e, vestigial pleurobranch (indicated by arrow) on somite XIV (thoracomere 8, above pereopod 5) in some parapagurids; f, biserial gill lamella; g, distally divided quadriserial gill lamella; h, deeply divided quadriserial gill lamella.

Mandible: i, Pylojacquesidae; j, Paguridae.

Maxillule: k, with external lobe (indicated by arrow) of endopod well developed, recurved; l, with external lobe (indicated by arrow) of endopod weakly developed or obsolete, not recurved.

Maxilliped 1: m, with exopodal flagellum; n, without exopodal flagellum.

Maxilliped 2: o, with epipod.

Maxilliped 3: p, with epipod; q, without epipod.

Abbreviations: arth = arthrobranch; ch = cheliped; epip = epipod; fla = flagellum; mxp = maxilliped 3; pleu = pleurobranch; 2–5 = coxae of pereopods 2–5. [e, from Lemaitre, 1989; f–h, l–n, q from Forest et al. 2000; i, from McLaughlin and Lemaitre, 2001c; j, from McLaughlin, 1974; k, o, p, from Forest, 1987; not to scale].

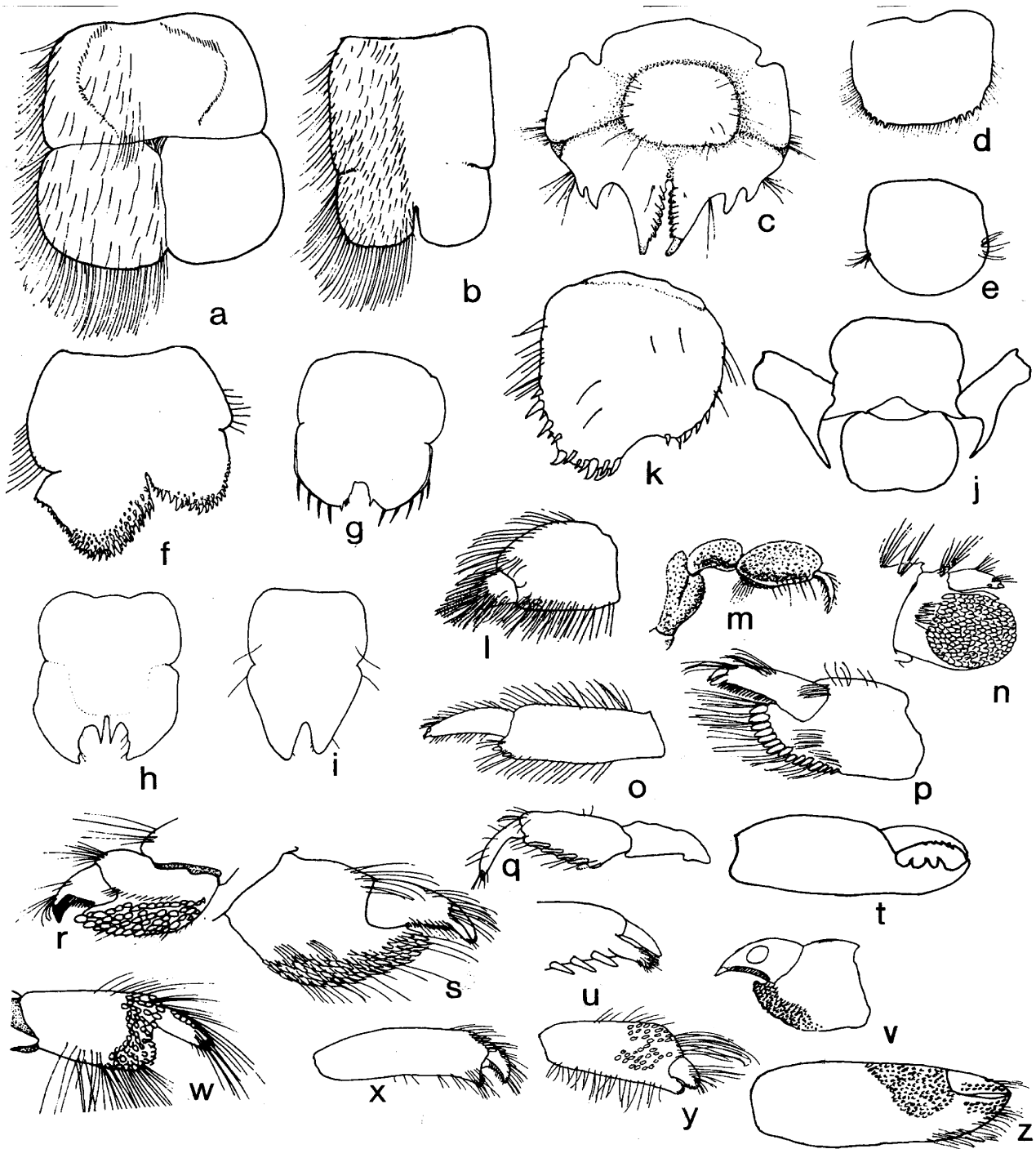


Figure 5. Representative telsons: a, b, Pylochelidae; c–j, Paguridae; k, Parapaguridae.

Sixth abdominal tergite, protopods of uropods and telson: j, *Munidopagurus*.

Dactyl and propodus of pereopod 4: l, o, simple; m, q, subchelate; n, r, semichelate with multiple rows of corneous scales in propodal rasp and no preungual process; p, u, t, semichelate with single row of corneous scales in propodal rasp and preungual process at base of claw; s, semichelate with multiple rows of corneous scales in propodal rasp and preungual process at base of claw; t, chelate; v, semichelate with “type A” (cf. McLaughlin, 1974) sensory structure on lateral face of dactyl.

Dactyl and propodus of pereopod 5: w, x subchelate; y, semichelate; z, chelate. [a, b, n, from Forest and McLaughlin, 2000; c, from Lewinsohn, 1982; d, e, from McLaughlin, 1982; f–i from McLaughlin, 1997; j, adapted from Provenzano, 1971; k, from Lemaitre, 1996; l, o–q, s, u, y, from McLaughlin, 1997; m, from McLaughlin and Lemaitre, 1997; q, w, from McLaughlin and Lemaitre, 2001c; v, from McLaughlin, 1974; x, after Lemaitre, 1998; not to scale].

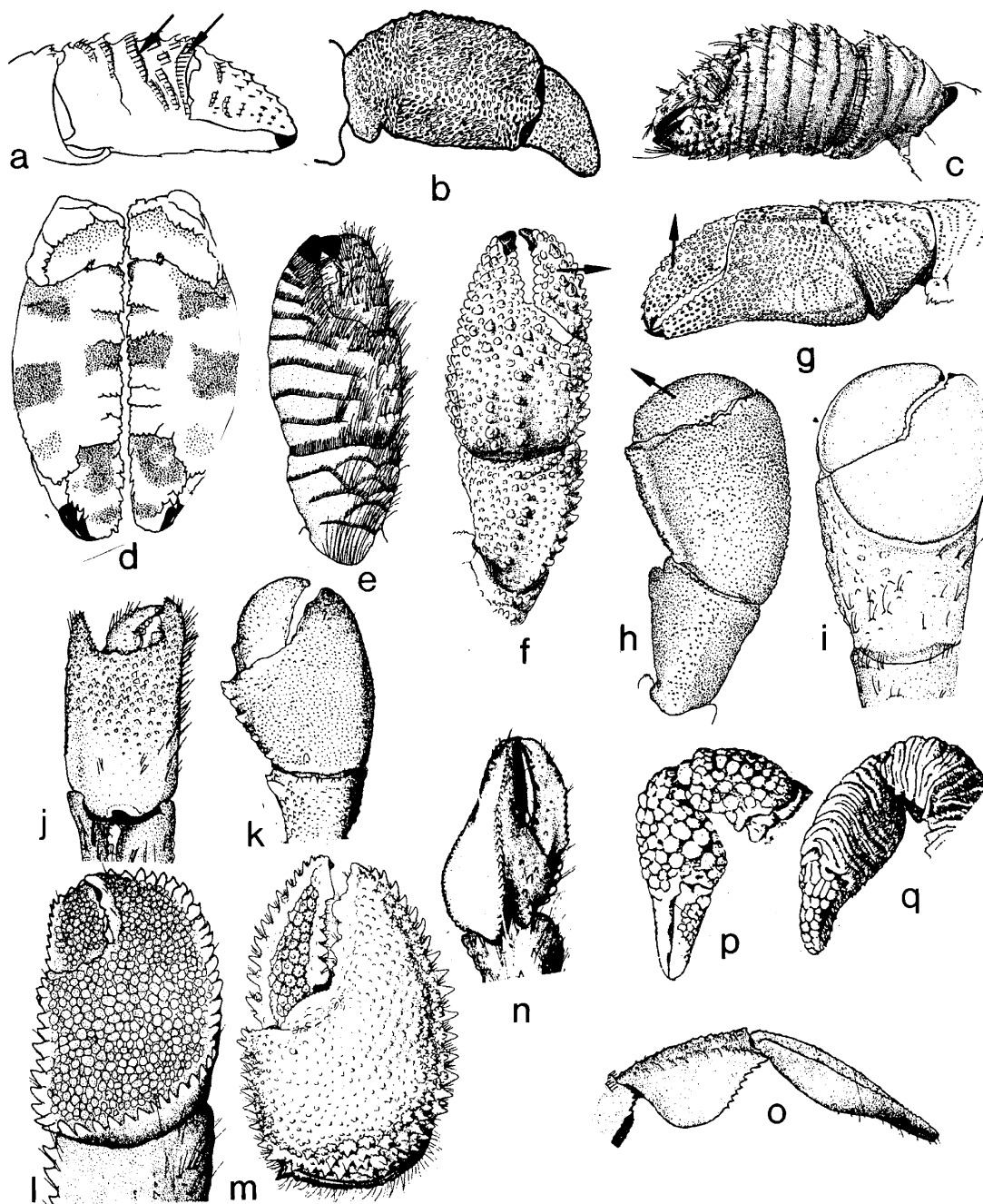


Figure 6. Chelipeds: a, left chela of *Ciliopagurus* (mesial view) showing stridulating mechanism (indicated by arrows); b, left chela of *Allodardanus* (mesial view) lacking stridulating mechanism; c, left chela and carpus of *Ciliopagurus* (lateral view); d, chelae of *Cancellus* together forming operculum; e, left carpus and chela of *Aniculus*; f, left chela and carpus of *Isocheles* (dorsal view), with dactyl opening horizontally (as indicated by arrow); g, left chela and carpus of *Loxopagurus* (dorsolateral view) with dactyl opening vertically (as indicated by arrow); h, right chela and carpus of *Paragiopagurus* (dorsal view) with dactyl opening obliquely (as indicated by arrow); i, right chela of *Pylojacquesia*; j, right chela of *Xylopagurus*; k, right chela of *Bathypaguopsis*; l, right chela of *Lophopagurus* (*Australeremus*); m, right chela of *Rhodochirus*; n, left chela of *Lophopagurus* (*Lophopagurus*); o, right carpus and chela of *Goreopagurus* (lateral view); p, right carpus and chela of *Oedignathus* (mesial view); q, right carpus and chela of *Dermaturus* (mesial view). [a, c, from Forest, 1952; b, after Haig and Provenzano, 1965; d, after Mayo, 1973; e, from McLaughlin and Hoover, 1995; f, g, from Forest and de Saint Laurent, 1968; h, from Lemaitre, 1996; i, from McLaughlin and Lemaitre, 2001c; j, from Lemaitre, 1995; k, from McLaughlin, 1994; l, n, from McLaughlin and Gunn, 1992; m, from Williams, 1984; o, from McLaughlin and Haig, 1995; k, l, after Vinogradov, 1950; not to scale].

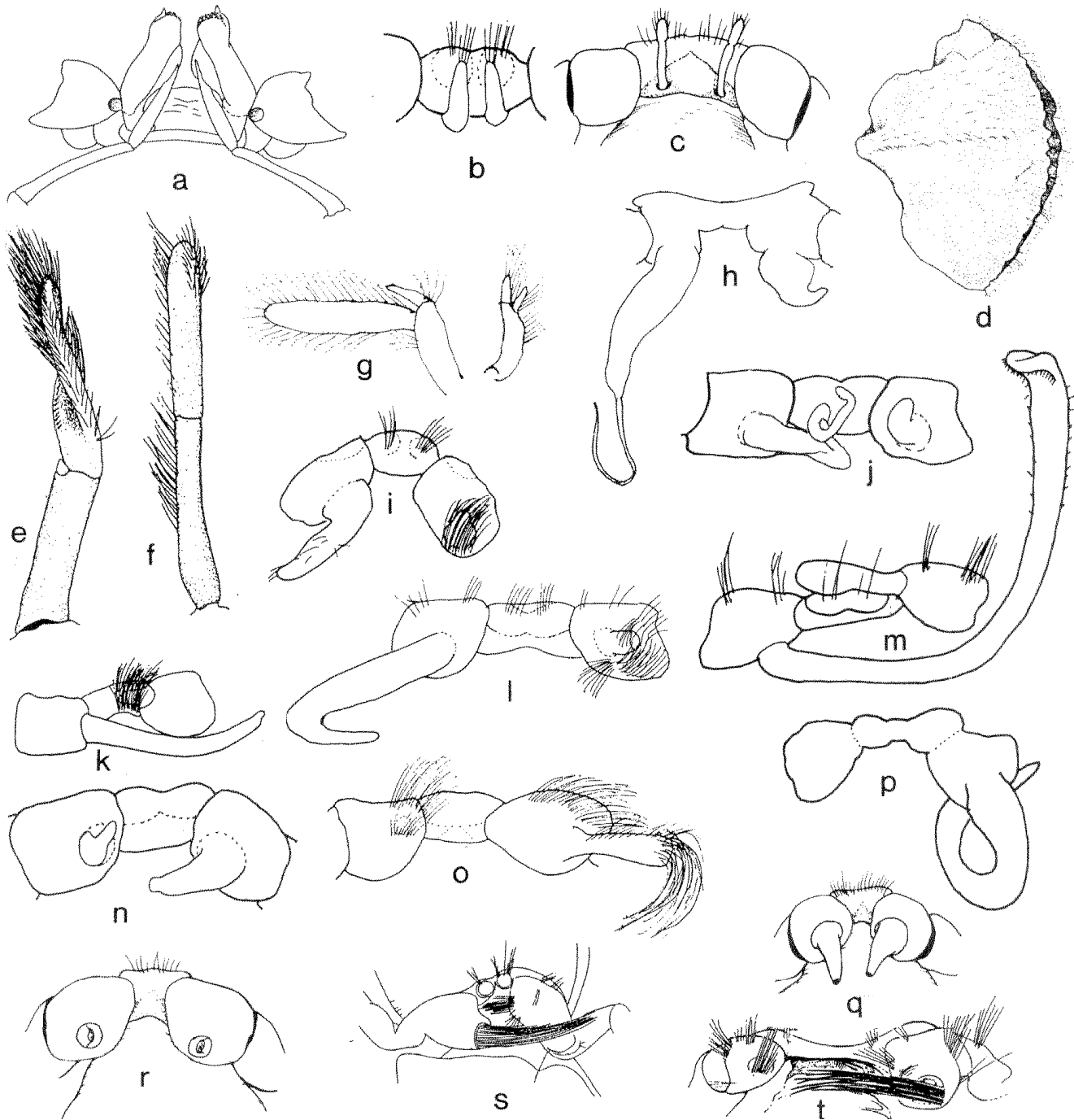


Figure 7. Secondary sexual appendages and structures: a, coxae of pereopods 5 and abdominal somites 1 and 2 of male with pleopods 1 and 2 paired, modified; b, c, coxae of pereopods 5 and abdominal somite 1 of female with pleopod 1 paired, modified; d, female brood pouch; e–g, male pleopod 2; h–q, male sexual tubes; r, male gonopores without sexual tube development; s, coxa of right pereopod 5 of male with gonopore masked by tuft of stiff setae; t, coxa of left pereopod 5 of male with gonopore masked by tuft of stiff setae. [a, from Forest et al. 2000; b, from McLaughlin and Haig, 1995; c, q, r, from McLaughlin and Lemaitre, 2001b; d, from McLaughlin and Provenzano, 1975; e, f, from Lemaitre, 1989; g, from Forest, 1995; i–n from McLaughlin, 1997; h, from Wang and McLaughlin, 2000; p, from McLaughlin, 1986; s, from Melin, 1939; t, from Forest, 1961; not to scale].



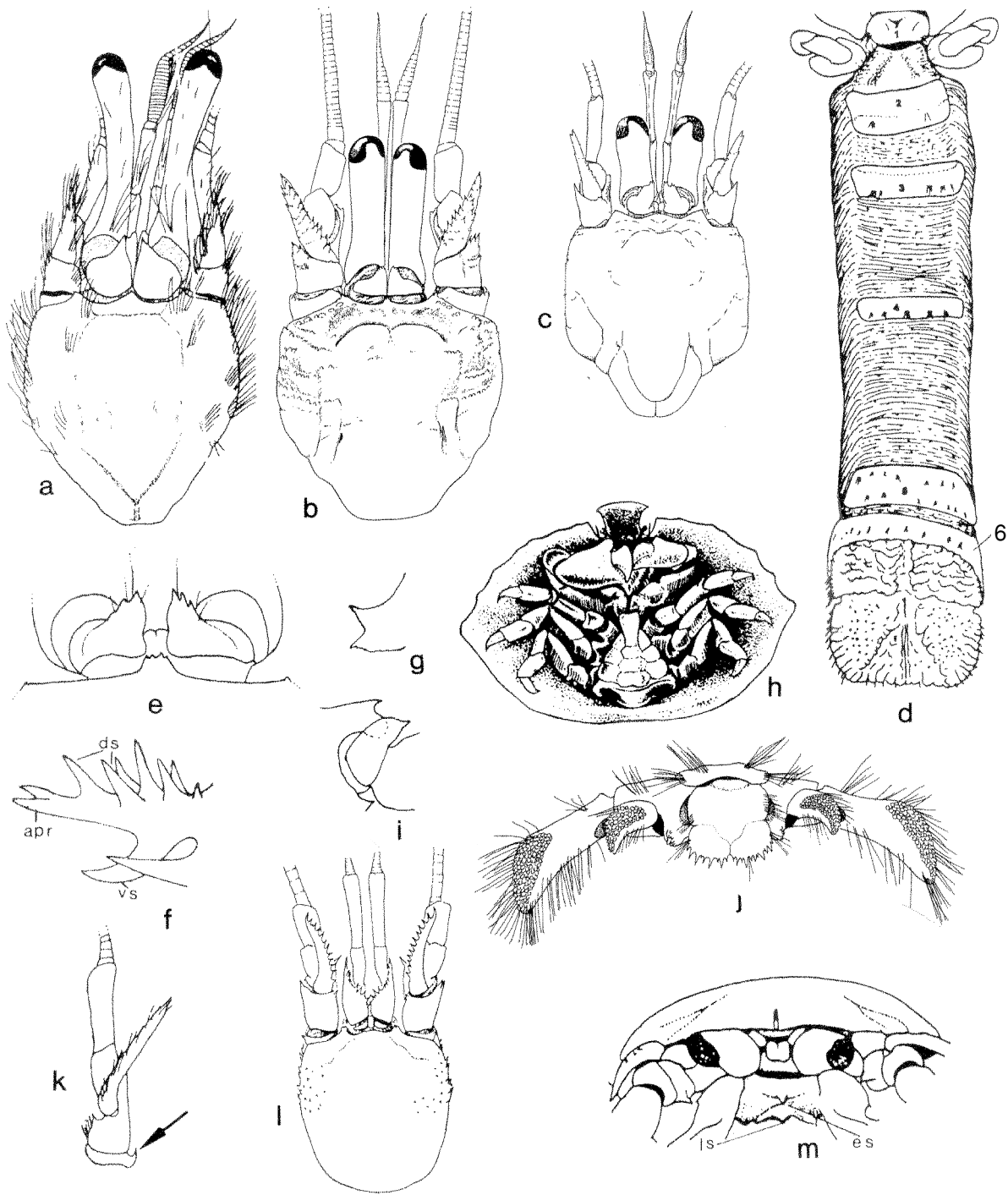


Figure 8. Additional morphological characters: a, c, shield with Y-shaped posterior groove; b, shield without Y-shaped posterior groove; d, last thoracic somite and abdomen of *Xylopagurus* (dorsal view); e, multifid ocular acicles; f, *Lithodes* rostral spine complex; g, dorsal and ventral rostral spines of *Glyptolithodes*; h, *Cryptolithodes* (ventral view) with carapace covering body and appendages; i, rostrum with epirostral spine (lateral view); j, symmetrical uropods and posterior portion of abdominal tergite 6, plus telson (dorsal view) k, right antennal peduncle with hooked spine (indicated by arrow) on lateral margin of segment 1; l, shield of *Typhlopagurus* showing spinose ocular and antennal acicles and lack of ocular peduncles; m, parapagurid epistome and labrum. Abbreviations: apr = anterior rostral process; ds = dorsal spine(s); es = epistomial spine; ls = labral spine; vs = ventral spine; 6 indicates abdominal tergite 6. [a, from McLaughlin and Hoover, 1996; b, from Forest and de Saint Laurent, 1968; c, from Forest and McLaughlin, 2000; d, from Lemaitre, 1995; e, McLaughlin and Murray, 1990; f, from Vinogradov, 1950; g, after Haig, 1974; h, from Makarov, 1938; i, from McLaughlin, 1997; j, from McLaughlin and Lemaitre, 1993; k, from McLaughlin, 1981; l, from de Saint Laurent, 1972; m, after Lemaitre, 1989; not to scale].

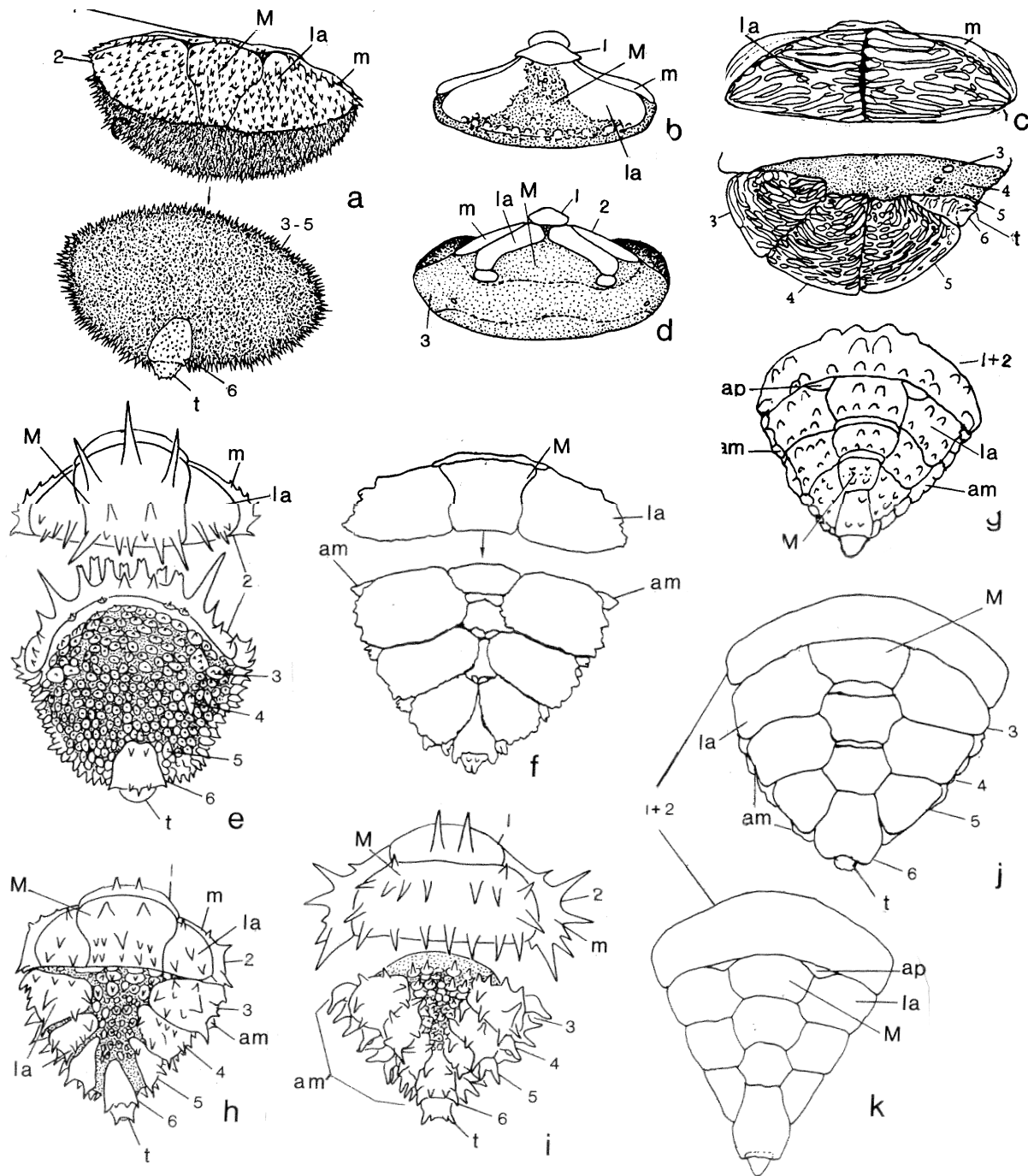


Figure 9. Lithodid abdominal tergites: a, *Acantholithodes* tergites 1 and 2, tergites 3–6 and telson; b, *Hapalogaster* tergites 1–3; c, *Placetron* tergites 1 and 2, tergites 3–6 and telson, showing female asymmetry in tergites 3–5; d, *Oedignathus* tergites 1–3; e, *Neolithodes* tergites 1 and 2, tergites 3–6 and telson; f, *Phyllolithodes* tergites 1 and 2, tergites 3–6 and telson; g, *Lopholithodes* tergite 1+2, tergites 3–6 and telson; h, *Paralithodes* tergites 1 and 2, tergites 3–6 and telson; i, *Lithodes* tergites 1 and 2, tergites 3–6 and telson; j, *Paralomis* tergite 1+2, tergites 3–6 and telson; k, *Cryptolithodes* tergite 1+2, tergites 3–6 and telson. Abbreviations: am = accessory marginal plates; ap = accessory plate; la = lateral plate; m = marginal plate; M = median plate; t = telson; tergites are numbered 1–6. [a–i, k from McLaughlin and Lemaitre, 2001a.; j adapted from Macpherson, 1988; not to scale].