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REVISION OF *PYLOPAGURUS* AND *TOMOPAGURUS* (CRUSTACEA: DECAPODA: PAGURIDAE), WITH THE DESCRIPTIONS OF NEW GENERA AND SPECIES

PART I. TEN NEW GENERA OF THE PAGURIDAE AND A REDESCRIPTION OF *TOMOPAGURUS* A. MILNE EDWARDS AND BOUVIER

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ABSTRACT

The pagurid genera *Pylopagurus* and *Tomopagurus* have been revised and, as a result, 10 new genera are proposed. In this first of a six part series the genus *Pylopagurus* is restricted, new genera are diagnosed and *Tomopagurus* is redescribed. Several characters in the generic diagnoses are used for the first time. One new species is described in *Tomopagurus* and diagnoses and figures are given of the other seven species herein assigned to this genus.

Of pagurids with 11 pairs of gills, only three genera, i.e., *Pylopagurus* A. Milne Edwards and Bouvier, 1891[1], *Ceratopagurus* Yokoya, 1933 and *Benthopagurus* Wass, 1963, initially were defined, in part, by the presence of paired first pleopods (gonopods) in females and no sexual modifications in males. The last genus subsequently was placed in synonymy with *Tomopagurus* A. Milne Edwards and Bouvier, 1893, as redefined by Forest and De Saint Laurent (1968). During studies of western Atlantic pagurids, a number of new species with gonopod bearing females were discovered, and several species assigned to *Pagurus* Fabricius were found also to have gonopod bearing females. Attempts to place these species in their appropriate genera quickly showed that no clear-cut distinctions existed among these genera.

A review of the literature has shown that at least 44 species have been assigned to *Pylopagurus*, four to *Tomopagurus* and one to *Ceratopagurus*. The last species is known only from its type locality, Japan, and Yokoya's (1933) generic and specific descriptions are too brief to permit further evaluation; the type material apparently is no longer extant (T. Sakai, personal communication). *Tomopagurus* has three representatives in the western Atlantic and one in the eastern Pacific; *Pylopagurus* species are abundant in both the Caribbean and western Atlantic and in the eastern Pacific, but representatives also are present in the Indo Pacific, Australian-New Zealand and South African regions. Part I of the series includes the restriction of *Pylopagurus* sensu stricto, diagnoses of 10 new genera and a review of *Tomopagurus* with the description of one new species. Descriptions of new species and diagnoses of known species assigned to the new genera and to *Pylopagurus* s. s. will be presented in parts II to VI.

Materials

Specimens used in this study have come from the collections of the Allan Hancock Foundation, University of Southern California (AHF), British Museum (BM), Dauphin Island Sea Lab, University of Alabama (DISL), Florida Institute of Oceanography, Florida State University System (FIO), Florida State Department of Natural Resources (DNR), Museum of Comparative Zoology, Harvard University (MCZ), Muséum National d'Histoire Naturelle (MNHN), National Museum of Natural His-

[1] Milne Edwards and Bouvier (1891) gave a brief, but sufficiently detailed description of *Pylopagurus* to meet the criteria for availability; *Pylopagurus discoidalis* (A. Milne Edwards, 1880) and *Pylopagurus ungulatus* (Studer, 1883) were cited as nominal species.

tory, Smithsonian Institution (USNM), Rosenstiel School of Marine and Atmospheric Science, University of Miami (RSMAS), Smithsonian Oceanographic Sorting Center (SOSC), and the Systematics Laboratory, National Marine Fisheries Service (NMFS).

KEY TO THE "PYLOPAGURID-LIKE" GENERA

1a. Telson typically with transverse suture; terminal margin bilobed, straight or concave 2
1b. Telson without transverse suture; terminal margin entire, convex 11
2a. Propodus of 4th pereopods with single row of scales 3
2b. Propodus of 4th pereopods with 2 or more rows of scales 9
3a. Uropods symmetrical or nearly so ..... *Pylopagurus* s.s.
3b. Uropods markedly asymmetrical 4
4a. Left chela with spinose or tuberculate median keel or crest ..... *Lophopagurus* new genus
4b. Left chela without spinose or tuberculate median keel or crest 5
5a. Spines of chelae with basal rosettes ..... *Rhodochirus* new genus
5b. Spines of chelae without basal rosettes 6
6a. Left chela with angle of articulation greater than 45° ..... *Australeremus* new genus
6b. Left chela with angle of articulation less than 45° 7
7a. Dactyl and fixed finger of left chela "spoon-shaped" ..... *Tomopagurus*
7b. Dactyl and fixed finger of left chela not "spoon-shaped" 8
8a. Right chela operculate; preungual process present ..... *Phimochirus* new genus
8b. Right chela not operculate; preungual process absent ..... *Haigia* new genus
9a. Uropods symmetrical or nearly so, with protopods produced posteriorly ..... *Agaricochirus* new genus
9b. Uropods markedly asymmetrical, with protopods not produced posteriorly 10
10a. Left chela triangular in cross-section, dactyl and fixed finger not dorsoventrally flattened ..... *Anisopagurus* new genus
10b. Left chela not triangular in cross-section, dactyl and fixed finger dorsoventrally flattened ..... *Manucomplanus* new genus
11a. Propodus of 4th pereopods with one row of scales ..... *Enallopagurus* new genus
11b. Propodus of 4th pereopods with two or more rows of scales ..... *Enallopaguropsis* new genus

Pylopagurus A. Milne Edwards and Bouvier, 1891 sensu stricto

Type species.—*Eupagurus discoidalis* A. Milne Edwards, 1880, by subsequent designation by Miyake, 1978: 119.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles triangular, often acutely so, with moderately strong submarginal spine; separated basally by equivalent or greater than basal width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds unarmed or with 1 or 2 spines on each side of median depression or cleft.

Right cheliped with chela ovate to subrectangular; angle of articulation of chela and carpus perpendicular or 5°–10° from perpendicular. Left cheliped with chela usually small, dactyl and fixed finger dorsoventrally compressed, palm without prominent keel or crest; angle of articulation of chela and carpus varying from 30°–90° from perpendicular. Sternite of 3rd pereopods with anterior projection small, subcircular, subovate or slender. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyls well developed, claw elongate, curved; preungual process prominent, positioned laterally near base of claw. Thoracic sternites of pereopods 3–5 often with capsulate setae.

Abdomen straight or flexed. Uropods symmetrical or nearly so. Telson with transverse suture; posterior lobes symmetrical or nearly so, terminal margins concave or oblique, armed with series of small to moderately strong spines. Males without paired pleopods, with 3 unpaired, usually biramous pleopods with endopods reduced or rudimentary, occasionally vestigal. Females with paired 1st

pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced or vestigial.

Species herein assigned to *Pylopagurus* s. s. include: *Pylopagurus discoidalis* (A. Milne Edwards, 1880); *Pylopagurus holmesi* Schmitt, 1921; *Pylopagurus longicarpus* Walton, 1954; *Pylopagurus stewarti* (Filhol, 1883); and *Pylopagurus serpulophilus* Miyake, 1978.

Lophopagurus new genus

Type species.—*Eupagurus thompsoni* Filhol, 1885.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles narrowly triangular, with moderately strong submarginal spine; separated basally by approximately basal width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds usually unarmed.

Right cheliped with palm of chela usually subrectangular; angle of articulation of chela and carpus perpendicular or 1°–15° from perpendicular. Left cheliped with chela broadly triangular in dorsal view and in cross-section, dorsal midline usually produced into prominent spinose or tuberculate keel or crest; angle of articulation of chela and carpus perpendicular or only slightly off perpendicular. Sternite of 3rd pereopods with anterior projection subsemicircular. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl well developed, claw elongate, curved; preungual process small to moderate at base of dactyl. Sternites of pereopods 3–5 with or without capsulate setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes symmetrical or nearly so, terminal margins straight or slightly rounded, armed with numerous small to moderately strong spines. Males without paired pleopods, with 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Species herein assigned to *Lophopagurus* include: *Pylopagurus thompsoni* (Filhol, 1885); *Pylopagurus lacertosus* (Henderson, 1888); *Pylopagurus nanus* (Henderson, 1888); and *Pylopagurus crenatus* (Borradaile, 1916); *Pylopagurus cristatus* (H. Milne Edwards, 1836) is questionably assigned to this genus.

Rhodochirus new genus

Type species.—*Pylopagurus rosaceus* A. Milne Edwards and Bouvier, 1893.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles triangular, with small submarginal spine; separated basally by basal width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds unarmed or with minute denticles on either side of midline.

Right cheliped with chela subovate, spines and tubercles with basal rosettes; articulation of chela and carpus approximately 15° from perpendicular. Left cheliped with chela usually moderately broad, spines and tubercles with basal rosettes; articulation of chela and carpus 45°–60° from perpendicular. Sternite of 3rd pereopods with anterior lobe subsemicircular, often slightly skewed. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl well developed, claw elongate, curved; preungual process well developed on lateral face near base of claw. Sternites of pereopods 3–5 of males with capsulate setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes asymmetrical, triangular, with terminal margins oblique and

armed with few small to large spines. Males without paired pleopods, with 3 unpaired, biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Species herein assigned to *Rhodochirus* include: *Pylopagurus rosaceus* A. Milne Edwards and Bouvier, 1893 and *Pylopagurus hirtimanus* Faxon, 1893. *Pylopagurus acutus* Forest and De Saint Laurent, 1968 is considered a synonym of *Rhodochirus rosaceus*.

Australeremus new genus

Type species.—*Eupagurus cooki* Filhol, 1883.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles acutely triangular, with submarginal spine; separated basally by basal width or less of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds with small spine on either side of midline. Right cheliped with chela subrectangular; angle of articulation of chela and carpus approximately 15° from perpendicular. Left cheliped with lateral margin of chela expanded and elevated; angle of articulation of chela and carpus 75°–90° from perpendicular. Sternite of 3rd pereopods with anterior lobe subovate. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl short, claw small; preungual process small. Sternites of pereopods 3–5 usually without capsulate setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes subequal, terminal margins rounded, armed with few moderately strong spines. Males without paired pleopods, with 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

In addition to the type species, *Pylopagurus cooki* (Filhol, 1883) *Pylopagurus kirki* (Filhol, 1883) is questionably assigned to this genus.

Phimochirus new genus

Type species.—*Eupagurus operculatus* Stimpson, 1859.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles narrow, often subrectangular, with small submarginal spine; separated basally by less than basal width of 1 acicle. Crista dentata well developed; accessory tooth present. Sternite of 3rd maxillipeds unarmed, midline occasionally with slight depression.

Right cheliped with chela operculate; angle of articulation of chela and carpus perpendicular. Left cheliped with chela small, subtriangular in cross-section, but not produced into prominent keel or crest; angle of articulation of chela and carpus 15°–20° from perpendicular. Sternite of 3rd pereopods with anterior lobe semisubovate. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl moderately short, claw usually elongate and curved; preungual process very prominent at base of claw laterally. Sternite of 5th pereopods often with clusters of capsulate setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes subequal, terminal margins oblique, each with series of moderately strong spines. Males without paired pleopods, with 3 unpaired biramous pleopods, endopods reduced. Females with paired 1st pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Species herein assigned to *Phimochirus* include: *Pylopagurus operculatus* (Stimpson, 1859); *Pylopagurus californensis* (Benedict, 1892); *Pylopagurus mexicanus* (Benedict, 1892); *Pylopagurus venustus* (Bouvier, 1898); *Pylopagurus roseus* (Benedict, 1892); *Pylopagurus randalli* Provenzano, 1961; and *Pylopagurus holthuisi* Provenzano, 1961. *Pylopagurus occlusus* (Henderson, 1888) and *Pylopagurus liochele* Barnard, 1947 questionably are assigned to this genus.

Haigia new genus

Type species.—*Pylopagurus diegensis* Scanland and Hopkins, 1969.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles roundly triangular, with submarginal spine; separated basally by basal width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds with spine on each side of midline.

Right cheliped with chela subquadrate to subrectangular; angle of articulation of chela and carpus approximately 15° from perpendicular. Left cheliped with lateral margin of chela somewhat expanded, chela triangular in cross-section, but not elevated into prominent keel or crest; angle of articulation of chela and carpus approximately 15° from perpendicular. Sternite of 3rd pereopods with anterior lobe semisubcircular. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl moderately short, claw long; preungual process apparently lacking. Sternites of pereopods 3–5 typically without capsulate setae.

Abdomen flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes subequal, terminal margins slightly excavated, straight, armed with series of small spines. Males without paired pleopods, with 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

At present this genus is represented only by the type speices, *Haigia diegensis*.

Agaricochirus new genus

Type species.—*Pylopagurus boletifer* A. Milne Edwards and Bouvier, 1893.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles triangular, with moderately strong submarginal spine; separated basally by equivalent or greater than basal width of 1 acicle. Crista dentata well developed; accessory tooth present. Sternite of 3rd maxillipeds with prominent spine on either side of usually concave midline.

Right cheliped with chela generally subovate, armature usually in form of "mushroom-like" tubercles. Left cheliped with chela moderately well developed; angle of articulation of chela and carpus varying from 60°–75° from perpendicular. Carpi of 2nd and 3rd pereopods without dorsodistal spine. Sternite of 3rd pereopods with anterior lobe very small or absent (except in *A. gibbosimanus*). Fourth pereopods with propodal rasp consisting of several rows of corneous scales; dactyl very short, claw prominent; preungual process lateral, very small. Sternite of 5th pereopods often with capsulate setae.

Abdomen straight or flexed, often very short. Uropods symmetrical or nearly so; exopods considerably larger than endopods; protopods produced posteriorly, often strongly so. Telson with transverse suture; posterior lobes symmetrical or nearly so, terminal margins unarmed. Males without paired pleopods, with 3 unpaired, usually uniramous pleopods. Females with paired 1st pleopods modified as gonopods, with 4 unpaired pleopods, 2nd–4th biramous, 5th uniramous.

Species herein assigned to *Agaricochirus* include: *Pylopagurus boletifer* A. Milne Edwards and Bouvier, 1893; *Pylopagurus alexandri* A. Milne Edwards and Bouvier, 1893; *Pylopagurus cavimanus* Chace, 1939; *Pylopagurus erosus* (A. Milne Edwards, 1880); *Pylopagurus gibbosimanus* (A. Milne Edwards, 1880); and *Pagurus hispidus* (Benedict, 1892).

Anisopagurus new genus

Type species.—*Pylopagurus bartletti* A. Milne Edwards and Bouvier, 1893.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles triangular, with 1 to several strong marginal or submarginal spines; separated basally by approximately basal width of 1 acicle. Crista dentata well developed, 1 or more accessory teeth present. Sternite of 3rd maxillipeds with very small to strong spine on either side of midline.

Right cheliped with chela suboperculate; angle of articulation of chela and carpus approximately 15° from perpendicular. Left cheliped with chela triangular in cross-section, occasionally with lateral margin expanded; angle of articulation of chela and carpus approximately 15° from perpendicular. Sternite of 3rd pereopods with anterior lobe subquadrate to subovate. Fourth pereopods with propodal rasp consisting of several rows of corneous scales; dactyl moderately long; preungual process moderately well developed at base of claw. Sternites of pereopods 3–5 sometimes with capsulate setae.

Abdomen typically flexed. Uropods markedly asymmetrical. Telson with transverse suture; posterior lobes subequal, margins rounded to slightly oblique, armed with few to numerous small spines. Males without paired pleopods, with 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Species herein assigned to *Anisopagurus* include: *Pylopagurus bartletti* A. Milne Edwards and Bouvier, 1893 and *Pylopagurus pygmaeus* (Bouvier, 1918).

Manucomplanus new genus

Type species.—*Eupagurus corallinus* Benedict, 1892.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles broadly triangular, with strong submarginal spine; separated basally by basal width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds with moderately strong spine on either side of midline.

Right cheliped with chela subovate to ovate; articulation of chela and carpus perpendicular. Left cheliped with chela broad, dactyl and fixed finger broad and dorsoventrally flattened, hiatus prominent; angle of articulation of chela and carpus 15°–30° from perpendicular. Sternite of 3rd pereopods with anterior lobe elongate and slender, often extremely so. Fourth pereopods with propodal rasp consisting of several rows of corneous scales; dactyl very short, claw short, preungual process well developed at base of claw. Sternites of 3rd–5th pereopods usually without capsulate setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes subquadrate to roundly triangular, subequal, terminal margins rounded or somewhat oblique, with few to several moderately strong spines often interspersed with smaller spines. Males without paired pleopods, with 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st

pleopods modified as gonopods, with 4 unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Species herein assigned to *Manucomplanus* include: *Pylopagurus corallinus* (Benedict, 1892); *Pylopagurus cervicornis* (Benedict, 1892); *Pylopagurus spinulosus* Holthuis, 1959; *Pylopagurus longimanus* Faxon, 1893; and *Pylopagurus varians* (Benedict, 1892). *Pylopagurus ungulatus* (Studer, 1883) is questionably assigned to this genus; this taxon is not *Pylopagurus ungulatus*: A. Milne Edwards and Bouvier, 1893. The latter is a misidentified specimen of *M. corallinus*.

Enallopagurus new genus

Type species.—*Pylopagurus spinicarpus* Glassell, 1938.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles triangular, with strong submarginal spine; separated basally by equivalent or greater than basal width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds with spine on either side of midline.

Right cheliped with chela suboperculate; angle of articulation of chela and carpus approximately 15° from perpendicular. Left cheliped with chela triangular in cross-section but not elevated into prominent keel or crest; angle of articulation of chela and carpus 15°–20° from perpendicular. Sternite of 3rd pereopods with anterior lobe subcircular to subovate. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl moderately well developed, claw moderately long; preungual process very small. Sternites of pereopods 3–5 often with small capsulate setae.

Abdomen straight or flexed. Uropods asymmetrical. Telson without transverse suture, margins entire, unarmed. Males without paired pleopods, with 3 unpaired uniramous pleopods. Females with paired 1st pleopods modified as gonopods, with 4 unpaired pleopods, 2nd–4th biramous, 5th uniramous.

Species herein assigned to *Enallopagurus* include: *Pylopagurus spinicarpus* Glassell, 1938; *Pylopagurus affinis* Faxon, 1893; and *Pylopagurus coronatus* (Benedict, 1892).

Enallopaguropsis new genus

Type species.—*Pylopagurus guatemoci* Glassell, 1937.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles acutely triangular, with moderately well developed submarginal spine; separated basally by approximate width of 1 acicle. Crista dentata well developed, accessory tooth present. Sternite of 3rd maxillipeds with strong spine on either side of concave midline.

Right cheliped with chela suboperculate; angle of articulation of chela and carpus perpendicular. Left chela subtriangular in cross-section but without prominent keel or crest; angle of articulation of chela and carpus approximately 60° from perpendicular. Sternite of 3rd pereopods with anterior lobe represented by single large capsulate seta. Fourth pereopod with propodal rasp consisting of several rows of corneous scales; dactyl moderately long, claw well developed; preungual process moderately well developed at base of claw. Sternites of pereopods 3–5 often with few large capsulate setae.

Abdomen typically straight. Uropods asymmetrical. Telson without transverse suture, margins entire, unarmed. Males without paired pleopods, with 3 unpaired pleopods with endopods reduced or absent. Females with paired 1st pleopods modified as gonopods, with 4 unpaired pleopods, 2nd–4th biramous, 5th with endopod reduced or absent.

Species herein assigned to *Enallopaguropsis* include: *Pylopagurus guatemoci* Glassell, 1937 and *Pylopagurus hancocki* Walton, 1954.

Geographical Distribution

Some interesting geographical patterns in the distribution of species as now reassigned are apparent. *Pylopagurus* s.s. remains cosmopolitan; however, species of *Lophopagurus* and *Australeremus* are known only from Australian-New Zealand waters. *Agaricochirus* and *Anisopagurus* are represented in the Atlantic only, whereas *Haigia*, *Enallopagurus*, and *Enallopaguropsis* are found exclusively in the Pacific. Species of *Rhodochirus*, *Enallopagurus*, *Phimochirus*, and *Manucomplanus* like *Tomopagurus*, occur in both the Atlantic and Pacific.

Tomopagurus A. Milne Edwards and Bouvier, 1893

Tomopagurus A. Milne Edwards and Bouvier, 1893: 70. Type species by monotypy *Tomopagurus rubropunctatus* A. Milne Edwards and Bouvier, 1893: 71. Gender: masculine.

Benthopagurus Wass, 1963: 134. Type species by original designation *Benthopagurus schmitti* Wass, 1963: 136. Gender: masculine.

Diagnosis.—Eleven pairs phyllobranch gills. Ocular acicles narrowly triangular, with small submarginal spine; usually separated basally by basal width or less of 1 acicle, occasionally separation exceeds basal width of 1 acicle. Crista dentata moderately well developed, accessory tooth present. Sternite of 3rd maxillipeds unarmed or with minute spinule on either side of midline.

Right cheliped with spinose or tuberculate, non-operculate chela; angle of articulation of chela and carpus 10°–25° from perpendicular; carpus with mesial face concave, often markedly so. Left cheliped with chela triangular in cross-section but usually not developed as keel or crest; dactyl and fixed finger "spoon-shaped" ventrally. Sternite of 3rd pereopods with anterior projection subovate to subsemicircular. Fourth pereopods with propodal rasp consisting of single row of corneous scales; dactyl well developed, claw elongate, curved; preungual process prominent, lateral near base of claw. Sternites of pereopods 3–5 of males often with capsulate setae, interspersed with typical setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes asymmetrical, triangular, terminal margins oblique, armed with several to many slender spines. Males usually without paired pleopods, with 3 unpaired biramous pleopods with endopods reduced; rarely with paired 1st pleopods reduced or vestigial. Females usually with paired 1st pleopods modified as gonopods (except in *Tomopagurus wassi* n. sp.), with 4 unpaired biramous pleopods, 2nd–4th with both rami moderately well developed, 5th with endopod reduced.

Species herein assigned to *Tomopagurus* include: *Tomopagurus rubropunctatus* A. Milne Edwards and Bouvier, 1893; *Tomopagurus cokeri* (Hay, 1917); *Tomopagurus maclaughlinae* Haig, 1976; *Tomopagurus wassi* n. sp.; *Pagurus purpuratus* (Benedict, 1892); *Tomopagurus cubensis* (Wass, 1963); *Pylopagurus chacei* Wass, 1963; and *Pagurus merimaculosus* Glassell, 1937.

Remarks.—As noted by Haig (1976), *Tomopagurus* originally was established for a single male specimen from Barbados, parasitized by *Peltogaster* sp. During studies of western Atlantic and Caribbean pagurids, Provenzano (in Forest and De Saint Laurent, 1968) found gonopod-bearing females assignable to *Pagurus rubrolineatus* Wass, 1963, known previously only from the male holotype. Provenzano's comparison of his female, as well as male, specimens of this taxon

with Milne Edwards and Bouvier's *T. rubropunctatus* showed that the two species were identical except for one character. The male of *T. rubropunctatus* had a pair of small gonopods on the first abdominal somite, whereas the males of *P. rubrolineatus* did not. Provenzano, Forest and De Saint Laurent presumed that the feminizing effect of infestation by *Peltogaster* sp. had induced the development of both female-type pleopods and paired gonopods; therefore, they placed *P. rubrolineatus* in synonymy with *T. rubropunctatus*.

The Provenzano, Forest and De Saint Laurent hypothesis is supported by the presence of at least one gonopod on a damaged male syntype of *Rhodochirus hirtimanus* parasitized by a rhizocephalan (personal examination). Numerous studies on the effects of rhizocephalan infestation have confirmed varying degrees of feminization of the male pleopods in pagurids (e.g., Potts, 1906; Nilsson-Cantell, 1926; Shiino, 1931; Reinhard, 1942; Oguro, 1955). Nielsen (1970) has reported the presence of a complete set of female pleopods in some infected males of *Pagurus prideauxi* Leach, a species in which pleopods are absent in normal males. Nielsen also has noted the varying degrees of reduction of the sexual tube in some parasitized males of *Anapagurus laevis* (Bell). A reduction in gonopores has been noted in parasitized specimens of both sexes (Reinhard, 1942; Oguro, 1955; Nielsen, 1970). Studies have shown that secondary male sexual characters in many crustaceans are under the control of the androgenic gland, and in the case of at least one hermit crab, *Diogenes pugilator* (Roux), rhizocephalan infestation results in some degeneration of this gland (Veillet and Graf, 1958; Charniaux-Cotton, 1960). The acquisition of a permanent female secondary sexual structure, oöstegites, in males of certain amphipods has been induced experimentally through the removal of the androgenic gland and the injection of an ovarian hormone (Charniaux-Cotton, 1960); however, simple elimination of the androgenic gland in the male did not lead to the development of oöstegites. The observations of female gonopods in infected male pagurids point to the need for more detailed studies of parasitism in the gonopod bearing genera.

During Provenzano's studies, he found that another of Wass' (1963) species, *Benthopagurus schmitti* Wass appeared to be identical with a previously described species, *Pagurus cokeri* Hay. Originally Hay (1917) described his new hermit crab from the western Atlantic on the basis of two male specimens and assigned it to *Pagurus* without considering that characters of the females might not be applicable to that genus. Females of *B. schmitti* were described as having paired first pleopods; however, among Provenzano's material were females both with and without gonopods. As all the specimens appeared to be identical, he concluded that not only was *B. schmitti* a synonym of *P. cokeri*, but that the presence of female gonopods was variable. As *Benthopagurus* differed from *Tomopagurus* only in the presence of gonopods, Forest and De Saint Laurent (1968) placed *Benthopagurus* in synonymy. In their redescription of *Tomopagurus* these authors included a statement regarding the variability of the gonopods in the female.

Among the specimens assigned to *Tomopagurus cokeri* (Hay), Wass and Provenzano both had two distinct taxa, *T. cokeri* sensu stricto, with gonopod-bearing females and *Tomopagurus wassi* n. sp. with females usually lacking gonopods. This is not the only instance of gonopod variability in the genus. Vestigial gonopods have been observed in some apparently non-parasitized males as well. Variability in the occurrence of gonopods in uninfected males also is reported for *Parapagurus* (De Saint Laurent, 1972), although the variation appears to be interspecific rather than intraspecific as in some species of *Tomopagurus*. Hazlett (1972 and personal communication) has found behavioral differences of consid-

erable magnitude between *T. cokeri* and *T. cubensis*; however, the behavioral patterns of the other taxa assigned to the genus have not been observed. There also are several morphological differences between the two species, but when all species assigned to the genus are considered collectively there are no well defined distinctions that would justify even species-group separation of *T. cubensis*.

KEY TO THE SPECIES OF *TOMOPAGURUS*

1a. First antennal segment with prominent, often hooked, lateral spine 2
1b. First antennal segment without prominent, often hooked, lateral spine 5
2a. Propodus and dactyl of left 3rd pereopod with lateral faces densely setose 3
2b. Propodus and dactyl of left 3rd pereopod with lateral faces not densely setose ..... *T. rubropunctatus*
3a. Propodus and dactyl of 2nd pereopods with dorsal surfaces unarmed 4
3b. Propodus and dactyl of 2nd pereopods with dorsal surfaces armed with granules or low tubercles ..... *T. maclaughlinae*
4a. Carpus of right 2nd pereopod with 1 spine on dorsal margin ..... *T. cokeri*
4b. Carpus of right 2nd pereopod with more than 1 spine on dorsal margin ..... *T. wassi* n. sp.
5a. Dorsal surface of right chela with spinulose or blunt tubercles 6
5b. Dorsal surface of right chela with prominent acute spines ..... *T. cubensis*
6a. Dactyl and propodus of 3rd pereopod with lateral faces convex, not densely setose 7
6b. Dactyl and propodus of 3rd pereopod with lateral faces concave, densely setose *T. purpuratus*
7a. Carpus of 2nd right pereopod with 1 or 2 strong spines on dorsal margin distally; Atlantic ..... *T. chacei*
7b. Carpus of 2nd right pereopod with several strong spines on dorsal margin; Pacific ..... *T. merimaculosus*

Tomopagurus rubropunctatus A. Milne Edwards and Bouvier, 1893
Figures 1a; 7d; 8d

Tomopagurus rubropunctatus A. Milne Edwards and Bouvier, 1893: 71, pl. 6, figs. 1–6 (type locality: Barbados, W. I., BLAKE station 290).—Forest and De Saint Laurent, 1968: 114.
Pagurus rubrolineatus Wass, 1963: 151, fig. 9 (type locality: Rosalind Bank, Caribbean Sea, 16°35'N 80°55'W, OREGON station 1890).—Forest and De Saint Laurent, 1968: 114.

Holotype of *Tomopagurus rubropunctatus*: ♂ (Shield length, SL = 6.9 mm) MCZ. Holotype of *Pagurus rubrolineatus*: ♂ (SL = 8.3 mm) USNM 108752.

Material Examined.—See Table 1.

Diagnosis.—Shield slightly wider than long; rostrum broadly rounded, typically without terminal spine; lateral projections acutely triangular, with strong marginal spine. Ocular peduncles moderately short, with corneae slightly dilated; ocular acicles acutely triangular, with strong submarginal spine; separated basally by two-thirds basal width of 1 acicle. First segment of antennal peduncle with moderately strong, usually hooked, lateral spine. Right chela with dorsal surface armed with moderately strong spines, spines of dorsomesial and dorsolateral margins not markedly stronger. Left chela with dorsal surface armed with moderately strong spines; dactyl with few spinules mesially. Carpi of 2nd pereopods with 1 or 2 spines on dorsal surface distally; dactyl with dorsal row of corneous spinules. Left 3rd pereopod with lateral faces of dactyl and propodus convex, not densely setose. Sternite of 3rd pereopods with anterior lobe subsemicircular; typically with few capsulate setae. Telson with terminal margins suboblique, each armed with several acute or blunt spines.

Distribution.—Western Atlantic and Caribbean Sea; 73–238 m.

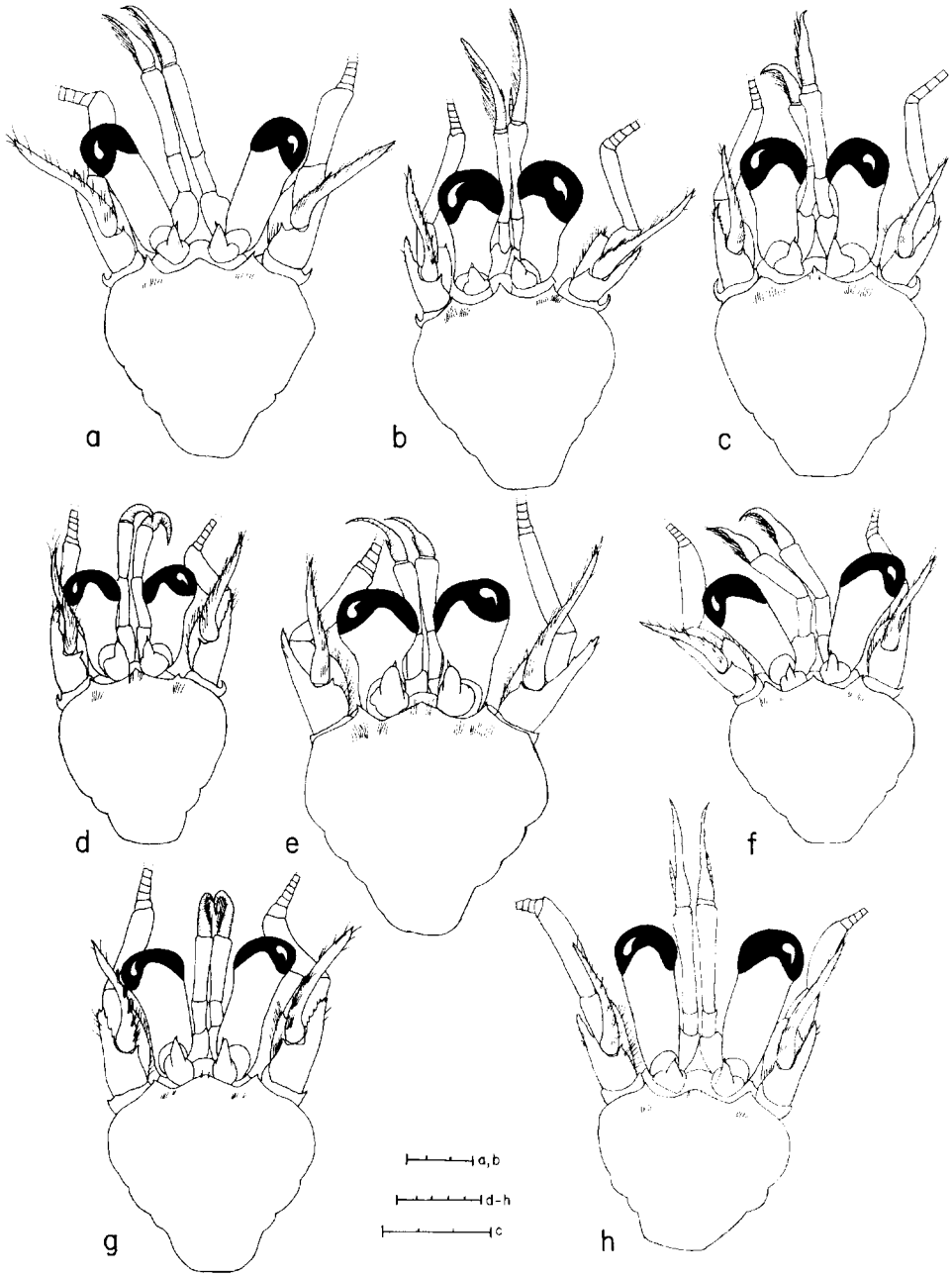

Figure 1. Diagrammatic shield and cephalic appendages: (a) *Tomopagurus rubropunctatus*; (b) *Tomopagurus wassi* new species; (c) *Tomopagurus maclaughlinae* (after Haig, 1976); (d) *Tomopagurus cokeri*; (e) *Tomopagurus cubensis*; (f) *Tomopagurus purpuratus*; (g) *Tomopagurus merimaculosus*; (h) *Tomopagurus chacei*. Scales equal 3 mm (a–c) and 5 mm (d–h).

Tomopagurus maclaughlinae Haig, 1976
Figures 1c; 2c; 3c; 4c

Tomopagurus maclaughlinae Haig, 1976: 27, figs. 1–3 (type locality: off Daphne Minor Island, Galapagos Islands, 0°24′30″S, 90°22′40″W, VELERO III Station 792-38).

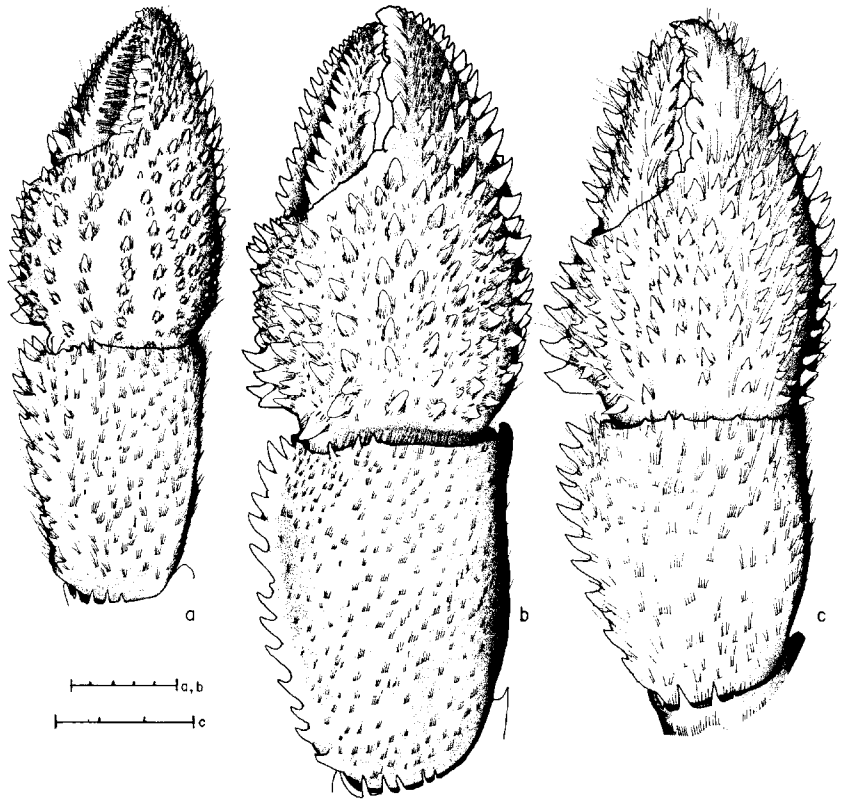

Figure 2. Right chelae and carpi: (a) *Tomopagurus cokeri*; (b) *Tomopagurus wassi* new species; (c) *Tomopagurus maclaughlinae* (from Haig, 1976). Scales equal 5 mm (a,b) and 3 mm (c).

Holotype.—♀ (SL = 5.9 mm) AHF 3823.

Material Examined.—See Table 2.

Diagnosis.—Shield approximately as long as broad; rostrum obtusely triangular, with acute terminal spine; lateral projections obtusely triangular, with strong

Table 1. *Tomopagurus rubropunctatus* Milne Edwards and Bouvier (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Western Atlantic							
26°01′N 79°10′W	143–210	GERDA 725 UMML 32:4981	8/3/65	1		7.7	RSMAS
Caribbean							
16°35′N 80°55′W	73	OREGON 1890 USNM 108752	8/24/57	1		8.3	NMFS
14°15.5′N 80°27.1′W	219–238	OREGON 4832 UMML 32:4982	5/12/64	2	2	3.1–5.1	NMFS
14°15.5′N 80°25.7′W	82–146	OREGON 4833 UMML 32:4983	5/12/64		1	5.2	NMFS
Off Barbados	133	BLAKE 290 MCZ	—	1		6.9	U.S. Coast Survey

Table 2. *Tomopagurus maclaughlinae* Haig (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Galapagos Islands							
0°24.5'S 90°22.7'W	128–146	VELERO III 792-38 AHF 3823	1/20/38		1	5.9	AHF

marginal spine. Ocular peduncles moderately short, with corneae strongly dilated; ocular acicles subtriangular, with strong submarginal spine; separated basally by two-thirds basal width of 1 acicle. First segment of antennal peduncle with strong hooked spine laterally. Right chela with dorsal surface armed with moderately strong spines, dorsomesial and dorsolateral marginal spines markedly stronger. Left chela with dorsal surface armed with moderately strong spines; dactyl with short row of spines on dorsal midline proximally. Dactyls and propodi of 2nd pereopods with granulate dorsal surfaces; carpi with several dorsodistal spines. Left 3rd pereopod with lateral faces of propodus and dactyl slightly concave and densely setose. Sternite of 3rd pereopods with anterior lobe subsemicircular, slightly skewed. Telson with terminal margins obliquely concave, right armed with 11 acute spines, left with 10.

Distribution.—Known only from type locality; 128–146 m.

Tomopagurus cokeri (Hay, 1917) sensu stricto
Figures 1d; 2a; 3a; 4a; 7a; 8a

Pagurus cokeri Hay, 1917: 73 (type locality: 30 mi. S of Cape Lookout lightship).—Hay and Shore, 1918: 412, fig. 16, pl. 30, fig. 2.—Forest and De Saint Laurent, 1968: 114.

Benthopagurus schmitti Wass, 1963: 136, fig. 2a–g (type locality: south of Tortugas), in part.—Forest and De Saint Laurent, 1968: 114, in part.

?*Benthopagurus cokeri*: Hazlett, 1966: 84, in part.

Tomopagurus cokeri: Forest and De Saint Laurent, 1968: 114, in part.—Haig, 1976: 27.

Holotype of *Pagurus cokeri*: ♂ (SL = 6.0 mm) USNM 49638. Holotype of *Benthopagurus schmitti*: ♀ (SL = 7.5 mm) USNM 108753.

Material Examined.—See Table 3.

Diagnosis.—Shield usually longer than broad; rostrum triangular, with acute terminal spine; lateral projections obtusely triangular, with strong marginal or submarginal spine. Ocular peduncles moderately short, with corneae usually strongly dilated; ocular acicles subovate to subtriangular, with prominent submarginal spine; separated basally by at least basal width of 1 acicle. First segment of antennal peduncle with prominent hooked or curved spine laterally. Right chela with dorsal surface armed with irregular longitudinal rows of moderately strong spines, dorsomesial and dorsolateral marginal spines moderately small. Left chela with dorsal surface armed with irregular rows of small spines; dactyl with row of small spines dorsomesially on proximal half. Dactyls and propodi of 2nd pereopods with short transverse rows of stiff setae dorsally; carpi each with single spine at dorsodistal margin. Left 3rd pereopod with lateral faces of dactyl and propodus each with longitudinal sulcus and dense tufts of stiff setae. Sternite of 3rd pereopods with anterior lobe semisubquadrate or broadly semisubovate and with dense cluster of stiff setae anteriorly. Telson with terminal margins oblique, armed with numerous small calcareous acute or blunt spines, lateral margins often similarly armed.

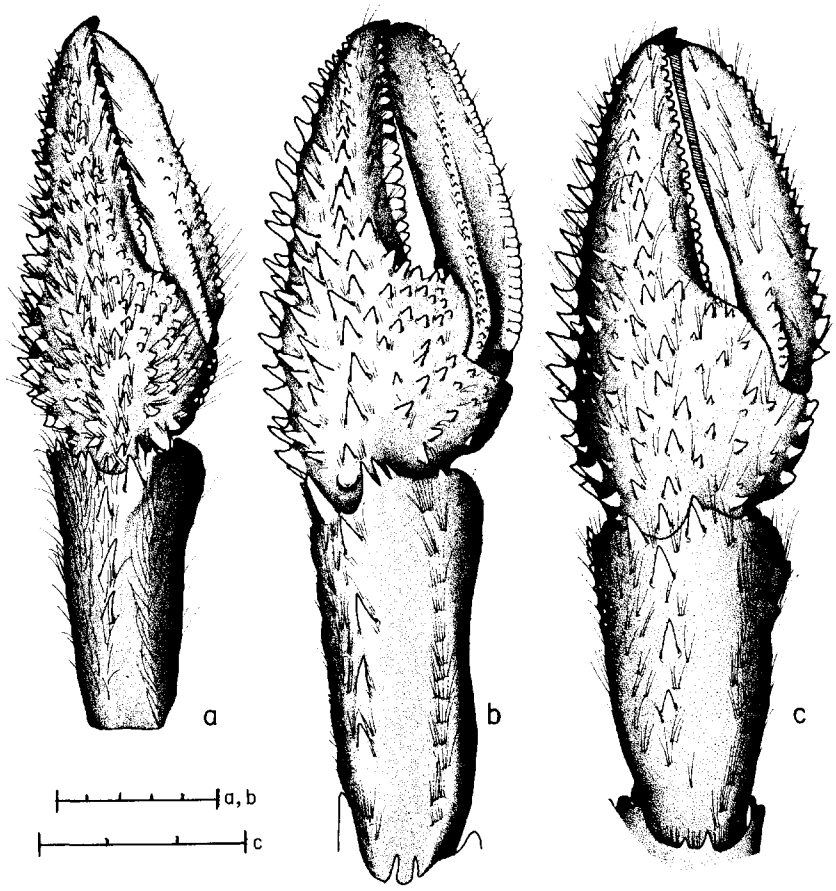

Figure 3. Left chelae and carpi: (a) *Tomopagurus cokeri*; (b) *Tomopagurus wassi* new species; (c) *Tomopagurus maclaughlinae* (from Haig, 1976). Scales equal 5 mm (a,b) and 3 mm (c).

Distribution.—Western Atlantic, Gulf of Mexico and Caribbean; 44–302 m.

Tomopagurus wassi new species
Figures 1b; 2b; 3b; 4b; 5; 6; 7b, c; 8b

Benthopagurus schmitti Wass, 1963: 136, in part, not fig. 2a–g.—Forest and De Saint Laurent, 1968: 114, in part.
Benthopagurus cokeri: Hazlett 1966: 84, in part.
Tomopagurus cokeri: Forest and De Saint Laurent, 1968: 114, in part.

Holotype.— ♀ (SL = 10.7 mm) USNM 108757.

Type locality.—Off Venezuela, OREGON station 1985, 09°41′N 59°47′W.

Material Examined.—See Table 4.

Description.—Shield as long or longer than broad, anterolateral margins sloping or slightly terraced, anterior margin between rostrum and lateral projections concave, posterior margin truncate; dorsal surface with tufts of short setae. Rostrum short to moderately long, acutely or obtusely triangular, occasionally slightly rounded, with or without terminal spine. Lateral projections obtusely triangular, terminating in usually acute, strong marginal spine.

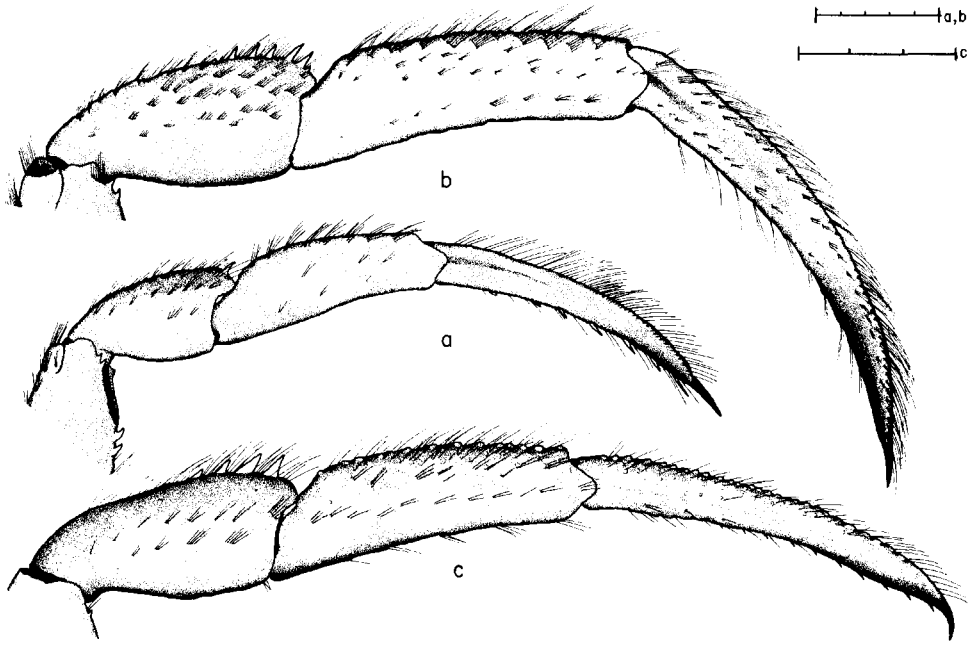

Figure 4. Second right pereopods: (a) *Tomopagurus cokeri*; (b) *Tomopagurus wassi* new species; (c) *Tomopagurus maclaughlinae* (from Haig, 1976). Scales equal 5 mm (a,b) and 3 mm (c).

Ocular peduncles short, corneae usually strongly dilated; dorsal and mesial faces with tufts of moderately short setae. Ocular acicles usually acutely triangular, dorsal surface slightly concave; terminating subacutely, usually with moderately strong submarginal spine; separated basally by at least basal width of 1 acicle.

Antennular peduncles moderately long, often exceeding ocular peduncles by three-fourths length of ultimate segment. Ultimate and penultimate segments each with row of fine setae on dorsal surface; basal segment with strong acute spine on lateral face dorsally and small spine on ventromesial distal margin.

Antennal peduncle moderately long, approximately equalling length of antennular peduncle; with supernumerary segmentation (cf. McLaughlin, 1974). Fifth and fourth segments each with few scattered setae. Third segment with strong spine on ventrodistal margin, partially obscured by tufts of stiff setae. Second segment with dorsolateral distal angle strongly produced, terminating in small, simple or bifid spine, mesial margin with row of small acute spines, lateral margin with 1 or 2 small spines, or unarmed; dorsomesial distal angle with strong spine, mesial margin with long setae. First segment with very prominent, acute hooked spine on dorsolateral margin, ventral margin produced, with few to several spinules or denticles laterally. Antennal acicle moderately long, often reaching distal half of 5th peduncular segment, somewhat arcuate; terminating in small simple or bifid spine; mesial margin with tufts of moderately long setae. Flagella long, every 3rd to 8th article with 1 or 2 short to moderately long setae.

Mandible without distinguishing characters. Maxillule (Fig. 5a) usually with 1 stiff bristle on moderately well developed internal endopodal lobe, external lobe produced, not recurved; proximal endite subtriangular. Maxilla (Fig. 5b) with endopod slightly exceeding scaphognathite in distal extension. First maxilliped

Table 3. *Tomopagurus cokeri* (Hay) (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Western Atlantic							
30 mi S Lookout lightship	—	— USNM 49638	8/15	2		6.0, 4.3	U.S. Bur. Fish.
30°3.5′N 77°33.5′W	183	SILVER BAY 2539 UMML 32:4663	12/5/60		1	6.1	NMFS
Gulf of Mexico							
South of Tortugas	144–256	— USNM 108753	7/2/32		1	7.5	W. L. Schmitt
24°40′N 80°41.5′W	183	SILVER BAY 2387 UMML 32:4665	10/26/60		1	4.6	NMFS
24°32′N 81°08′W	100	GERDA 977 UMML 32:4455	2/8/68		1	7.1	RSMAS
24°30′N 80°50′W	220	GERDA 135 UMML 32:4457	6/21/63	1	1	8.5, 9.0	RSMAS
24°29.5′N 80°50′W	191	GERDA 134 UMML 32:4449	6/21/63	1		4.6	RSMAS
24°29′N 80°50′W	275–302	GERDA 132 UMML 32:4465	6/21/63		1	5.9	RSMAS
24°26′N 80°58′W	198	GERDA 836 UMML 32:4655	7/11/67		1	7.3	RSMAS
24°25′N 81°25′W	176	GERDA 360 UMML 32:4447	9/15/64	1		5.6	RSMAS
24°24′N 80°52′W	222–230	GERDA 972 UMML 32:4659	2/5/68		1	4.4	RSMAS
24°24′N 81°59′W	137	SILVER BAY 2425 UMML 32:4662	10/29/61	1		6.7	NMFS
24°23.5′N 81°59′W	210–219	SILVER BAY 2426 UMML 32:4666	10/29/61		1	6.5	NMFS
24°22′N 81°11′W	187–198	GERDA 835 UMML 32:4656	7/11/67		1	6.7	RSMAS
24°21.6′N 81°58.2′W	179	FISH HAWK 7279 USNM 107821	2/14/02	1	3	3.5–7.0	U.S. Bur. Fish.
24°19′N 81°07′W	234	GERDA 863 UMML 32:4454	8/29/67		1	6.3	RSMAS
24°18′N 81°07′W	223	GERDA 864 UMML 32:4657	8/29/67	1	1	5.5, 5.6	RSMAS
24°18′N 82°33′W	186–199	GERDA 432 UMML 32:4448	11/28/64		1	5.3	RSMAS
Caribbean							
19°58′N 91°47′W	44	SILVER BAY 1118 UMML 32:4661	4/12/59	1		4.8	NMFS
Southwestern Atlantic							
06°29′N 52°30′W	201–220	OREGON 2461 UMML 32:4663	9/10/58	1		7.4	NMFS

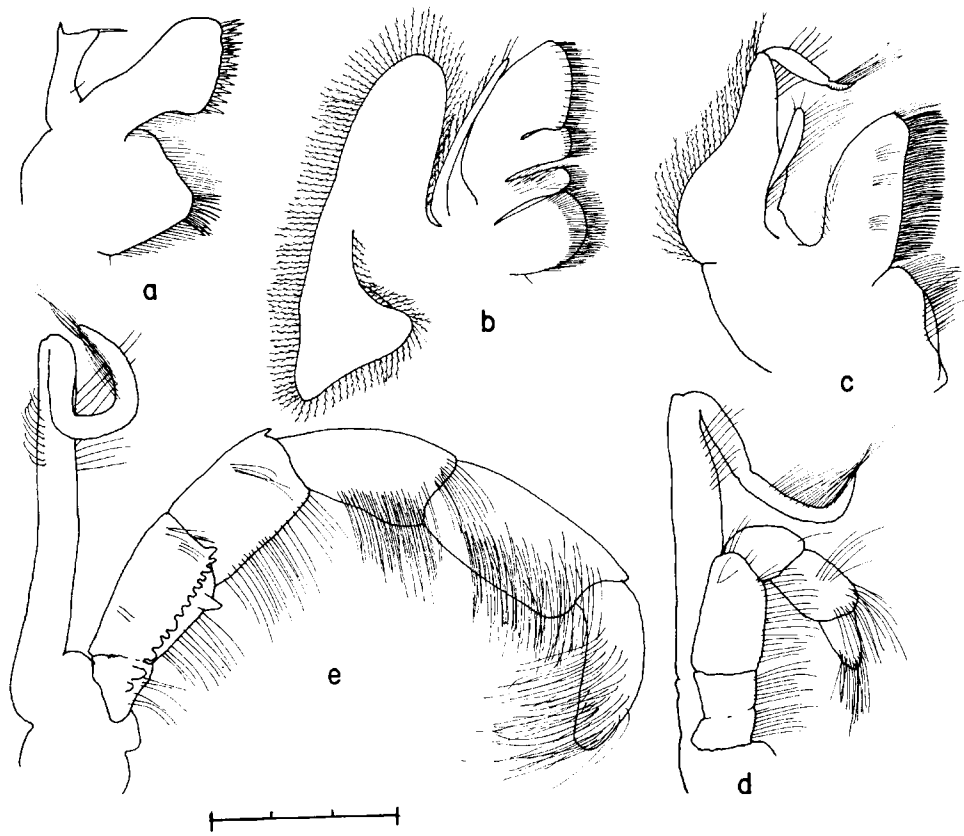

Figure 5. *Tomopagurus wassi* new species: Mouthparts.—(a) maxillule; (b) maxilla; (c) 1st maxilliped; (d) 2nd maxilliped; (e) 3rd maxilliped. Scale equals 3 mm.

(Fig. 5c) with basal segment of exopod protuberant. Second maxilliped (Fig. 5d) with basis-ischium fusion incomplete. Third maxilliped (Fig. 5e) with crista dentata moderately well developed, accessory tooth present; merus with small spine at dorsodistal margin. Sternite of 3rd maxillipeds with small spinule on either side of midline.

Chelipeds unequal, right larger than left. Right cheliped with dactyl moderately long, approximately equal to or slightly longer than palm; cutting edge with strong calcareous teeth and short row of corneous teeth distally, terminating in small corneous claw; dorsal surface elevated in midline and with irregular row of conical or tubular strong spines, decreasing in size distally, dorsal surface mesially and laterally with numerous tufts of moderately short setae, dorsomesial margin with row of strong spines; mesial and ventral faces with tufts of moderately long setae. Palm moderately short, one-half to two-thirds length of carpus; dorsomesial margin with irregular row of long and short or strong slender spines, dorsal surface with irregular rows of moderately strong conical spines usually encircled by short stiff setae; fixed finger often with several spines and numerous tufts of short stiff setae; dorsolateral margin with short spines proximally and irregular, often double row of stronger spines distally, lateral face spinulose or tuberculate; mesial and ventral faces often with transverse spinulose ridges and tufts of setae. Carpus short to moderately long, often equalling length of merus, frequently quite broad

and strongly inflated dorsoventrally, mesial face usually strongly concave; dorsomesial margin with row of very strong, often slender, acute spines, dorsal surface with numerous transverse ridges or short rows of tufts of very short setae, distal margin usually with few small spines and often with 1 or 2 spines slightly proximal to margin, dorsolateral margin unarmed or with few small spines distally; lateral face with scattered tufts of setae, distolateral margin with row of moderately strong spines, decreasing in size ventrally; mesial face with prominent ridge proximal to distal margin and occasionally 1 or 2 small spines; ventral surface often slightly spinulose or tuberculate. Merus subtriangular; dorsal margin with row of low ridges and tufts of setae proximally, becoming transverse rows of small spines or spinules distally and extending onto mesial and lateral faces dorsally, distal and distolateral margins each with row of slender strong spines and tufts of long setae, lateral face with low transverse ridges and tufts of setae; ventrolateral margin with row of small spines or tubercles, increasing in size and becoming acute spines distally, ventral surface often glabrous distally, tuberculate or spinulose proximally; mesial face with few transverse ridges ventrally, ventromesial margin with row of moderately strong, often tubular, spines.

Left cheliped moderately long, often reaching beyond base of dactyl of right. Dactyl very long, 4 or 5 times length of palm; cutting edge with row of very fine corneous teeth, terminating in small corneous claw, slightly overlapped by fixed finger; with prominent hiatus; dorsal surface with single or double row of small tubercles extending approximately three-quarters length of dactyl in midline, occasionally nearly reaching tip, dorsomesial margin with row of moderately strong tubercles or blunt spines, decreasing in size distally and with tufts of long stiff setae; mesial and ventral faces with tufts of long setae. Palm very short, approximately one-quarter or less length of carpus, subtriangular in cross-section; dorsolateral margin with double irregular row of strong, sometimes corneous-tipped spines, decreasing in size on fixed finger; dorsal surface with irregular rows of acute, often corneous-tipped spines, strongest in the midline and with numerous tufts of short setae; ventral surface with few spinules proximally and laterally and tufts of long stiff setae. Carpus approximately three-quarters length of merus, subtrapezoidal in shape; dorsolateral margin with row of very strong acute spines tending to cluster distally, dorsomesial margin with row of small spines, decreasing in size distally and with tufts of moderately long stiff setae; mesial face with small protuberances and tufts of setae, few spinulose ridges ventrally extending onto ventral surface; ventrodistal margin with irregular row of small spines, ventral surface spinulose or tuberculate and with tufts of long setae; lateral face with transverse, spinulose or tuberculate ridges, becoming spinose distally and with tufts of long setae, laterodistal margin with few strong spines dorsally and row of corneous-tipped spines ventrally. Merus subtriangular; dorsal margin with transverse low ridges, becoming spinulose distally and extending on to lateral and mesial faces dorsally, distal margin dorsally, laterally and mesially with strong slender acute spines; lateral face slightly ridged and with tufts of long setae, ventrolateral margin with row of strong spines; mesial face with scattered tufts of setae, ventromesial margin with row of small spines, decreasing in size distally; ventral surface spinulose or tuberculate. Ischium with cluster of small tubercles or spines on ventral surface laterally, ventromesial margin with single or double row of tubercles or denticles and with tufts of long setae. Coxa with 1 or 2 prominent acute spines on ventrodistal margin, ventrolateral margin slightly spinulose or denticulate, ventromesial margin with tufts of long setae.

Ambulatory legs usually slightly overreaching right cheliped, generally similar from right to left. Dactyls equalling or exceeding length of propodi; in lateral

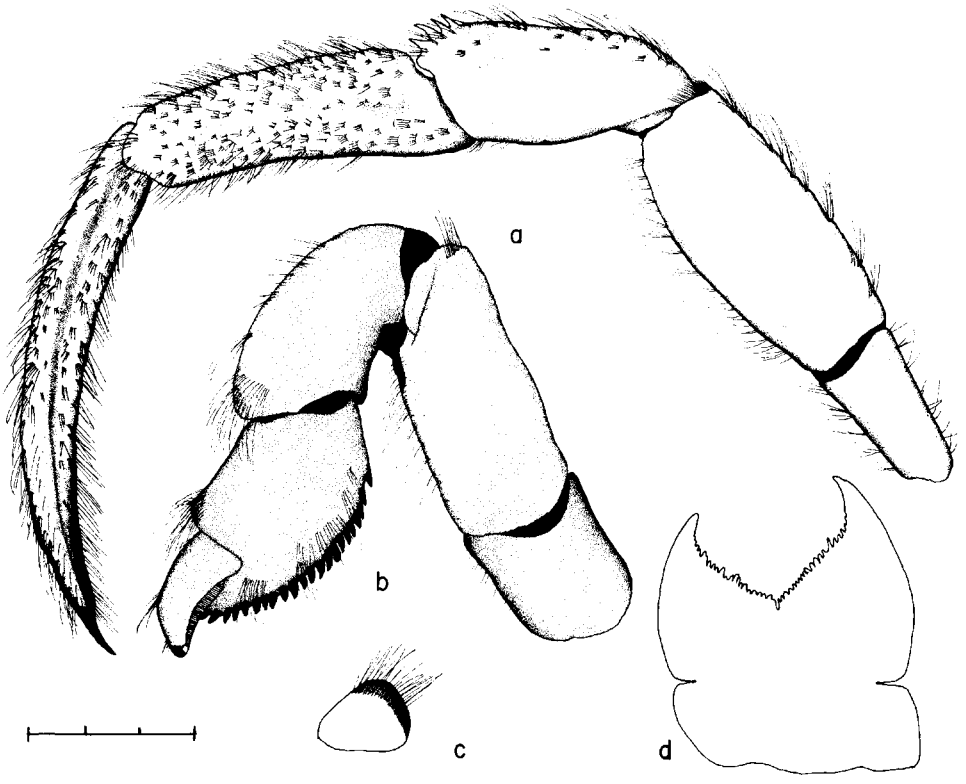

Figure 6. *Tomopagurus wassi* new species: (a) 3rd left pereopod; (b) 4th left pereopod; (c) anterior lobe of sternite of 3rd pereopods; (d) telson. Scale equals 3 mm.

view, curved ventrally, in dorsal view, twisted; terminating in strong corneous claws; dorsal surfaces with irregular rows of tufts of long stiff setae; lateral faces each with longitudinal sulcus flanked by tufts of setae, much more dense on left 3rd pereopod; ventral surfaces each with row of corneous spinules, increasing in size distally; mesial faces each with longitudinal sulcus, at least in proximal half, and tufts of stiff setae. Propodi usually slightly longer than carpi; dorsal surfaces with low transverse ridges, often spinulose on 2nd pereopods, and tufts of setae; mesial and ventral surfaces with scattered tufts of setae; lateral faces with irregular rows of tufts of setae or with slight longitudinal sulcus and dense tufts of setae (left 3rd pereopod). Carpi one-half to full length of merus; dorsal surfaces with row of strong spines (right 2nd pereopod) or with few strong spines; lateral faces with transverse short rows of setae; ventral and mesial faces with scattered setae. Meri laterally compressed; dorsal surfaces with transverse ridges and tufts of setae; lateral and mesial faces with few scattered setae; ventral margins with single or double rows of small spines (2nd pereopods) or with low spinules or tubercles (3rd pereopods). Ischia each with row of small spinules or tubercles on ventromesial margin (2nd pereopods) or row of long setae. Coxae each with row of long setae on ventromesial margin. Sternite of 3rd pereopods with anterior lobe broadly subsemicircular, with patch of short stiff setae distally.

Females typically without paired 1st pleopods modified as gonopods. Telson with posterior lobes asymmetrical, often markedly so; separated by shallow to moderately prominent median cleft; terminal margins oblique, armed with row of

calcareous spines or teeth; lateral margins often weakly calcified, occasionally slightly spinulose or denticulate.

Color.—In preservative, no distinctions in color between *T. cokeri* and *T. wassi* can be ascertained. All specimens are generally straw-colored. In freshly preserved specimens of *T. wassi* the ocular peduncles are light orange dorsally; the shield is tinged with orange anteriorly and laterally. The chelae and carpi of both chelipeds are light orange; the meri each have have orange dorsodistal margins and are circumscribed medially by an orange band. The ambulatory legs are lightly tinged with orange on the propodi; the carpi are orange on the ventrolateral faces, and the meri each have a prominent vertical stripe of orange medially and are tinged with orange distally and proximally. [Color is based on color illustrations of Dr. A. J. Provenzano.]

Distribution.—Southeastern United States, Straits of Florida, Gulf of Mexico, Caribbean, to northern Brazil; 75–360 m.

Affinities.—*T. wassi* is most closely allied with *T. cokeri* from the Atlantic and *T. maclaughlinae* from the Galapagos Islands. It may be distinguished from *T. cokeri* by the presence of a row of strong spines on the carpus of the 2nd right pereopod; this segment in *T. cokeri* bears only a single dorsodistal spine. *T. wassi* is distinguished from *T. maclaughlinae* by lack of granules or tubercles on the dorsal surfaces of the dactyls and propodi of the 2nd pereopods that are present in the latter species.

Remarks.—As previously indicated, Wass (1963) named a new species, *Benthopagurus schmitti,* from the western Atlantic, because its females bore paired 1st pleopods modified as gonopods. In his remarks (1963: 139), Wass commented that the paired pleopods were not easily observed and were sometimes missing from preserved material. Review of his material in the collections of the National Museum of Natural History, Smithsonian Institution has shown that three paratypes represented a distinct taxon. One of these specimens has been selected as the holotype of *Tomopagurus wassi.*

Provenzano recognized that *B. schmitti* was conspecific with the earlier described *Pagurus cokeri,* a species originally known only from two male specimens (cf. Hazlett, 1966). With subsequent collections, Provenzano (in Forest & De Saint Laurent, 1968) found that paired gonopods were present in some females but lacking in others. These authors assumed that gonopod variation was inherent in the species. In the material examined during this present study, no female specimens bearing gonopods were found with more than a single spine on the dorsodistal margin of the carpus of the 2nd right pereopod. Conversely, all females lacking gonopods had the carpi of the 2nd pereopods armed with a row of strong spines dorsally. Other morphological differences between *T. wassi* and *T. cokeri* exist, but these are subject to considerable intraspecific variation and, therefore, not of value in distinguishing between the taxa. As with the females, males of *T. wassi* are best distinguished by the presence of a row of spines on the dorsal surface of the carpus of the 2nd pereopod.

Hazlett (1966) observed the behavior patterns of two specimens which he referred to as *Benthopagurus cokeri.* The specimen from GERDA station G-462 is *Tomopagurus wassi.* I have not had the opportunity to examine the specimen from GERDA station G-482. As both *T. cokeri* and *T. wassi* appear to be sympatric over part of their ranges, I have questionably assigned the second Hazlett specimen to *T. cokeri* s.s. until such time as it may be critically examined.

This species is named for Dr. Marvin L. Wass.

Tomopagurus cubensis (Wass, 1963)
Figures 1e; 7e; 8e

Benthopagurus cubensis Wass, 1963: 134, fig. 1a–d (type locality: north of Matanzas Province, Cuba, ATLANTIS station 3480, 23°10′N, 81°28′W).—Hazlett, 1972: 820.
Tomopagurus cubensis: Forest and De Saint Laurent, 1968: 114 (by implication).

Holotype.—♀ (SL = 6.8 mm) MCZ 12682.

Material Examined.—See Table 5.

Diagnosis.—Shield as broad or broader than long; rostrum obtusely triangular, usually without terminal spine; lateral projections acutely triangular, with strong marginal spine. Ocular peduncles moderately short, with corneae strongly dilated; ocular acicles subtriangular, with acute submarginal spine; separated basally by approximately four-fifths basal width of 1 acicle. First segment of antennal peduncle without strong hooked or curved spine laterally. Right chela with strong slender spines on dorsal surface; dorsomesial and dorsolateral marginal spines not appreciably stronger. Left chela with dorsal surface spinose, dactyl with median row of spines, at least on proximal two-thirds. Dactyls, propodi and carpi of 2nd pereopods each with dorsal row of spines. Left 3rd pereopod with lateral face of propodus not densely setose. Sternite of 3rd pereopods with anterior lobe subquadrate, often with capsulate setae. Telson with posterior lobes subtriangular, terminal margins and dorsal surfaces each with numerous small calcareous spines and spinules.

Distribution.—Western Atlantic and Caribbean; 183–366 m.

Tomopagurus chacei (Wass, 1963) new combination
Figures 1h; 7h; 8g

Pylopagurus chacei Wass, 1963: fig. 11a–g (type locality: off Surinam, OREGON station 2289, 07°25′N 54°35′W).

Holotype.—♂ (SL = 3.6 mm) USNM 108963.

Material Examined.—See Table 6.

Diagnosis.—Shield as broad or broader than long; rostrum broadly rounded, without terminal spine; lateral projections triangular, often acutely so, with strong or moderately strong marginal spine. Ocular peduncles moderately short, with corneae slightly dilated; ocular acicles acutely triangular, with strong submarginal spine; separated basally by basal width or less of 1 acicle. First segment of antennal peduncle unarmed or with small spinule laterally. Right chela with raised, slightly spinulose tubercles on dorsal surface, dorsomesial and dorsolateral margins with acute or subacute spines, not appreciably enlarged. Left chela with raised, slightly spinulose tubercles on dorsal surface laterally; dactyl unarmed or with few low tubercles proximally. Dactyls and propodi of 2nd pereopods with stiff setae on dorsal surfaces; carpi with 1 or 2 spines near dorsodistal margin. Left 3rd pereopod with lateral faces of dactyl and propodus convex, not particularly setose; carpus with 1 spine on dorsodistal margin. Sternite of 3rd pereopods with anterior lobe semisubovate. Telson with posterior lobes asymmetrical, terminal margins oblique, each armed with moderately weak to moderately strong calcareous spines or spinules.

Distribution.—Western Atlantic and Caribbean; 84–192 m.

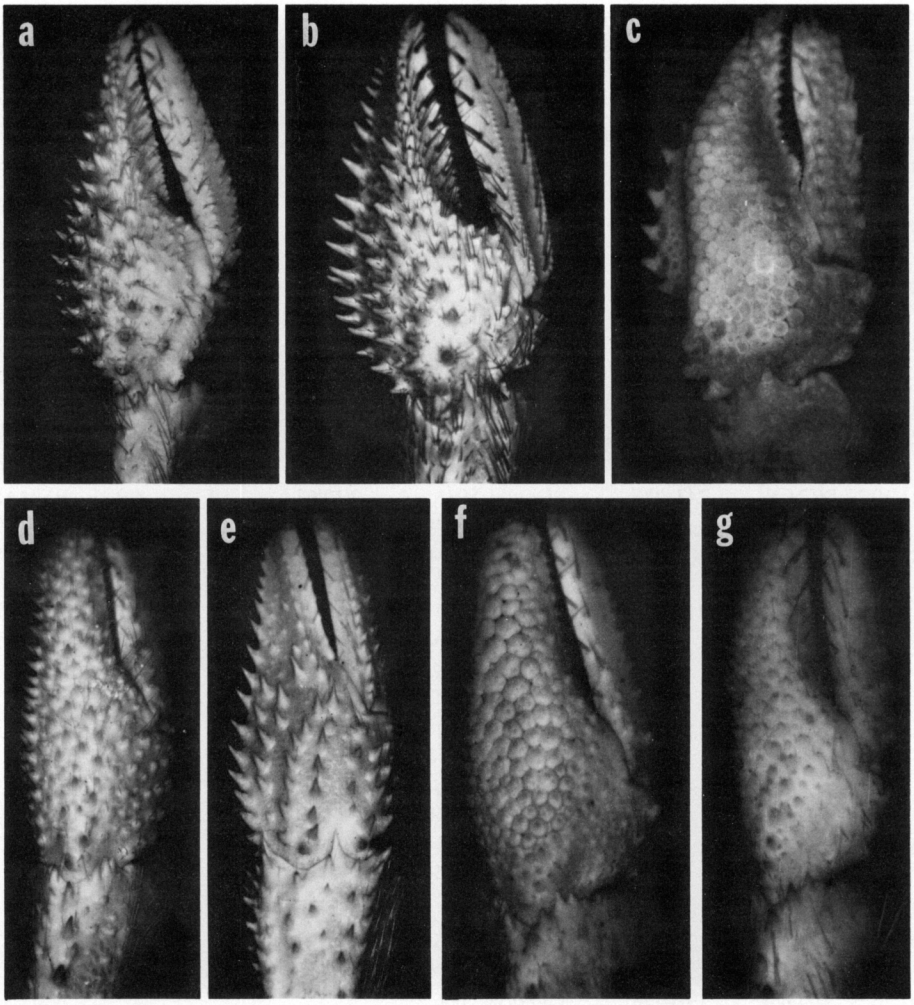

Figure 8. Left chelae: (a) *Tomopagurus cokeri* (5.7×); (b) *Tomopagurus wassi* new species (5.7×); (c) *Tomopagurus purpuratus* (11.8×); (d) *Tomopagurus rubropunctatus* (8.2×); (e) *Tomopagurus cubensis* (6.2×); (f) *Tomopagurus merimaculosus* (9.2×); (g) *Tomopagurus chacei* (13.9×).

ginal spine. Ocular peduncles moderately short, corneae dilated; ocular acicles acutely triangular, with small submarginal spine; separated basally by approximately two-thirds basal width of 1 acicle. First segment of antennal peduncle usually with small spine or spinule laterally. Right chela with raised slightly spinulose tubercles on dorsal surface, dorsomesial and dorsolateral margins with weak to moderately strong spines. Left chela with raised, slightly spinulose tubercles, particularly dorsolaterally; dactyl with few tubercles proximately in midline and laterally. Dactyls and propodi of 2nd pereopods with stiff setae dorsally; carpi with 2 to several spines on dorsal margin. Left 3rd pereopod with lateral faces of dactyl and propodus convex, not particularly setose; carpus with 1 spine on dorsodistal margin. Sternite of 3rd pereopods with anterior lobe subsemicircular. Telson with posterior lobes roundly triangular, terminal margins obliquely concave, each with moderately strong calcareous spines.

Table 4. *Tomopagurus wassi* n. sp. (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Western Atlantic and Gulf of Mexico							
34°07'N 76°06'W	183	SILVER BAY 2190 UMML 32:4664	7/21/60	2		3.4, 3.6	NMFS
29°56.5'N 87°03'W	73–146	OREGON 26 UMML 32:4667	6/14/50		1	2.7	NMFS
24°34'N 83°28'W	183	OREGON 4370 UMML 32:4451	8/6/63	1		10.6	NMFS
24°19'N 82°43'W	174–201	GERDA 462 UMML 32:4658	1/25/65		1	9.3	RSMAS
Caribbean and Southwestern Atlantic							
21°13'N 86°25'W	247–283	GERDA 947 UMML 32:4660	1/27/68		1	3.4	RSMAS
21°10'N 86°21'W	242–320	GERDA 893 UMML 32:4464	9/10/67		1	8.9	RSMAS
21°00.5'N 86°23'W	307–330	PILLSBURY 594 UMML 32:4653	3/15/68		1	3.3	RSMAS
17°13'N 87°55'W	219–311	OREGON 3637 UMML 32:4462	6/10/62	1	1	7.3, 8.0	NMFS
13°40'N 60°54'W	230	OREGON 5956 UMML 32:4452	3/10/66	1		11.6	NMFS
11°50'N 73°05'W	320–350	OREGON 4911 UMML 32:4453	5/31/64	1		13.1	NMFS
11°09'N 74°26.5'W	180–195	OREGON 4859 UMML 32:4458	5/19/64		1	12.1	NMFS
09°41'N 59°47'W	275	OREGON 1985 USNM 108757, 150270	3/11/57	1	1	7.9–10.7	NMFS
07°35'N 54°23'W	250	—	7/28/67	1	1	9.3–12.0	—
07°27'N 54°27'W	220–247	OREGON 2286 USNM 108759	9/9/59		1	—	NMFS
07°26'N 54°49'W	192–220	OREGON 2066 USNM 108760	9/8/58	1		—	NMFS
00°18'N 44°17'W	275	OREGON 4226 UMML 32:4459, 60	3/9/63		3	6.3–8.8	NMFS
00°18'N 44°23'W	183	OREGON 4225 UMML 32:4461	3/9/63	1		6.9	NMFS

Tomopagurus merimaculosus (Glassell, 1937) new combination
Figures 1g; 7g; 8f

Pagurus merimaculosus Glassell, 1937: 259 (type locality: Gulf of California, 3 miles northeast of Cape Pulmo, ZACA station 136, 23°29'30"N 109°25'W).

Holotype.—♂ (SL = approximately 7 mm) Amer. Mus. Natl. Hist. 12221.

Material Examined.—See Table 7.

Diagnosis.—Shield broader than long; rostrum obtusely triangular, without terminal spine; lateral projections triangular, with small to moderately strong mar-

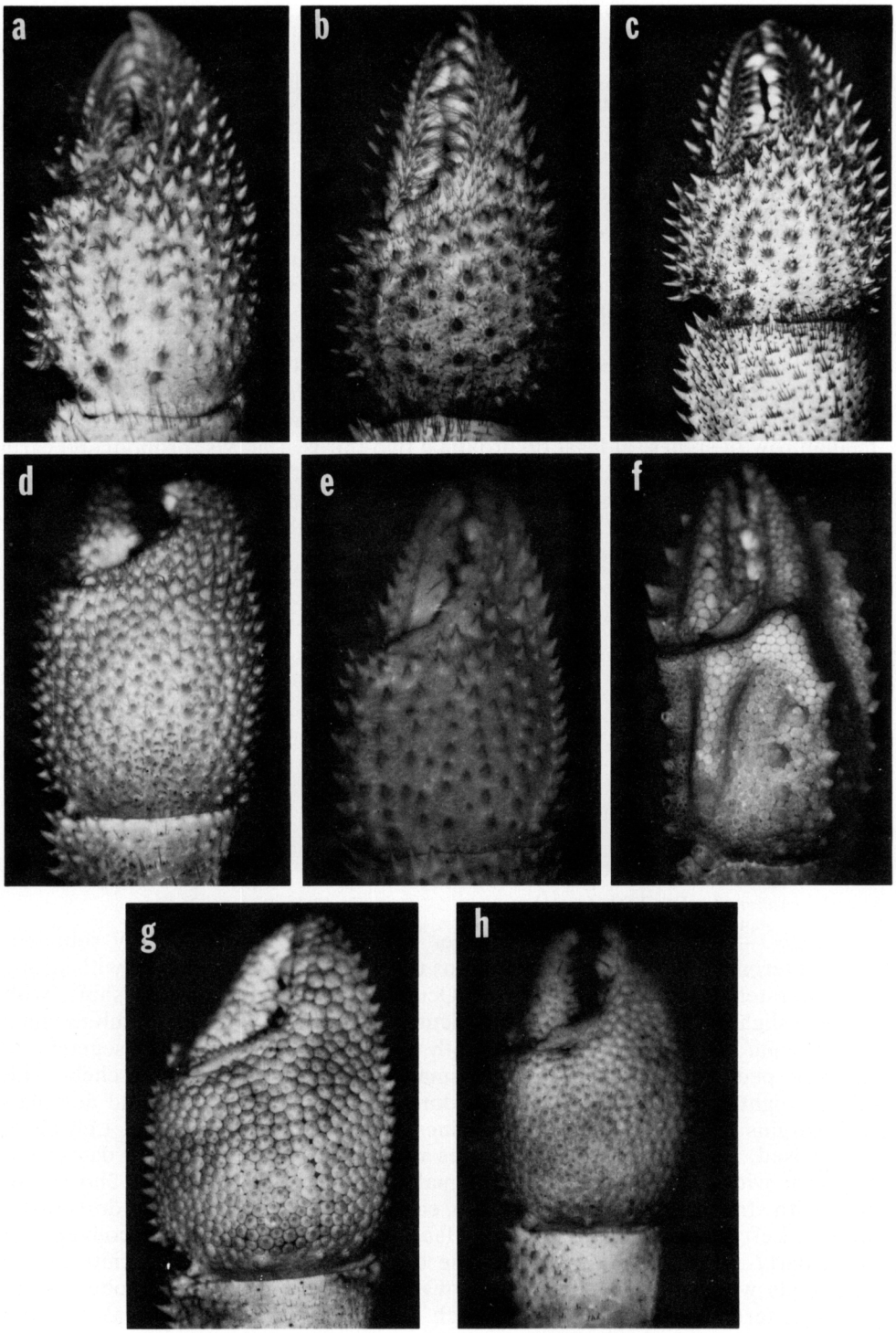

Figure 7. Right chelae: (a) *Tomopagurus cokeri* (6.4×); (b) *Tomopagurus wassi* new species (7.5×); (c) *Tomopagurus wassi* new species (2nd specimen, 4.2×); (d) *Tomopagurus rubropunctatus* (6.7×); (e) *Tomopagurus cubensis* (6.9×); (f) *Tomopagurus purpuratus* (8.3×); (g) *Tomopagurus merimaculosus* (6.2×); (h) *Tomopagurus chacei* (8.3×).

Table 5. *Tomopagurus cubensis* (Wass) (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Western Atlantic and Caribbean							
26°28′N 78°45′W	366	GERDA 503 UMML 32:4475	2/4/65	2		7.8, 8.8	RSMAS
26°08′N 79°11′W	311–329	GERDA 509 UMML 32:4471	3/2/65	1	2	7.9–8.1	RSMAS
24°08′N 80°08′W	252	SILVER BAY 2445 UMML 32:4542	11/3/60	2		5.8, 9.3	NMFS
23°10′N 81°28′W	366	ATLANTIS 3480 MCZ 12682	5/11/39		1	6.8	MCZ
16°05′N 81°21′W	183	OREGON 4928 UMML 32:4545	6/8/64		1	5.3	NMFS
14°14.2′N 80°28.5′W	275–292	OREGON 4834 UMML 32:4469	5/12/64	1		8.3	NMFS
14°15.5′N 80°27.1′W	220–238	OREGON 4832 UMML 32:4543	5/12/64	3		4.9–5.8	NMFS
—	229–256	PILLSBURY 198 UMML 32:4544	8/11/64	1		5.2	RSMAS

Table 6. *Tomopagurus chacei* (Wass) (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Caribbean and Southwestern Atlantic							
12°30′N 71°48′W	192	OREGON 5684 UMML 32:4710	10/9/65		1	5.7	NMFS
11°19.7′N 62°01.2′W	121–131	PILLSBURY 479 UMML 32:4709	8/8/66		1	3.1	RSMAS
11°14.5′N 61°46.2′W	137–143	PILLSBURY 849 UMML 32:4706	7/2/69		1	5.3	RSMAS
10°50′N 66°55′W	97	OREGON 4461 UMML 32:4713	10/13/63		1	3.0	NMFS
10°32′N 60°23′W	93–115	PILLSBURY 838 UMML 32:4709	6/30/69	1		4.1	RSMAS
10°09′N 76°05′W	163–183	OREGON 4904 UMML 32:4715	5/28/64		1	5.2	NMFS
10°04′N 76°06′W	183–219	OREGON 4903 UMML 32:4714	5/28/64	1		3.2	NMFS
07°30′N 55°00′W	183	OREGON 4304 UMML 32:4712	8/24/63		1	4.3	NMFS
07°25′N 54°35′W	137–146	OREGON 2289 USNM 108963	9/8/58	1		3.6	NMFS
06°07′N 52°19′W	84–91	PILLSBURY 650 AHF	7/8/68	1	1	2.4, 3.2	RSMAS

Table 7. *Tomopagurus merimaculosus* (Glassell) (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Costa Rica, Pacific coast							
Off Bahia Herradura	55	SEARCHER 455 AHF 1973-12	3/10/72	1	1	7.1–7.9	Los Angeles Co. Museum & Univ. Costa Rica
Gulf of Dulce	35–88	VELERO III 941-39 AHF	3/26/39	1		7.5	AHF

Distribution.—Gulf of California, Mexico to Colombia; 35–183 m (J. Haig, pers. comm.).

Tomopagurus purpuratus (Benedict, 1892) new combination
Figures 1f; 7f; 8c

Eupagurus purpuratus Benedict, 1892: 15 (type locality: Off Hood Island, Galapagos Islands, ALBATROSS station 2813).

Pagurus purpuratus: Boone, 1932: 7, fig. 2a–c. *Pagurus bunomanus* Glassell, 1937: 262, nomen nudum.—1938: 3 (type locality: Puerto Refugio, Angel de la Guardia I., Gulf of California).

Holotype of *Eupagurus purpuratus*: ♂ (SL = 3.7 mm) USNM 16715. Holotype of *Pagurus bunomanus* (SL = 7.9 mm) AHF 365.

Material Examined.—See Table 8.

Diagnosis.—Shield approximately as broad as long; rostrum obtusely triangular or broadly rounded, with or without small terminal spine; lateral projections obtusely triangular, with small marginal spine. Ocular peduncles moderately short, with corneae slightly dilated; ocular acicles acutely triangular, with strong submarginal spine; separated basally by one-half to entire basal width of 1 acicle. Right chela with dorsal surface prominently sculptured and with raised blunt or spiniform tubercles, dorsomesial and dorsolateral margins with widely spaced, strong blunt spines. Left chela elevated in midline, occasionally excavated dorsolaterally, dorsolateral margin broadly expanded; surface with raised, usually blunt tubercles; dactyl with tuberculate dorsal surface. Dactyls of 2nd pereopods each with dorsal row of corneous spinules or stiff bristles; propodi and carpi each with row of strong spines dorsally. Left 3rd pereopod with lateral faces of dactyl and propodus deeply concave, each with 1 or 2 rows of prominent tubercles and lateral and ventral rows of dense setae. Sternite of 3rd pereopods with anterior lobe subquadrate, occasionally with capsulate setae. Telson with posterior lobes asymmetrical and triangular, terminal margins oblique, each with row of calcareous spines, occasionally lateral margins also with several strong spines.

Distribution.—Gulf of California, Mexico to Colombia, Revillagigedos and Galapagos groups of oceanic islands; 36.5–274 m (J. Haig, pers. comm.).

DISCUSSION

As originally described, the principal characters of the genus *Pylopagurus*, sensu lato, were the presence of paired female gonopods, "mushroom-shaped" tubercles on the chelae and the operculate shape of the right chela. Wass (1963) used the latter two characters to differentiate his genus *Benthopagurus* from *Pylopagurus*. However, Wass did not consider that during the interim a number

Table 8. *Tomopagurus purpuratus* (Benedict) (Material examined)

Locality	Depth (m)	Station Deposition	Date	Sex ♂	Sex ♀	SL (mm)	Collector
Gulf of California							
Puerto Refugio	25–50	VELERO III 542-36 AHF	3/4/36	1	1	6.7, 7.9	AHF
Panama, Pacific coast off Bahia Honda	55–91	VELERO III 863-38 AHF	3/1/38	1	1	5.9, 7.1	AHF
Galapagos Islands							
Off Hood Island	73	ALBATROSS 2813 USNM 16715	1888	1		3.7	U.S. Coast Survey
Albemarle Island	—	VELERO III 149-34 AHF	1/34		1	5.6	AHF
Between Albany and James Islands	—	VELERO III 183-34 AHF	1/24/34	2		2.8, 3.6	AHF

of species had been assigned to *Pylopagurus* simply because the females possessed paired gonopods; more often than not these taxa lacked mushroom-shaped tubercles, and frequently the right chelae were not really operculate. When Forest and De Saint Laurent (1968) placed *Benthopagurus* in synonymy with *Tomopagurus*, they remarked that they were confident that *Tomopagurus* was distinct from *Pylopagurus*, but that the only character they could propose to separate the two genera was the less than satisfactory character of the operculate right chela of the latter genus. As may be seen in the present diagnoses of *Tomopagurus*, *Pylopagurus* s.s. and the newly proposed genera, a series of new or relatively new characters form the basis of the generic definitions, e.g., angle of articulation of chela and carpus, shape of the anterior lobe of the sternite of the 3rd pereopods, preungual process and propodal rasp of the 4th pereopods, symmetry of the uropods and telson, etc. The presence of paired gonopods in the female does, with few exceptions, set all of these genera apart from other genera of the Paguridae. As the phylogenetic significance of these new characters is still under investigation, it is premature to attempt to discuss intergeneric relationships at this point. It is, however, possible to evaluate interspecific relationships and these will be discussed as each genus subsequently is reviewed.

Interspecific Relationships of *Tomopagurus* Species

Tomopagurus, as currently interpreted, is perhaps the least homogeneous of all the proposed taxa. Prior to Haig's (1976) description of *T. maclaughlinae* from the Galapagos Islands, only *T. rubropunctatus*, *T. cokeri* sensu lato and *T. cubensis* were recognized. The former two species easily could be distinguished from the latter by the presence of a prominent hooked spine on the 1st segment of the antennal peduncle and a right cheliped with a relatively short and broad carpus. When Hazlett (1972) reported significant behavioral differences between *T. cokeri* s.l. and *T. cubensis*, it was a temptation to consider the possiblity of two distinct genera based on these differences. The discovery of an eastern Pacific species very closely related, morphologically, to *T. cokeri* s.l. has made it possible to more clearly evaluate the significance of particular morphological characters. While *T. maclaughlinae* shares with both *T. cokeri* s.l. and *T. rubropunctatus* the apparently unique character of a hooked spine on the 1st segment of the

antennal peduncle and the typically short and broad carpus of the right cheliped, it shares the strongly modified propodus and dactyl of the 3rd left pereopod only with *T. cokeri*. In this latter character *T. rubropunctatus* is much closer to *T. cubensis*. Another particularly noticeable character shared by *T. maclaughlinae* and *T. cokeri* s.l. is the elongate, flattened dactyl of the left chela. In contrast, the dactyls of the left chelae of *T. rubropunctatus* and *T. cubensis* are quite similar. However, when characters such as the generic characters cited in the diagnosis are considered, all four taxa are found to be relatively closely related. *T. wassi* quite obviously can either be derived from, or provide the stem stock for *T. cokeri* s.s.; the former would seem the most reasonable interpretation. Although the absence of a character such as paired gonopods, as is the condition in the genus *Pagurus*, has been considered to be the primitive state, the absence of female gonopods in *T. wassi* probably is a secondarily derived character. In most other characters *T. wassi* agrees well with the morphological specializations (e.g., hooked antennal spine, modified dactyl and propodus of the 3rd left pereopod, etc.) of *T. cokeri*. Both of these western Atlantic species are most closely related to *T. maclaughlinae*.

In having raised or somewhat "mushroom-shaped" tubercles, the Atlantic species, *Pylopagurus chacei* and the Pacific species, *Pagurus merimaculosus* and *Pagurus purpuratus* would fit the Milne Edwards and Bouvier diagnosis of *Pylopagurus* sensu lato, and in fact Haig (personal communication) had found that the females of the latter two species did possess paired 1st pleopods modified as gonopods. Application of the diagnostic characters as defined for *Tomopagurus* has shown that these three species correctly are assignable to this genus. Although all three species lack the prominent hooked spine on the 1st segment of the antennal peduncle, the dactyl and propodus of the left 3rd pereopod of *T. purpuratus* are modified similarly to those of *T. cokeri*, *T. wassi* and *T. maclaughlinae*; whereas the dactyls of the left chelipeds of *T. chacei* and *T. merimaculosus* more closely resemble those of *T. rubropunctatus* and *T. cubensis*. All characters considered, *T. chacei* from the Atlantic and *T. merimaculosus* from the Pacific appear more closely related to one another than to other species of the genus with similar geographic distributions.

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