

## A NEW FAMILY FOR A NEW GENUS AND NEW SPECIES OF HERMIT CRAB OF THE SUPERFAMILY PAGUROIDEA (DECAPODA: ANOMURA) AND ITS PHYLOGENETIC IMPLICATIONS

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### A B S T R A C T

A new family, Pylojacquesidae, is proposed for *Pylojacquesia colemani*, new genus and species. Although the new family, with its monotypic genus, exhibits characters of both superfamilies of the Section Paguridea, it is tentatively assigned to the Paguroidea until additional material becomes available that would permit a more detailed study. The new family Pylojacquesidae is diagnosed, and its type genus and species are described and illustrated. The possible phylogenetic relationships of the new genus are discussed. A key to all the families of hermit crabs is presented.

Prior to the classic study of MacDonald *et al.* (1957), all hermit crabs were included in a single superfamily, the Paguroidea, with pagurids and diogenids ranked as subfamilies within the family Paguridae. However, MacDonald *et al.* found what they believed to be sufficient evidence among the larvae to separate hermit crabs into two distinct superfamilies, the Paguroidea, including the family Lithodidae and the subfamily Pagurinae, and the Coenobitoidea, including the families Pylochelidae, Coenobitidae, Lomidae (as Lomisidae), and the subfamily Diogeninae. Both the Pagurinae and Diogeninae were raised by MacDonald *et al.* to familial rank. However, McLaughlin (1983a) regarded the Lomidae as distinct from all hermits, and subsequently she (McLaughlin, 1983b) argued against MacDonald's *et al.* implied polyphyly in hermits. In the classification proposed by McLaughlin (1983a, b), the family Lomidae was elevated to superfamily rank, the superfamily Coenobitoidea was suppressed, and the remaining families were reunited within the single superfamily Paguroidea. Although Forest (1987) supported McLaughlin's (1983b) view of monophyly among hermit crab families, he felt strongly that the difference between coenobitoids and paguroids was sufficient to justify the reinstatement of the Coenobitoidea and, with the Paguroidea, return to the use of the hierarchical Section Paguridea (cf. Holthuis, 1959).

The new, albeit monotypic, taxon described herein is sufficiently distinct from all other hermit crab families to justify the establishment of a new family. Despite the fact that Pylojacquesidae shares characters of both the Coenobitoidea and Paguroidea, a third superfamily has not been deemed appropriate. Initially, we were prompted to propose the suppression of the superfamily Coenobitoidea once again, and reunite the existing families, i.e., Coenobitidae, Diogenidae, Lithodidae, Paguridae, Parapaguridae, and Pylochelidae, under the superfamily Paguroidea and add the new family Pylojacquesidae for *Pylojacquesia*, new genus. This action was strongly opposed by Professor Jacques Forest, who stressed (Forest, 1987, personal communication) that the thoracic endophragmal systems of the two superfamilies were so different that suppression of the Coenobitoidea was entirely unjustified. Information concerning the endophragmal systems remains, at present, still unpublished; however, the salient differences have been pointed out to us. Given the paucity of material upon which Pylojacquesidae is established, we have not been able to determine the characteristics of this system in the new family. Consequently, at least for the present, we are assigning Pylojacquesidae to the superfamily Paguroidea. Nonetheless, it is equally possible that further study will show by the characters of the endophragmal system that Pylojacquesidae could be con-

sidered a coenobitoid, or a link between the two superfamilies.

In having 13 pairs of phyllobranchiate gills, paired and modified first pleopods in the female, and no secondary sexual modifications in the male, *Pylojacquesia*, new genus, exhibits affinities with the pagurid genus, *Pylopaguropsis* Alcock, 1905. Similarly, the modified female gonopods and operculate right cheliped suggest at least a superficial relationship with a second pagurid genus, *Pylopagurus* A. Milne-Edwards and Bouvier, 1891. The carapace shape and structure of the left cheliped in *Pylojacquesia*, new genus, are reminiscent of the pagurid genus *Xylopagurus* A. Milne-Edwards, 1880, whereas the structure of the telson, rounded rostral lobe, and the very elongate, albeit spinose, ocular acicles might even imply an affinity with the pagurid genus *Catapagurus* A. Milne-Edwards, 1880. Alternatively, the nearly approximate position of the third maxillipeds, as well as lack of fusion of the first abdominal and last thoracic somites would advocate an assignment of *Pylojacquesia*, new genus, to the Diogenidae. The 13 pairs of gills, the absence of an accessory tooth on the *crista dentata*, and modified female first pleopods, which characterize *Pylojacquesia*, new genus, are characters shared by genera of both the Paguridae and Diogenidae. However, the new genus also possesses characters that more clearly suggest its singularity. These include the notable separation of thoracic sternites XI–XIV (cf. Pilgrim, 1973) (sternites of the third maxillipeds, chelipeds, and pereopods 2–5) (Fig. 1a); the presence of a fused, or pair of small, calcified tergal plates on the first abdominal somite (Fig. 2a), but without characteristic “bulge” (cf. Richter and Scholtz, 1994); partially calcified sternal projection on the first abdominal somite (Fig. 2c); and most importantly, a prominently toothed mandible (Fig. 3b, c).

The taxon, *Pylojacquesia colemani*, new genus and species, is described from two specimens collected off Brisbane, eastern Australia during the voyage of the S.M.S. “Gazelle” in 1875. These specimens are housed in the collections of the Naturhistorisches Forschungsinstitut Museum für Naturkunde zu Berlin, Berlin, Germany (ZMB). The measurement shield length (sl) provides an indication of animal size. General terminology follows that of McLaughlin

(1974), with specialized terminology of the shield after Lemaitre (1995), designation of thoracic sternites after Pilgrim (1973), categorization of the fourth pereopods after McLaughlin (1997), and gill structure after McLaughlin and de Saint Laurent (1998).

#### SYSTEMATICS

Superfamily Paguroidea Latreille, 1802

Family **Pylojacquesidae**, new family

*Type Genus*.—*Pylojacquesia*, new genus.

*Etymology*.—The name is derived from the type genus *Pylojacquesia*, new genus.

*Diagnosis*.—Cephalothorax with *linea transversalis* and cervical groove distinct. Ocular peduncles well developed, corneas pigmented or not; ocular acicles elongate. Antennular and antennal peduncles well developed; antennal peduncle with supernumerary segmentation.

Mandible with prominent corneous teeth. First maxilliped with multiarticulate flagellum. Third maxillipeds basally separated by narrow protrusion of sternal plate; *crista dentata* moderately well developed, without accessory tooth. Thoracic sternites IX–XI (sternites of third maxillipeds, chelipeds, and second pereopods) fused but with sutures apparent; sternites XII–XIV (sternites of pereopods 3–5) well separated.

First abdominal somite contiguous with last thoracic somite, but suture clearly discernable. Abdominal somites membranous, except for calcified tergite of sixth and partially calcified sternite and tergite(s) of first. Pleopods 3–5 developed on left side only. Uropods well developed.

***Pylojacquesia***, new genus

*Type Species*.—*Pylojacquesia colemani*, new species.

*Gender*.—Feminine.

*Etymology*.—From the Greek *pylo* meaning gate keeper and indicative of the operculate right chela of the type species, combined with *jacquesia* to honor Professor Jacques Forest, Muséum national d’Histoire naturelle, Paris, in recognition of his many contributions to carcinology in general and hermit crabs in particular.

*Diagnosis*.—Thirteen pairs of generally biserial phyllobranchiate gills (Fig. 3a). Rostrum

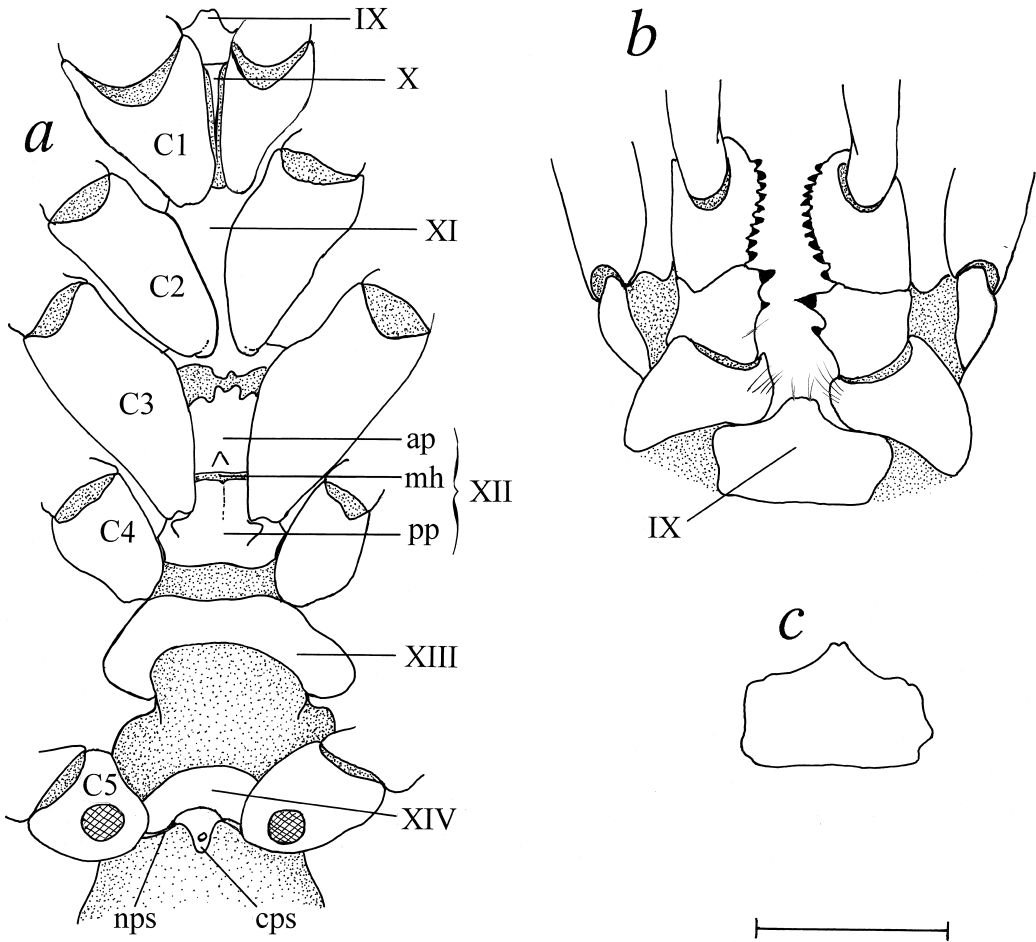


Fig. 1. *Pylojagquesia colemani*, new genus and species, *a*, *b*, allotype (sl = 4.0 mm), ZMB 5204: *a*, sternum, ventral view; *b*, sternite IX, coxae, bases, ischia, and parts of meri and exopods of third maxillipeds, ventral view; *c*, sternite IX, ventral view. Scale equals 1 mm. Stippling indicates membranous regions. Roman numerals indicate sternites. Abbreviations: C1–5, coxae of first to fifth pereopods; ap, anterior portion; mh, membranous “hinge”; pp, posterior portion; cps, calcified portion of sternite of first abdominal somite; nps, non-calcareous portion of sternite of first abdominal somite.

rounded. Ocular acicles very elongate, spinose. Mandible (Fig. 3*b*, *c*) partially calcified, with several exceptionally well-formed, chitinous teeth on incisor process; molar process absent; palp 3-segmented. Maxillule (Fig. 3*d*) with reduced internal endopodal lobe; external endopodal lobe produced, not recurved. Maxilla (Fig. 3*e*) with elongate, slender endopod. First maxilliped (Fig. 3*f*) with subrectangular-shaped exopod. Second maxilliped (Fig. 3*g*) with exopod appreciably longer than endopod. Third maxilliped (Fig. 3*h*) with well-developed *crista dentata*, no accessory tooth. Third maxillipeds nearly approximate basally, separated by small, sub-

quadrate (allotype, Fig. 1*b*) or subtriangular (holotype, Fig. 1*c*) anteromedian sternal projection. Thoracic sternites XII (sternite of third pereopods) and XIII (sternite of fourth pereopods) (Fig. 1*a*) each separated from preceding sternite by moderately broad membranous area; anterior and posterior portions of sternite XII separated by distinctly membranous “hinge.”

Chelipeds asymmetrical, right largest. Fourth pereopods with several rows of sharp, corneous scales in propodal rasp. Fifth pereopods subchelate.

Males with paired gonopores, no sexual tubes; no paired pleopods, unequally bira-

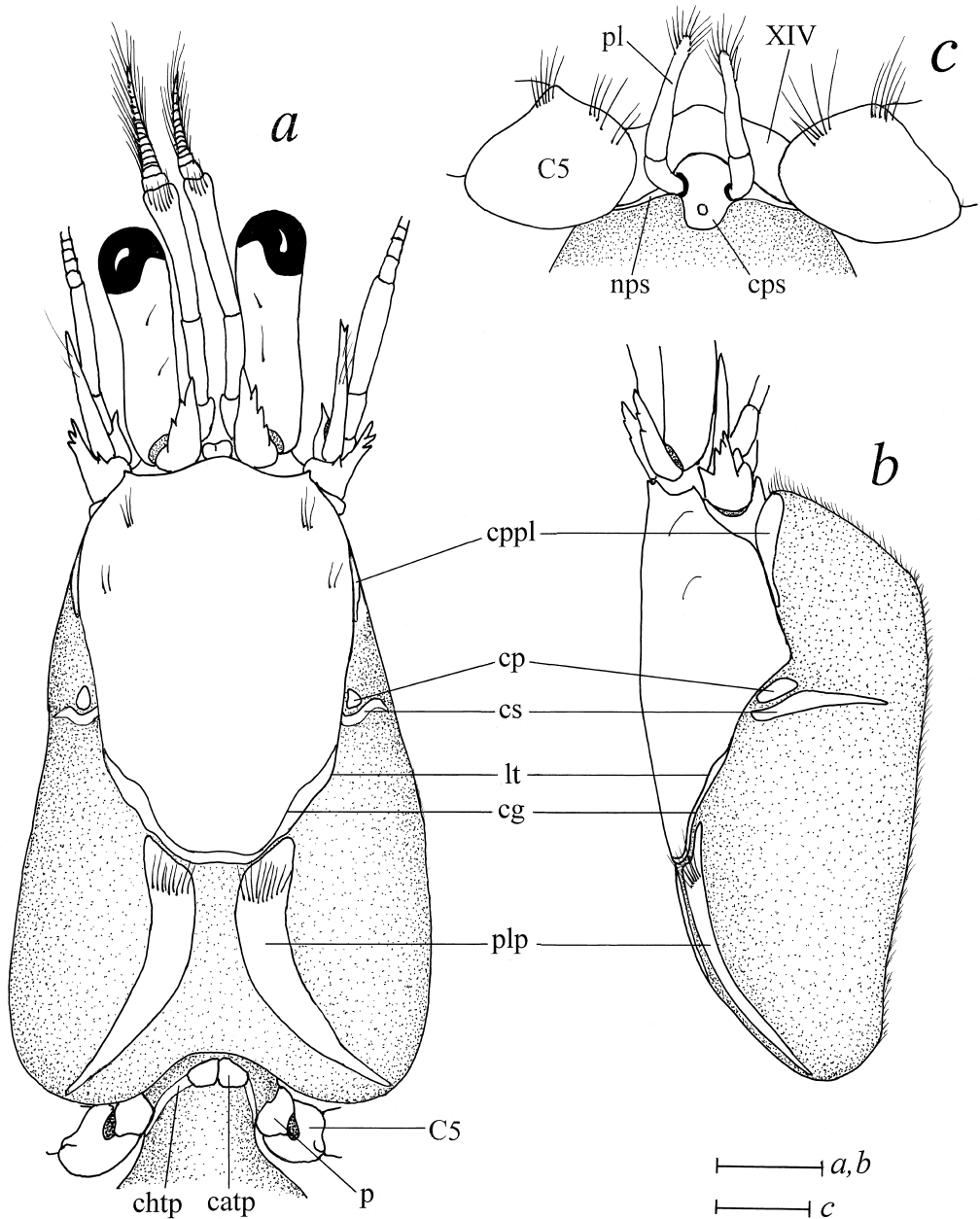


Fig. 2. *Pylojacquesia colemani*, new genus and species, holotype (sl = 3.9 mm), ZMB 5204: *a*, cephalothorax, cephalic appendages, and first abdominal somite, dorsal view; *b*, same in lateral view, excluding distal part of cephalic appendages and first abdominal somite; *c*, sternite XIV, coxae of fifth pereopods, and sternum and pleopods of first abdominal somite, ventral view. Scales equal 1 mm (*a*, *b*), and 0.5 mm (*c*). Stippling indicates membranous regions. Abbreviations: cppl, calcified portion of pterygostomial lobe; cp, calcified patch; cps, calcified projection of sternum of first abdominal somite; cs, calcified strip; lt, *linea transversalis*; cg, cervical groove; plp, posterolateral plates; C5, coxa of fifth pereopod; p, pleura of last thoracic somite; catp, calcareous tergal part of first abdominal somite; chtp, chitinous tergal part of first abdominal somite.

mous unpaired left pleopods 3–5. Females with paired gonopores; paired, modified first pleopods; unpaired, unequally biramous left pleopods 2–5.

Abdomen with sternite and tergite of first somite at least partially calcified (Figs. 1a, 2a); tergite of sixth somite well calcified, but not modified as operculum. Uropods symmetrical. Telson with broad, U-shaped median cleft.

*Remarks.*—McLaughlin and de Saint Laurent (1998) corrected the long-standing misinterpretation of phyllobranchiate and trichobranchiate gills. These authors pointed out that all hermit crab gills are phyllobranchiate, in that the gill elements almost always are inserted biserially in regular pairs along the rachis. These authors proposed the use of the terms biserial and quadriserial to distinguish between lamellae that were entire as opposed to those divided into two elements. The gill lamellae of *Pylojacquesia*, new genus, are intermediate between the two conditions, with an incomplete division occurring (Fig. 3a).

The term “teeth”, as used in descriptive morphology, has several meanings, even when applied exclusively to structures of the mouthparts. On the third maxilliped, for example, the chitinous, spiniform projections on the basis and those comprising the *crista dentata* of the ischium (Fig. 1b, 3h, 6a–e, g) are referred to as “teeth.” In contrast, mandibular “teeth”, such as those referred to by Asakura (2000) in species of *Pylopaguropsis*, are small projections or irregularities of the incisor grinding surface of the well-calcified mandible. In *Pylojacquesia*, new genus, the mandibular “teeth” are very prominent and acute, chitinous projections of the normal grinding margin of the otherwise calcified mandible (Fig. 3a, b).

*Pylojacquesia colemani*, new species

Figs. 1–4, 5a–d, f, g

*Eupagurus* sp. Studer, 1889: 266 (in part).

*Type Locality.*—Off Brisbane, eastern Australia (26°51.1'S, 153°29.6'E).

*Etymology.*—This species is named for Dr. Charles Oliver Coleman, curator of Crustacea of the Museum für Naturkunde zu Berlin, who kindly made his collection available for study.

*Material Examined.*—Holotype female (sl = 3.9 mm), allotype (sl = 4.0 mm), “Gazelle” trawl no. 40, 26°51.1'S, 153°29.6'E, 139.1 m, 27 September 1875, ZMB 5204.

*Description.*—Shield (Fig. 2a) somewhat vaulted, approximately 1.50 times longer than broad; dorsal surface smooth, but with moderately shallow depressed area posterior to each lateral projection and 2 faint lateral swellings, each with sparse tuft of setae. Anterior margin weakly concave between rostrum and slightly produced lateral projections, posterior margin truncate. Accessory portions of shield narrow but clearly delineated, cervical groove and *linea transversalis* not confluent posteriorly. Rostrum very weakly produced as broadly rounded rostral lobe. Lateral projections obtusely triangular, each with small, laterally directed spinule. Branchiostegite (Fig. 2b) cuticle very thin, with weakly calcified strip in region of strut near anterior termination of cervical groove close to *linea anomurica*, and adjacent small calcified patch. No *sulcus verticalis* apparent, and *linea anomurica* only faintly detectable. Cuticle of posterior carapace extremely thin, posterior median plate visible, not calcified; posterolateral plates (cf. Pilgrim, 1973) partially calcified (Fig. 2a), each with transverse row of long setae.

Ocular peduncles moderately long, 0.60–0.65 length of shield; row of very sparse tufts of setae on dorsomesial surface, and distinct foramen on mesial face at mid-length; corneas not dilated. Ocular acicles elongate, slender, with very prominent terminal spine and 2 or 3 smaller spines on lateral margin; interocular lobe with areas of calcification laterally.

Antennular peduncles, when fully extended, slightly overreaching distal margins of corneas. Ultimate segments each with tuft of long setae adjacent to dorsodistal margin. Penultimate segments with few sparse tufts of setae. Basal segments each with slender, acute spine on lateral surface of statocyst lobe.

Antennal peduncles reaching to bases of corneas or slightly beyond, but not overreaching distal margins. Fifth and fourth segments with few scattered setae. Third segments ventrally produced to approximately mid-ventral length of fourth, each with prominent terminal spine. Second segments each with dorsolateral surface prominently produced, armed with 2–4 spines; dorsal surface with small spine, usually removed from dorsomesial margin. First segments produced ventrally, each with 0–3 spines on ventrolateral margin. Acicles slender, reaching beyond

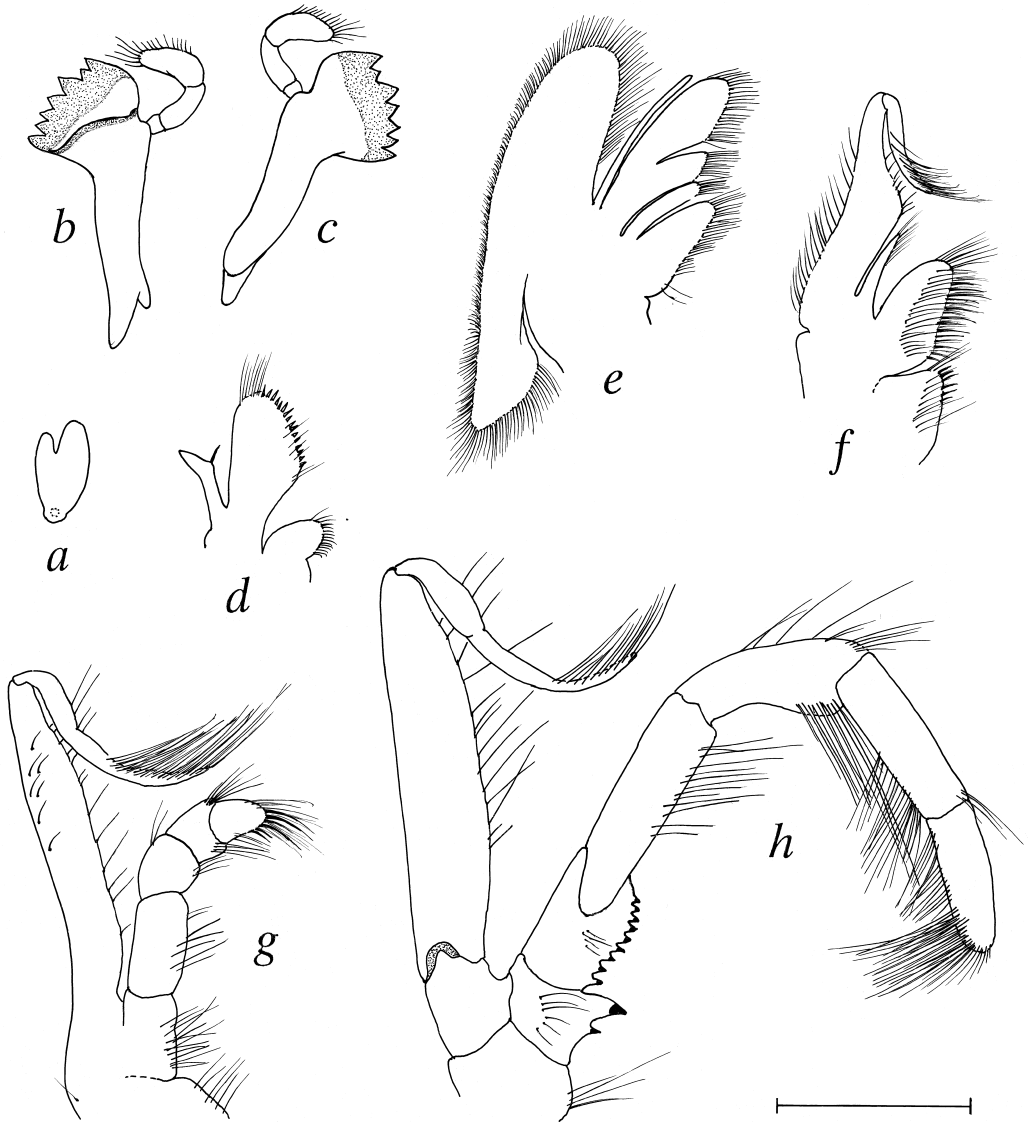


Fig. 3. *Pylojacquesia colemani*, new genus and species, right mouthparts and gill, allotype (sl = 4.0 mm), ZMB 5204: a, lamella; b, mandible, internal view; c, same, external view; d, maxillule, internal view; e, maxilla, internal view; f, first maxilliped, internal view; g, second maxilliped, internal view; h, third maxilliped, internal view. Scale equals 1 mm.

midpoint of fifth antennal segment; terminating in strong, simple or bifid spine.

Right cheliped (Fig. 4a–c) operculate, much larger than left; chela subcircular (female holotype) to slightly subovate (allotype); longer in male (Fig. 4a) than in female (Fig. 4b); dactyl broad, approximately 0.50 width of palm (dorsal view); with dorsal surface slightly convex, smooth, but slightly pitted and with faint creases, particularly laterally; dorsomesial margin raised as low, smooth to

weakly crenulate ridge; mesial and ventral surfaces with few rows of widely spaced pits from which sparse tufts of setae arise; cutting edges of dactyl and fixed finger each with row of closely spaced, very small, subacute to blunt, calcareous teeth alternating with minute, corneous teeth; terminating in very small, corneous claws. Palm and fixed finger circumscribed by low, smooth to crenulate marginal ridge mesially and laterally, and submarginal proximally, circumscribed dor-

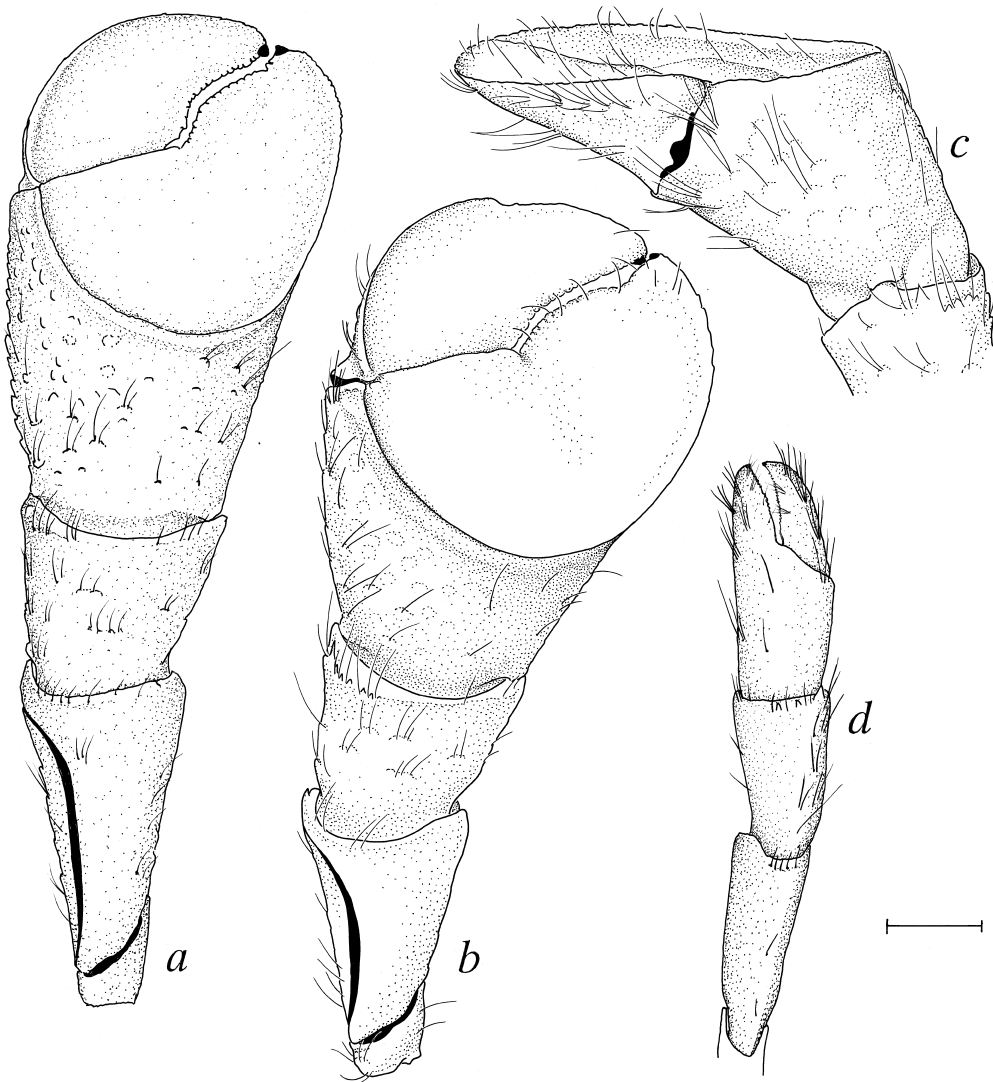


Fig. 4. *Pylojacquesia colemani*, new genus and species, ZMB 5204: *a*, right cheliped of male allotype (sl = 4.0 mm), dorsal view; *b*, right cheliped of female holotype (sl = 3.9 mm), dorsal view; *c*, chela of same, mesial view; *d*, left cheliped of female holotype, dorsal view. Scale equals 1 mm.

sal surface (Fig. 4c) flattened to slightly convex, smooth, but faintly pitted and creased, particularly in male; dorsoproximal surface, mesial, lateral and ventral faces all with small tubercles, low, weakly spinulose ridges, and sparse tufts of setae (male), or practically smooth, with only widely scattered, minute granules and few setae (female). Carpus short, subtrapezoidal; dorsomesial distal angle with acute spine, dorsal, lateral and mesial surfaces of male all with short, transverse, smooth or spinulose ridges, only faintly de-

lineated in female; pair of very small spines adjacent to dorsodistal margin present in both sexes; ventral surface with few setae. Merus with few transverse ridges and sparse setae dorsally, laterally, and mesially, much less pronounced in female. Ischium unarmed.

Left cheliped (Fig. 4d) with dactyl slightly longer than palm, unarmed but with several tufts of long setae dorsally and ventrally; cutting edge with row of very small, corneous teeth, terminating in small, calcareous claw. Palm and fixed finger similarly unarmed but

with several tufts of long setae on all surfaces; cutting edge of fixed finger with row of very small, calcareous teeth, terminating in small corneous claw. Carpus with prominent spine at dorsomesial distal angle and 1 or 2 small spines on dorsodistal margin; surfaces all unarmed but with several tufts of long setae. Merus similarly unarmed, but also with several tufts of long setae. Ischium unarmed.

Ambulatory legs (Fig. 5*a–c*) similar from left to right (holotype with only third left and right; allotype with second right, third left); laterally compressed. Dactyls moderately short and broad, longer than propodi; with very long, blade-shaped, terminal claws; dorsal margins each with row of widely spaced, low protuberances and spiniform bristles; ventral margins each with 4 or 5 corneous spines. Propodi 1.30–1.40 times length of carpi; each usually with corneous spine at ventrodorsal margin and few tufts of setae on ventral surfaces; dorsal margins each with few tufts of setae. Carpi each with moderately prominent spine at dorsodistal margin and smaller spine on dorsal surface near proximal margin. Meri and ischia unarmed, but with few tufts of setae. Sternite XII (sternite of third pereopods) (Fig. 1*a*) with small calcareous spine on anterior portion posteromedially; posterior portion with blunt projection on each side near posteromesial angle of coxa.

Fourth pereopods (Fig. 5*d*) semichelate; dactyl with row of long, thin, corneous spines on ventral margin in distal half, terminal claw also long; no preungual process present; propodus with several rows of sharp, corneous scales in rasp. Fifth pereopods (Fig. 5*f*) subchelate; dactyl with single row of small, corneous scales.

Abdomen straight; calcified portion of sternite of first somite forming prominent, posteriorly directed, projection (Fig. 1*a*). Female paired first pleopods (Fig. 2*c*) long, slender, 2-segmented; distal segment with few marginal setae distally, approximately twice length of proximal segment. Uropods (Fig. 5*g*) symmetrical, endopods appreciably smaller than exopods, both rami with well-developed rasps of corneous scales. Tergite of sixth abdominal somite (Fig. 5*g*) well calcified, divided into anterior and posterior sections by prominent transverse suture. Telson (Fig. 5*g*) without division into anterior and posterior lobes; terminal margin with broad, median U-shaped concavity, allotype with 2

minute spine-like projections on either side of faintly indicated median cleft. Telson of holotype abnormal, left portion laterad of concavity not developed, 4 tiny bristles on right outer margin of concavity.

*Color*.—"Red" (Studer, 1889).

*Habitat*.—Sand substrate with mussel fragments, sea urchins spines, and small rock particles, in serpulid worm tubes of *Protula* sp. A single, relatively large and wide-spread species of *Protula* of uncertain identity, and which tends to be solitary, is known to occur in Australia (K. Fauchald, personal communication).

*Distribution*.—Known only from the type locality, off Brisbane, Australia.

*Remarks*.—In his report of the catch for trawl number 40, Studer (1889) reported three species of hermit crabs (all as *Eupagurus* sp.). One species reportedly occupied shells of *Murex* and *Xenophora*, while the other two were found in worm tubes. Of the hermits in the Berlin collection from that station, we identified two shell-inhabiting species, *Pagurus sinuatus* (Stimpson, 1858) (ZMB 27347) and *Pagurixus jervienseis* McLaughlin and Haig, 1984 (ZMB 27348). The species inhabiting serpulid tubes has proved to be *Lophopagurus (Australeremus) triserratus* (Ortmann, 1892) (ZMB 27349). The remaining species, described herein as *Pylojacquesia colemani*, new species (ZMB 5204), according to Studer (1889) was found in tubes of *Protula* sp.

Noticeable sexual dimorphism is apparent in the armature and proportions of the right cheliped, as indicated in the description (Fig. 4*a, b*). Other differences between the holotype and allotype, such as the number of spines on the dorsolateral projection of the second antennal segment or the number of spines on the first segment of the peduncle most probably reflect simple intraspecific variation. The shield of the allotype is not as well calcified as that of the holotype, but it is impossible to say whether or not this is simply an artifact of preservation.

#### DISCUSSION

As previously noted, certain characters of *Pylojacquesia*, new genus, are shared with the Diogenidae, while others are common to the Paguridae and to a lesser extent the Para-



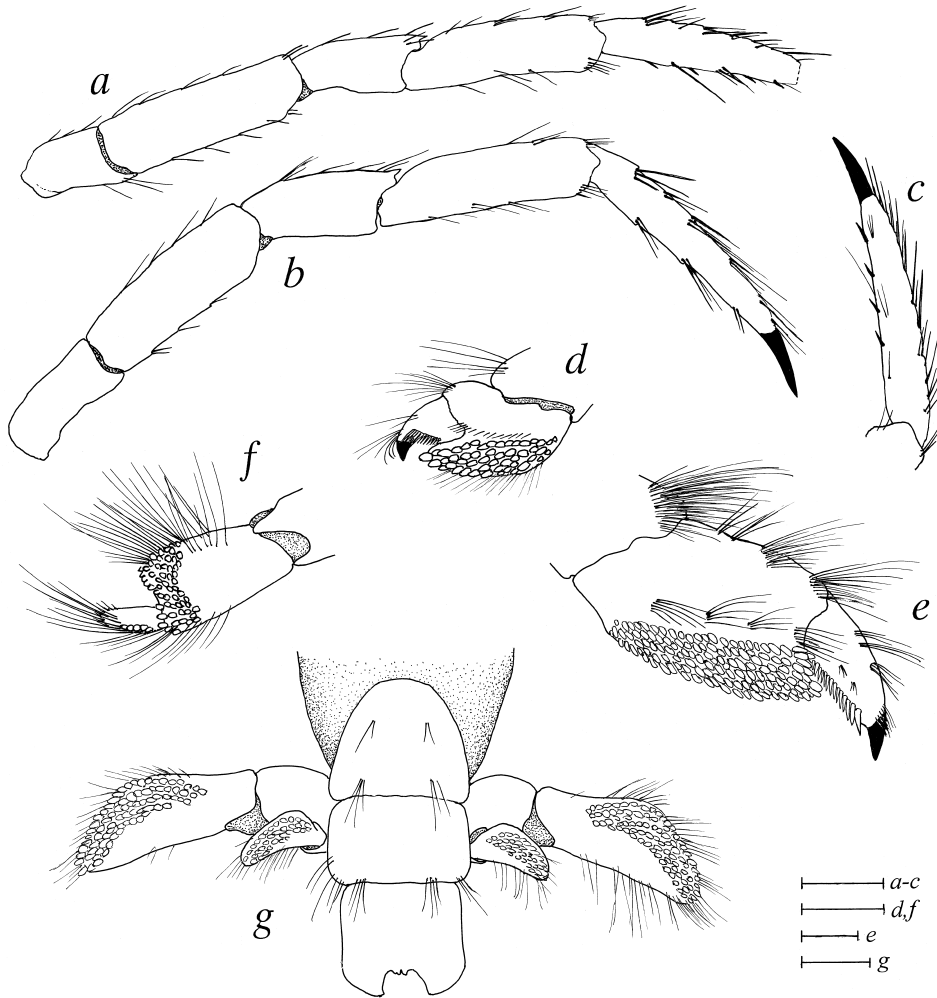


Fig. 5. *a-d, f, g*, *Pylojacquesia colemani*, new genus and species, *a, g*, allotype (sl = 4.0 mm), ZMB 5204; *b-d, f*, holotype (sl = 3.9 mm), ZMB 5204; *e*, *Mixtopagurus paradoxus* A. Milne-Edwards, 1880, *e*, male (sl = 11.9 mm), Gulf of Mexico, USNM 92321: *a*, right second pereopod, lateral view (tip damaged); *b*, right third pereopod, lateral view; *c*, dactyl of same, mesial view; *d, e*, dactyl and propodus of left (*d*) and right (*e*) fourth pereopods, lateral view; *f*, dactyl and propodus of left fifth pereopod, lateral view; *g*, tergite of sixth abdominal somite, uropods, and telson, dorsal view. Scales equal 1 mm (*a-c, e*), and 0.5 mm (*d, f, g*). Stippling indicates membranous regions.

paguridae, Lithodidae, and Pylochelidae. Still others appear to be unique to the new genus *Pylojacquesia*. When evaluating monophyly in "asymmetrical" hermit crabs, Richter and Scholtz (1994) adjudged the asymmetrical abdomen an apomorphic character, with examples of symmetry in the position of the telson secondarily acquired. The straight abdomen and symmetrical uropods, together with the operculate right cheliped of *P. colemani*, new species, most probably are habitat adaptations. Nonetheless, the several distinctive morphological aspects of this genus,

if considered from a phylogenetic point of view, are enigmatic.

Richter and Scholtz (1994) regarded the occurrence of paired first and second pleopods the plesiomorphic condition in males. While only in some female parapagurids has a rudimentary or vestigial right second pleopod been observed (Lemaitre, 1989, 1990, 1999), the occurrence of paired, first pleopods in females was also deemed plesiomorphic by Richter and Scholtz (1994). The presence of paired, modified first pleopods is much more prevalent in genera of the Paguridae than

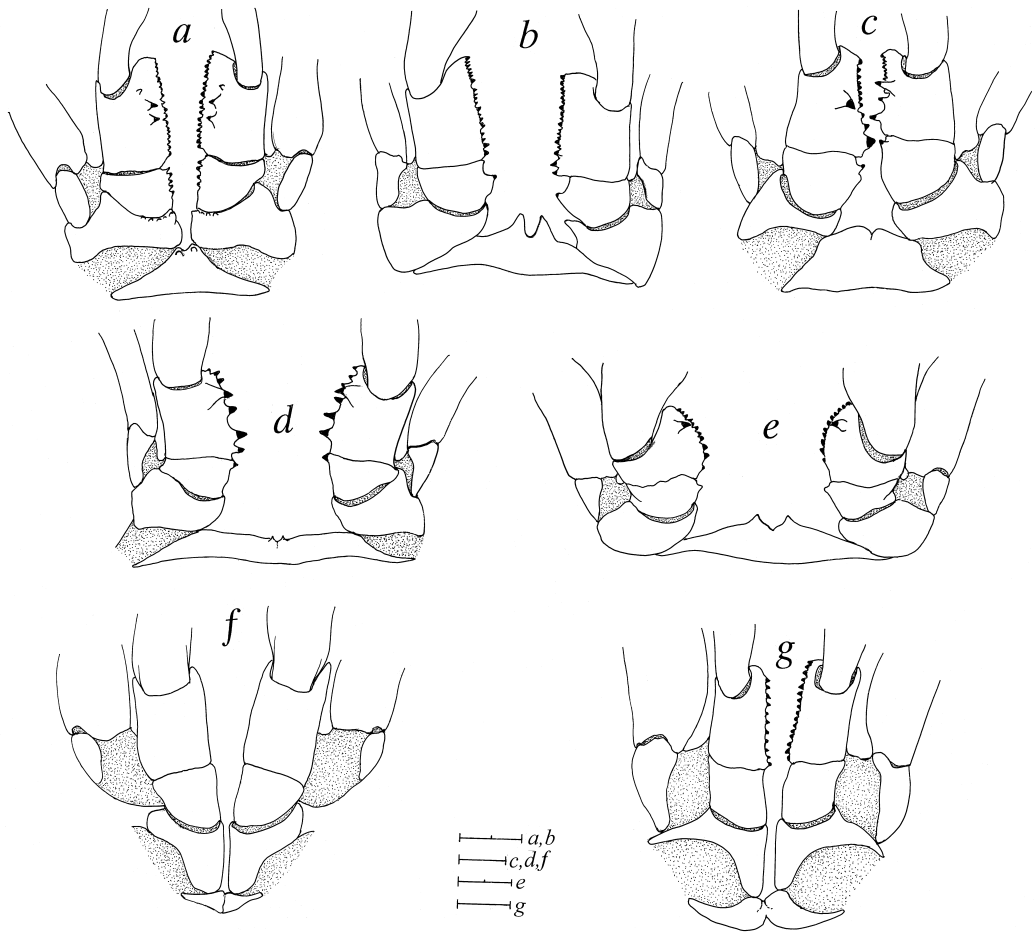


Fig. 6. Sternite IX and coxae, bases, ischia, and parts of meri and exopods of third maxillipeds in representatives of hermit crab families, ventral view. *a*, Pylochelidae, *Mixtopagurus paradoxus* A. Milne-Edwards, 1880, Gulf of Mexico, USNM 92321; *b*, Parapaguridae, *Parapagurus pilosimanus* Smith, 1879, northeastern coast of United States, USNM 216842; *c*, Paguridae, *Xylopagurus cancellarius* Walton, 1950, eastern Pacific, USNM 128863; *d*, Paguridae, *Pagurus pollicaris* Say, 1817, northeastern coast of United States, USNM 9308; *e*, Lithodidae, *Dermaturus mandtii* Brandt, 1850, Alaska, USNM 267705; *f*, Coenobitidae, *Coenobita clypeatus* (Fabricius, 1787), Caribbean Sea, USNM 154545; *g*, Diogenidae, *Clibanarius vittatus* Bosc, 1802, Caribbean Sea, USNM 7572. Scales equal 2 mm (*a*, *b*, *e*), and 1 mm (*c*, *d*, *f*, *g*). Stippling indicates membranous regions.

other hermit crab families, and in structure, female first pleopods of *Pylojacquesia*, new genus (Fig. 2c), appear “pagurid-like”, albeit longer.

The presence of a *crista dentata* was regarded by Richter and Scholtz (1994) to be apomorphic for reptant decapods (their “Eureptantia” exclusive of the Polychelidae) but they were uncertain whether the presence of one or more accessory teeth should be considered plesiomorphic or apomorphic. McLaughlin and Lemaitre (1997), however, adjudged the absence of an accessory tooth to be a plesiomorphic state. *Pylojacquesia*,

new genus, lacks an accessory tooth, a condition common to genera of the Diogenidae.

McLaughlin and Lemaitre (1997) illustrated a great variety of fourth pereopods, and in none, nor any of the species of which we are familiar, except for *Mixtopagurus paradoxus* Milne-Edwards, 1880 (Fig. 5e), is the ventral margin of the dactyl armed with such an elongate row of slender, corneous spines as is seen in *Pylojacquesia*, new genus (Fig. 5d). Species of *Xylopagurus* also have a row of unusually strong corneous spines on the ventrolateral margin of the dactyl (Lemaitre, 1995), but these spines are short. The signif-

icance or phylogenetic meaning of this dactylar condition cannot be determined at the present time. The fifth pereopods of the new genus are subchelate, a condition seen only in a few Pylochelidae (cf. Forest, 1987), and in *Solitariopagurus* Türkay, 1986, and *Alainopagurus* McLaughlin, 1997, among the Paguridae (McLaughlin and Lemaitre, 1997). Scholtz and Richter (1995) regarded the lack of a chelate fifth pereopod as plesiomorphic.

In addition to their data on the larvae, MacDonald *et al.* (1957) used the position of the bases of the third maxillipeds to divide the hermit crab families into superfamilies, just as Bouvier (1940) had done with his "parallel series." The bases of the maxillipeds of *Pylojacquesia*, new genus (Fig. 1b), cannot be regarded as widely separated, although they are disassociated by a small median projection of the sternite. Such a projection does not seem to occur in genera of the other families. Based on the criterion of maxilliped position, *Pylojacquesia*, new genus, must be judged as allied with the Pylochelidae (Fig. 6a), but also with the Coenobitidae (Fig. 6f), and Diogenidae (Fig. 6g). In some tubedwelling Paguridae such as species of *Xylopagurus* (Fig. 6c), the third maxillipeds are not as widely separated as is the norm in this family (e.g., species of *Pagurus*, Fig. 6d); the sternite does not have a median projection. The pagurid condition of the third maxillipeds exhibited by *Xylopagurus*, however, may represent an adaptation to the constricted conditions of its life in tube dwellings.

As noted by Richter and Scholtz (1994), and confirmed by McLaughlin and Lemaitre (1997), no thoraco-abdominal fusion is apparent in the families Pylochelidae, Coenobitidae, or Diogenidae. These latter authors reported a tendency toward fusion in the Parapaguridae. While in most members of the Paguridae and Lithodidae complete fusion has occurred, there are exceptions. McLaughlin and Lemaitre (1997) referred to incomplete fusion in the pagurid genera *Xylopagurus*, *Labidochirus* Benedict, 1892, and *Phimochirus* McLaughlin, 1981. In *Pylojacquesia*, new genus, while the first abdominal somite is contiguous with the last thoracic, both somites are readily identifiable and separated by a distinct suture. No recognizable fusion has occurred.

Complete calcification of the first abdominal tergite and at least partial calcification

of its respective sternite is characteristic of the Pylochelidae. At least partial calcification of the tergite is not uncommon in genera of the Coenobitidae, Diogenidae, Parapaguridae, the lithodid subfamily Lithodinae, and even some genera of the Paguridae, e.g., *Porcellanopagurus* Filhol, 1885, *Solitariopagurus*. Similarly, some calcification of the sternite is present in some of these genera, although it is less frequently observed. What is different in *Pylojacquesia*, new genus, is that while the tergite exhibits a small area of calcification (Fig. 2a), no characteristic posterior "bulge" in the tergite (cf. Richter and Scholtz, 1994: 195, fig. 3D) is observed, and the sternal calcification includes a prominent, posteriorly directed projection (Fig. 1a).

Other than position of the third maxillipeds and the shape of the anterior lobe of the sternite of the third pereopods (XII), the sternal plates of hermit crabs have received limited published attention. Sternites IX–XI (sternites of the third maxillipeds, chelipeds, and second pereopods) in *Pylojacquesia*, new genus, do not appear to differ from the condition described by Pilgrim (1973) for *Pagurus bernhardus* (Linnaeus, 1758). However, rather than the thin, flexible hinge separating sternites XI and XII, an appreciably broader membranous area is present in the new genus, *Pylojacquesia*. Similarly, the membranous areas separating sternites XII from XIII (sternites of third and fourth pereopods), and XIII from XIV (sternites of fourth and fifth pereopods) are considerably larger in this new genus. Extrapolating from Scholtz and Richter's (1995) proposition that fusion of all thoracic sternites, or at least the last two, reflects the plesiomorphic condition, the broadly separated sternites of *Pylojacquesia*, new genus, might be regarded as more highly evolved than any other hermit crab genus.

The toothed and chitinized condition of the mandible is unquestionably the most morphologically unique character of *Pylojacquesia*, new genus. To the best of our knowledge, it has no counterpart among genera of the Anomura, although at least one other species, the parapagurid *Paragiopagurus insolitus* Lemaitre, 1997, has been reported to have a mandible with an incisor process consisting of several irregularly shaped teeth (Lemaitre, 1997: 589, fig. 8a). However, in the latter species the teeth are blunt and only the tips are corneous. In both the Anomura and

Brachyura, the mandible of the adult has been described and/or illustrated as having the molar process lost entirely. The teeth on the incisor process are also lost or reduced, producing a relatively smooth medial edge (e.g., Patwardhan, 1935a; Snodgrass, 1950; Caine, 1975; Barker and Gibson, 1978; McLaughlin, 1982; Factor, 1989; Scholtz and Richter, 1995). Among other reptant decapods, a toothed incisor process is not uncommon (e.g., Huxley, 1880; Patwardhan, 1935b; Snodgrass, 1950; Poore, 1975, 1994; Wales *et al.*, 1976; Robertson and Laverack, 1979; Suthers and Anderson, 1981; Factor, 1989; Scholtz and Richter, 1995). While Poore (1994) considered the anterior truncated, blade-like portion and posterior toothed margin of the mandible of thalassinideans as representing the plesiomorphic condition, a toothed cutting edge was regarded as apomorphic. A smooth anterior portion and weakly toothed posterior portion was also described by Forest and de Saint Laurent (1981) for *Neoglyphea inopinata* Forest and de Saint Laurent, 1975.

Although the mandibular teeth of *Neoglyphea inopinata* are described as being corneous, as they also are in *Pylojacquesia*, new genus, that is where the similarity ends. The mandible of *N. inopinata* is clearly divided into anterior and posterior portions, as it is in most thalassinideans (Poore, 1994); the teeth are small and restricted to the posterior portion (Forest and de Saint Laurent, 1981). A corneous edge on the incisor process has been documented by Lemaitre (1995) for species of the pagurid genus *Xylopagurus*, and by Forest (1987) for at least three pylochelid genera, *Parapylocheles* Alcock, 1901, *Cancellocheles* Forest, 1987, and *Mixtopagurus* A. Milne-Edwards, 1880, but teeth are lacking in all of these.

Factor (1989), in discussing mandibular development in larval decapods, indicated that in reptants the trend from larval to postlarval to adult was toward loss of the molar element, loss of teeth, and strengthening of the medial edge to produce a shield-shaped incisor. However, in the first postlarval stage of *Naushonia crangonoides* Kingsley, 1897, as described by Goy and Provenzano (1978), four well-developed teeth are present on this margin.

There is no trace of a molar process in the mandible of *Pylojacquesia*, new genus; how-

ever, while there may have been a reduction in number, there has been no loss of incisor teeth. That, together with the partial calcification of the mandible itself, suggests that this structure may represent an advanced larval or megalopal condition that has been retained in the adult. Several instances of neoteny in Crustacea were summarized by Matsuda (1979).

Regrettably, the mandible has often not been considered to have morphological significance, except with reference to the mandibular palp. In most descriptions of anomuran larvae, the mandibles are asymmetrical, and both incisor and molar processes are apparent in the zoeal stages. Although asymmetry and molar processes may be lost with the molt to the megalopa, a chitinous megalopal mandible is not common. However, a chitinous, and weakly toothed medial margin is illustrated, although not commented upon by Konishi (1986) for the megalopal stage of the lithodid, *Hapalogaster dentata* (de Haan, 1844). A mandible with only a marginally toothed incisor process is described for the ultimate zoeal stage in another lithodid, *Paralomis histrix* (de Haan, 1846) by Konishi and Taishaku (1994). In both species, larval development is abbreviated (cf. Gore, 1985). A chitinous, albeit smooth, incisor medial margin is illustrated by Carvacho (1988) for the first crab stage in *Pagurus bernhardus*, with increasing calcification in subsequent stages. These examples, while not in themselves substantive evidence, do lend support to the proposition that the mandible of *Pylojacquesia*, new genus, might be an example of neoteny (*sensu* Hurlley, 1959) or pedomorphosis (*sensu* Klingenberg, 1998).

Clearly, *Pylojacquesia*, new genus, combines morphological characters of the Diogenidae, Paguridae, and additional characters heretofore not known for either. With the exception of the unusual separation of the thoracic sternites, the majority of characters would appear to be plesiomorphic by current interpretation. If Scholtz and Richter (1995) are correct in their assessment of the apomorphic condition of the telson being one with a vertical and a horizontal suture, the structure of the telson in *P. colemani*, new species, would unquestionably also be plesiomorphic. Thus, one might hypothesize that *Pylojacquesia*, new genus, represents a spe-

cialized, primitive hermit crab positioned near the base of the ancestral lineage, before the position of the third maxillipeds and other familial characters had become genetically fixed. Alternatively, it might be argued that our interpretations of plesiomorphy and apomorphy in hermit crabs are not altogether accurate, and that *Pylojacquesia colemani*, new species, actually represents a highly advanced and specialized species.

#### KEY TO FAMILIES OF HERMIT CRABS

1. Fourth pereopods developed as normal walking legs; body "crab-like" in form; abdomen recurved and carried under cephalothorax . . . . . Lithodidae (Paguroidea)
- Fourth pereopods not developed as normal walking legs; body not "crab-like" in form; abdomen usually not recurved and carried under cephalothorax . . . . . 2
2. Mandible with incisor process mostly corneous, armed with prominent, acute teeth (Fig. 3*b, c*); sternite XI distinctly separated from sternite XII by membranous area (Fig. 1*a*) . . . . . Pylojacquesidae, new family (Paguroidea)
- Mandible with incisor process calcareous or at most with only mesial edge corneous, lacking acute teeth; sternite XI not distinctly separated from sternite XII, fused . . . . . 3
3. Third maxillipeds generally widely separated basally (Fig. 6 *b–e*); chelipeds unequal or less frequently subequal, right largest . . . . . 4
- Third maxillipeds generally approximate basally (Fig. 6*a, f, g*); chelipeds equal, subequal or unequal, left frequently largest . . . . . 5
4. Exopod of first maxilliped with flagellum . . . . . Paguridae (Paguroidea)
- Exopod of first maxilliped without flagellum . . . . . Parapaguridae (Paguroidea)
5. Antennules with flagella "stick-like" (semiterrestrial) . . . . . Coenobitidae (Coenobitoidea)
- Antennules with flagella not "stick-like" . . . . . 6
6. Paired pleopods on abdominal somites 2–5 . . . . . Pylochelidae (Coenobitoidea)
- No paired pleopods on abdominal somites 4 and 5 . . . . . Diogenidae (Coenobitoidea)

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#### LITERATURE CITED

Alcock, A. 1901. A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the Royal Indian Marine Survey Ship *Investigator*. Calcutta: i–iv, 1–286.

- . 1905. Anomura. Fasc. I. Pagurides.—Catalogue of the Indian decapod Crustacea in the collections of the Indian Museum 2: i–xi, 1–197.
- Asakura, A. 2000. A review of Japanese species of *Pylopaguropsis* Alcock, 1905 (Decapoda: Anomura: Paguridae).—Crustacean Research 29: 70–108.
- Barker, P. L., and R. Gibson. 1978. Observations on the structure of the mouthparts, histology of the alimentary tract, and digestive physiology of the mud crab *Scylla serrata* (Forskål) (Decapoda: Portunidae).—Journal of Experimental Marine Biology and Ecology 32: 177–196.
- Benedict, J. D. 1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum.—Proceedings of the United States National Museum 15: 1–26.
- Bosc, L. A. G. 1802. Histoire naturelle des crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. 2. De Guilleminet, Paris, 296 pp.
- Bouvier, E.-L. 1940. Faune de France. 37. Décapodes Marcheurs. Pp. 1–404. Paul Lechevalier, Paris.
- Brandt, J. F. 1850. Vorläufige Bemerkungen über eine aus zwei noch unbeschriebenen Gattungen und Arten gebildete Unterabtheilung (Hapalogastrica) der Tribus Lithodea, begleitet von einer Charakteristik der eben genannten Tribus der Anomuren.—Bulletin de la Classe physico-mathématique de l'Académie Impériale des Sciences de Saint Pétersbourg 8(17-17): 266–269.
- Caine, E. A. 1975. Feeding and masticatory structures of selected Anomura (Crustacea).—Journal of Experimental Marine Biology and Ecology 18: 277–301.
- Carvacho, A. 1988. Développement juvénile de *Pagurus bernhardus* L. (Crustacea Decapoda).—Cahiers Biologie Marine 29: 109–133.
- de Haan, W. 1833–1850. Crustacea. In: P. F. von Siebold, *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. i–xxxii, ix–xvi, 1–243, pls. A–J, L–Q, 1–55, circ. tab. 2. Lugduni-Batavorum, Leiden.
- Fabricius, J. C. 1787. *Mantissa insectorum sistens eorum species nuper detectas adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus*. 1. Pp. xx, 1–348. Hafniae.
- Factor, J. R. 1989. Development of the feeding apparatus in decapod crustaceans. Pp. 185–203 in B. E. Felgenhauer, L. Watling, and A. B. Thistle, eds. Functional Morphology of Feeding and Grooming in Crustacea. Crustacean Issues 6. A. A. Balkema, Rotterdam.
- Filhol, H. 1885. Description d'un nouveau genre de Crustacés provenant de la Nouvelle-Zélande.—Bulletin de la Société Philomatique de Paris (7)9: 47, 48.
- Forest, J. 1987. Les Pylochelidae ou "Pagures symétriques" (Crustacea Coenobitoidea). Pp. 1–254 in Résultats des campagnes MUSORSTOM.—Mémoires du Muséum national d'Histoire naturelle, Série A, Zoologie 137.
- , and M. de Saint Laurent. 1975. Présence dans la faune actuelle d'un représentant du groupe mésozoïque des Glyphéides: *Neoglyphea inopinata* gen. nov., sp. nov. (Crustacea Decapoda Glypheidae).—Compte Rendu hebdomadaire des Séances de l'Académie des Sciences Paris, série D 281: 155–158.
- , and ———. 1981. La morphologie externe de *Neoglyphea inopinata*, espèce actuelle de Crustacé Dé-

- capode Glyphéide. Pp. 51–84 in Résultats des Campagnes MUSORSTOM, 1. Philippines (18–28 mars 1976). Mémoires d'ORSTOM, 91.
- Gore, R. H. 1985. Molting and growth in decapod larvae. Pp. 1–65 in A. M. Wenner, ed. Crustacean Growth: Larval Growth. Crustacean Issues 2. A.A. Balkema, Rotterdam.
- Goy, J. W., and A. J. Provenzano, Jr. 1978. Larval development of the rare burrowing mud shrimp *Naushonia crangonoidea* Kingsley (Decapoda; Thalassinidea; Laomediidae).—Biological Bulletin 154: 241–261.
- Holthuis, L. B. 1959. The Crustacea Decapoda of Suriname (Dutch Guiana).—Zoologische Verhandlungen 44: 1–296.
- Hurley, D. E. 1959. Notes on the ecology and environmental adaptations of the terrestrial Amphipoda.—Pacific Science 13: 107–129.
- Huxley, T. H. 1880. The Crayfish. An introduction to the study of zoology. International Scientific Series, 28. xxviii, 371 pp. D. Appleton & Co., New York. Reprinted 1973, The MIT Press, Cambridge, Massachusetts and London.
- Kingsley, J. S. 1897. On a new genus and two new species of macrurous Crustacea.—Bulletin of the Essex Institute (for 1895): 95–99, pls. 1–3.
- Klingenberg, C. P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny.—Biological Reviews 73: 79–123.
- Konishi, K. 1986. Larval development of the stone crab, *Haplogaster dentata* (De Haan, 1844) (Crustacea: Anomura: Lithodidae) reared in the laboratory.—Journal of the Faculty of Science, Hokkaido University, (4) Zoology 24: 155–172.
- , and H. Taishaku. 1994. Larval development in *Paralomis hystrix* (De Haan, 1846) (Crustacea, Anomura, Lithodidae) under laboratory conditions.—Bulletin of the National Research Institute for Aquaculture 23: 43–54.
- Latreille, P. A. 1802. Histoire Naturelle, générale et particulière des Crustacés et des Insectes. 3: 1–480. F. Dufart, Paris.
- Lemaitre, R. 1989. Revision of the genus *Parapagurus* (Anomura: Paguroidea: Parapaguridae), including re-descriptions of the western Atlantic species.—Zoologische Verhandlungen 253: 1–106.
- . 1990. A review of eastern Atlantic species of the family Parapaguridae (Decapoda, Anomura, Paguroidea).—Journal of Natural History 24: 219–224.
- . 1995. A review of the hermit crabs of the genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), including descriptions of two new species.—Smithsonian Contributions to Zoology 570: 1–27.
- . 1997. Crustacea Decapoda: Parapaguridae from the KARUBAR Cruise in Indonesia, with descriptions of two new species. Pp. 573–597 in A. Crosnier and P. Bouchet, eds. Résultats des Campagnes MUSORSTOM, 16.—Mémoires du Muséum national d'Histoire naturelle 172.
- . 1999. Crustacea Decapoda: A review of the species of the genus *Parapagurus* Smith, 1879 (Parapaguridae) from the Pacific and Indian Oceans. Pp. 303–378 in A. Crosnier, ed. Résultats des Campagnes MUSORSTOM, 20.—Mémoires du Muséum national d'Histoire naturelle 180.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species Cum Characteribus, Differentiis, Synonymis, Locis*. Edition 10. 1, Pp. i–iii, 1–824. Holmiae.
- MacDonald, J. D., R. B. Pike, and D. I. Williamson. 1957. Larvae of the British species of *Diogenes*, *Pagurus*, *Anapagurus* and *Lithodes* (Crustacea, Decapoda).—Proceedings of the Zoological Society London 128: 209–257.
- Matsuda, R. 1979. Abnormal metamorphosis and arthropod evolution. Pp. 137–256 in A. P. Gupta, ed. Arthropod Phylogeny. Van Nostrand Reinhold Co., New York.
- McLaughlin, P. A. 1974. The hermit crabs (Crustacea Decapoda, Paguridae) of northwestern North America.—Zoologische Verhandlungen 130: 1–396.
- . 1981. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: Part II. *Rhodochirus* McLaughlin and *Phimochirus* McLaughlin.—Bulletin of Marine Science 31: 329–365.
- . 1982. Comparative morphology of crustacean appendages. Pp. 197–256 in D. E. Bliss, ed. The Biology of Crustacea. Vol. 2. L. G. Abele, ed. Embryology, Morphology, and Genetics. Academic Press, New York.
- . 1983a. A review of the phylogenetic position of the Lomidae (Crustacea: Decapoda: Anomala).—Journal of Crustacean Biology 3: 431–437.
- . 1983b. Hermit crabs—Are they really polyphyletic?—Journal of Crustacean Biology 3: 608–621.
- . 1997. Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. Pp. 433–572 in A. Crosnier and P. Bouchet, eds. Résultats des Campagnes MUSORSTOM, 16.—Mémoires du Muséum national d'Histoire naturelle 172.
- , and J. Haig. 1984. A review of *Pagurixus* (Decapoda, Anomura, Paguridae) and descriptions of new species.—Crustaceana 47: 121–148.
- , and R. Lemaitre. 1997. Carcinization in the Anomura—fact or fiction? I. Evidence from adult morphology.—Contributions to Zoology, Amsterdam 67: 79–123.
- , and M. de Saint Laurent. 1998. A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae).—Proceedings of the Biological Society of Washington 111: 158–187.
- Milne-Edwards, A. 1880. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey steamer “Blake”, Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les Crustacés.—Bulletin of the Museum of Comparative Zoölogy, Harvard College 8: 1–68.
- , and E.-L. Bouvier. 1891. Observations générales sur les paguriens recueillis dans la mer des Antilles et le Golfe du Mexique, par le Blake et le Hassler, sous la direction de M. Alexandre Agassiz.—Bulletin de Société Philomatique (8) 3: 102–110.
- Ortmann, A. 1892. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, IV. Die Abteilungen Galatheidea und Paguridea.—Zoologischen Jahrbüchern. Abtheilung für Systematik, Geographie und Biologie der Thiere 6: 241–326, pls. 11, 12.
- Patwardhan, S. S. 1935a. On the structure and mecha-

- nism of the gastric mill in Decapoda. III. The structure of the gastric mill in Anomura.—Proceedings of the Indian Academy of Science 1B: 405–413.
- . 1935b. On the structure and mechanism of the gastric mill in Decapoda. IV. The structure of the gastric mill in reptantous Macrura.—Proceedings of the Indian Academy of Science 1B: 414–422.
- Pilgrim, R. L. C. 1973. Axial skeleton and musculature in the thorax of the hermit crab, *Pagurus bernhardus* [Anomura: Paguridae].—Journal of the Marine Biological Association of the United Kingdom 53: 363–396.
- Poore, G. C. B. 1975. Systematics and distribution of *Callinassa* (Crustacea, Decapoda, Macrura) from Port Phillip Bay, Australia, with the descriptions of two new species.—Pacific Science 29: 197–209.
- . 1994. A phylogeny of the families of Thalassinidea (Crustacea: Decapoda) with keys to families and genera.—Memoirs of the Museum of Victoria 54: 79–120.
- Richter, S., and G. Scholtz. 1994. Morphological evidence for a hermit crab ancestry of lithodids (Crustacea, Decapoda, Anomala, Paguroidea).—Zoologischer Anzeiger 223: 187–219.
- Robertson, R. M., and M. S. Laverack. 1979. The structure and function of the labrum in the lobster *Homarus gammarus* (L.).—Proceedings of the Royal Society, London B 206: 209–233.
- Say, T. 1817. An account of the Crustacea of the United States.—Journal of the Academy of Natural Sciences of Philadelphia 1: 155–169.
- Scholtz, G., and S. Richter. 1995. Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca).—Zoological Journal of the Linnean Society 113: 289–332.
- Smith, S. I. 1879. The stalk-eyed crustaceans of the Atlantic coast of North America north of Cape Cod.—Transactions of the Connecticut Academy of Arts and Sciences 5: 27–136.
- Snodgrass, R. E. 1950. Comparative studies on the jaws of mandibulate arthropods.—Smithsonian Miscellaneous Collections 116: 1–85.
- Stimpson, W. 1858. *Prodromus descriptionis animalium evertibratorum, quae in expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federate missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit*. VII.—[Preprint (December 1858) from] Proceedings of the Academy of Natural Science of Philadelphia 1858 [1859]: 225–252.
- Studer, Th. 1889. Die Forschungsreise S. M. S. “Gazelle” in den Jahren 1874 bis 1876 unter Kommando des Kapitän zur See Freiherrn von Schleinitz herausgegeben von dem Hydrographischen Amt des Reichs-Marine-Amtes. 3. Zoologie und Geologie, i–iv + 322 pp.
- Suthers, I. M., and D. T. Anderson. 1981. Functional morphology of mouthparts and gastric mill of *Ibacus peronii* (Leach) (Palinura: Scyllaridea).—Australian Journal of Marine and Freshwater Research 32: 931–944.
- Türkay, M. 1986. Crustacea Decapoda Reptantia der Tiefsee des Roten Meeres.—Senckenbergiana Maritima 18: 123–185.
- Wales, W., F. L. Macmillan, and M. S. Laverack. 1976. Mandibular movements and their control in *Homarus gammarus*. I. Mandible morphology.—Journal of Comparative Physiology 6: 177–191.
- Walton, B. C. 1950. Some new and rare Pacific pagurids.—Journal of the Washington Academy of Sciences 40: 188–193.

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