A Review of the Hermit Crabs of the Genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), Including Descriptions of Two New Species

RAFAEL LEMAITRE

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 570

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ABSTRACT

Lemaitre, Rafael. 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*, number 570, 27 pages, 17 figures, 1995.—The examination of all available material of hermit crabs of the genus *Xylopagurus* A. Milne Edwards revealed the existence of two new species previously confounded with *X. rectus* A. Milne Edwards. As a result, the genus now contains five species, four of which are known only from the Caribbean Sea, and one of which is from the tropical eastern Pacific. A critical review of all species of *Xylopagurus*, and a discussion of unusual or unique features, are presented. The two new species, *X. anthonii* and *X. tenuis*, are described. A redescription of the type species of the genus, *Xylopagurus rectus* A. Milne Edwards, sensu stricto, is included, as well as diagnoses of *X. cancellarius* Walton and *X. tayrona* Lemaitre and Campos. A key for the identification of the species is presented. With the exception of the recently described *X. tayrona*, all species are fully illustrated, and complete synonymies are presented.

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Contents

A Review of the Hermit Crabs of the Genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), Including Descriptions of Two New Species

Rafael Lemaitre

Introduction

During the 1879 cruise of the United States Coast Survey Steamer *Blake*, several specimens of an unusual hermit crab were collected near the coast of the Caribbean islands of Dominica and St. Vincent (A. Milne Edwards, 1880). The hermit crabs were found living in cylindrical cavities in pieces of wood; the posterior opening was tightly sealed by a strongly calcified portion of the abdomen, and a massive, strongly armed right cheliped protected the anterior opening. A. Milne Edwards observed that these hermit crabs entered their wood housing head first, instead of backing in, as their shell-living counterparts did. Based largely on these morphological novelties and distinct mode of life, A. Milne Edwards (1880) erected the new genus *Xylopagurus* and species *X. rectus* for them. Using the same material, A. Milne Edwards and Bouvier (1893) subsequently supplemented the description of this genus and species. Since then, a substantial amount of material assumed to be *X. rectus* has been collected from the Caribbean. The majority of this material has remained deposited in various museums, unreported. An exception to this is Benedict's (1901) report of two specimens of *X. rectus* from Puerto Rico. Provenzano (1971) also indicated that specimens of *X. rectus* were collected during cruises of the University of Miami's R/V *John Elliott Pillsbury*, but included only a brief comment on the larvae.

In addition to *Xylopagurus rectus*, two more species of *Xylopagurus* have been described: *X. cancellarius* Walton, 1950, from the eastern Pacific, and recently, *X. tayrona* Lemaitre and Campos, 1993, from the Caribbean Sea. Discovery of the third species prompted a review of all available material previously identified as *X. rectus*. The review showed that two additional new species had been confounded under the name *X. rectus*, bringing to five the total number of species in the genus. This increase in number of species in the genus, and the discovery of several new or insufficiently described diagnostic characters, has made it necessary to present a detailed description or diagnosis of each of the species. Furthermore, the presence of unusual features of diagnostic importance, such as the operculate sixth abdominal tergite and the sulci of the cephalothorax, has made it essential to define the terminology employed.

The material used for this investigation remains deposited at the following museums and institutions: Museum of Comparative Zoology, Harvard University (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Rosenstiel School of Marine and Atmospheric Sciences, University of Miami (UMML). An attempt was made to examine the material of *Xylopagurus cancellarius* deposited at the Allan Hancock Foundation (now Natural History Museum of Los Angeles County), but this was not possible because it apparently was lost in the mail. The following abbreviations are used: SL, shield length (to the nearest 0.1 mm), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield; ORSTOM-SMCB, French government "Office de la Recherche Scientifique et Technique Outre-Mer, Service Mixte de Contrôle des Armées"; and ov, ovigerous female(s). In the material examined, the station numbers are preceded by abbreviations for ship names as follows: A, *Atlantis;* B, U. S. Coast Survey Steamer *Blake;* FH, *Fish Hawk;* SB, R/V *Silver Bay;* O, M/V *Oregon;* P, R/V *John Elliott Pillsbury;* and V, *Velero III.*

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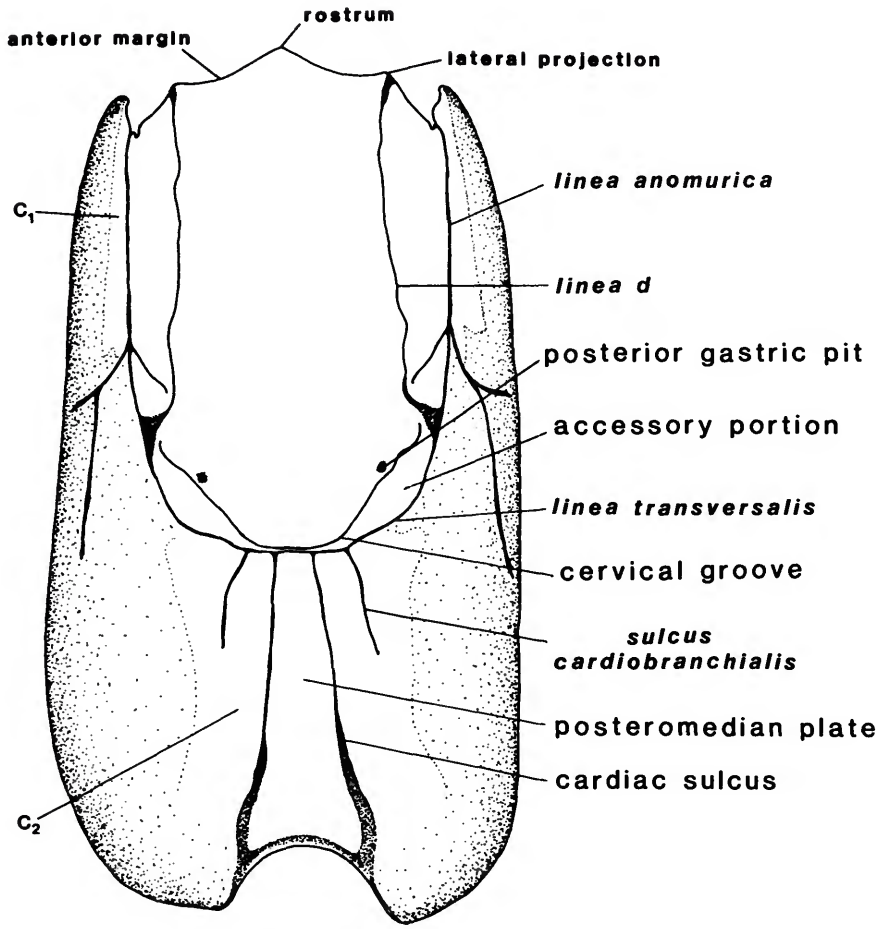


FIGURE 1.—Diagrammatic cephalothorax showing lineae and sulci found in species of *Xylopagurus* A. Milne Edwards. (c_1: calcified portion of wall of branchiostegite; c_2: calcified portion of posterior carapace).

ACKNOWLEDGMENTS.—I wish to thank my colleague N.H. Campos for attracting my attention to the species of the genus *Xylopagurus;* A. Johnston, M.M. Criales, J. Forest, J. García-Gómez, J. Haig, P.A. McLaughlin, and N. Voss, for arranging loans or facilitating access to material of *Xylopagurus* deposited in their respective museums or institutions; and J. Poupin, for permitting the examination of recent collections made by him in the Caribbean island of Guadeloupe. This study benefitted from the criticisms and suggestions of P.A. McLaughlin, and J.W. Martin. Molly K. Ryan illustrated the sixth abdominal tergites presented in Figure 7, and Rose A. Ragnacci assisted with the preparation of the plates.

Special Morphological Features and Terminology

Terms used to describe the general morphology of the species and sulci of the cephalothorax (Figure 1) follow McLaughlin (1974:11, figs. 1-5), except for the sulcus cardiobranchialis (= "sulcus a'" of McLaughlin), and the cardiac sulcus (= "sulcus cardiobranchialis" of McLaughlin). The original terminology proposed by Boas (1926:24, fig. 16) and Pilgrim (1973:367, fig. 1) for these two sulci is used, following the clarification provided by Morgan and Forest (1991). On either side of the posterior region of the cephalic shield there is a shallow pit; they are referred to as the posterior gastric pits (Glaessner, 1969).

The shield of *Xylopagurus anthonii,* new species, has a distinct suture that extends from near the posterolateral angle to the anterior margin just lateral to the lateral projection (Figure 1). The suture widens at either end, forming a small subtriangular weakly calcified area. This suture is designated linea d, following Boas (1880:189, fig. 141, letter d), and subsequent carcinologists (Jackson, 1913:502, text-fig. 1; Makarov, 1938:119, fig. 43; Pilgrim, 1973:366, fig. 1).

On the cephalothorax, a pair of well calcified regions are delineated anteriorly by the anterior prolongation of the cervical groove, and posteriorly by the linea transversalis. This region, designated here as "accessory portion," is incompletely

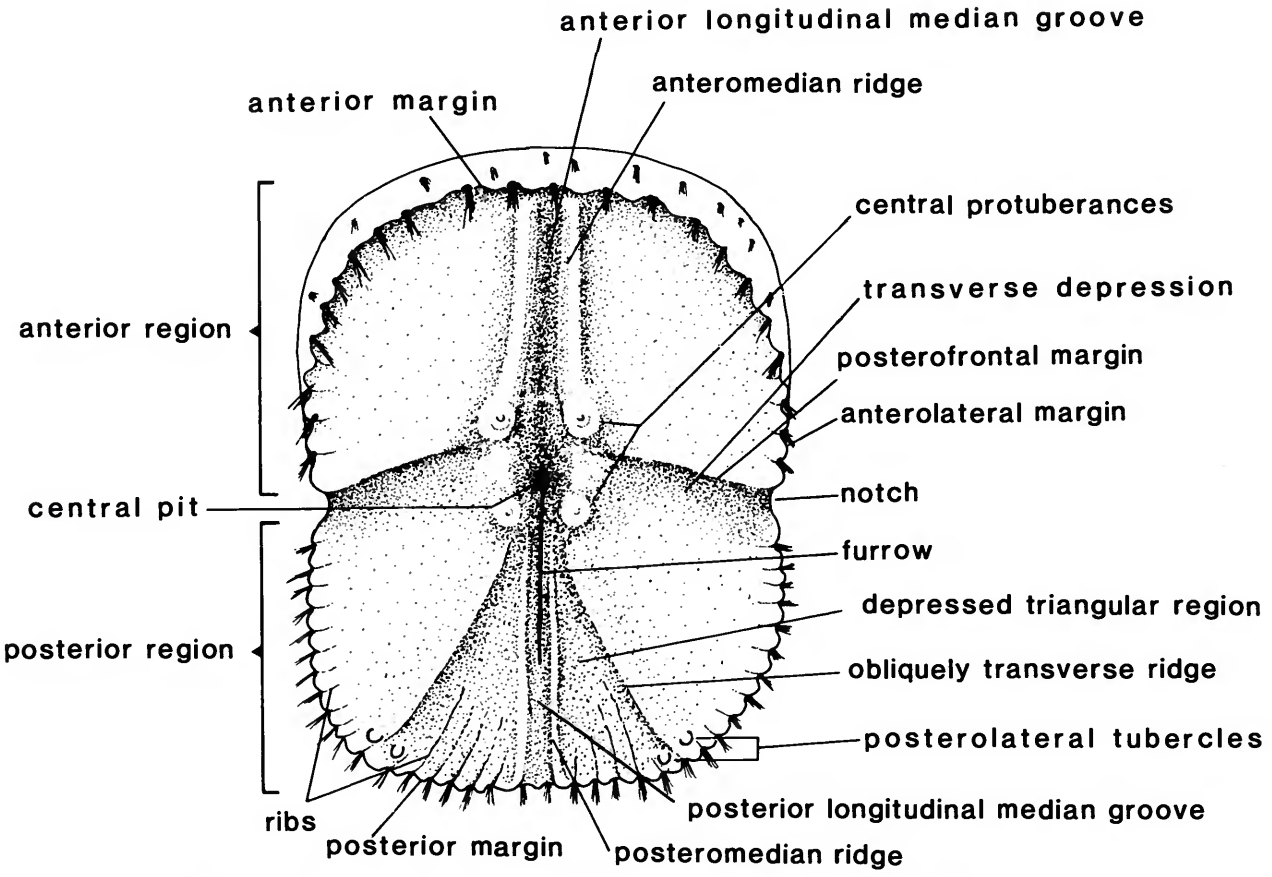


FIGURE 2.—Diagrammatic operculate tergite of sixth abdominal somite, showing terminology used in text.

delimited from the shield at the point where the linea d curves laterally (Figure 1). Although clearly delimited in many species of hermit crabs, this presumably homologous, calcified part of the cephalothorax has not received a name. McLaughlin (1974:341) described similar regions for *Labidochirus* and referred to them in the text as "islands"; however, McLaughlin did not name these in her fig. 91. On the branchiostegite, adjacent and parallel to the linea anomurica, there is a narrow calcified portion (c_1) extending from the anterior margin of the branchiostegite to the point where the linea anomurica curves away from the shield (Figure 1). This calcified portion is probably equivalent to the inner pterygostomial plate described by Pilgrim (1973:368, fig. 1, letter i.ptp) for *Pagurus bernhardus*. The posterior carapace has a well calcified region (c_2) that covers the posteromedian plate and portions of the carapace wall lateral to this plate (Figure 1).

The tergite of the sixth abdominal somite is strongly calcified, and operculate in shape. This tergite consists of a well-calcified plate-like structure divided into four equal or subequal quadrants by an anterior and posterior longitudinal median groove and a median or submedian transverse depression. The two anterior quadrants form the anterior region, the two posterior quadrants the posterior region. The latter can be delimited anteriorly by a distinct posterofrontal margin. A prominent notch on each side separates the regions laterally. A central pit frequently is present. The anterior and anterolateral margins are raised and usually broadly crenulate. On the anterior region, the longitudinal median groove can be flanked on either side by an elevated anteromedian ridge that can end posteriorly in a central protuberance adjacent to the transverse depression. The posterior region has a distinct depressed triangular region basally encompassing nearly the entire posterior margin, and with its blunt apex near the central pit. This triangular region is divided by the posterior longitudinal median groove, which can be flanked on either side by a low posteromedian ridge (often best observed in dorsolateral view of the tergite). A distinct furrow often extends from the central pit posteriorly between the posteromedian ridges. The depressed triangular region is delimited laterally by obliquely transverse ridges that can be set off anteriorly by a pair of central protuberances and frequently extend posteriorly to the posterior margin. The posterolateral and posterior

margins are crenulate or tuberculate, with the crenulations or tubercles often delineated by short or moderately short ribs.

Xylopagurus A. Milne Edwards, 1880

Xylopagurus A. Milne Edwards, 1880:37 [type-species: *Xylopagurus rectus* A. Milne Edwards, 1880:37, by monotypy; gender: masculine].—A. Milne Edwards and Bouvier, 1893:106.—Alcock, 1905:190.

DIAGNOSIS.—Thirteen pairs of phyllobranchiate gills. Shield distinctly longer than broad, with pair of posterior gastric pits. Accessory portions of carapace partially fused to shield. Branchiostegite with narrow calcified portion (c_1) adjacent and parallel to linea anomurica. Posterior carapace with dorsal surface (c_2) well calcified medially, with lineae and grooves as illustrated (Figure 1). Cardiac sulci extending posteriorly from linea transversalis to posterior margin of carapace, each sulcus widening posteriorly. Ocular acicles developed as broad ovate plates armed marginally. Second antennal segment with distolateral angle developed as broad subrectangular projection armed with spines on distal margin. Antennal acicle elongate and strong, subrectangular, armed with spines distally. Mouthparts as exemplified by those of type species (see Figure 5). Mandible (Figure 5*a*) with corneous edge on incisor process proximally, and 1–2 strong teeth distally. Maxillule (Figure 5*b*) with stiff bristle on moderately developed internal endopodal lobe, external lobe well developed, strongly recurved ventrally. Maxilla (Figure 5*c*) with endopod not reaching distal margin of scaphognathite, tapering distally. First maxilliped (Figure 5*d*) with exopod narrow basally, endopod equaling exopod in distal extension. Second maxilliped (Figure 5*e*) without distinguishing characters. Third maxilliped (Figure 5*f*) with ischium having well developed crista dentata and strong accessory tooth; merus and carpus each with small dorsodistal spine; exopod with row of hook-like setae on mesial margin distally. Palm of right cheliped with prominent spiniform dorsomesial projection distally. Fourth pereopod with propodus strongly produced ventrally; propodal rasp well developed, ovate, consisting of numerous minute scales (e.g., Figure 6*e*). Abdomen (e.g., Figures 3*b*, 8*a*) with tergites entire, those of 2nd to 5th somites represented by narrow calcified plates; tergite of sixth abdominal somite strongly calcified, operculate, obliquely closing off posterior opening of housing. Telson and uropods symmetrical; telson broader than long, without transverse suture. Males with paired first and second pleopods modified as gonopods, lacking pleopods on third to fifth somites. Females with paired gonopores, and unpaired, biramous left second to fourth pleopods; second pleopod slightly smaller than third and fourth, third and fourth subequal.

The following species are included in this genus: in the western Atlantic, *X. rectus* A. Milne Edwards, 1880 sensu stricto, *X. tayrona* Lemaitre and Campos, 1993, *X. anthonii*, new species, and *X. tenuis*, new species; and in the eastern Pacific, *X. cancellarius* Walton, 1950. All are found living in hollow pieces of reeds, in open-ended cylindrical cavities in pieces of wood, or in empty polychaete tubes.

Key to the Species of *Xylopagurus*

1. Operculate tergite of sixth abdominal somite with two pairs of prominent, conical protuberances near center . . . . . ***X. cancellarius*** Walton, 1950
   Operculate tergite of sixth abdominal somite without prominent, conical protuberances near center 2
2. Cephalic shield with pair of longitudinal sutures (linea d) extending from near termination of cervical groove to anterior margin in proximity of lateral projections . . . . . ***Xylopagurus anthonii,*** new species
   Cephalic shield without pair of longitudinal sutures (linea d) 3
3. Operculate tergite of sixth abdominal somite without anterior longitudinal median groove, anterior and posterior regions separated laterally by narrow V-shaped notch (see Lemaitre and Campos, 1993:564, fig. 5b); dactyls of ambulatory legs with 30 or more corneous spines on ventral margin . . . . . ***X. tayrona*** Lemaitre and Campos, 1993
   Operculate tergite of sixth abdominal somite with anterior longitudinal median groove, anterior and posterior regions separated laterally by broad U-shaped notch [e.g., Figure 8b]; dactyls of ambulatory legs with no more than 11 corneous spines on ventral margin 4
4. Posterior region of tergite of sixth abdominal somite with low posteromedian ridges extending to posterior margin; carpus of right cheliped evenly convex dorsally (specimens SL≤7.0 mm only) . . . . . ***X. rectus*** A. Milne Edwards, 1880, sensu stricto
   Posterior region of tergite of sixth abdominal somite without posteromedian ridges; carpus of right cheliped triangular in cross-section . . . . ***X. tenuis,*** new species

Xylopagurus rectus A. Milne Edwards, 1880, sensu stricto

FIGURES 3–6, 7a, 8

Xylopagurus rectus A. Milne Edwards, 1880:37 [in part]; 1883, fig. 9.—Filhol, 1885:132, fig. 40.—Agassiz, 1888:40, figs. 233, 234.—A. Milne Edwards and Bouvier, 1893:108 [in part], pl. 8: figs. 1–13.—Perrier, 1893:1037.—Young, 1900:384.—Pérez, 1934:27, fig. 17.—Rabaud, 1941:262, fig. 22.—Gordan, 1956:342 [in part].— Russell, 1962:19, fig. 13.

Not *Xylopagurus rectus*.—Benedict, 1901:143.—Schmitt, 1935:207, fig. 67. [= *Xylopagurus tenuis*, new species; see "Remarks"].

TYPE MATERIAL.—All from off Dominica, 15°17′20″N, 61°24′22″W, B-192, 138 fms (252.4 m), 30 Jan 1879: holotype, ♂ (SL 7.0 mm), MCZ 4097; paratypes, 4♂ (SL 3.1–4.3 mm), 1♀ (SL 4.0 mm), 1♀ ov (SL 5.5 mm), MCZ 4097; 1♂ (SL 6.5 mm), 1♀ ov (SL 5.0 mm), MNHN Pg. 462.

ADDITIONAL MATERIAL.—1♀ (SL 3.9 mm), north of Puerto Rico, 18°32′N, 66°21′15″W, sta 23, 260 fms (475.5 m), 4 Feb 1933, Johnson-Smithsonian Deep-Sea Expedition, USNM 265164. 3♀ ov (SL 4.8–6.0 mm), 17°50′N, 77°52′W, O-3549, 311 m, 16 May 1962, USNM 265144. 1♀ (SL 5.4 mm), 17°17′N, 87°59′W, O-3636, 229 m, 10 Jun 1962, UMML 32:2477. French Antilles, Guadeloupe, west coast of Basse Terre, ORSTOM-SMCB, coll. G. Leblond and J. Poupin: 2♀ ovs (SL 7.2, 5.5 mm), sta A 37, 16°22,65′N, 61°48,72′W, 200 m, Apr 1993; 5♂ (SL 6.0–11.0 mm), 3♀ ovs (SL 7.7–8.6 mm), sta A 117, 16°02,46′N, 61°46,86′W, 250 m, Apr 1993; 1♂ (SL 4.8 mm), sta B 117, 15°57,82′N, 61°43,02′W, 170 m, Mar 1993.

REDESCRIPTION.—Shield (Figure 4*a*) distinctly longer (1.4 times) than wide, evenly convex. Dorsal surface glabrous except for scattered minute pits and setal tufts, sometimes with some iridescence (preserved specimens); with short, low dorsal ridge posterior to rostrum, and shallow depressed region posterior to each lateral projection. Rostrum acutely subtriangular, exceeding lateral projections. Anterior margin nearly straight. Lateral projections broadly subtriangular. Anterolateral margins sloping, with distinct indentation on distolateral angle. Branchiostegite with anterior margin rounded, setose.

Ocular peduncles stout, combined length of peduncle and cornea about 1/2 length of shield; cornea dilated. Ocular acicles (Figure 4*a–c*) developed as broad ovate plate armed marginally with 9–13 spines; acicles separated basally by basal width of 1 acicle.

Antennular peduncle reaching to distal margin of cornea (peduncle not fully extended in Figure 4*a*). Ultimate segment less than 2.6 times as long as broad. Ultimate and penultimate segments subequal in length, with scattered setae. Basal segment with ventrodistal spine, setose lobe on lateral face proximally, and usually small spine on lateral face. Dorsal flagellum approximately 2 times as long as ultimate segment; ventral flagellum usually with 10 articles.

Antennal peduncle (Figure 4*a,d–f*) not exceeding distal margin of cornea, supernumerary segment present. Fifth segment with long setae on lateral and mesial margins. Fourth segment with scattered setae dorsally, and short transverse row of long setae on ventral face distally. Third segment with blunt ventrodistal angle. Second segment with distolateral angle developed as very broad subrectangular projection armed with 8–11 small spines on distal margin; dorsomesial distal angle armed with 1–3 spines. First segment unarmed, with tuft of setae on lateral face. Acicles elongate, distal margin armed with 5–7 small spines, and often with small spine dorsally; acicle more elongate, slender, in small specimens (SL<3.0 mm), and terminating in strong bifid or trifid spine (Figure 4*f*). Flagellum

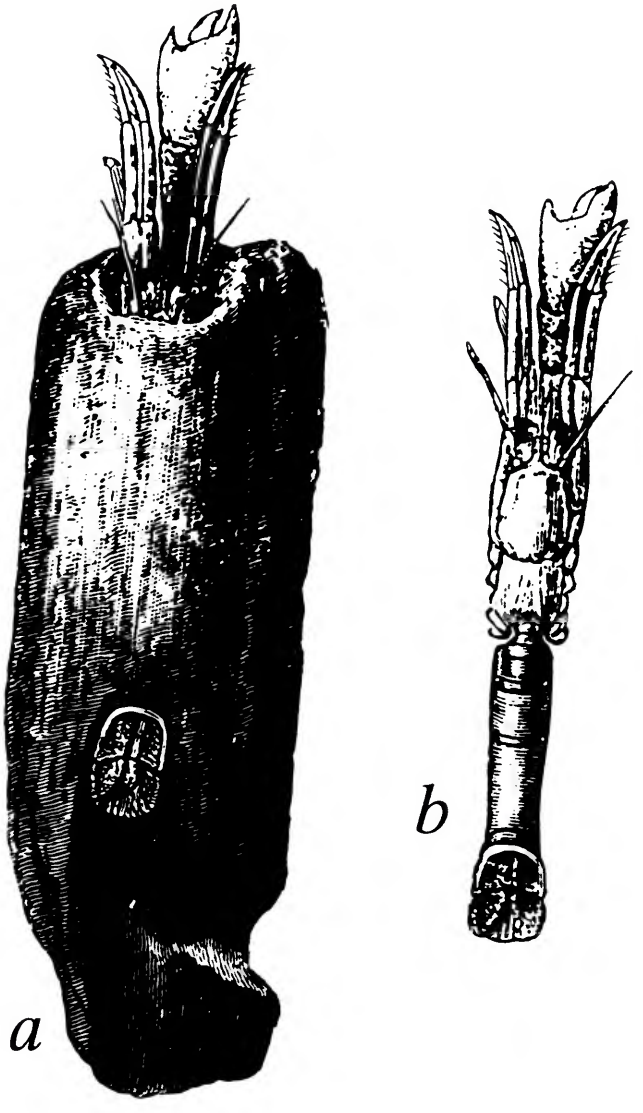


FIGURE 3.—*Xylopagurus rectus* A. Milne Edwards, 1880, sensu stricto: *a*, specimen in wood housing; *b*, specimen removed from wood housing (modified from Filhol, 1885).

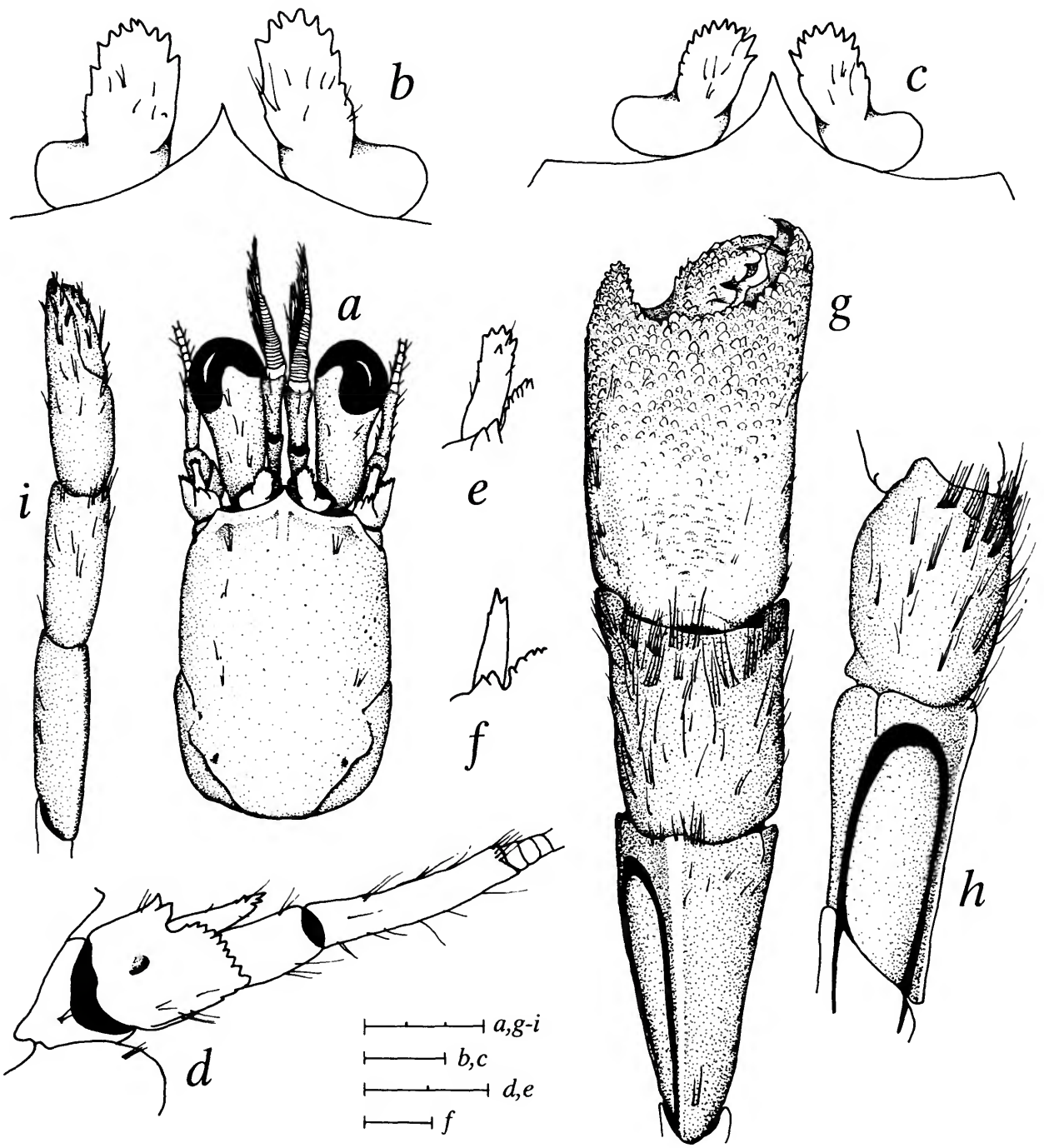


FIGURE 4.—*Xylopagurus rectus* A. Milne Edwards, 1880, sensu stricto; all male holotype SL 7.0 mm, except for *c,f.* paratypes (MCZ 4097): *a*, shield and cephalic appendages; *b*, ocular acicles and rostrum of same; *c*, ocular acicles and rostrum of female SL 5.5 mm; *d*, right antennal peduncle, lateral view; *e*, antennal acicle of same, dorsal view; *f*, antennal acicle of male SL 3.9 mm; *g*, right cheliped, dorsal view; *h*, merus and carpus of same, mesial view; *i*, left cheliped, dorsal view. (Scales = 3 mm for *a,g-i;* 0.5 mm for *b,c;* 2 mm for *d,c;* 0.5 mm for *f*).

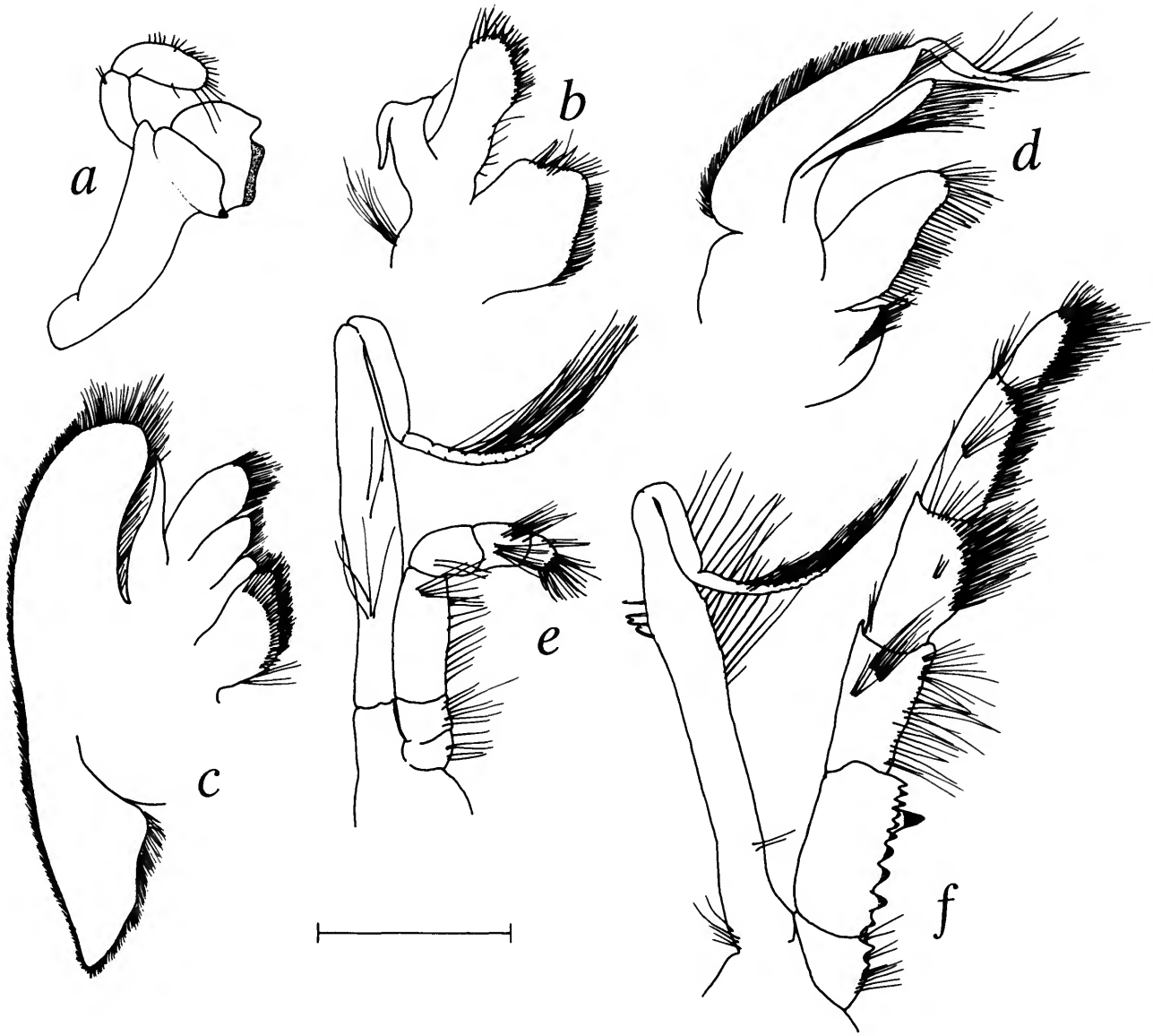


FIGURE 5.—*Xylopagurus rectus* A. Milne Edwards, 1880, sensu stricto; female SL 4.8 mm (USNM 265144); left mouthparts, internal view: *a*, mandible; *b*, maxillule; *c*, maxilla; *d*, first maxilliped; *e*, second maxilliped; *f*, third maxilliped. (Scale = 1 mm.)

reaching to about midlength of right chela, each article usually with 4–5 short and long setae.

Mouthparts as illustrated (Figure 5).

Chelipeds markedly dissimilar. Right cheliped (Figure 4*g*,*h*) strong, massive, fingers each terminating in blunt calcareous claw. Dactyl with tubercles and strong spines on dorsal face, and row of setal tufts parallel to cutting edge; mesial margin with setal tufts and small tubercles; cutting edge with 1 massive, molar-like calcareous tooth (only partially visible in Figure 4*g*) proximally, and with 3–5 small calcareous teeth distally; ventral surface smooth except for scattered setal tufts. Fixed finger slightly overreaching dactyl; dorsal face with strong tubercles and spines, and dorsomesial row of setal tufts; cutting edge with 2 strong, blunt calcareous teeth proximally, and 3 small teeth distally (not visible in Figure 4g); ventral face smooth except for ventromesial row of setal tufts. Palm 1.1 to 1.5 times as long as wide; spiniform dorsomesial projection approximately 1/2 as long as dactyl, with tubercles and spines

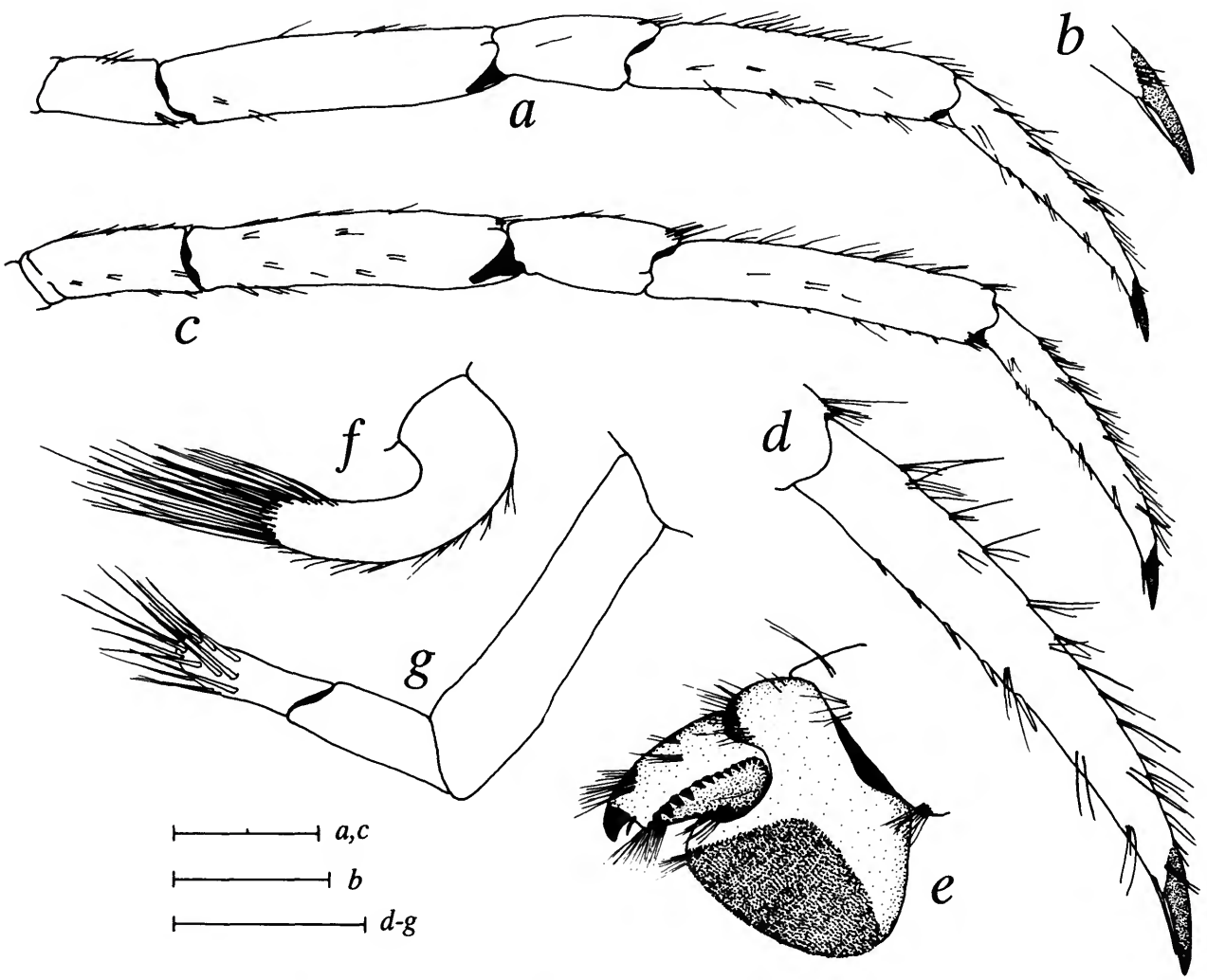


FIGURE 6.—*Xylopagurus rectus* A. Milne Edwards, 1880, sensu stricto; *a–d*, female paratype SL 5.5 mm (MCZ 4097); e–g, male holotype SL 7.0 mm: *a*, right second pereopod, lateral view; *b*, tip of dactyl of same; *c*, right third pereopod, lateral view; *d*, dactyl of same; *e*, propodus and dactyl of left fourth pereopod, lateral view; *f*, male left first pleopod, lateral view; *g*, male left second pleopod, lateral view. (Scales = 2 mm for *a,c;* 1 mm for *b;* 1 mm for *d,g*.)

on dorsal and mesial faces; dorsal surface armed on distal half with strong tubercles and spines (largest on medial region), smooth and with scattered setal tufts proximally; dorsomesial and dorsolateral margins each delimited at least distally by irregular row of small tubercles or spines; mesial face with numerous small tubercles and spines on distal third; lateral face smooth except for setal tufts; ventral face with scattered small tubercles and setal tufts. Carpus longer than wide, dorsal surface evenly convex (specimens SL≤7.0 mm) or triangular in cross-section (specimens SL>7.0 mm), with transverse rows of long setae on distal third, and scattered long setae proximally; ventral face smooth, but with scattered setal tufts. Merus twice as long as wide, triangular in cross-section, unarmed, but with scattered setae (dark band on Figure 4*g,h* represents molting suture). Left cheliped (Figure 4*i*) slender, short, reaching to distal margin of carpus of right cheliped. Fingers subequal to length of palm, terminating in corneous claw, opposing faces of fingers concave; cutting edges each with row of minute, fused

corneous teeth; dorsal and ventral surfaces with setal tufts. Palm unarmed, but with scattered setae. Carpus and merus subequal in length, unarmed, but with scattered setae.

Ambulatory legs (Figure 6*a–d*) similar from right to left. Dactyls each terminating in corneous claw, with tuft of setae near base of claw on lateral and mesial faces; ventral margin very broadly curved (more strongly curved distally), armed with 3–7 corneous spines; with row of long setae dorsally, and setal tufts on dorsolateral and dorsomesial faces. Ischia, meri, carpi, and propodi unarmed except for row of 4–8 spinules on ventral margin of each propodus; segments with few setae on dorsal and ventral margins, lateral and mesial faces with scattered setae or with tufts of short setae often arranged in longitudinal rows. Sternite of third pereopods narrow, anterior lobe naked, flat, sloping down anteriorly.

Fourth pereopod (Figure 6*e*) with dactyl subtriangular, terminating in corneous claw curved laterad; with setal tufts on dorsolateral and ventrolateral margins; ventrolateral margin with row of strong corneous spines directed slightly laterad and slender spine near base of claw. Propodus with rasp forming ovate area covering nearly half lateral face and consisting of numerous minute densely packed scales arranged in straight rows to form grid. Merus and carpus unarmed, but with scattered setae.

Fifth pereopod subchelate; propodus with long setae on dorsal and ventral margins; rasp formed of conical or lanceolate scales. Merus and carpus unarmed, but with scattered setae.

Operculate tergite of sixth abdominal somite (Figure 7*a*) with raised crenulate margins bearing evenly spaced tufts of long setae (more broadly spaced on anterior margin). Dorsal surface divided into anterior and posterior regions by broad transverse depression. Anterior and posterior regions separated laterally by wide U-shaped notch (Figures 7*a*, 8*b*). Anterior region with very uneven surface and many short irregular ridges; anterior longitudinal median groove distinct, flanked on each side by sharply elevated anteromedian ridge. Posterior region with numerous rounded pits, and distinct posterofrontal margin; depressed triangular region delimited laterally by well defined obliquely transverse ridges, longitudinal furrow usually reaching to central pit and flanked by low posteromedian ridges extending to posterior margin. Posterior region laterally with short ribs directed concentrically (ribs usually longer on depressed triangular region).

Telson (Figure 8*b–d*) not visible in dorsal view of abdomen, more than 2 times as broad as long. Lateral margins with tuft of short setae. Dorsal surface with 3 depressions (2 deep lateral, and 1 shallow medial). Terminal margin divided into very broad subequal lobes by shallow (sometimes obsolete) cleft, and armed with small spines bearing corneous tips.

Uropods (Figure 8*b*) robust. Protopod with dorsal face flattened; posterodorsal margin corneous, proximally with broad triangular and subrectangular teeth, and row of long setae; ventrodistal angle produced into prominent blunt spine with row of setae laterally. Rasp of endopod and exopod formed of strong conical and lanceolate scales; endopod with small denticles on anterior margin; rasp of exopod occupying almost entire surface of lateral face, scales stronger and more spaced proximally.

First pleopods of males (Figure 6*f*) 1-segmented, curved anteriorly, and with long dense setae distally; second pleopods (Figure 6*g*) 3-segmented, directed anteriorly, with long setae distally. Ovigerous females with eggs ranging from 12 to 50 in specimens examined, eggs approximately 1–1.5 mm in diameter.

REMARKS.—As previously mentioned, the material used by A. Milne Edwards (1880) in his brief description of *Xylopagurus rectus* came from *Blake* stations 192 and 223, collected at Dominica and St. Vincent, respectively. Subsequently, A. Milne Edwards (1883) illustrated his species but did not include a descriptive text. The *Blake* material was again used by A. Milne Edwards and Bouvier (1893) when a more detailed description of *X. rectus* was published. Although A. Milne Edwards (1880) did not select a holotype for his taxon, he did indicate in his later 1893 publication with Bouvier that the type was the largest male from *Blake* station 192. The illustrations presented by A. Milne Edwards (1883), and by A. Milne Edwards and Bouvier (1893), do represent *X. rectus* sensu stricto. However, examination of the type material has revealed that the male from off St. Vincent (station 223) actually represents *X. tenuis*, new species. One of A. Milne Edwards and Bouvier's illustrations (pl. 8: fig. 1) was evidently used by several authors (Pérez, 1934; Rabaud, 1941; Russell, 1962) in discussions of adaptations and evolution in hermit crabs. In his popular account of deep sea life, Filhol (1885, fig. 40) included an engraving depicting *Xylopagurus rectus* with and without its wood housing, based on specimens sent to him by A. Milne Edwards. The engraving was inverted during the printing process, and inaccurately shows the chelipeds and spiniform projection of the right palm on the wrong side. This same inverted engraving was re-published later by Agassiz (1888, figs. 233, 234) in his narrative of the cruises of the *Blake*. The operculate tergite of the sixth abdominal somite depicted by these authors clearly shows the presence of posteromedian ridges, leaving no doubt that their figures represent *X. rectus* sensu stricto. A modified and corrected reproduction of this engraving is presented in Figure 3.

DISTRIBUTION.—Caribbean Sea: Off Belize, Jamaica, Guadeloupe, and Dominica; 170 to 311 m.

HABITAT.—Pieces of wood.

AFFINITIES.—See *Xylopagurus tenuis*, new species.

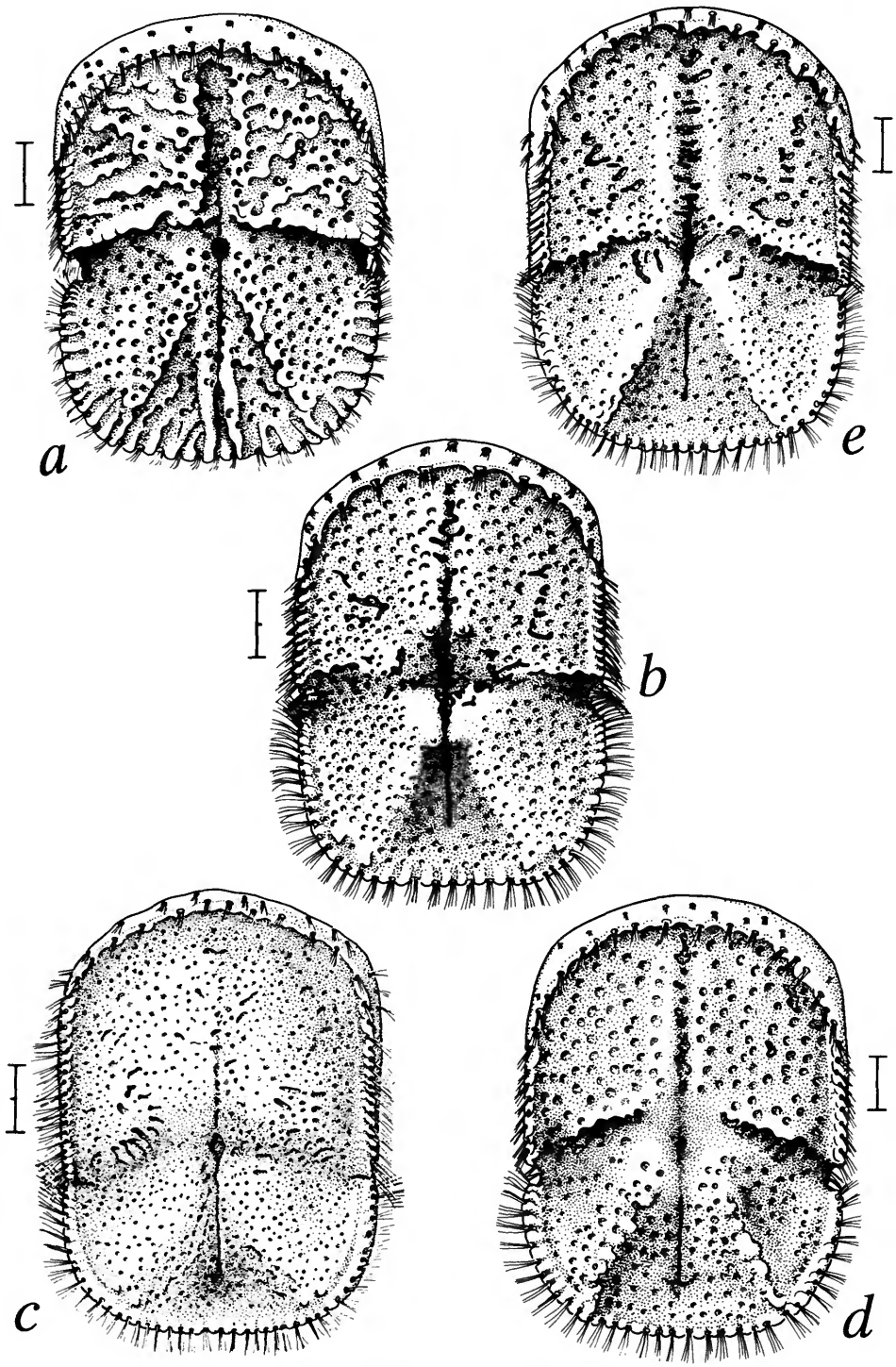


FIGURE 7.—Operculate tergite of sixth abdominal somite in species of *Xylopagurus* A. Milne Edwards, 1880, dorsal view: *a, X. rectus* A. Milne Edwards, 1880, sensu stricto, male holotype (MCZ 4097); *b, X. cancellarius* Walton, 1950, male SL 12.1 mm (USNM 128863); *c, X. tayrona* Lemaitre and Campos, 1993, female holotype (USNM 251902); *d, X. anthonii*, new species, female holotype (USNM 265145); *e, X. tenuis*, new species, male holotype (USNM 265150). (Scales = 1 mm for *a,d,e;* 2 mm for *b,c.*) (*c*, from Lemaitre and Campos, 1993.)

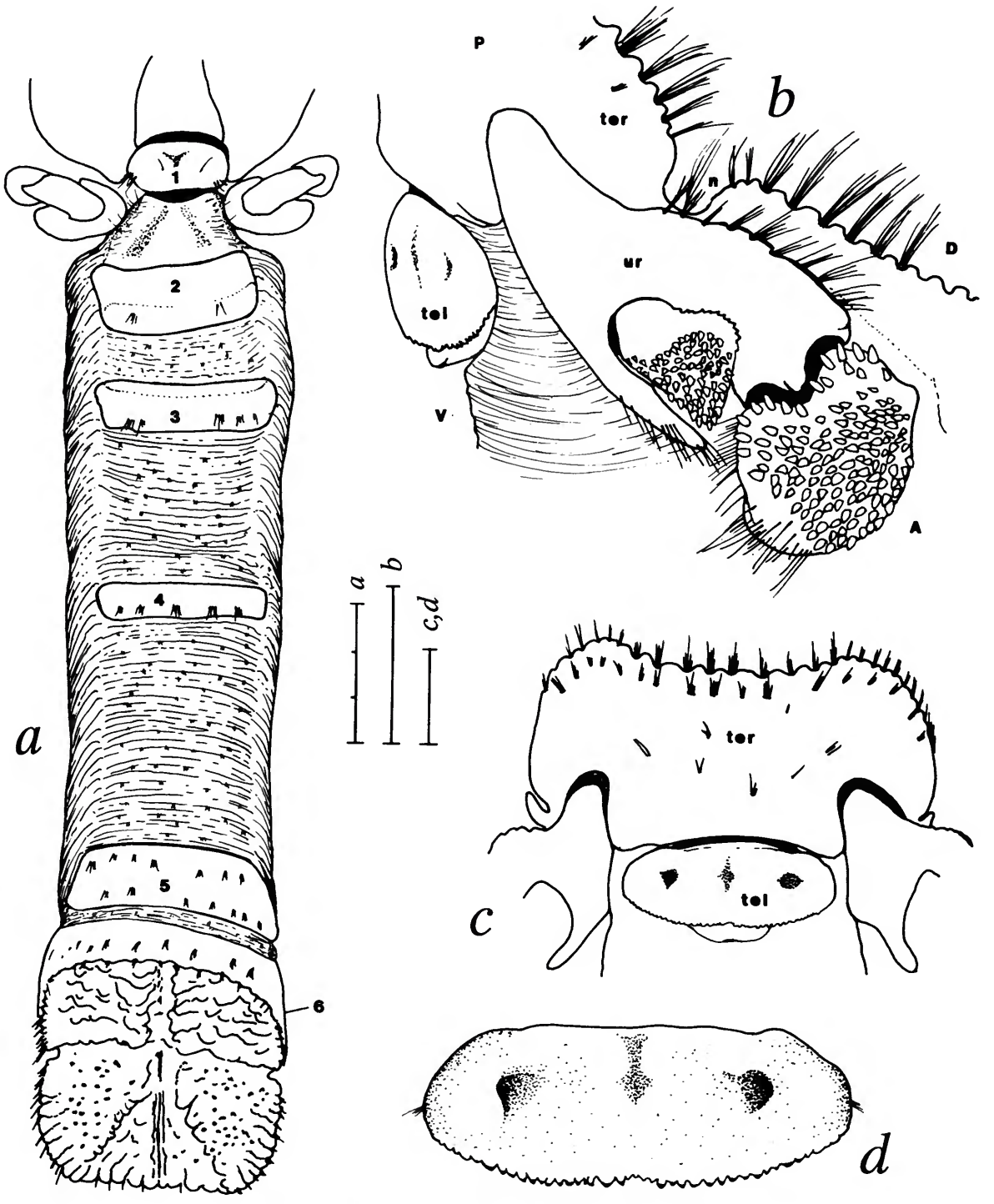


FIGURE 8.—*Xylopagurus rectus* A. Milne Edwards, 1880, sensu stricto; *a*, male holotype (MCZ 4097); *b–d*, female paratype SL 5.5 mm (MCZ 4097): *a*, abdomen, dorsal view; *b*, right uropod, part of margin of sixth abdominal tergite, and telson, lateral view; *c*, posterior part of abdomen in ventral view, showing part of sixth abdominal tergite, and telson; *d*, telson, dorsal view. (Scales = 3 mm for *a;* 1 mm for *b,c;* 0.5 mm for *d.*). Abbreviations are as follows: 1–6, abdominal tergites; tel, telson; ter, sixth abdominal tergite; ur, uropod; A, anterior; D, dorsal; P, posterior; V, ventral.

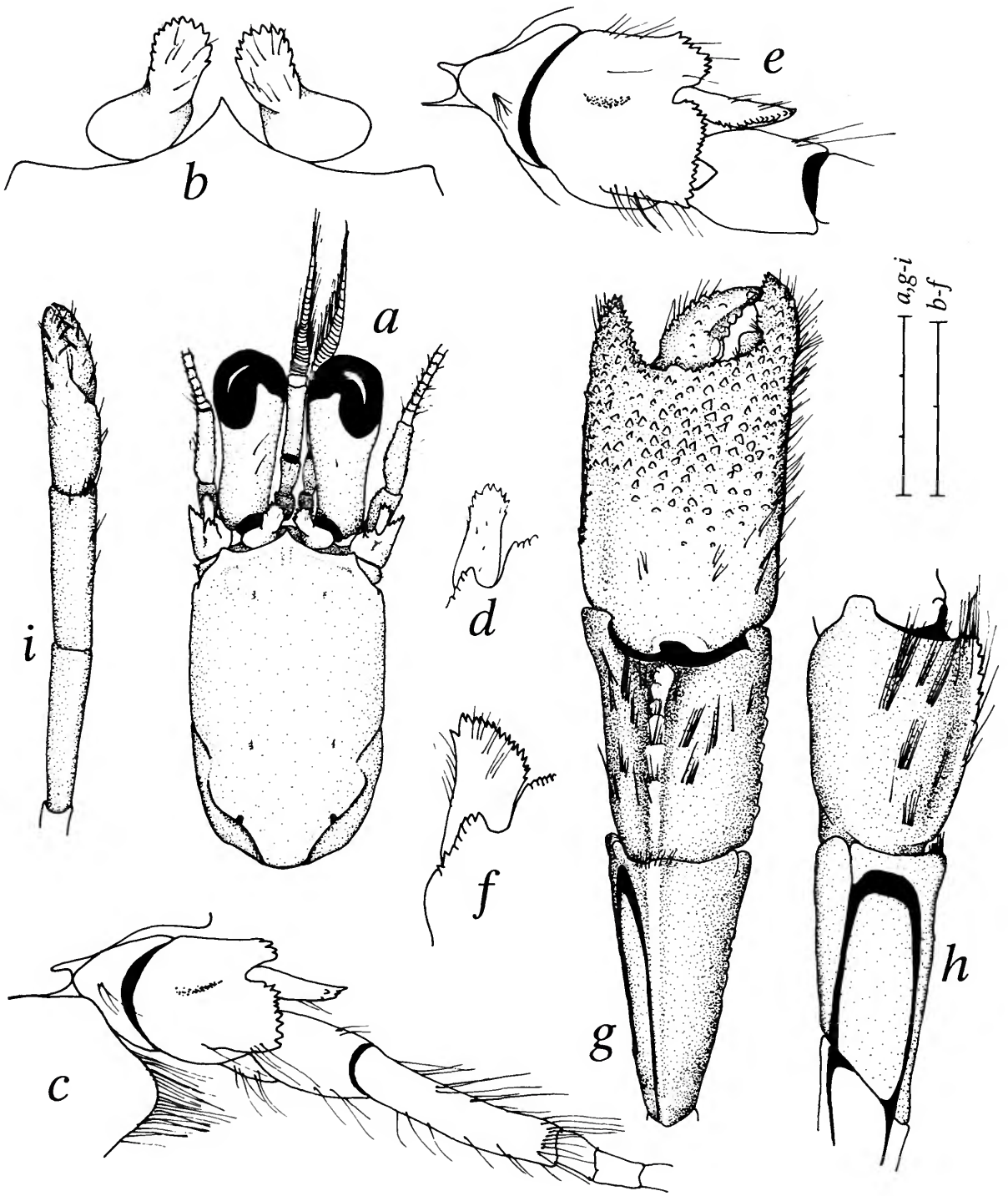


FIGURE 9.—*Xylopagurus cancellarius* Walton, 1950; female holotype (USNM 90384) except for *e,f,* male SL 12.1 mm (USNM 128863): *a,* shield and cephalic appendages; *b,* ocular acicles and rostrum, dorsal view; *c,* right antennal peduncle, lateral view; *d,* antennal acicle of same, dorsal view; *e,* first to third segments of right antennal peduncle, lateral view; *f,* antennal peduncle of same, dorsal view; *g,* right cheliped, dorsal view; *h,* merus and carpus of same, lateral view; *i,* left cheliped, dorsal view. (Scales = 3 mm for *a,g–i;* 1 mm for *b–d;* 2 mm for *e,f.*)

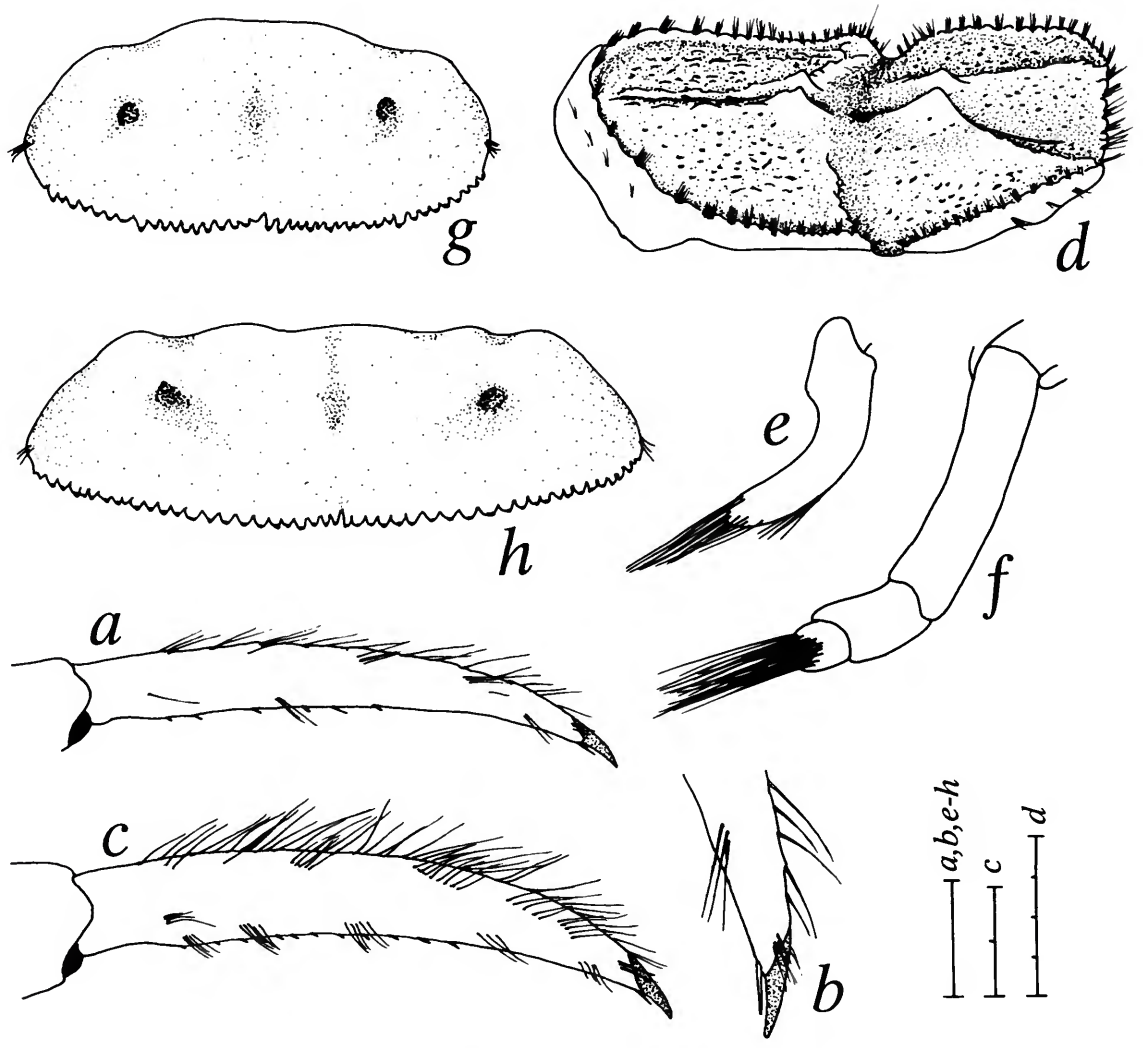


FIGURE 10.—*Xylopagurus cancellarius* Walton, 1950; *a,b,g*, female holotype; *c,d,h*, male SL 12.1 mm (USNM 128863); *e,f*, male SL 10.8 mm (USNM 244296): *a*, dactyl of right third pereopod, lateral view; *b*, tip of dactyl of same; *c*, dactyl of right third pereopod, lateral view; *d*, sixth abdominal tergite, dorsolateral view; *e,f*, male left first (e) and second (f) pleopods, lateral view; *g,h*, telson, dorsal view. (Scales = 1 mm for *a,b,e,f,h;* 2 mm for *c;* 4 mm for *d;* 0.5 mm for *g*.)

Xylopagurus cancellarius Walton, 1950

FIGURES 7*b*, 9, 10

Xylopagurus cancellarius Walton, 1950:190, fig. 2.

Xilopagurus cancellarius.—Ríos et al., 1990:78, figs. 1, 2. [misspelling of *Xylopagurus cancellarius*].

HOLOTYPE.—♀ (SL 5.8 mm), off Port Utría, Pacific coast of Colombia, V-238-34, 37 m, 15 Feb 1934, USNM 90384.

ADDITIONAL MATERIAL.—1♂ (SL 12.1 mm), Costa Rica, beach, intertidal, 12 Nov 1969, USNM 128863. 1♀ (SL 7.5 mm), Gulf of Nicoya, Costa Rica, sta BN-8, 25 m (?), Feb 1980, coll. H. Dean and S. House, USNM 265162. 1♀ (SL 4.2 mm), outside peninsula at Port Utría, Colombia, V-236-34, 73 m) 15 Feb 1934, USNM 265156. 1♂ (SL 10.8 mm), off Bahía Buenaventura, Colombia, 72 m, 29 Sep 1990, coll. M. Londoño, USNM 244296.

DIAGNOSIS.—Rostrum acutely subtriangular, exceeding lateral projections. Ocular acicles (Figure 9*a,b*) terminating in raised ovate projection armed with 12–14 marginal spines. Ultimate antennular segment more than 2 times longer (2.4 to 2.8 times) than broad. Second antennal segment (Figure 9*c,e*) with distolateral angle produced into subrectangular projection

armed with 10–19 small spines on distal margin; dorsomesial distal angle armed with 4–8 spines. Antennal acicles subrectangular, strongly developed and broad in large specimens (SL≥12.0 mm; see Figure 9*a,d,f*), distal margin armed with 7–17 small spines. Antennal flagellum densely setose, each article with about 8–10 short and long setae. Right cheliped (Figure 9*g,h*) with dactyl bearing few scattered tubercles dorsally; palm with dorsal surface armed with numerous spines and tubercles at least on distal half; carpus subtriangular in cross-section, dorsal margin well delimited (often somewhat raised) and armed anteriorly with tubercles bearing setal tufts, lateral and mesial faces with transverse rows of setae; merus less than 2 times as long as broad, subtriangular in cross-section (dark band on Figure 9*g,h* represents molting suture). Left cheliped (Figure 9*i*) unarmed, dorsal surface of merus, carpus and palm evenly convex, with setal tufts in large specimens (SL≥12.0 mm). Dactyls of ambulatory legs (second and third pereopods; Figure 10*a–c*) each with 5–14 small, widely spaced corneous spines on ventral margin in addition to long bristle near base of claw. Operculate tergite of sixth abdominal somite (Figures 7*b*, 10*d*) with 2 pairs of prominent conical, central protuberances (each often terminating in blunt spine) and usually 1 pair of small posterolateral tubercles on each side; dorsal surface divided into anterior and posterior regions by broad transverse depression, and with numerous shallow rounded pits and scattered short irregular grooves; anterior and posterior regions separated laterally by broad U-shaped notch; anterior region with distinct longitudinal median groove; posterior region with longitudinal furrow extending to about midline of posterior region. Telson (Figure 10*g,h*) more than 2 times as broad as long, becoming somewhat shorter and broader with increasing size; terminal margin divided into 2 very broadly rounded lobes separated by often obsolete cleft, and armed with small corneous-tipped spines.

DISTRIBUTION.—Tropical eastern Pacific: Costa Rica and Colombia; intertidal to 73 m (possibly deeper, see "Remarks").

HABITAT.—Wood or hollow reeds of *Typha* sp. (Walton, 1950; Ríos et al., 1990).

REMARKS.—Aside from the material examined, two males have been reported by Ríos et al. (1990:78) from near the mouth of the Juradó River, on the Pacific coast of Colombia. Ríos et al. observed that *X. cancellarius* uses the right cheliped and operculate tergite of the sixth abdominal somite to protect the entrance to the wood housing, and described the function of the telson in removing the excrement. They also suggested that this species is omnivorous.

As previously mentioned, it has not been possible to examine the material identified as *X. cancellarius* deposited at the Allan Hancock Foundation. Records from this Foundation indicate that their collections contain ten specimens obtained in the eastern Pacific from Costa Rica (Bahía Herradura), Panamá (off Isla Ladrones; Gulf of Chiriquí), and Colombia (Puerto Utría, including one male paratype), in depths ranging from 20 fms (36.6 m) to 60 fms (109.7 m).

Xylopagurus tayrona Lemaitre and Campos, 1993

FIGURE 7*c*

Xylopagurus rectus.—Provenzano, 1971:251 [first zoea; see "Remarks"]. [Not *Xylopagurus rectus* A. Milne Edwards, 1880.]

Xylopagurus tayrona Lemaitre and Campos, 1993:554, figs. 3–5.

DIAGNOSIS.—Rostrum subtriangular, slightly in advance of lateral projections. Lateral projections broadly subtriangular. Second segment of antennal peduncle with dorsomesial distal angle armed with 7–8 small spines. Antennal acicles short, terminating in fan-like distal margin armed with 14–16 small spines. Carpus of right cheliped triangular in cross-section, dorsal margin usually crest-like, armed with series of transverse rows of small tubercles. Dactyls of ambulatory legs armed on ventral margin with 30 or more corneous spines. Operculate tergite of sixth abdominal somite (Figure 7*c*) with anterior region nearly flat (at most with small, shallow rounded pits), lacking anterior longitudinal median groove and anteromedian ridges; anterior and posterior regions separated laterally by narrow V-shaped notch (see Lemaitre and Campos, 1993:564, fig. 5b); posterior region with posterofrontal margin and oblique transverse ridge broadly rounded.

DISTRIBUTION.—Southern Caribbean: off Venezuela and Colombia; 91 to 229 m.

HABITAT.—Pieces of wood.

REMARKS.—Provenzano (1971:251) reported that the first zoeal stage of *Xylopagurus rectus* was obtained from a female specimen captured during one of the R/V *John Elliott Pillsbury* cruises. He compared these zoeae with the larvae of species of *Pylopaguropsis, Munidopagurus,* and *Lithopagurus*. In that report, Provenzano did not specifically identify the female from which the larvae had been obtained. However, from the labels accompanying Provenzano's *X. rectus* material, and Provenzano's unpublished notes (P.A. McLaughlin, pers. comm.), it has been possible to establish that the *Xylopagurus* larvae were hatched from a female collected at station P-783, off the northern coast of Colombia. The only species of *Xylopagurus* collected at that station was *X. tayrona;* thus, Provenzanos's comments should correctly apply to this species.

Xylopagurus anthonii, new species

FIGURES 7*d*, 11–13

HOLOTYPE.—♀ov (SL 8.7 mm), O-3585, 09°12′N, 81°30′W, 247–256 m, 25 May 1962, USNM 265145.

PARATYPES.—1♀ (SL 11.8 mm), O-3637, 17°13′N, 87°55′W, 219–310 m, 10 Jun 1962, USNM 265146; 2 ♂ (SL 7.0, 9.3 mm), 1♀ (SL 5.7 mm), P-340, 09°13.5′N, 77°46′W, 304–362 m, 9 Jul 1966, USNM 265147, 265148; 1♂ (SL 7.1 mm), O-3585, 09°12′N, 81°30′W, 247–256 m, 25 May 1962, UMML 32: 2476; 1♀ (SL 6.0 mm), P-445, 09°03′N, 81°25′W, 338–342 m, 21 Jul 1966, USNM 265149.

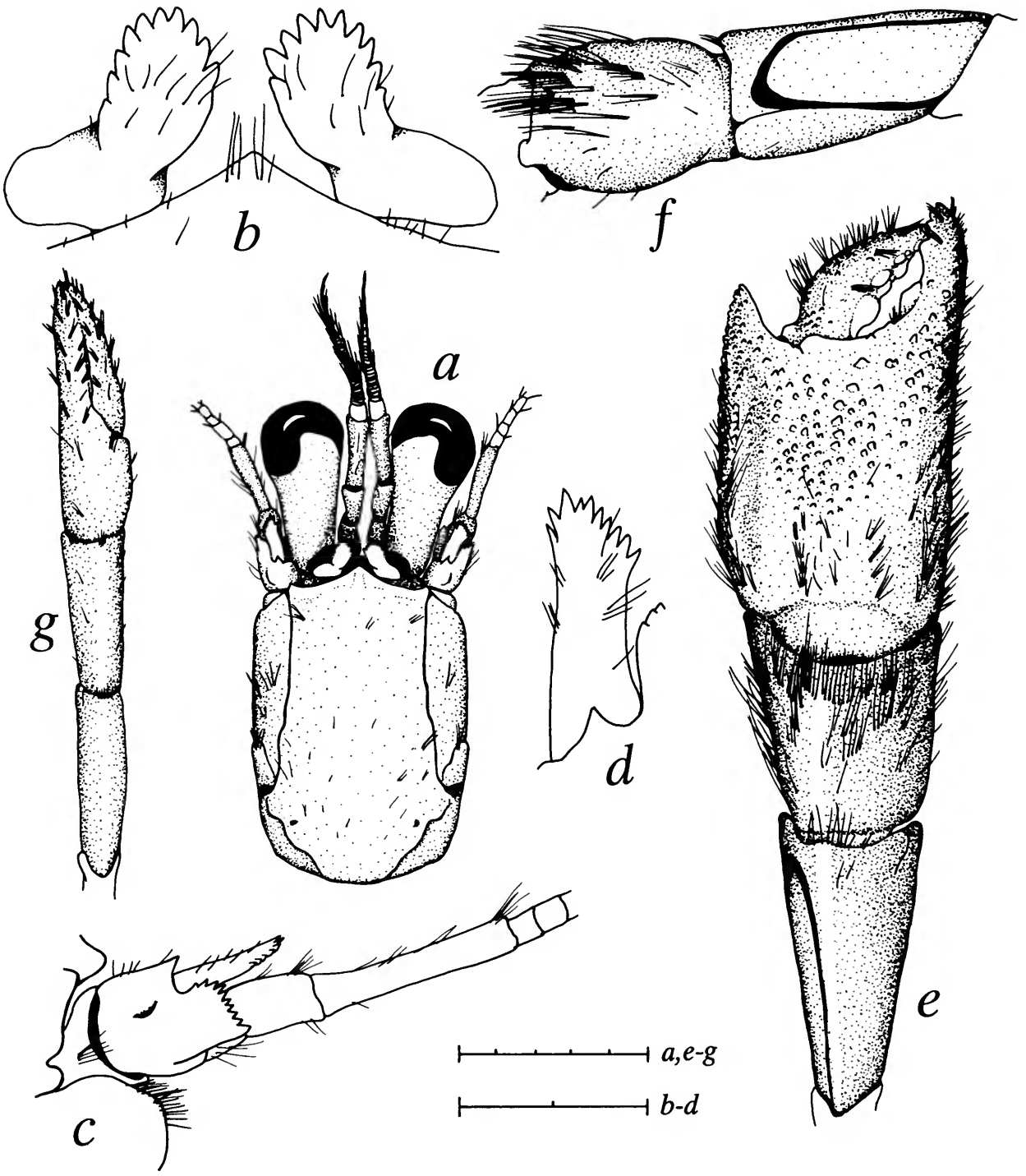


FIGURE 11.—*Xylopagurus anthonii*, new species; female holotype (USNM 265145): *a*, shield and cephalic appendages; *b*, ocular acicles and rostrum; *c*, right antennular peduncle, lateral view; *d*, antennal acicle of same, dorsal view; *e*, right cheliped, dorsal view; *f*, merus and carpus of same, mesial view; *g*, left cheliped, dorsal view. (Scales = 5 mm *a,e–g;* 1 mm for *b,d;* 2 mm for *c*.)

DESCRIPTION.—Shield (Figure 11*a*) distinctly longer (1.5 times) than wide, evenly convex. Dorsal surface glabrous except for few scattered minute pits and setal tufts, and short, low dorsal ridge posterior to rostrum; with pair of sutures (linea d) each extending from termination of cervical groove to anterior margin just laterad of lateral projection. Rostrum subtriangular, slightly exceeding lateral projections. Anterior margin nearly straight. Lateral projections acute, subtriangular. Anterolateral margins sloping, with distinct indentation on distolateral angle. Branchiostegite with anterior margin rounded, setose.

Ocular peduncles stout, combined length of peduncle and cornea about half length of shield; cornea dilated. Ocular acicles (Figure 11*a,b*) developed as broad ovate plate armed marginally with 9–12 spines; separated basally by basal width of 1 acicle.

Antennular peduncle reaching to distal margin of cornea (peduncle not fully extended in Figure 11*a*). Ultimate segment 3 to 3.5 times as long as broad, slightly longer than penultimate segment, both segments with scattered setae. Basal segment with ventrodistal spine, setose lobe on lateral face proximally, and usually small spine on lateral face. Dorsal flagellum long, nearly twice as long as ultimate segment; ventral flagellum usually with 12 articles.

Antennal peduncle (Figure 11*a,c*) not exceeding distal margin of cornea, supernumerary segment present. Fifth segment with long setae on lateral and mesial margins. Fourth segment with long setae on ventral face distally and scattered setae on lateral face. Third segment with blunt ventrodistal angle. Second segment with distolateral angle developed as very broad subrectangular projection armed with 9–10 small spines on distal margin; dorsomesial distal angle armed with 1–2 small spines. First segment unarmed, but with tuft of setae on lateral face. Acicles (Figure 11*a,d*) elongate, strong, terminating obliquely and with 9–10 marginal spines. Flagellum reaching to about distal margin of right palm, each article with 2–5 usually long setae up to 6 flagellar articles in length.

Chelipeds markedly dissimilar. Right cheliped (Figure 11*e,f*) strong, massive. Fingers each terminating in blunt calcareous claw. Dactyl with scattered, small spines and setal tufts on dorsal face, and row of setal tufts parallel to cutting edge; mesial margin with few tubercles and setal tufts; cutting edge with 1 large, low, molar-like tooth proximally and 5 small sharp or blunt teeth distally; ventral surface smooth except for row of setal tufts on ventromesial margin. Fixed finger slightly overreaching dactyl; dorsal face with small spines or tubercles proximally; dorsolateral margin with row of small spines; cutting edge proximally with 2 large molar-like teeth, and distally with 3 small teeth; ventral face smooth except for mesial row of setal tufts parallel to cutting edge. Palm approximately 1.4 times as long as wide (as much as 1.9 times as long as wide in small specimens, SL<6.0 mm); spiniform dorsomesial projection one-third as long as dactyl, with numerous small spines on dorsolateral and mesial faces; dorsal surface armed on distal third with moderately dense tubercles and spines (largest on medial region), smooth and with 2 short longitudinal rows of setal tufts proximally; dorsomesial and dorsolateral margins each delimited by irregular rows of small spines or long setae; mesial face smooth except for row of blunt spines on distal margin and scattered small spines distally; lateral and ventral faces with scattered small tubercles and setal tufts. Carpus as long as wide, with evenly convex dorsal surface bearing several distinct transverse rows of setae; ventral face smooth, but with scattered setal tufts. Merus longer than wide, triangular in cross-section, unarmed, but with scattered setae (dark band on Figure 11*e,f* represents molting suture).

Left cheliped (Figure 11*g*) slender, short, reaching to distal margin of carpus of right cheliped. Fingers distinctly longer than palm, terminating in corneous claw, opposing faces of fingers concave; cutting edge of fixed finger with closely spaced, minute corneous teeth; cutting edge of dactyl with row of minute, fused corneous teeth; dorsal and ventral surfaces with numerous setal tufts. Palm unarmed, but with scattered setae. Carpus and merus subequal in length, unarmed, but with scattered short setae.

Ambulatory legs (Figure 12*a–c*) similar from right to left. Dactyls each terminating in corneous claw, with cluster of short setae near base of claw on lateral and mesial faces; ventral margin broadly curved, armed with 13–16 corneous spines; with row of long setae dorsally, and 3 or 4 short oblique rows of setae dorsolaterally and dorsomesially. Ischia, meri, carpi, and propodi unarmed except for row of 8–9 minute spinules on ventral margin of each propodus; segments with setae or setal tufts on dorsal and ventral margins, lateral and mesial faces with scattered setae or with longitudinal rows of short setae. Sternite of third pereopods narrow, anterior lobe naked, flat, sloping down anteriorly.

Fourth pereopod (Figure 12*d*) with dactyl subtriangular, terminating in corneous claw curved laterad; dactyl with setal tufts on dorsolateral and ventrolateral margins, ventrolateral margin with row of strong corneous spines directed slightly laterad and slender spine near base of claw. Propodus with rasp forming ovate area covering nearly half lateral face, consisting of numerous minute densely packed scales arranged in straight rows to form grid. Merus and carpus unarmed, but with scattered setae.

Fifth pereopod (Figure 12*e*) subchelate; propodus with long setae on dorsal and ventral margins; rasp formed of conical or lanceolate scales. Merus and carpus unarmed, but with scattered setae.

Operculate tergite of sixth abdominal somite (Figures 7*d*, 13*a*) with raised crenulate margins bearing evenly spaced tufts of long setae (more separated on anterior margin). Dorsal surface divided into anterior and posterior regions by broad transverse depression. Anterior and posterior regions separated laterally by wide U-shaped notch (Figures 7*d*, 12*f*). Anterior

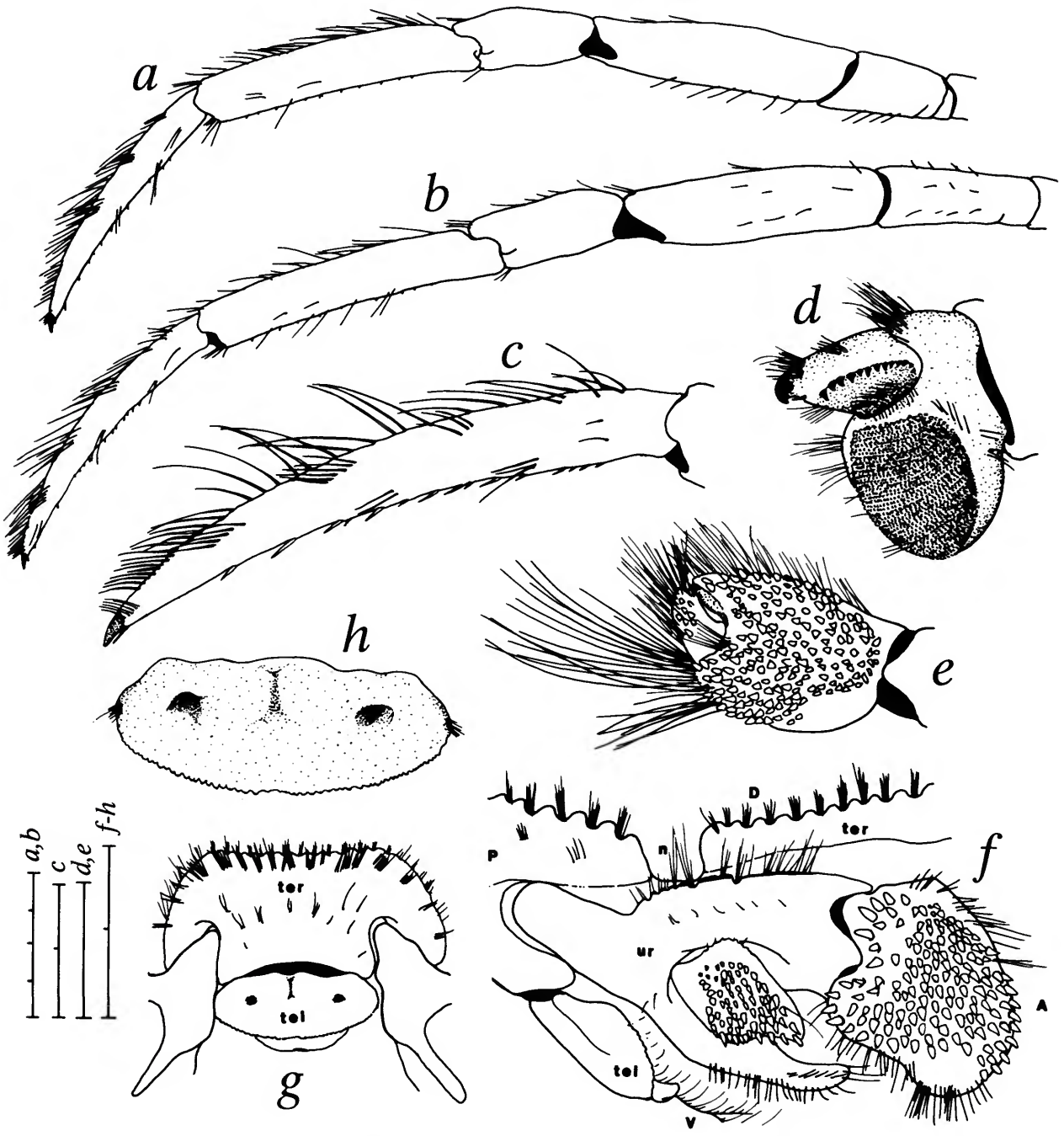


FIGURE 12.—*Xylopagurus anthonii*, new species; female holotype (USNM 265145): *a*, left second pereopod, lateral view; *b*, left third pereopod, lateral view; *c*, dactyl of same, lateral view; *d*, propodus and dactyl of left fourth pereopod, lateral view; *e*, propodus and dactyl of left fifth pereopod, lateral view; *f*, right uropod, part of lateral margin of sixth abdominal tergite, and telson, lateral view; *g*, posterior part of abdomen in ventral view, showing portion of sixth abdominal tergite, and telson; *h*, telson, dorsal view. (Scales = 4 mm for *a,b;* 2 mm for *c,f–h;* 1 mm for *d,e*. Abbreviations are as for Figure 8.)

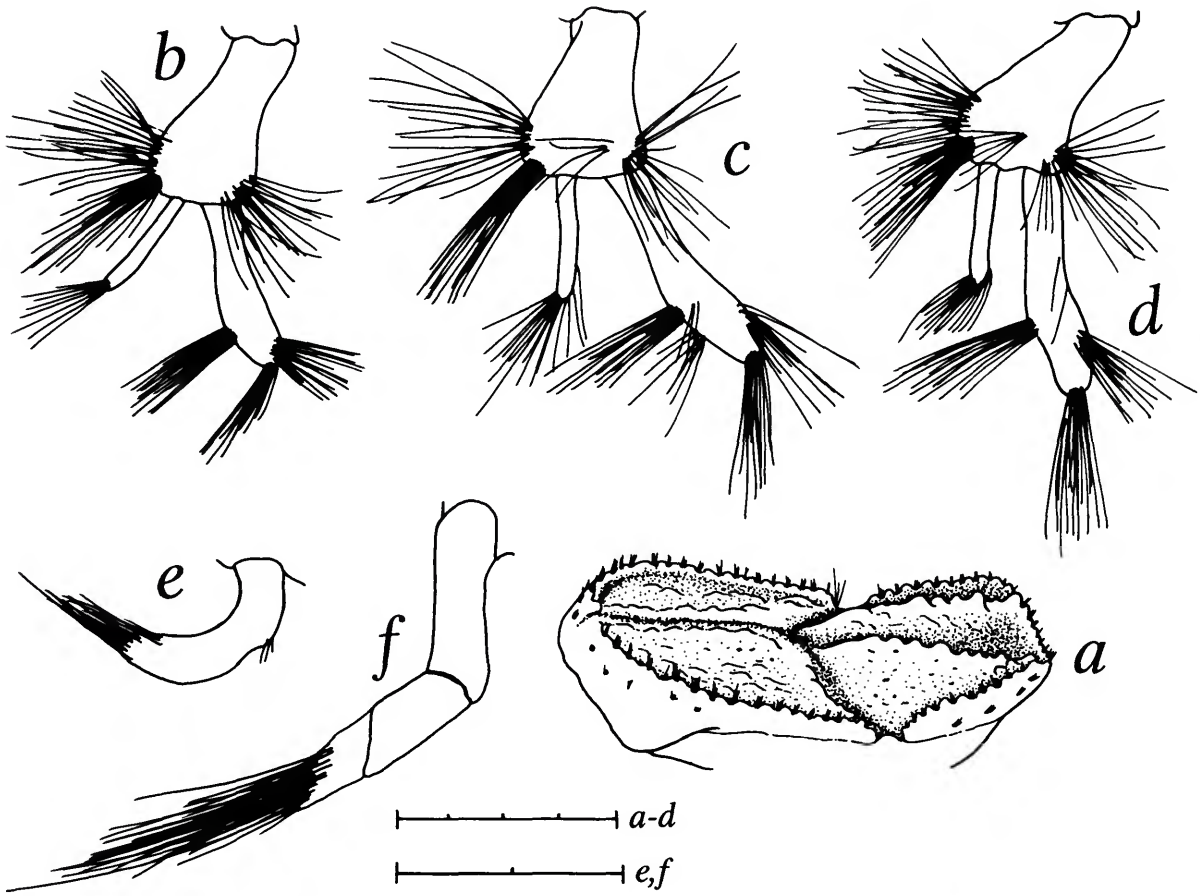


FIGURE 13.—*Xylopagurus anthonii*, new species; *a–d*, female holotype (USNM 265145); *f,g*, male paratype SL 7.1 mm (UMML 32:2476): *a*, tergite of sixth abdominal somite, dorsolateral view; *b–d*, female left second (b), third (c) and fourth (d) pleopods, lateral view; *e,f*, male left first (e) and second (f) pleopods, lateral view. (Scales = 4 mm for *a–d*; 2 mm for *e,f*.)

region with surface having numerous rounded pits, anterior longitudinal median groove flanked on each side by weakly elevated anteromedian ridge. Posterior region with numerous rounded pits, and distinct posterofrontal margin; longitudinal furrow sometimes extending to central pit; depressed triangular region with well defined obliquely transverse ridges each with row of 6–8 distinct tubercles, and often pair of small posterolateral tubercles.

Telson (Figure 12*f–h*) not visible in dorsal view, more than 2 times broader than long. Lateral margins with tuft of short setae. Dorsal surface with 3 depressions (2 deep lateral and 1 shallow median). Terminal margin divided into very broadly rounded lobes by shallow (sometimes inconspicuous) cleft, and armed with small corneous-tipped spines.

Uropods (Figure 12*f*) robust. Protopod with dorsal face flattened; posterodorsal margin corneous, proximally with broad triangular and subrectangular teeth, and row of tufts of long setae; ventrodistal angle produced into prominent blunt spine with row of setae laterally. Rasp of endopod and exopod formed of strong conical and lanceolate scales; endopod with small denticles on anterior margin; rasp of exopod occupying almost entire surface of lateral face, scales stronger and more spaced proximally.

First pleopod of males (Figure 13*e*) 1-segmented, curved anteriorly, and with long dense setae distally; second pleopod (Figure 13*f*) 3-segmented, distal segment directed anteriorly and with long setae distally. Ovigerous females with eggs approximately 1.6 mm in diameter.

ETYMOLOGY.—The specific name is given in honor of Anthony J. Provenzano, Jr., whose pioneer studies and collecting efforts laid the modern foundations of our knowledge of the western Atlantic hermit crab fauna.

DISTRIBUTION.—Western Caribbean: Off Panama and Belize; 219 to 362 m.

HABITAT.—Pieces of wood or empty, corneous polychaete tubes.

REMARKS.—This new species can immediately be distinguished from all others in the genus by the presence of sutures or linea d on the shield, and the presence on the operculate tergite of the sixth abdominal somite of distinct tubercles on the obliquely transverse ridges of the depressed triangular region.

Xylopagurus tenuis, new species

FIGURES 7*e*, 14, 15

Xylopagurus rectus A. Milne Edwards, 1880:37 [in part].—A. Milne Edwards and Bouvier, 1893:108 [in part; not pl. 8: figs. 1–13; = *Xylopagurus rectus* A. Milne Edwards, 1880].—Benedict, 1901:143.—Schmitt, 1935:207, fig. 67 [see "Remarks" under *Xylopagurus rectus*].

HOLOTYPE.—1♂ (SL 9.4 mm), 19°48′N, 70°26′W, 274 m, SB-5167, 15 Oct 1963, USNM 265150.

PARATYPES.—1♂ (SL 3.7 mm), 23°12′N, 78°49′W, O-10861, 150 fms (274.3 m), 15 Dec 1969, USNM 265163; 2♂ (SL 5.2, 6.3 mm), 3♀ (SL 5.7–6.0 mm), 22°55′N, 78°36′W, SB-3510, 274 m, 7 Nov 1961, USNM 265151; 1♂ (SL 3.7 mm), 22°13′N, 81°11′W, A-3320, 338 m, 4 Apr 1939, MCZ 12872; 1♀ (SL 4.8 mm), 22°07′N, 81°08′W, A-2963A, 292–348 m, 25 Feb 1938, MCZ 13336; 1♂ (SL 8.2 mm), SB-5165, 19°48′N, 70°30.5′W, 91 m, 15 Oct 1963, USNM 265152; 1♀ ov (SL 9.1 mm), P-1303, 18°21′N, 69°14.3′W, 311–322 m, 21 Jul 1970, USNM 265153; 1♂ (SL 6.4 mm), SB-5193, 18°16′N, 67°22′W, 274 m, 18 Oct 1963, USNM 265154; 1♂ (SL 9.5 mm), 2♀ (SL 6.7, 9.4 mm), 18°13′N, 67°21′W, O-2648, 366 m, 6 Oct 1959, UMML 32:4997; 1♂ (8.9 mm), 17°50′N, 77°52′W, O-3549, 311 m, 16 May 1962, USNM 265155; 2♂ (SL 3.2, 4.1 mm), Mayaguez Harbor, Puerto Rico, FH-6063, 139, 20 Jan 1899, USNM 42561.

Paratype of *Xylopagurus rectus* A. Milne Edwards, 1880: 1♂ (SL 4.0 mm), off St. Vincent, 13°08′24″N, 61°13′50″W, B-223, 267 m, 18 Feb 1879, MCZ 4098.

DESCRIPTION.—Shield (Figure 14*a*) distinctly longer (1.6–1.8 times) than wide, evenly convex, usually with some iridescence (preserved material). Dorsal surface glabrous except for few scattered minute pits and setal tufts, and short, low dorsal ridge posterior to rostrum. Rostrum acutely subtriangular, slightly exceeding lateral projections. Anterior margin nearly straight. Lateral projections subtriangular. Anterolateral margins sloping, with distinct indentation on distolateral angle. Branchiostegite with anterior margin rounded, setose.

Ocular peduncles stout, combined length of peduncle and cornea about half or more length of shield; cornea dilated. Ocular acicles (Figure 14*a,b*) developed as broad ovate plate usually showing iridescence (preserved material), and armed marginally with 9–12 spines; separated basally by basal width of 1 acicle.

Antennular peduncle reaching to distal margin of cornea (peduncles not fully extended on Figure 14*a*). Ultimate segment 3 to 4 times longer than broad, and approximately 1.5 times as long as penultimate segment. Ultimate and penultimate segments with scattered setae. Basal segment with ventrodistal spine, setose lobe on lateral face proximally, and usually small spine on lateral face. Dorsal flagellum long, twice as long as ultimate segment; ventral flagellum with 7 articles.

Antennal peduncle (Figure 14*a,c*) not exceeding distal margin of cornea, supernumerary segment present. Fifth segment with long setae on lateral and mesial margins. Fourth segment with setae on dorsal and ventral face distally. Third segment with blunt ventrodistal angle. Second segment with distolateral angle developed as very broad subrectangular projection armed with 8–9 spines on distal margin; dorsomesial distal angle armed with 3–7 small spines. First segment unarmed, but with tuft of setae on lateral face. Acicles (Figure 14*a,d,e*) short, broad, terminally straight and with 10–14 marginal spines (or elongate and terminating in 2–4 spines, and often also with small spine on dorsal surface, in small specimens SL<5.0 mm). Flagellum reaching to about mid-length of right chela, each article usually with 4–5 short and long setae.

Chelipeds markedly dissimilar. Right cheliped (Figure 14*f,g,i–k*) strong, fingers each terminating in blunt calcareous claw. Dactyl with scattered small tubercles on dorsal face, and row of setal tufts parallel to cutting edge; mesial margin with few weak tubercles; cutting edge proximally with 1 massive, molar-like calcareous tooth proximally (only partially visible on Figure 14*f,i*), and 3–6 smaller molar-like calcareous teeth; ventral surface smooth, except for row of setal tufts on ventromesial margin. Fixed finger slightly overreaching dactyl; dorsal face with scattered small spines or tubercles, and setal tufts; cutting edge with 2 strong, blunt calcareous teeth proximally, and with 3 or 4 small teeth distally; ventral face smooth except for row of setal tufts parallel to cutting edge. Palm approximately 1.3 to 1.7 times as long as wide; spiniform dorsomesial projection approximately half as long as dactyl, with numerous small spines on dorsal and mesial faces; dorsal face with numerous spines or tubercles on distal third to one-half (spines and tubercles well spaced and less numerous in small specimens SL<5.0 mm), smooth and with setal tufts proximally; dorsomesial margin delimited (at least distally) by irregular rows of small spines; mesial face with numerous small tubercles and spines on distal fourth; lateral face convex, with setal tufts; ventral face smooth except for scattered setae. Carpus longer than wide, dorsal face varying from weakly triangular in cross-section and unarmed to distinctly triangular with row of small spines on dorsal margin; dorsal surface with transverse rows of long setae; ventral face smooth except for scattered setal tufts. Merus about twice as long as wide (more slender in small specimens SL<5.0 mm), triangular in cross-section, unarmed, and with scattered setae (dark band on Figure 14*f,g* represents molting suture).

Left cheliped (Figure 14*h*) slender, short, reaching to about distal margin of carpus of right cheliped, surfaces with some

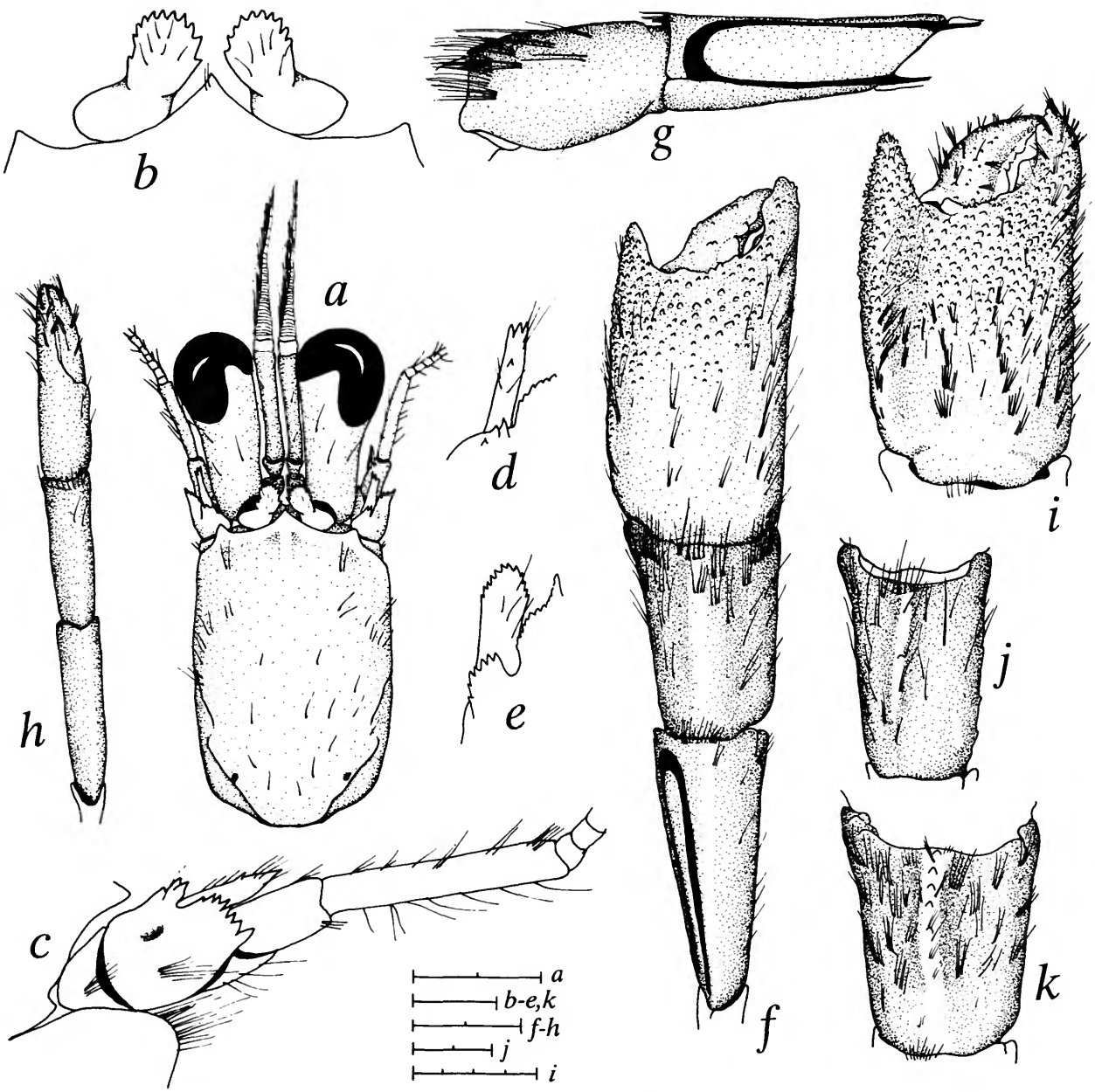


FIGURE 14.—*Xylopagurus tenuis*, new species; *a–d,f–h*, female paratype SL 4.8 mm (MCZ 13336); *e*, female paratype SL 6.0 mm (USNM 265151); *i*, male holotype (USNM 265150); *j*, male paratype SL 4.1 mm (USNM 42561); *k*, male paratype SL 8.9 mm (USNM 265155): *a*, shield and cephalic appendages; *b*, ocular acicles and rostrum, dorsal view; *c*, right antennal peduncle, lateral view; *d*, antennal acicle of same; *e*, antennal acicle, dorsal view; *f*, right cheliped, dorsal view; *g*, merus and carpus of same, mesial view; *h*, left cheliped, dorsal view; *i*, right chela, dorsal view; *j,k*, carpus of right cheliped, dorsal view. (Scales = 2 mm for *a*; 0.5 mm for *b–e*; 2 mm for *f–h,j*; 1 mm for *k*; 4 mm for *i*.)

iridescence (preserved specimens). Fingers subequal to length of palm, terminating in corneous claw; opposing faces of fingers moderately concave; cutting edges each with row of minute, fused corneous teeth; dorsal and ventral faces with setal tufts. Palm unarmed, but with scattered setae. Carpus and merus subequal in length, unarmed, each with dorsal face evenly convex and nearly naked or at most with scattered short setae.

Ambulatory legs (Figure 15*a–c*) similar from right to left, with some iridescence (preserved specimens). Dactyls each terminating in corneous claw, with tuft of setae near base of claw on lateral and mesial faces; ventral margin broadly curved, armed with 3–11 (usually 5 or 6) small corneous spines; with row of long setae dorsally, and 3 or 4 short oblique rows of setae dorsolaterally and dorsomesially. Ischia, meri, carpi, and propodi unarmed except for row of 4–7 corneous spinules on ventral margin of each propodus; segments with setae or setal tufts on dorsal and ventral margins, lateral and mesial faces with scattered setae. Sternite of third pereopods narrow, anterior lobe naked, flat, sloping down anteriorly.

Fourth pereopod (Figure 15*d*) with dactyl subtriangular, terminating in corneous claw curved laterad; dactyl with setal tufts on dorsolateral and ventrolateral margins, ventrolateral margin with row of strong corneous spines directed slightly laterad and slender spine near base of claw. Propodus with rasp forming ovate area covering nearly half of lateral face and consisting of numerous, minute densely packed scales arranged in straight rows to form grid. Merus and carpus unarmed but with scattered setae.

Fifth pereopod (Figure 15*e*) subchelate; propodus with long setae on dorsal and ventral margin; rasp formed of conical or lanceolate scales. Merus and carpus unarmed but with scattered setae.

Operculate tergite of sixth abdominal somite (Figure 7*e*) with raised crenulate margins formed by evenly spaced tubercles separated by tufts of long setae (more separated on anterior margin). Dorsal surface divided into anterior and posterior regions by broad transverse depression. Anterior and posterior regions separated laterally by wide U-shaped notch (Figures 7*e*, 15*g*). Anterior region with surface moderately uneven, or at most with widely spaced short, irregular ridges; anterior longitudinal median groove flanked on each side by sharply elevated anteromedian ridge, and usually with series of short, transverse shallow grooves or furrows. Posterior region with numerous rounded pits, and distinct posterofrontal margin; depressed triangular region with well defined obliquely transverse ridges (occasionally with pair of small posterolateral tubercles on one or both sides); longitudinal furrow usually not extending to central pit.

Telson (Figure 15*f–h*) not visible in dorsal view of abdomen, more than 2 times as broad as long. Lateral margins with tuft of short setae, dorsal surface with 3 depressions (1 deep on each side, 1 shallow medially). Terminal margin divided into broadly rounded lobes by shallow (sometimes inconspicuous) cleft, and armed with small spines bearing corneous tips.

Uropods (Figure 15*g*) robust. Protopod with dorsal face flattened; posterodorsal margin corneous, proximally with broad triangular and subrectangular teeth, and row of tufts of long setae; ventrodistal angle produced into prominent blunt spine with row of setae laterally. Rasp of endopod and exopod formed of strong conical and lanceolate scales; endopod with small denticles on anterior margin; rasp of exopod occupying almost entire surface of lateral face, scales stronger and more spaced proximally.

First pleopod of males (Figure 15*i*) 1-segmented, curved anteriorly, and with long dense setae distally; second pleopod (Figure 15*j*) 3-segmented, distal segment directed anteriorly and with long setae distally.

DISTRIBUTION.—Caribbean Sea: Off Cuba, Jamaica, Hispaniola, Puerto Rico, and St. Vincent; 139 to 366 m.

HABITAT.—Pieces of wood.

ETYMOLOGY.—The specific name is from the Latin *tenuis*, meaning thin, and refers to the slender appearance of this species, specially the young individuals.

AFFINITIES AND VARIATIONS.—This new species is morphologically the most variable among species of the genus, and closely resembles *X. rectus*. The two species can be confused if variations are not taken into account. The most reliable character that can be used to distinguish between the two is the shape of the operculate sixth abdominal tergite. In both *X. tenuis* and *X. rectus*, the posterior region of the sixth abdominal tergite has a longitudinal furrow; however, the furrow in *X. rectus* is flanked by low posteromedian ridges extending to the posterior margin of the tergite, whereas *X. tenuis* lacks these ridges. In both species the anterior region of the operculate sixth abdominal tergite is uneven, with short, irregular ridges and pits, and there is a distinct anterior longitudinal median groove flanked by anteromedian ridges. In *X. rectus*, however, the short ridges and pits are frequently more numerous and the pits deeper, than in *X. tenuis*.

The shape of the carpus of the right cheliped, although variable in *X. tenuis* and *X. rectus*, does provide some supplemental means of distinguishing between the two, at least in specimens up to a size of about 7.0 mm in SL. The dorsal surface of the carpus in *X. tenuis* is always triangular (Figure 14*f,j,k*). However, in *X. rectus*, the dorsal surface varies from evenly convex in specimens SL≤7.0 mm (Figure 4*g*) to a triangular condition in large specimens.

Study and measurement of specimens of different sizes shows that substantial variations related to growth exist in relative length of the antennular peduncle, and relative length and armature of the palm of the right cheliped. In *X. tenuis*, the length/width ratio of the ultimate antennular segment varies substantially with increasing size of the specimen. The segment is typically more elongated and slender in small individuals than in large ones. The length/width ratio varies from 4.4 in a small specimen (SL 3.7 mm) to 3.0 in a large specimen (SL 9.4 mm). In contrast, the length/width ratio of the ultimate antennular segment of *X. rectus* is much less variable, ranging from 2.2 to 2.6.

In *X. tenuis*, the length/width ratio of the palm of the right cheliped varies with increasing size. This ratio varies from 1.7 in a small specimen (SL 3.7 mm) to 1.3 in a large specimen (SL 9.4 mm). In *X. rectus*, the ratio varies from 1.1 to 1.5. The armature of the dorsal face of the right palm in small specimens of *X. tenuis* consists of mostly small, widely-spaced tubercles or spines on the distal third (Figure 14*f*). In larger specimens, the spines and tubercles become more dense and can cover the

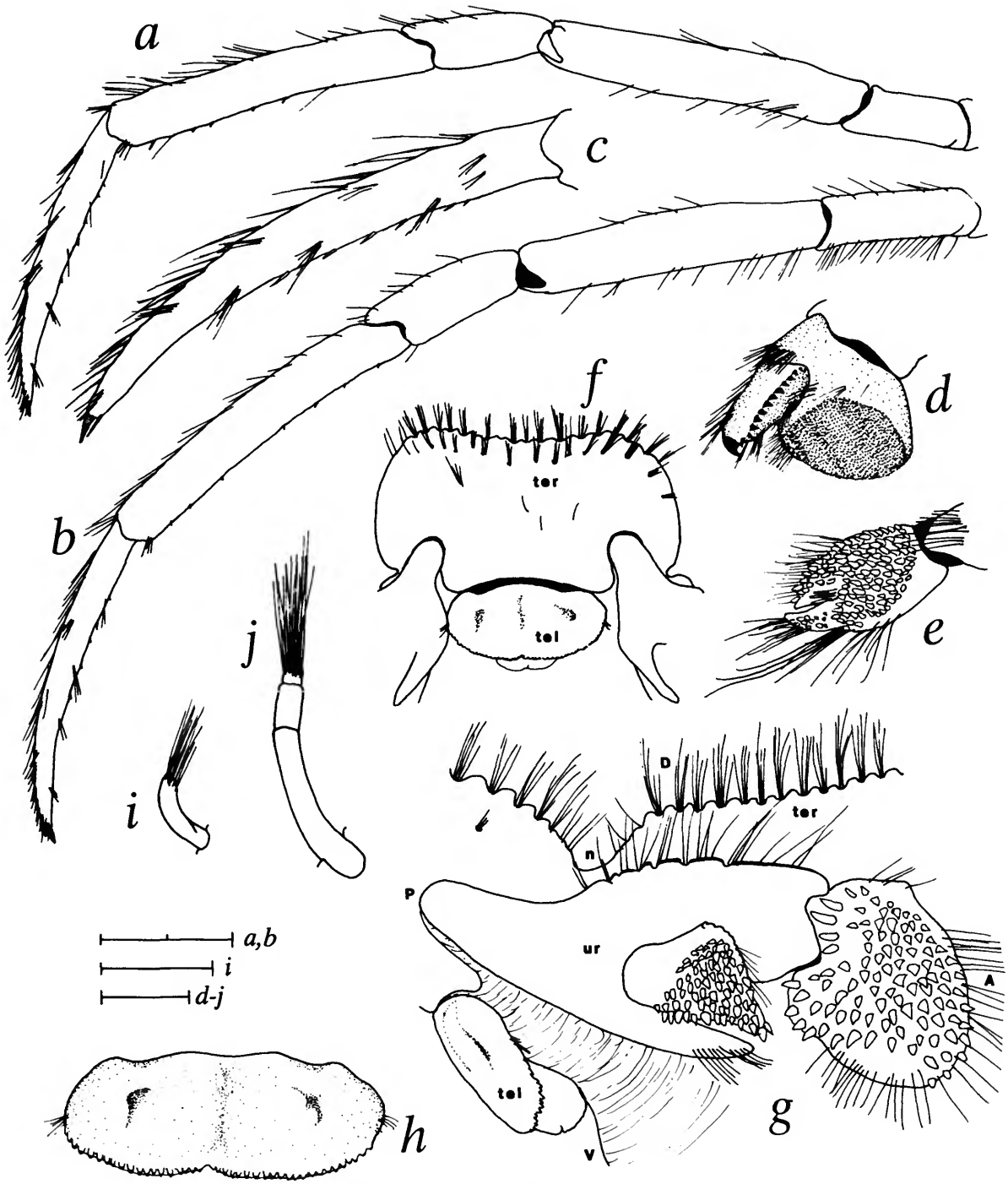


FIGURE 15.—*Xylopagurus tenuis*, new species; *a–h*, female SL 4.8 mm (MCZ 13336); *i,j*, male SL 4.1 mm (USNM 42561): *a*, left second pereopod, lateral view; *b*, left third pereopod, lateral view; *c*, dactyl of same, lateral view; *d*, propodus and dactyl of left fourth pereopod, lateral view; *e*, propodus and dactyl of left fifth pereopod, lateral view; *f*, posterior part of abdomen in ventral view, showing portion of sixth abdominal tergite, and telson; *g*, right uropod, part of lateral margin of sixth abdominal tergite, and telson, lateral view; *h*, telson, dorsal view; *i,j*, male left first (i) and second (j) pleopods, lateral view. (Scales = 2 mm for *a,b;* 0.5 mm for *d,e,g–h,j;* 1 mm for *f;* 1 mm for *i*. Abbreviations are as for Figure 8.)

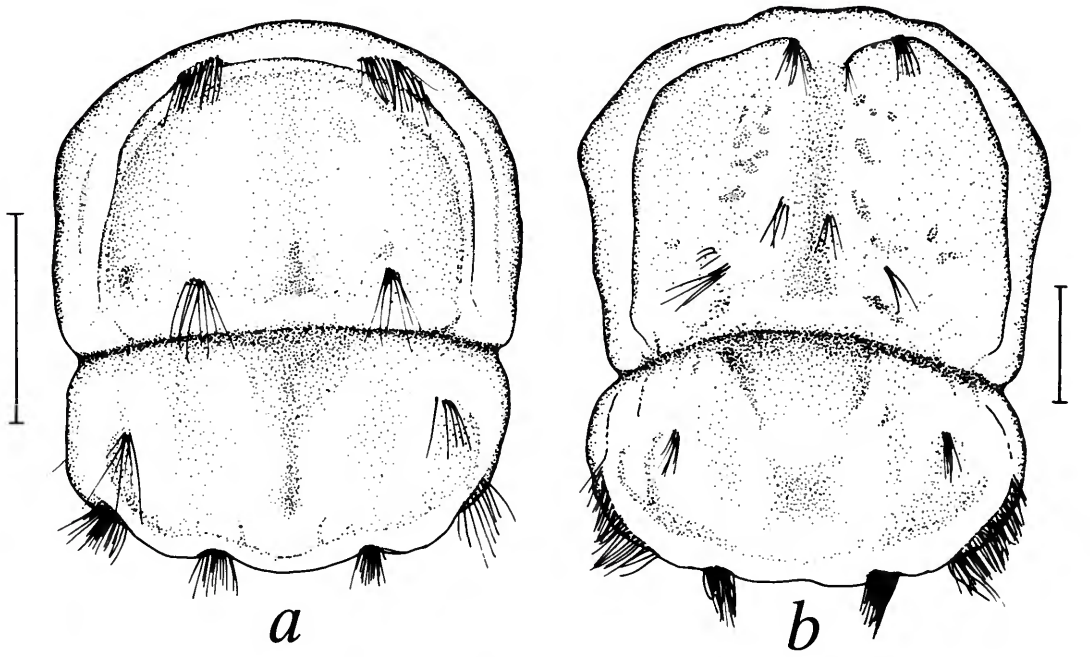


FIGURE 16.—Operculate tergite of sixth abdominal somite, dorsal view: *a, Discorsopagurus schmitti* (Stevens, 1925), female SL 2.8 mm, eastern Pacific, northwest coast of North America (USNM 265172); *b, Orthopagurus minimus* (Holmes, 1900), male SL 5.6 mm, eastern Pacific, coast of California (USNM 103772). (Scales = 1 mm.)

distal half of the palm (Figure 14*i*). The armature of the palm in *X. rectus* is not as variable, being dense, and consisting of strong spines and tubercles on at least the distal half of the palm (Figure 4*g*).

Discussion

Several structures in species of *Xylopagurus* are unusual or unique among hermit crabs (= superfamilies Paguroidea and Coenobitoidea). The length of the linea d as seen in *X. anthonii*, for example (see Figures 1, 11*a*), is greater than is known in other hermit crabs. When linea d is present in other hermit crabs, it does not reach the anterior margin of the shield. In contrast, the linea d in *X. anthonii* extends longitudinally across the shield to the anterior margin, and consists of a distinct, uncalcified suture. The functional and evolutionary significance of this suture as seen in *X. anthonii*, is unclear. In the freshwater anomuran crabs of the family Aeglidae, the lineae on the carapace are known to increase the flexibility of the carapace, and also allow for the movement of portions of the carapace to increase the apparent size of the crab (Feldmann, 1984:384; Martin and Abele, 1988:30). Schram (1986:287) suggested that the longitudinal lines of the carapace of "reptant" decapods represent lines of weak calcification to accommodate molting sutures. It is intriguing that given the similarity in mode of life adopted by the species of *Xylopagurus* (i.e., enclosed in cylindrical cavities in pieces of wood or polychaete tubes) and the specialized but similar morphology developed by all five species of the genus, only *X. anthonii* has developed this linea. The function of this morphological feature, however, cannot be evaluated until living specimens are studied and their molts obtained.

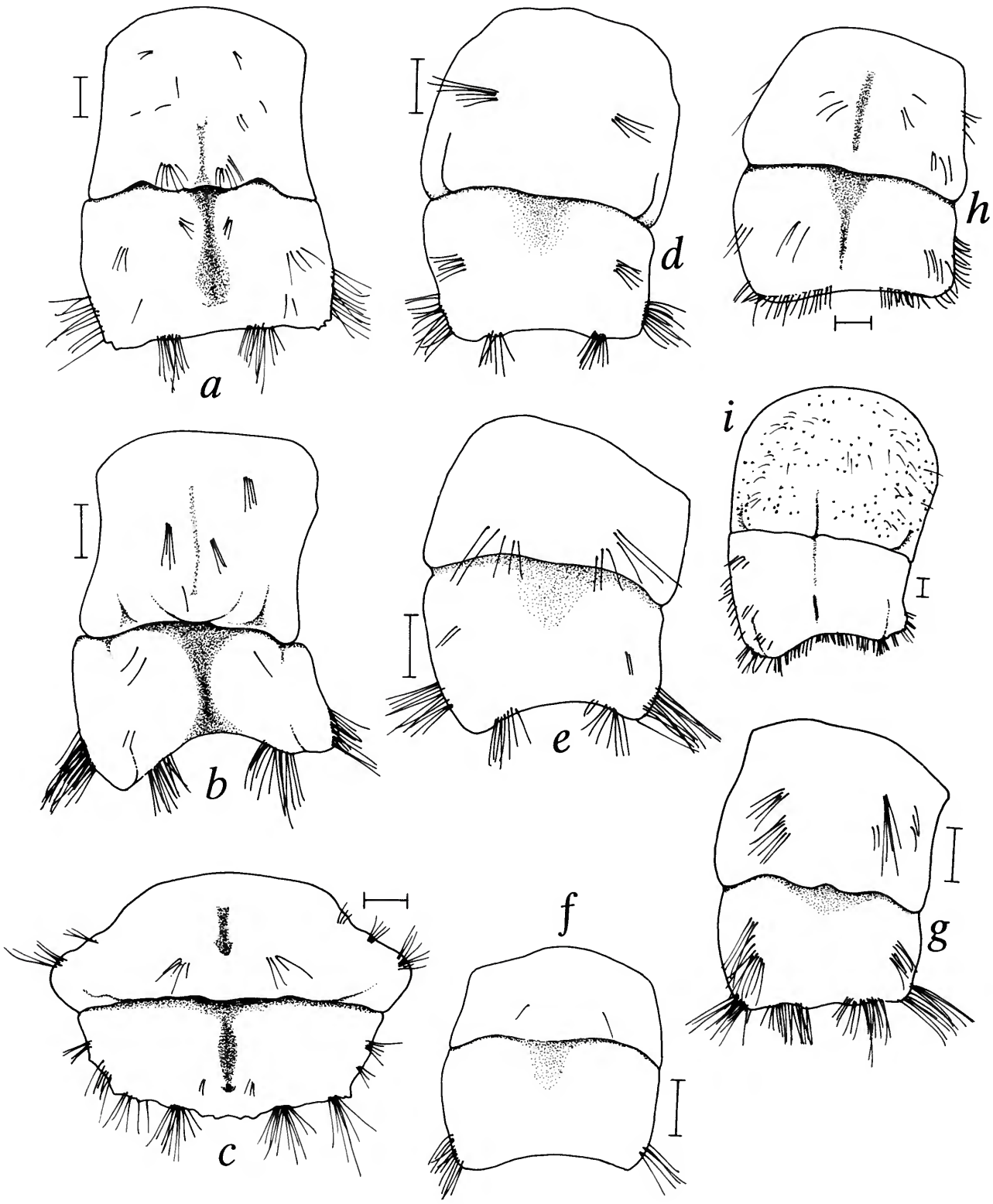
Species of *Xylopagurus* exhibit a development of the ocular and antennal acicles similar to that seen in members of the family Diogenidae. In the development of the second antennal segment, the armature in species of *Xylopagurus* approaches that of one group of species of the diogenid genus *Diogenes*. The development of the ocular acicles in species of *Xylopagurus* is somewhat similar, albeit not necessarily homologous, to that seen in species of the diogenid genus *Dardanus*.

The most visible and striking structure found in species of *Xylopagurus* is the strongly calcified and operculate tergite of the sixth abdominal somite. The development of an operculate sixth tergite, however, is not unique to species of *Xylopagurus* and evidently represents a case of convergent adaptation in some species of tube-dwelling paguroids. Two tube-dwelling species, *Discorsopagurus schmitti* (Stevens, 1925) and *Orthopagurus minimus* (Holmes, 1900), also have an operculate sixth abdominal tergite (Figure 16) very similar, albeit less sculptured dorsally, to that of species of *Xylopagurus*. *Discorsopagurus schmitti* lives in attached or loose tubes of the polychaetes *Sabellaria cementarium* and *Serpula vermicularis*,

and *O. minimus* usually inhabits *Dentalium* shells (Caine, 1980; Hart, 1982). As in species of *Xylopagurus*, the sixth abdominal tergite of *D. schmitti* and *O. minimus* is strongly calcified, has raised margins and setal tufts, and also serves to block the posterior entrance of the tube. Examination of other species from randomly selected genera in all hermit crab families quickly revealed similarities in the sixth abdominal tergite among these species and those of *Xylopagurus*. The tergite of species examined from other genera (see Figure 17) all have a distinct, transverse, narrow groove or furrow, equivalent to the transverse depression in *Xylopagurus* that divides the tergite into anterior and posterior regions. Additionally, there is a weak, usually short anterior longitudinal median groove in some Parapaguridae (Figure 17*h*), Diogenidae (Figure 17*a–c;* see also Forest, 1988:775, fig. 4, for *Clibanarius* and *Bathynarius*), Pylochelidae (see Forest, 1987), and Coenobitidae (Figure 17*i*). A posterior longitudinal median groove is present in all species examined, although this groove is less marked in the Paguridae (Figure 17*d–g*). Calcification of the tergite is weakest in the Paguridae, and strongest in the Diogenidae and Coenobitidae. The degree of calcification as well as the shape and armature of the sixth abdominal tergite in species of *Xylopagurus* clearly represents an extreme development of this tergite among hermit crabs.

There have been some attempts to elucidate the systematic position of the genus *Xylopagurus* within the family Paguridae. Saint Laurent-Dechancé (1966) placed *Xylopagurus* in her *Pylopaguropsis* group, based on adult morphology and limited larval evidence. She defined this group as genera whose species have 13 pairs of gills (10 arthrobranchs and three pleurobranchs); a strong accessory tooth on the ischium of the third maxilliped; paired pleopods on the first or second, or both, abdominal segments in the male, or on the first abdominal somite in the female; and no sexual tubes. In addition to *Xylopagurus*, the genera *Pylopaguropsis* Alcock, 1905, *Munidopagurus* A. Milne Edwards and Bouvier, 1893, *Tomopaguroides* Balss, 1912, and *Tomopaguropsis* Alcock, 1905, were included in the group. When Provenzano (1968) described the genus *Lithopagurus*, he added it to the *Pylopaguropsis* group. Subsequently, Provenzano (1971:251) observed that several unusual larval features (i.e., armature of antennal scale, carapacial spines, lateral spines of fifth abdominal somite, and shape of telson) found in the first zoea of *X. rectus* (= *X. tayrona*) were shared with the larvae of species of *Lithopagurus*, *Munidopagurus*, and *Pylopaguropsis*, and cited these as evidence linking these genera. The evidence linking these genera provided by Saint Laurent-Dechancé, and Provenzano, seems strong. However, conclusive evidence in support of close evolutionary affinities among the genera of the *Pylopaguropsis* group must await full evaluation of the morphology and character polarity in the larvae and adults of the currently recognized 49+ hermit crab genera.

FIGURE 17.—Tergite of sixth abdominal somite of species in selected hermit crab genera of the families Diogenidae *(a–c)*, Paguridae *(d–g)*, Parapaguridae *(h)*, and Coenobitidae *(i)*: *a, Petrochirus* (*P. diogenes* (Linnaeus), Caribbean Sea, Bahamas, USNM 88644); *b, Paguristes* (*P. puncticeps* Benedict, Caribbean Sea, Jamaica, USNM 104203); *c, Cancellus* (*C. parfaiti* A. Milne Edwards, Eastern Atlantic, Gulf of Guinea, USNM 128735); *d, Pagurus* (*Pagurus pollicaris* Say (western Atlantic, northeast coast of United States, USNM 9308); *e, Labidochirus* (*L. splendescens* (Owen), eastern Pacific, northwest coast of North America, USNM); *f, Catapagurus* (*C. sharreri* A. Milne Edwards, western Atlantic, northeast coast of United States, USNM 5886); *g, Tomopagurus* (*T. wassi* McLaughlin, Caribbean Sea, St. Lucia, USNM 184329); *h, Parapagurus* (*P. andreui* Macpherson, southwestern Indian Ocean, USNM); *i, Coenobita* (*C. clypeatus* (Fabricius), Caribbean Sea, British Virgin Islands, USNM 240232). (Scales = 1 mm for *a–d,g–i;* 0.5 mm for *e;* 0.25 mm for *f.*)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