A Review of the Genus *Cancellus* (Crustacea: Diogenidae) with the Description of a New Species from the Caribbean Sea

BARBARA SHULER MAYO
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*Barbara Shuler Mayo*
Mayo, Barbara Shuler. A Review of the Genus Cancellus (Crustacea: Diogenidae) with the Description of a New Species from the Caribbean Sea. Smithsonian Contributions to Zoology, number 150, 65 pages, 25 figures, 1973.—All available literature dealing with the genus Cancellus is reviewed. Of the ten nominal species in the genus, eight are probably valid. Reports made by previous authors on the biology, ecology, and behavior of these specialized hermit crabs are included along with new observations.

New material of six nominal species of Cancellus was examined: Cancellus ornatus and C. spongicola from the West Indies are redescribed and illustrated. C. calypso Forest and St. Laurent, 1967, was found to be within the range of variation of C. ornatus and is considered a synonym. Cancellus tanneri from the eastern Pacific is redescribed and illustrated. The morphology of the few specimens available was practically identical to that of C. ornatus, and it appears that the two are closely related. The eastern Atlantic species, C. parfaiti, is redescribed and figured; it seems to be closely related to C. spongicola. Cancellus typus, the Australian species, is redescribed and illustrated. Although distinct, it has several characters in common with C. parfaiti. The holotype of Cancellus canaliculatus (Herbst) from the "east Indies" is redescribed and illustrated. It is generally similar to C. parfaiti, but can be distinguished easily. A specimen of C. investigatoris from Japanese waters is redescribed and illustrated. This species, also known from Indian coasts, is similar to C. parfaiti as noted by Alcock (1905), and is distinct from C. canaliculatus. Cancellus macrothrix, the aberrant species from South Africa, is reviewed. It shows characters which may be more primitive and more typically diogenid than those of the other species. Cancellus viridis, a new species from the Caribbean, is described and figured. Its morphology is much like that of C. ornatus. This species brings the total number in the genus to nine if the aberrant C. macrothrix is included. A key to all described species is given.
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A Review of the Genus *Cancellus*  
(Crustacea: Diogenidae)  
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New Species from the Caribbean Sea

*Barbara Shuler Mayo*

**Introduction**

*Cancellus* is a distinctive genus of hermit crabs in the family Diogenidae. Most animals of this genus live in pieces of rock, sponge, coral, or other firm substances, rather than in gastropod shells as is more typical for pagurid crabs. When the animal withdraws within the generally cylindrical cavity, the aperture is closed by an operculum formed by the modified chelipeds and anterior ambulatory legs.

Species have been listed in Alcock's catalogue of the Indian decapod crustaceans (1905) and in Gordon's bibliography (1956), but no review of the genus has been attempted previously. With the new material available, it is now possible to redescribe the western Atlantic species. Material of all known species, except *Cancellus macrothrix*, has been made available for study. This paper brings together and summarizes all work done to date on each of the nominal species. The synonymies are complete with the possible exception of *Cancellus typus*, the Australian species, which has an extensive popular literature.

**Acknowledgments.**—Because of the sparsity and widespread distribution of the animals studied, I was dependent on many sources for specimens. I would like to thank the following for making material available: Dr. Des Griffin of the Australian Museum, Sydney; Dr. R. B. Manning of the National Museum of Natural History, Washington, D.C.; Dr. H. W. Levi of the Museum of Comparative Zoology, Cambridge, Massachusetts; Dr. H. E. Gruner of the Zoologisches Museum, Berlin; Mr. John Garth of the Allan Hancock Foundation, Los Angeles; Mr. David Camp of the Florida Department of Natural Resources, St. Petersburg; Dr. Roy Ölerod of the Naturhistoriska Riksmuseum, Stockholm; and Dr. S. Miyake of Kyushu University, Fukuoka, Japan.

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LITERATURE REVIEW.—The first description of a species recognized today as belonging in the genus *Cancellus* was given by J. F. W. Herbst in 1804. According to his brief and very general note, the carapace of *Cancer canaliculatus* from the "East Indies" was "as usual" but the animal could be distinguished from all other crabs by the "claws." While there is no question that this was a *Cancellus*, neither the illustration nor the description was sufficiently detailed to permit specific identification. The holotype is redescribed and illustrated in this paper.

Olivier (1811) moved Herbst's *Cancer canaliculatus* to the genus *Pagurus* and stated that the animal was found on the "coasts of the Indian Ocean." His encyclopedic treatment of the species seemed to be based solely on Herbst's work rather than on any additional material.

H. Milne Edwards (1836) formally established the genus *Cancellus* as separate from other genera in the tribe "Pagurien"; the distinguishing features were the symmetry of the abdomen and the lack of appendages between the thorax and the last abdominal segment. He described and figured one male from an unknown location as *Cancellus typus* and pointed out that *Pagurus canaliculatus* figured by Herbst appeared to be close to his new species.

H. Milne Edwards included a description of the genus *Cancellus* and the species *C. typus* in his *Histoire Naturelle des Crustacés*, published in 1837. This report contained the same information presented previously (1836), and referred to the single male specimen.

Dana (1852) divided the Paguridea into two families: the Paguridae and the Cenobitidae. He proposed the further division of the Paguridae into two subfamilies based on the structure of the abdomen: the asymmetrical Pagurinae, which included the genus *Pagurus* and four new genera (*Bernhardus, Calcinus, Diogenes, and Paguristes*); and the symmetrical Cancellinae, with the single genus *Cancellus*.

This classification was repeated in another paper in 1852 in which Dana added several genera to the Pagurinae, while *Cancellus* remained the only genus in Cancellinae.

Zietz read a paper to the Royal Society of South Australia in 1887, describing *Gryllopagurus lithodomus* from St. Vincent Gulf as a new genus and species. The description and figures were published in 1888.

*Cancellus typus* was included in a list of the fauna of Port Jackson (near Sydney, New South Wales, Australia) compiled by Whitelegge in 1889. In a paper on *Scyllarus sculptus*, Whitelegge (1889) briefly mentioned *Cancellus typus*, pointing out that it had been described without a definite habitat but had subsequently been found in South Australia and in Port Jackson.

A. Milne Edwards and Bouvier published a paper in 1891 dealing with hermit crabs of the genus *Cancellus*. They described a new species, *Cancellus parfaiti*, from the Cape Verde Islands. They remarked on the use of the chelipeds and ambulatory legs as an "operculum" for the dwelling of the crab. Moreover, they pointed out the similarities and differences between *Cancellus* and the other pagurids, and defined the relationship of *Cancellus* to the superficially similar *Pylocheles*. The characters used to distinguish *C. parfaiti* from *C. typus* were listed. *Cancer canaliculatus* Herbst...
was formally placed in the genus *Cancellus*, and note was made of the characters, according to Herbst's description and figure, which served to separate it from the closely related *C. typus*. Finally, they stated that *Cancellus* was composed of three species: *C. typus* H. Milne Edwards, *C. canalicularus* (Herbst), and *C. parfaตi*. Apparently they had no knowledge of Zietz's *Gryllopagurus lithodomus* from Australia. *C. parfaตi* was mentioned in a preliminary note on the hermit crabs collected from the *Travailleur* and *Talisman*, published by A. Milne Edwards and Bouvier in 1892. This note concerned the same animals reported in 1891, but indicated that the species had been collected by Parfait at Annobon and at Île du Prince.

Perrier (1893) reported the occurrence of *C. parfaตi* off Senegal, but it is not known whether this was a new location or simply a restatement of a previous report.

A. Milne Edwards (1893) referred to *Cancellus* in the report of the Blake pagurids, again pointing out that the similarities between *Cancellus* and *Pylocheles* were due only to adaptations to a similar mode of life.

The same year, Faxon (1893) gave a preliminary description of a new species, *Cancellus tanneri*, from the Gulf of Panama. The complete description, accompanied by several figures, appeared in 1895. He reviewed the literature and summarized the characters that could be used to distinguish *C. tanneri* from the three species discussed by A. Milne Edwards and Bouvier (1891).

In the scientific results of the *Travailleur* and *Talisman*, A. Milne Edwards and Bouvier (1900) redescribed and figured *Cancellus parfaตi*. Their description and figures were the most detailed and specific for any species in the genus at that time. They distinguished *C. parfaตi* from the three other *Cancellus* known to them, and stated that their specimens, collected by Commandant Parfait, came from “île du Prince (îles du Cap-Vert) et Annobon.”

Benedict (1901) added two new species to the genus *Cancellus* in a rather short publication on new symmetrical hermit crabs from the West Indies dredged by the *Albatross* in 1885. *Cancellus ornatus* was described from a single female from the Gulf of Mexico, and *C. spongicola* from one male taken in the vicinity of Arrowsmith Bank in the Caribbean. The descriptions are brief and incomplete, and the few figures are nonspecific.

Sayce recorded *Cancellus typus* in a report of the results of dredging at Port Phillip in Australia in 1902. He gave the crab the common name of “boring hermit.”

In 1905, the pagurid part of Alcock’s monograph of the Indian decapod crustaceans was published. This volume dealt with the Paguridea, including the families Pylochelidae, Paguridae, Coenobitidae, and Lithodidae. A worldwide key to the recognized genera of each family was given, and *Cancellus* was included in the Paguridae. Alcock listed *Gryllopagurus* as a synonym of *Cancellus* and gave a description of the genus. He described *Cancellus investigatoris* from off the coast of Ceylon as a new species extremely similar to *C. parfaตi* A. Milne Edwards and Bouvier. A very useful table of the genera and species of pagurids appears at the end of Alcock’s publication. It includes the pertinent references for each species and the approximate depth range from which they were reported. He listed eight species of *Cancellus*: *C. canalicularus* (Herbst), *C. investigatoris* Alcock, *C. typus* Milne Edwards, *C. tanneri* Faxon, *C. ornatus* Benedict, *C. spongicola* Benedict, *C. parfaตi* A. Milne Edwards and Bouvier, and *C. lithodomus* Zietz.

Southwell (1906) reported one specimen of *C. investigatoris* from the Indian Ocean in Herdman’s *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Mannar* [sic, = Mannar]. Later (1910), he noted and figured, among other things, the coralline “habitatculum” or dwelling of a specimen of *C. investigatoris*.

In 1921, Balss reported a new location for *C. parfaตi* off Angola, based upon a single ovigerous female.

*Cancellus macrothrix* was described by Stebbing in 1924. According to Barnard (1950), “it is difficult to extract any specific characters from Stebbing’s description and figures.” The type-specimen came from Algoa Bay, near Port Elizabeth on the southeastern coast of South Africa.

“The Crustaceans of South Australia, Part 1,” by Hale was published in 1927. This volume, one of the *Handbooks of the Fauna and Flora of South Australia*, was a general reference written in a popular style with many photographs and nontechnical descriptions. *Cancellus typus* was briefly described under the common name of miner hermit crab.
In British, Australian and New Zealand Antarctic Expedition 1929–1931 Reports, Hale (1941) described and figured the early stage of Cancellus typus. He included Gryllopagurus lithodomus in the synonymy, and commented that Zietz’s material was dried and the eviscerated types filled with cotton wool.

In the same year, Rabaud (1941) mentioned C. parfaiti in a paper on pagurid adaptations.

Two popular accounts of C. typus appeared in 1944 and 1947 by Elizabeth Pope in Australian Museum publications. She commented that the crab lives in a hole in a stone, rather than in a snail shell like most other hermits.

In 1950, Barnard compiled a new description of Cancellus macrothrix Stebbing, the South African species, unreported since the original description in 1924. One of his specimens was from Algoa Bay, the type-locality; the other two were taken off East London and Cape Morgan. He commented on several “glaucothoes” which had been collected with one of the female specimens.

Dakin (1952) mentioned Cancellus typus in his popular book, Australian Seashores, and included two photographs of the crab.

A year later, Pope (1953) wrote a magazine article about Cancellus typus. She told of Zietz’s animals from St. Vincent Gulf and reported subsequent locations: in other parts of South Australia; Western Port, Port Phillip, and off Cape Everard in Victoria; and in Sydney Harbour and Port Jackson in New South Wales. “A Cancellus boring into a stony polyzoan colony” collected from the F.I.S. Endeavour off Devonport, Tasmania, was reported in her paper; this specimen was among the material examined in the present study.

In 1956, Balss wrote that the genus Cancellus, with its “stretched out” abdomen, was composed of nine species, circumtropically distributed in the littoral zone, and that they lived in coral rocks, in hollowed-out rocks, or in sponges. He used Hale’s (1927) photograph showing C. typus enconced in a fragment of rock.

In the introductory section of the scientific results of the Calypso expeditions, Forest (1959) mentioned Cancellus parfaiti taken on a cruise in the Gulf of Guinea in 1956.

Two years later, in an Atlantide report, Forest (1961) reported three specimens of C. parfaiti taken by the Galathea near São Tomé in 1950. In addition, he reported having collected many C. parfaiti off the coast of Dakar in 1955.

In 1966, Forest formally reported the three specimens of C. parfaiti collected by the Calypso near São Tomé in 1956.

The most recently described species was Cancellus calypso Forest and St. Laurent (1967). The description was based on one female specimen taken in a colony of bryozoans near the island of Abrolhos off the coast of Brazil. The very detailed description and clear figures are the most precise given for any animal in this genus. Forest and St. Laurent pointed out that the species was very close to C. ornatus Benedict. Diagnoses of the family Diogenidae and the genus Cancellus and a key to the genera of the western Atlantic diogenids were included in their paper.

The only behavioral study of a Cancellus was done by Hazlett (1969). He reported the “stone fighting” behavior of several specimens of Cancellus spongicola observed in the laboratory, and compared it to that of other diogenids.

MATERIALS AND METHODS.—Most specimens examined in this study were taken during oceanographic cruises of the research vessels John Elliott Pillsbury and Gerda of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida. The letters P and G in station numbers refer to the Pillsbury and Gerda stations, respectively. A few specimens were collected from the M/V Silver Bay and the M/V Oregon of the U.S. Fish and Wildlife Service, Pascagoula, Mississippi. The type-specimens of Cancellus ornatus and C. spongicola were borrowed from the National Museum of Natural History, Washington, D.C.; illustrations and photographs of these were made for study and comparison. The holotype of Cancellus canaliculatus was borrowed from the Zoologisches Museum, Berlin. Camera lucida sketches for study of the type-specimens of C. Tanneri from the Museum of Comparative Zoology, Harvard College, Cambridge, were made by Miss Barbara Stolen. One of the two specimens of C. Tanneri available was obtained from the Allan Hancock Foundation, Los Angeles, California, and the other was borrowed from the Naturhistoriska Riksmuseet, Stockholm. The C. typus material was borrowed from the Australian Museum, Sydney. The specimen of C. in-
vestigatoris was borrowed from Kyushu University, Fukuoka, Japan.

Most of the animals were captured using bottom nets (otter trawls) or dredges and were immediately preserved in formalin. All were subsequently transferred to ethyl alcohol. Ionol, an antioxidant color preservative, was added in some cases, but it was not very effective.

Some live specimens were brought into the laboratory and were maintained for several months. Several animals produced as many as four moults that were preserved in 10 percent buffered formalin.

The shield length, shield width, and sex were noted for each specimen; shield length is the measurement listed in material sections unless otherwise indicated. Occasionally other measurements were made for the purpose of comparison. Measurements were made using an ocular micrometer.

Sex determination was based on the position of the gonopores and the presence or absence of pleopods on the abdomen. The male has gonopores on the fifth coxal segment and lacks pleopods; the female has gonopores on the third coxal segment and four biramous pleopods on one side of the abdomen. Some secondary sexual characteristics which vary among the species are described in the individual species accounts.

Illustrations were made with the aid of a Wild M-5 microscope and drawing apparatus. Significant morphological features are labeled on the diagrams on Figure 1.

A list of the technical terms and abbreviations used in the descriptions follows. The definitions usually apply to all hermit crabs but are intended for the genus *Cancellus* only.

cardiac region: the median calcined area posterior to the cervical groove and anterior to the first abdominal segment.

cephalothoracic shield: the part of the carapace anteromedial to the cervical groove, and anterior to the *linea transversalis*.

cl.: length of the carapace measured from tip of rostral projection to transverse margin of posterior carapace between membranous lobes.

Mx₁, Mx₂: maxillae; sometimes called maxilla and maxillule, respectively.

Mxp₁–Mxp₅: first through third maxillipeds- opercular surface: the area on the dorsal (in this genus, anterior) surface of a pereiopod contributing to the discoidal operculum formed when the appendages are drawn in.

Phylum: ARTHROPODA.

Class: CRUSTACEA.

Subclass: MALACOSTRACA.

Order: DECAPODA.

Suborder: REPTANTIA.

Section: ANOMURA.

Superfamily: COENOBITOIDEA (= Paguridea Serie Pagurienne Bouvier 1940).


Family DIOGENIDAE Ortmann, 1892

Fourteen pairs of gills on each side, namely: 10 arthrobranchs and one pleurobranch on P₅, P₆, P₇, and P₈. In certain genera, 13 pairs only, pleurobranch lacking on P₅. Branchial lamellae usually undivided, sometimes divided into two lobes.

Mxp₅, approximated at base. Ischium of these appendages with *crista dentata* developed or not, according to the genus, always lacking an accessory tooth.

Chelipeds equal, subequal or very unequal; in which case, the left is largest, except in *Petrochirus*.
On the male, no paired pleopods and four unpaired pleopods (Pl₁-Pl₅) except in Paguristes and Paguropsis, where Pl₁ and Pl₅ are paired, and in Cancellus, where there are no pleopods on somites 1 to 5.

On the female, no paired pleopods and four unpaired pleopods (Pl₁ to Pl₄) except in Paguristes and Paguropsis, where there are paired Pl₁. (Translated from Forest and St. Laurent, 1967.)

**Genus Cancellus H. Milne Edwards, 1836**

Cryllopagurus Zietz, 1888:298.

**TYPE-SPECIES.**

_Cancellus typus_ H. Milne Edwards, 1836, by original designation.

**DIAGNOSIS.**

Fourteen pairs of gills with undivided lamellae. Antennal flagella short, with very short setae.

No lateral lobe on the endopodite of Mx. _Crista dentata_ well developed on the ischium of Mxp.

Chelipeds equal, modified, forming an operculum with the distal articles of P and P; claws corneous.

On the male, no unpaired pleopods. On the female, four large biramous unpaired pleopods, P to P. Abdomen and uropods symmetrical. (Translated from Forest and St. Laurent, 1967.)

**DESCRIPTION.**

Cephalothoracic shield usually shorter than maximum shield width; laterally convex; frontal margin with inflated rim, postorbital indentations. Anterior surface of shield sculptured, posterior part smoother; indentations in postero-lateral margins.

Cardiac region calcified, at least in part; calcification usually decreasing posteriorly. Anteromesial part of brachial regions calcined, but most of area submembranous.

Ocular scales broad at base; inner part projected anteriorly to a triangle or tubercle which may terminate in one or more teeth or spinules.

Ocular peduncles shorter than shield length; cornea inflated slightly or not inflated, with basal emargination dorsally.

Antennular peduncle when extended approximately same length as ocular peduncle; basal segment usually armed with two or more teeth.

Antennal acicle reaching one-fourth to one-half length of ocular peduncle, terminating in two or more teeth distally; other teeth usually present on outer or inner margins; basal segment deeply indented, armed distally with two heavy teeth, one projecting anterolaterally, the other anteromesially.

Chelipeds equal, modified; dorsal surface of carpus with sharp angle, wrist flexed such that dorsal surface of propodus and distal half of carpus are anterior and perpendicular to the longitudinal plane of the animal. These anterior surfaces, together with surfaces of distal segments of P, forming discoidal operculum closing round opening of carinoecium. Opercular surfaces flattened or concave, usually tuberculate, often with shallow channels between rows of tubercles. Dorsal margin of carpus at flexure often raised in distinct lobate crest. Most surfaces on all segments of chelipeds and P relatively smooth except for opercular surfaces and angular margins. Inner dorsal margins of manus usually lobate at sharp angle separating opercular surface from smooth, flat inner face. Dorso-lateral margin of opercular face of manus usually rounded with tubercles diminishing laterally or channels becoming shallower. Some species with patch of rugose striae on ventrolateral surface of manus. Scattered setae in clusters over most surfaces, tufts of strong setae distally on both dactylus and fixed finger or propodus. Tips of dactylus and fixed finger dark, corneous, sometimes toothed at abutting edges. Most species with row or rows of corneous teeth or tubercles on inner face of dactylus just under row of tubercles at dorsomesial margin.

P with flattened or concave opercular surface on distal 3 segments; these surfaces tuberculate, other surfaces smooth. Mesial surfaces of distal 6 segments lightly concave or molded, fitting smoothly against lateral surface of P. Merus of P flattened laterally but distal part expanded on dorso-lateral corner. (Merus and part of carpus of P fitting against concavity behind this distal expansion of P merus). Flexure of carpus similar to P but usually not as sharp; sometimes with raised crest at flexure. Lobation always distinct on sharp expanded dorso-lateral edge of propodus; in some species outer margins of carpus and dactylus also lobate. Clusters of setae along most angular margins of opercular surfaces. Dactylus terminating in curved dark corneous tip; longitudinal row of forward-projecting corneous denticles along ventral margin.

P without distinct opercular surface (except as described for _C. macrothrix_), most surfaces smooth, dorso-lateral edge with tubercles, teeth, setae; scattered tufts of setae on ventral and distal parts of most segments. Mesial surfaces of basis, ischium, merus, and proximal part of carpus flattened or slightly concave to lie smoothly against convex lateral surfaces of P. Some species with distinct lobes on dorso-lateral edge of propodus. Dactylus terminating in curved dark corneous tip; longitudinal row of corneous denticles on ventromesial margin.

P subchelate; pad of corneous granules cover-
ing most of distolateral surface of propodus. Dactylus often with longitudinal row of corneous granules. Most other surfaces smooth. Outer curved edge of carpus with fringe of long setae. 

P₂ chelate; pad of corneous granules covering anterolateral surface of propodus. Usually one or more rows of corneous granules on dactylus and fixed finger; tips spooned, usually with corneous teeth on abutting distal margins.

Margins of most coxal segments, particularly those of P₄ with fringes of setae, often long and plumose.

Fifth coxal segment on males of some species rounded as in females, but most species with some modification ranging from expanded prolongation to shallow concavity on coxa.

Abdomen ellipsoidal or spherical, not coiled in typical pagurid manner, but often with gentle flexure bringing tail fan to ventral position. First abdominal tergite small, usually calcified, located close to cardiac region at junction of thorax and abdomen. Remnants of other abdominal terga on some species, appearing as hardened transverse strips, partly calcified in some species, particularly on large individuals. Females with 4 biramous pleopods on one side of abdomen, hardening of terga more apparent at insertion of pleopods. Pleopods lacking entirely on males.

Sixth abdominal tergite strongly calcified, symmetrical, hexagonal; transverse furrow and lateral notches dividing plate into anterior and posterior sections; rounded transverse carina and blunt lateral projections immediately anterior to furrow and notches respectively.

Uropods equal; exopod larger than endopod, both with pads of corneous granules distally.

Telson symmetrical; usually with slight swelling medially.

Remarks.—Of the nine known species of Cancellus, three are found in the West Indian region: Cancellus ornatus Benedict, C. spongicola Benedict, and C. viridis, new species. The only other region with more than one species is the “east Indies” with C. investigatoris Alcock, definitely described from the Indian Ocean, and C. canaliculatus (Herbst) of questionable location. The other species are C. parfaiti A. Milne Edwards and Bouvier from the eastern Atlantic and western coasts of Africa, C. Tanneri Faxon from the eastern Pacific, C. macrothrix Stebbing from South African coasts, and the Australian species, C. typus H. Milne Edwards (see Table 1).

An outstanding feature of this genus is the formation of an operculum by the distal segments of the chelipeds and anterior ambulatory legs. Typically, the distal parts of only the first pair of walking legs, along with the chelipeds, take part in the formation; the South African species, C. macrothrix, however, also uses the second pair. Barnard (1950) has pointed out that this is anomalous, and even questions whether that species should be considered a Cancellus. Since no specimens of C. macrothrix were available for examination, the species is included here for completeness, and its taxonomic position is left undisturbed.

Another obvious characteristic of the genus is the apparent symmetry of the abdomen, including the telson and uropods. The abdomen is spherical or ellipsoidal and the male lacks pleopods. The presence of four biramous pleopods on one side or the other of the female abdomen demonstrates the superficiality of the symmetry. Alcock (1905) stated that Paguropsis was the only pagurid genus having unpaired pleopods which may occur on either the left or right side of the abdomen of the female. All previous reports of Cancellus indicated that the pleopods were usually on the left side, illustrating the relation to the asymmetrical, more typical hermit crabs which inhabit gastropod shells. However, in the only species of which a number of individuals have been collected, C. spongicola, ten of fourteen females had their pleopods on the right side. Two C. ornatus, of eight females reported, have been noted to bear them on the right. One of the two females of C. typus examined had pleopods on the right side. Unfortunately there have not been enough specimens collected to obtain ratios for any species but C. spongicola, or to allow a generalization about the genus as a whole. It is likely, though, that some, if not all, of the species of Cancellus are losing or have lost the pagurid tendency for the females to bear pleopods on the left side, since “left-sided” animals living in a cylindrical hole apparently have no advantage over crabs bearing them on the right.

The question arises whether Cancellus, rather than advancing beyond the pagurid nature to a superficial symmetry, has instead not yet reached the true asymmetry displayed by the more typical pagurids. If this is the case it would be difficult to...
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<td>Barnard, 1950</td>
<td>S Africa</td>
<td>Alga Bay and off East London</td>
<td>31 and</td>
<td>1 &lt; 2</td>
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<td></td>
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<td>S Africa</td>
<td>off Cape Morgan</td>
<td>31</td>
<td>1 &lt; 2</td>
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account for the fact that the animals never have pleopods on both sides, and that some species have them only on the left side—a pagurid character. It is difficult to understand why pleopods should be borne on one side if the animal has always lived in a cylindrical cavity.

The only family of truly symmetrical hermit crabs is the Pylochelidae. A. Milne Edwards and Bouvier (1891) suggested that Pylocheles is a "macruran," closely related to the thalassinids, which has acquired pagurid characteristics in adapting to life in hollowed-out stones, bamboo, or other cylindrical cavities, whereas Cancellus is probably a true hermit crab which has abandoned gastropod shells to assume a mode of life, and consequently an external form, similar to that of Pylocheles. Boas (1926), in his study of symmetrical pagurids, maintained that the pylochelids were indeed pagurids, although in a more primitive position than the more typical hermit crabs. He agreed, however, that the symmetry of Cancellus was secondarily derived, and their similarity to Pylocheles was a result of their adaptation to life in similar cavities. In the dwelling, Cancellus can be distinguished easily from the Pylochelidae since the opercular surface is formed by a pair of ambulatory legs as well as the chelipeds, rather than by the flattened chelipeds alone as in the Pylochelidae. The abdomen of the pylochelids differs from that of Cancellus in that all the pleopods are paired, and the dorsal surface of the abdomen bears distinct, calcified terga; the whole animal looks very much like a small thalassinid.

Both the opercular formation and the body symmetry of Cancellus are related to the unusual habit of living in cylindrical cavities. They have been reported in pieces of calcareous rock, granular stones, siliceous sponges, calcareous algae, and dead coral. Only the anomalous South African species, C. macrothrix, has been collected inhabiting a gastropod shell.

Balss (1956) remarked that it was not known in what manner the tubes which Cancellus inhabits were formed. He speculated that the hole was probably made by a worm (since, he said, the crab could not bore it), possibly like a sipunculid of the genus Aspidosiphon which lives in "snail houses" that have been secondarily overgrown by corals. Some specimens have been found in pieces of coal which indicate they might not necessarily be dependent on other animals to provide a tube that is secondarily overgrown.

Balss repeated Boas' (1926) assumption that Cancellus, like Pylocheles, must abandon its permanent dwelling for feeding purposes. Two young females kept alive in our laboratory for eleven months after capture were never seen out of their stone dwellings. When walking from one side of a four-inch finger bowl to the other in response to the presence of food, they dragged the stone with them. Presumably they came out of the dwelling to moult since the moults were found outside the stones. Although the stones used by these specimens were heavier in relation to body weight than the mollusc shells used by typical pagurids, they did not appear too heavy or bulky for the animals to carry. Some specimens, however, have been taken in stones, pieces of coral, and calcareous algae which were so large and heavy that they could not possibly have been carried with ease if the hermit crab managed to move them at all. Therefore, it appears that the animals drag their dwellings about if possible or practical; it is not definitely known whether they frequently leave an immovable dwelling to obtain food, since this activity has not been observed. The abdomen of Cancellus is almost as soft and vulnerable as that of typical pagurids, and it would be in greater danger outside the dwelling than would Pylocheles with its more protected "macruran-like" abdomen.

With regard to Pope's (1953) proposal that the raps on the posterior ambulatory legs and uropods could be used as digging organs, it should be pointed out that all of the gastropod-shell inhabiting pagurids possess these "anti-skid" surfaces (Alcock, 1905) that are used to hold the animal inside its dwelling (Bohn, 1902; Russell, 1962). There is no evidence that these horny surfaces on Cancellus are used for active digging. It seems more likely that the pads, pressed against the inside of the tube, continually wear away material, perhaps allowing the crab to enlarge the cavity to keep pace with growth. All sponges and some stones which had served as dwellings for animals examined by this author were friable. One large Cancellus was taken in a piece of siliceous sponge; the burrow demonstrated the same curving away from the surface as described by Pope (1953), and there were many small shallow cavities that could have served as starting niches for smaller crabs.
Since the holes in the more durable rocks were much like those formed by animals known to drill, such as the boring clams, it is probable that the crab inhabited them secondarily.

Specimens of Cancellus parfaiati, the west African species, often live in clumps of melobesiid algae (Forest, 1959, 1961, 1966). Forest remarked that melobesiids taken at littoral stations other than where Cancellus had been collected often had a characteristic cylindrical cavity which he said showed that they had previously been occupied.

In all species except C. macrothrix, the sixth abdominal tergite is symmetrical and strongly calcified. This plate, sometimes together with the telson and uropods, may be used to effectively block the posterior opening of the hole, as in the genus Xylopagurus (Alcock, 1905). Although many of the dwelling cavities were open only at one end, the others showed clearly the advantages a crab would derive from having both ends protected.

In some species (C. spongicola, C. parfaiati, and C. typus) the ventrolateral surface of the manus of the cheliped has a distinct patch of regular striae resembling part of the stridulatory mechanism (pars stridens) in many decapods. That function is suggested for this structure, but since stridulation has not been observed in members of this genus, a positive statement cannot be made. In some species (C. ornatus and C. tanneri) this area on the manus is irregularly ridged or tuberculate; in C. viridis, new species, it is practically smooth.

Information about the life history of Cancellus consists of brief descriptions of young associated with adult females of C. typus and C. macrothrix (Hale, 1941; Barnard, 1950). Both cases indicate direct development, with the young clinging to the abdominal appendages until at least the glaucothoe or juvenile stage. Provenzano (personal communication) reports a zoeal stage present in C. spongicola.

Generalizations about relationships within the genus are not yet justified due to the small amount of material collected. Based on morphological similarities of the available specimens, however, there appear to be two groups of species (or species complexes). Species in the first group (C. typus, C. parfaiati and C. investigatoris) are characterized by a divided frontal rim on the shield, a flattened opercular surface on the chelipeds, a patch of regular striae on the ventrolateral surface of the chelipeds, and an unarmed frontal margin on the sixth abdominal tergite. Those in the second group (C. ornatus, C. tanneri, and C. viridis, new species) have a continuous inflated frontal rim, the opercular surface of the chelipeds concave, no patch of regular striae on the ventrolateral surface of the chelipeds, and heavy spines on the sixth abdominal tergite. This division is not absolute: C. typus, while it is associated with the first group, has the fifth coxal segments on the male concave, as do the species in the second group. C. canaliculatus has the divided frontal rim, only slightly concave opercular surface of the chelipeds, but no patch of striae on the chelipeds; the morphology of the sixth abdominal tergite is not known, but this species also appears to be intermediate in the nature of its characters. C. spongicola seems to be allied more closely with the first group than the second, but some of its characters (the frontal rim of the shield and armature of the sixth abdominal tergite, for example) are intermediate between those of each group. C. macrothrix may show characters of a more primitive Cancellus, as explained in the species account.

Key to Species of Cancellus

(This key should not be used independently of the full descriptions appearing in the text)

1. Telson and uropods symmetrical; abdomen with gentle anteroventral flexure, not spirally coiled; operculum formed by chelipeds and P2; carpus of cheliped and P2 strongly projected ........................................ 2
2. Telson and uropods not symmetrical; abdomen spirally coiled; operculum formed by chelipeds, P2 and P3; carpus of cheliped and P2 not strongly projected; South African species ......................................................... 9. C. macrothrix Stebbing
3. Frontal rim of shield continuous between blunt lateral teeth; anterior margin of sixth abdominal tergite with many strong or truncate spines; opercular surface of cheliped concave or with longitudinal groove .........................................................
Frontal rim of shield divided into at least three parts by depression behind eyes; anterior margin of sixth abdominal tergite nearly smooth; opercular surface of cheliped flat or slightly concave

3 (2). Ocular scale with more than one terminal tooth or spine; fifth coxal segments of male flattened; overall color of live or recently preserved specimens green; western Atlantic species ................................. 3. C. viridis, new species

Ocular scale with one triangular tooth; fifth coxal segments of male concave and expanded; overall color than green

4 (3). Lateral face of merus and propodus of P2 noticeably longer than twice the width of these segments; calcified part of cardiac region subrectangular, broader than long, posterior margin straight; overall color cream with purple, dark red or brown; checker board pattern on opercular surface, western Atlantic species 2. C. ornatus Benedikt

Length of lateral face of merus and propodus of P2 barely twice or less than twice the width; calcified part of cardiac region longer than broad, posterior margin a rounded point; color (according to Faxon) white with red spots, spots tending to coalesce in bands on ocular peduncles and legs; eastern Pacific species ............................................... 4. C. tanneri Faxon

5 (2). Manus of cheliped with distinct patch of parallel striae on ventrolateral surface .............................. 6

Manus of cheliped with forward projecting tubercles or ridges on ventrolateral surface, but no distinct patch of striae; dorsal projection of carpus of cheliped divided into two lobes; dorsolateral margin of manus of cheliped with toothed transverse projections, becoming lobular distally; an indentation in lateral surface below distalmost projections ................................................... 7. C. canaliculatus (Herbst)

6 (5). Ocular scale usually with more than one terminal tooth or spine; narrow raised rim parallel to and just behind angular frontal margin, divided into four parts by depressions at apex of rostrum and behind eyes ........................................................................ 7

Ocular scale usually with one terminal tooth or spine; frontal rim of shield inflated, divided into three parts by depressions behind eyes ........................................................................ 8

7 (6). Cornea inflated; ocular peduncle two-thirds to three-fourths shield length; smooth; basal segment of antennular peduncle with four broad teeth on anterolateral margin; two spines or heavy teeth on raised dorsal edge of antennal acicle; anterior margin of sixth abdominal tergite smooth; overall color orange, pink and cream; eastern Atlantic species .......................................................... 5. C. parvifil A. Milne Edwards and Bouvier.

Cornea not as wide as distal part of ocular peduncle; ocular peduncle about one-half length of shield with spines on mesial proximal surface; three or four spines on raised edge of antennal acicle; one or more low, tooth-like protuberances on anterior margin of sixth abdominal tergite; western Pacific species 8. C. investigatoris Alcock

8 (6). Anterior surface of shield with transverse sculpturing behind straight transverse depression; cheliped with deep transverse channels on dorsolateral margin; eyes slightly wider than eyestalks; reduced or truncate spines on anterior margin of sixth abdominal tergite; setae on appendages and body, but not extremely hirsute; fifth coxal segments of male round; overall color orange and cream; western Atlantic species .......................................................... 1. C. spongicola Benedict

Sculpturing on anterior part of shield in form of round granules or tubercles, but no deep transverse channels; eyes slightly narrower than eyestalks; anterior margin of sixth abdominal tergite smooth; appendages and body hirsute; fifth coxal segments of male expanded and concave; color of preserved material (according to Zietz) reddish, limbs marked with large dark red spots, some forming bands on the legs; Australian species ........................................................................................................................... 6. C. typus Milne Edwards

1. Cancellus spongicola Benedict, 1901

Figures 2-4

Cancellus spongicola Benedict, 1901:773, figs. 3, 4.—Alcock.

Material.—1 ♂, 6.5 mm, holotype; Albatross sta. 2354, Arrowsmith Bank; 20°59'30"N, 86°23'45"W; 238 m; in a siliceous sponge; 22 January 1885; USNM 9549.—1 ovigerous ♀ (yielded larvae), 8.6 mm; G−232, south of Bimini; 25°36'−39"N, 79°20.5'−21"W; 439−421 m; no dwelling taken; 29−30 Janu-
Figure 2—Cancellus spongicola Benedict. Male, sl. 7.1 mm, G-387: a, carapace (setae omitted on right side); b, coxal segments. Male, sl. 9.7 mm, G-798: c, antennular peduncle, lateral view. Female, sl. 5.2 mm, G-591: d, sixth abdominal tergite and telson; e, left uropod, dorsal view.
SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

mary 1964; 10' otter trawl; UMML 4137.—3 $, 7.1 mm, 4.4 mm, 3.8 mm; 1 $, 5.0 mm; G–387, north of Grand Bahama Island; 27°17'N, 79°15'W; 412 m; all in pieces of siliceous sponge; 19 September 1964, 5' screen dredge; USNM 128741 (illustrated), 128742, 128743, 128751.—1 $, 4.7 mm; G–633, north of Bimini; 25°59'–26°01'N, 79°19'–18'W; 439–458 m; in a piece of calcareous rock; 19 September 1964, 5' screen dredge; USNM 128746.—1 $, 9.7 mm; G–633, north of Bimini; 25°59'–26°01'N, 79°19'–18'W; 439–458 m; in a piece of calcareous rock; 30 June 1965; 10' otter trawl; USNM 128747.—1 $, 3.9 mm; G–897, Arrowsmith Bank; 21°10'N, 86°25'W; 247–284 m; in a piece of rock; 27 January 1968; triangular dredge; UMML 4133.—1 $, 3.3 mm; G–899, Arrowsmith Bank; 20°59'N, 86°24'W; 40–165 m; 1 $ without dwelling, 1 $ in a siliceous sponge, 9" in a piece of coral rock; 10 September 1967; 10' otter trawl; USNM 128747.—1 $, 3.9 mm; G–947, Arrowsmith Bank; 21°13'N, 86°25'W; 247–284 m; in a piece of rock; 15 March 1968; box dredge; UMML 4134.—1 $, 3.7 mm; 1 $, 5.2 mm; G–951, Arrowsmith Bank; 21°06'N, 86°28'W; 192–298 m; 1 $ in sponge, 9 without dwelling; 28 January 1968; 10' otter trawl; USNM 128748.—2 $, 3.5 mm, 2.3 mm; 2 $, 4.0 mm, 3.6 mm; G–952, Arrowsmith Bank; 21°02'N, 86°26'W, 586–92 m; no dwellings taken; 28 January 1968; 10' otter trawl; USNM 128745.—1 $, 6.2 mm; Oregon sta. 4941, Arrowsmith Bank; 20°59'N, 86°29'W; 201 m; 2 $ in calcareous rock; 12 June 1964; 6' tumbler dredge; USNM 128750.

DESCRIPTION.—Cephalothoracic shield shorter than maximum width (sl./sw.=0.80–0.95), slightly convex anteroposteriorly. Anterior margin inflated, dorsally flattened, merging with rounded anterolateral margin; postorbital indentations angular. Triangular rostrum with tiny denticle at apex, barely exceeding blunt lateral projections. Depression in surface of frontal margin on each side of rostrum behind ocular scales. Subdiamond or triangular-shaped depression behind rostrum connected to triangular depressions behind antennal acicles by narrow groove; margin of groove straight anteriorly, but curved posteriorly, bordering 2 raised sculptured semicircular areas; scattered short setae in depressions. Gastric pits elongate slits near postero-lateral margin of shield. Sculpturing on anteri- lateral margin limited to longitudinal furrow or irregular row of pits with setae. Indentations in posterolateral margin with postorbital indentations giving shield slightly three-lobed appearance, especially in larger specimens.

Cardiac region broader than long; several (usually 4 to 6) groups of setae along anterior margin. Ocular scales with mesial half projecting anteriorly to triangle, terminating in sharp point or spinule; setae on anterior margin and dorsal surface. Ocular peduncle about three-fourths length of shield, slightly arcuate and narrower in middle; smooth with scattered setae along inner dorsal margin. Cornea slightly inflated, rounded, faceted, with angular emargination in dorsal part of basal line. Antennular peduncle reaching almost to distal part of cornea; basal segment with 2, sometimes 3, teeth anteroventrally; flagellum composed of as few as 13 segments in smallest specimens and as many as 24 in large ones.

Antennal flagellum approximately same length as ocular peduncle. Fifth article of antennal pedun- cle reaching about one-half to two-thirds length of ocular peduncle. Acicle reaching one-third to one-half length of ocular peduncle with 3 anterior or anterolateral spines, one on inner margin posterior to these; occasionally an additional spine on inner or outer margin.

Posterior dorsal margin of carpus of cheliped in 3 or 4 tuberculate lobes. Ocular peduncle of manus
**Figure 3.** *Cancellus spongicola* Benedict, male, sl. 7.1 mm, G-387: *a*, left cheliped; *b*, left pereiopod 2; *c*, left pereiopod 3. (All lateral views.)
flat; evenly tuberculate; rounded protuberance mesially on distal margin of opercular surface; angle between opercular and inner faces sharp, 6 deep fissures dividing margin into 7 tuberculate lobes; 7 or more deep transverse rounded channels on dorsolateral margin extending down onto lateral face of manus, often with shorter shallower channels between deep ones; distinct patch of 8 or more closely spaced dorsoventral striae on ventrolateral surface; 2 or 3 ridges with several anteriorly projecting teeth and setae on ventral surface. Inner surface of dactylus with 2 rows of corneous projections, 3 to 6 in upper row, 2 to 5 in row beneath; several tubercles with similar corneous projections (resembling the corneous granules on rasps of P₄, P₅, and uropods) on dorsal inner margin above rows.

Opercular face of P₂ flat to very slightly concave, covered with low tubercles. Inner dorsal margin of carpus divided into small groups of tubercles by six or seven shallow fissures; outer margin with 5 toothed lobes separated by deeper fissures. Inner margin of propodus divided into 7 or 8 groups of tubercles, usually paired; fissures between groups extending about one-third distance across dorsal surface; outer margin separated into five toothed lobes, occasionally subdivided to form 6 or 7 lobes, usually no teeth on sides of lobes in lateral view. Inner dorsal margin of dactylus with 6 or 7 small groups of tubercles of diminishing height; outer ridge with three or four tuberculate lobes proximally, diminishing in size to small separate teeth distally; three horny denticles on ventral margin of dactylus, one denticle immediately behind corneous tip.

Merus and carpus of P₃ smooth proximally with low, anteriorly projecting teeth more distinct toward dorsal distal ends of these segments. Dorsal ridge of propodus with 5 toothed projections, larger distally. Dactylus with 7 or more dorsal teeth diminishing in height distally; ventral margin with 3 corneous denticles and one adjacent to dark tip.

Propodus of P₄ with round pad of corneous granules covering two-thirds of outer face. Dactylus extending one-half to two-thirds distance to end of pad, with 1 to 3 corneous denticles near distal end. Carpus with small tooth near articulation with propodus.

Dactylus of P₅ more than one-third length of propodus. Elongate pad of granules on propodus extending onto dactylus, diminishing to single row of granules.

Fifth coxal segment rounded on males and females. Fourth coxal segment with many plumose setae on all margins.

Females with 4 biramous pleopods on one side of abdomen. On females, “remnants” of 4 abdominal terga discernible at insertion of pleopods, particularly on large specimens. Hardened areas (but not calcified) only on abdomen of largest males. Small individuals of both sexes with spherical abdomens covered with short setae.

Length of sixth abdominal tergite approximately two-thirds maximum width. Anterior to rounded lateral projections on forward part of plate, a heavy lateral spine on each side. On anterolateral margin, rounded ridge with 4 or 5 groups of spines and setae, often reduced, irregular and truncate medially. On anterior lobe in front of carina, a deep curved depression; lateral to this on each side, a protuberance armed with a spine, setae, or both. Other spines symmetrically arranged over surface. Posterior lobe divided by medial longitudinal depression; raised, rounded areas on either side with several spines and setae. Posterolateral margin with 3 or 4 blunt triangular teeth on each side; posterior margin with 3 or 4 similar teeth on each side (12 to 14 teeth total).

Protopod with 2 rounded protuberances posteriorly; on some specimens, a group of setae between protuberances; occasionally a third protuberance beneath others. Anterior to these on dorsal surface, a single rounded protuberance, spine, or small group of setae.

Telson rounded, slightly wider than long. A depression around medial swelling. Rounded protuberances with setae and spines scattered over surface.

COLOR.—The overall color pattern of preserved material is light orange with pale straw or white mottling. All anterior appendages, including ocular peduncles, antennal acicles and peduncles, and pereiopods, have orange mottling; the color is generally more intense on exposed and dorsal surfaces. A white knob on the dorsal distal margin of the manus is distinct against the orange surface of the cheliped. There are suggestions of mottled bands on the meri of the chelipeds and ambulatory legs. There are concentrations of color in the post-
FIGURE 4.—*Cancellus spongicola* Benedict, male, sl. 7.1 mm, G-587: *a*, left pereiopod 2, mesial view; *b*, left pereiopod 3, mesial view; *c*, left pereiopod 4, lateral view; *d*, left pereiopod 5, lateral view.
orbital indentations of the frontal margin of the shield, in some of the depressions, and on the raised anterior semicircular areas in the gastric region. The branchial regions are also pigmented, particularly in the anteromesial areas. The tail fan is very pale in comparison to the rest of the animal. The corneous tips on the fingers of the chelipeds and ambulatory legs are dark brown to black.

**Type.**—USNM 9549. (See “Material.”)

**Type-LocalitY.**—Arrowsmith Bank, off the Yucatan Peninsula, Caribbean Sea.

**Distribution.**—Bimini; north of Grand Bahama Island; near Serrana Bank (off Honduras); Arrowsmith Bank. Most of the animals in the collections made by the Gerda and Pillsbury came from Arrowsmith Bank and Bimini. In depths of 33 m to 586 m. (See summary of species records, Table 1.)

**Remarks.**—Of 18 specimens with their dwellings preserved, 12 were in siliceous sponges, 5 were in pieces of calcareous rock, and one inhabited a piece of dead coral. While most of the sponges were friable enough to have been rasped out by the crab, the holes in the more durable rock were probably drilled by another animal, very possibly one of the boring clams (Donald R. Moore, personal communication).

**Discussion.**—*Cancellus spongicola* can be separated easily from the other western Atlantic species of *Cancellus* by the flat opercular surface of the chelipeds (as opposed to the distinctly concave or longitudinally grooved manus of the other species), the deep grooves on the dorsal external surface of the manus, and the patch of striae near the ventral margin. Also, the triangular rostrum and dorsally flattened frontal swellings of the carapace, with its postorbital indentations, are distinctive. The lobes on P₂ are usually rectangular and toothed only on the upper surface while in other species they are expanded, thinner, and tuberculate on all margins. The dorsal margin of the propodus of P₂ usually has five distinct groups of teeth, while in other species the teeth are arranged irregularly. The orange markings on live or recently preserved material are characteristic.

*Cancellus spongicola* appears to be most closely related to *C. parvai* A. Milne Edwards and Bouvier, a West African species, but the differences between the two are many and distinct: *C. parvai* has a raised ridge (in four parts) on the rim along the frontal margin and a granulated area on the anterior part of the shield which are not present in *C. spongicola*. The chelipeds of *C. parvai*, like *C. spongicola*, have the patch of striae on the ventral outer surface of the manus, but lack entirely the deep transverse channels on the dorsal outer margin. The opercular surface of the manus of *C. parvai* is more concave. The dactylus of P₂ of *C. parvai* is only barely toothed, rather than lobed as in *C. spongicola*. The anterior margin of the sixth abdominal segment is smooth in *C. parvai*, and the telson is longer with respect to width and more rectangular. The ocular scales of *C. parvai* are often armed with two or three tiny denticles, whereas the scales of *C. spongicola* always have one strong triangular tooth.

Of 14 female specimens of *C. spongicola* examined, 10 had pleopods on the right side and 4 had them on the left.

In large animals, the eyes are usually slightly wider than the eyestalks; smaller specimens have eyes noticeably wider, and the eyestalks are broader relative to their length (and shorter relative to shield length). The indentations in the upper surface of the frontal margin are less distinct on small specimens, and the frontal margin may be more rimlike (as opposed to the broad dorsally flattened frontal swelling in larger specimens). In the largest specimens the shield width increases relative to the shield length.

The black corneous area on the ends of the dactylus and propodus of the chelipeds may vary in length, and appears to wear down with use, since that area on an animal which had just moulted was obviously longer than that on the moult.

Observations of the behavior of six of the specimens from Arrowsmith Bank were recorded by Hazlett (1969). He concluded that patterns of "stone movement" were clearly diogenid rather than pagurid, and were even closer to patterns of other hermit crabs in the subfamily Diogeninae than to those in the subfamily Dardaninae.

2. *Cancellus ornatus* Benedict, 1901

**Figures 5-8**


*Cancellus calypso* Forest and St. Laurent, 1967:96-98, figs. 54-59.
FIGURE 5.—Cancellus ornatus Benedict. Male, sl. 9.4 mm, G-503: a, left antennular peduncle, lateral view; c, carapace; d, coxal segments. Male, sl. 6.2 mm, Silver Bay Sta. 5497: b, left antennular peduncle, lateral view; e, fifth coxal segments.
Material.—1 ♀, 5.5 mm, holotype; Albatross sta. 2405, NE Gulf of Mexico; 28°45'N, 85°02'W; 55 m; no dwelling taken; 15 March 1885; USNM 9784.—1 ♀, 9.4 mm; G-503, south of Grand Bahama Island; 26°31'-29'N, 78°51-45'W; 366 m; in a piece of siliceous sponge; 14 February 1965; 10' otter trawl; USNM 128737.—1 ♀, 2.7 mm; P-707, northwest of Trinidad; 11°21-23'N, 62°21'W; 76 m; in a piece of calcareous rock; 19 July 1968; 10' otter trawl; UMML 4131.—1 ♀, 4.8 mm; P-708, northwest of Trinidad; 11°24-26'N, 62°40.5'W; 69-73 m; in a piece of calcareous rock; 19 July 1968; 10' otter trawl; UMML 4132.—1 ♀, 7.9 mm; P-734, west of La Tortuga, southeast Caribbean; 11°01-02'N, 65°34-36'W; 68 m; no dwelling taken; 22 July 1968; 10' otter trawl; RMNH Reg. No. Crust. D 26549.—1 ♀, 6.0 mm; P-854, off Grenada, Windward Islands; 12°02'N, 61°36'W; 66-84 m; no dwelling taken; 3 July 1969; 10' otter trawl; USNM 128738.—1 ♀, 8.2 mm; Oregon sta. 6715, near Sombrero, Leeward Islands; 18°36'N, 63°27'W; 201-238 m; no dwelling taken; 30 May 1967; 6' tumbler dredge; USNM 128739.—1 ♀, 6.2 mm; Silver Bay sta. 3497, southwest of Great Inagua Island; 20°58'N, 73°44'W; 265 m; in a piece of siliceous sponge; 4 November 1961; 40' two seam trawl; USNM 128740.

Description.—Cephalothoracic shield shorter than maximum width (si./sw. = 0.80-0.95); anterior margin between antennal peduncles with rounded postorbital indentations, bordered by continuous flattened "collar-like" rim, slightly broader laterally. Rostrum broad, a rounded triangle with slightly concave sides, barely exceeding blunt lateral projections. Anterior margin of rostrum finely serrate. Occasionally a tiny spinule or spinules on anterior margin of rim at lateral terminations. Crescentic transverse depression behind frontal rim, parallel to rim on its anterior margin, wider behind ocular peduncles and diamond shaped behind rostrum; scattered setae in depressions. Small swelling in depression immediately behind rostral apex; short, mediolongitudinal groove posterior to swelling separating 2 semicircular transversely sculptured areas. Similar irregular transverse sculpturing on anterolateral surface of shield, extending mesially behind frontal rim to a point posterior to ocular peduncles. Central gastric region smooth with scattered pits at bases of setae. Gastric pits round to oval. Setae on anterior and lateral margins of shield. Indentations on posterolateral margins and postorbital indentations giving shield three-lobed appearance.

Calculated part of cardiac region broader than long; several groups of fine setae across anterior margin; posterior margin straight, posterolateral corners rounded.

Mesial half of ocular scale projected anteriorly to a triangle with setae, armed distally with one spinule. Ocular peduncle two-thirds to three-fourths length of shield, broader proximally and distally, more slender at a point even with antennal acicle. Inner and dorsal surfaces of ocular peduncle slightly flattened forming a rounded ridge at their boundary, with irregular row of broad low tubercles and associated setae; proximal tubercles with one or two spinules. Cornea slightly inflated; basal margin with triangular emargination on dorsal surface.

Antennular peduncle reaching cornea when extended. Basal segment usually with 3 or 4 well-developed spines anteroventrally on large animals. Antennular flagellum approximately equal to or slightly shorter than ocular peduncles.

Antennular flagellum longer than ocular peduncle, reaching about middle of ocular peduncle. Acicle reaching about one-third length of ocular peduncle; armed with 3 anterior or anterolateral teeth, one on inner margin behind these; occasionally additional tooth or teeth on inner or outer margin. Sometimes additional tooth under outer tooth on basal segment of peduncle.

Ocular peduncle reaching about one-third length of ocular peduncle, armed with 3 anterior or anterolateral teeth, one on inner margin behind these; occasionally additional tooth or teeth on inner or outer margin. Sometimes additional tooth under outer tooth on basal segment of peduncle.

Opercular face of cheliped irregularly tuberculate with longitudinal concavity; tubercles often denticulate or spinelike. Dorsolateral margin of manus rounded with indistinct short transverse channels; slightly larger widely spaced tubercles in indistinct longitudinal row lateral to concavity, row more distinct in smaller specimens; inner margin divided into about 6 groups of tubercles with setae, separated by fissures at bases between groups; these usually subdivided, forming up to 9 toothed lobes; on central margin of manus, several transverse ridges with forward-projecting spinules and setae; lateral to these, other transverse ridges extending dorsally on lateral surface. Lateral and mesial faces of manus smoothly reticulate with short setae and fine sculpturing. Inner surface of dactylus with 2 rows of corneous denticles, 4 to 6 denticles in dorsal row, 2 to 4 in row below; several tubercles in row on inner dorsal margin of...
FIGURE 6.—Cancellus ornatus Benedict. Female, sl. 6.0 mm, P-854: a, chelipeds and pereiopods 2 (shaded areas indicate color pattern). Male, sl. 9.4 mm, C-503: b, left cheliped, lateral view; c, left pereiopod 3, mesial view; d, left pereiopod 2, mesial view.
dactylus armed with denticles. Posterior and lateral borders of opercular face of carpus with projecting ridge divided into about 4 toothed lobes with setae.

Opercular face of P₂ tuberculate, carpus and propodus slightly concave, dactylus flat. Inner dorsal margin of carpus irregularly toothed, most teeth armed with a tiny denticle; outer ridge divided into 4 or 5 toothed lobes. Inner margin of propodus with 6 small groups of armed tubercles and one toothed distal lobe; tubercles on face of propodus in irregular transverse rows—more distinct toward inner margin; some tubercles armed with as many as 7 or 8 denticles; outer margin in 5 distinct lobes with setae, occasionally one subdivided into two shallow lobes; lobes foliaceous and expanded, their margins frequently touching; lateral surface near bases of fissures between lobes with several many-denticled protuberances; tiny denticle on distal lower margin of propodus at insertion of dactylus. Inner margin of dactylus with row of about 10 armed tubercles of diminishing height with interspersed tufts of heavy setae; 4 to 8 corneous denticles on ventral margin of dactylus with one flattened against dark tip; outer margin in 5 to 10 sections, proximal 4 or 5 are tuberculate lobes, remainder are armed tubercles diminishing in size distally. Length of merus and propodus noticeably greater than twice the width of these segments, measured on lateral surface.

Dorsal surface of carpus of P₃ broadening distally with several armed tubercles. Dorsal surface of propodus rough with 8 or 9 prominent tubercles armed with forward-projecting spinules and associated setae; denticle on distal lower margin of propodus. Dactylus with dorsal row of about 5 to 10 armed teeth and tufts of setae; ventral margin with a row of 5 to 7 corneous denticles, one adjacent to corneous tip. Length of merus and propodus usually noticeably greater than twice the width of these segments.

Corneous pad on P₄ oval, slightly longer than wide. Dactylus slender, extending to about two-thirds reach of pad, with row of 4 to 6 tiny denticles. One or two spines on distal end of carpus at insertion of propodus.

Dactylus of P₅ more than one-third length of propodus. Corneous pad extending onto dactylus as row of about 10 corneous granules.

Margins of fourth coxal segments with heavy fringe of long fine setae.

Fifth coxal segments of male broadly depressed in center with gonopore on rounded anterior margin, slightly mesial to center of segment. Tufts of short strong setae on inner adjacent margins of coxae.

Abdomen ellipsoidal, covered with many short setae. Females with 4 biramous pleopods on one side of abdomen; large females with hardened transverse strips at base of and mesial to pleopods.

Sixth abdominal tergite broadly hexagonal; its length two-thirds maximum width. Anterior lobe larger than posterior. Blunt triangular lateral projections at ends of rounded transverse carina with a single strong spine, sometimes bifid, inserted anterior to them near lateral borders. Ridge on each side of forward margin armed with 8 to 11 strong uneven spines. Shallow longitudinal depression in center of plate. Raised areas with spines and setae scattered over anterior lobe. Raised area on either side of posterior lobe with scattered spines and setae. Posterolateral border with toothed ridge. Medial ridge on rear margin with 2 groups of teeth, most posterior teeth armed with tiny spinules.

Surface of protopod with 2 or 3 tufts of setae, depressed to margins; backward projection with 2 to 4 blunt teeth or rounded protuberances; single spine projecting posteriorly from underneath.

Telson broader than long, with many short setae on posterior margin, several on surface and other margins. Two anterolateral depressions on either side in front of a raised central area. Surface uneven with scattered short setae.

Color.—The general color pattern in several recently preserved specimens is dark violet on a cream-colored background with scattered red and orange markings. There are large dark violet areas on the carapace, particularly on the anterior sculptured areas. Orange and red markings are mainly in depressions. There is a distinct red spot on each side of the shield just anterior to the gastric pit, and a broad pigmented spot on the side of the thorax just below the lateral margins of the carapace. The anterolateral corners of the cardiac region also have a concentration of color.

The dorsal surface of the ocular peduncle is violet with small diffuse patches of red and with white or cream-colored tubercles; the undersurface is
**Figure 7.** *Cancellus ornatus* Benedict, male, sl. 9.4 mm, G-503: a, left pereiopod 2; b, left pereiopod 3; c, left pereiopod 5; d, left pereiopod 4. (All lateral views.)
white with orange patches. There is an indistinct longitudinal line along the lateral surface.

The maxillipeds have a pigmented band around most of the segments.

The antennules are pale orange or cream with yellow flagella.

The ocular scales have distinct patches of color on a cream-colored or white background. The antennal acicles have red markings; there is a pigmented band around the middle of the fifth article of the antennal peduncle.

The chelipeds show dark violet patches on the lateral opercular surfaces and on the inner raised margins, with a large diffuse violet area on the inner face of the manus.

The opercular surfaces of the chelipeds and first ambulatory legs have somewhat rectangular areas of pigmentation which give an impressive checkerboard effect when the legs are drawn together. Most undersurfaces of legs and the coxal segments are cream with scattered red markings. The ambulatory legs are generally cream with violet banding; the bands around the proximal part of each propodus are continuous. There is a broad violet band covering most of the dorsal and outer surfaces of each carpus. The meri have large purple patches on the dorsal surfaces, narrowing ventrally. There are red spots on some of the violet areas.

P₄ is cream with a red-violet patch in the middle of the upper surface of the carpus and merus.

P₃ is pearlescent with a few scattered red marks.

There are many small red spots on the abdomen.

Red patches are arranged symmetrically on the sixth abdominal tergite and telson, frequently at the bases of certain setae; there are four conspicuous ones medially on the forward part of the segment and one near each end of the transverse carina; two spots appear on each side of the posterior lobe. There is a distinct patch of red in the middle of the posterior border. Four tiny spots are arranged in a curved transverse row across the front part of the telson. The uropods are cream, slightly pearlescent, with scattered light red patches.

One strikingly colored female specimen exhibited the same general patterns described, but the pigment was brownish violet or brownish red instead of violet. This animal had three distinct spots of this color across each of the transverse hardened elements on the abdomen mesial to the pleopods. The general background color varied from cream to light orange brown.

The violet color seems to fade very rapidly from preserved animals; the red and orange markings persist for a longer time.

**Type.**—USNM 9784.

**Type-Locality.**—Northeast Gulf of Mexico.

**Distribution.**—See “Material.” The only other animal collected was a small female (total length, 1.8 mm) taken near Abrolhos off the coast of Brazil by the Calypso, sta. 81, 18°06.5'S, 38°42'W, 37 m, 28 November 1961. There has never been more than one specimen taken at a location. Other material is from depths of 55–366 m. Both male specimens came from deeper waters (366 m, 265 m) than five of the females which were taken from 55–84 m. One female came from 201–238 m.

**Remarks.**—Of the four specimens taken with dwellings, two males were in pieces of siliceous sponge, and two females were in pieces of calcareous rock. The sponges were friable and open at one end only. The rocks were harder and open at both ends.

**Discussion.**—Two small specimens taken near Trinidad since the description of Cancellus calypso Forest and St. Laurent, 1967 (from the coast of Brazil), show characteristics intermediate between the tiny individual described as C. calypso and the much larger type-specimen of C. ornatus as well as other individuals positively identified as C. ornatus. This indicates that C. calypso is probably a juvenile of C. ornatus. A. J. Provenzano had suggested that it was a distinct species (in Litt.).

Forest and St. Laurent (1967) stated that the Cancellus captured by the Calypso differed from C. ornatus in the number of spines on the ridge at the anterior margin of the sixth abdominal tergite. The specimen taken by the Calypso has nine spines on the left and seven on the right. The type specimen of C. ornatus has six on the left and eight on the right. Benedict’s original description (1901) of the spination, “ . . . a group of four on one side of the notch and six on the other . . .”, is slightly misleading since he counted the two lateral spines of each group separately. The small female specimens have nine to twelve on each side. The larger specimens of C. ornatus (from Gerda, Oregon and Pillsbury stations) have eight to ten spines on each side. Thus the number of spines is varia-
Table 2.—Range of characters, Cancellus ornatus Benedict (+ indicates indistinct formation of additional lobes or projections)

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Sex</th>
<th>sl. mm</th>
<th>Circletip, manus</th>
<th>Osicular surface</th>
<th>Pereiopod 2, lobes on outer margin</th>
<th>Pereiopod 3, ventral teeth on dactylus</th>
<th>Sixth abdominal tergite</th>
<th>Telson anterior spines</th>
<th>Postopod dorsal surface</th>
<th>Uropods posterior margin</th>
<th>Exopod fronsal anterior margin</th>
<th>Fifth coxal segments</th>
</tr>
</thead>
<tbody>
<tr>
<td>P-707</td>
<td>♀</td>
<td>2.7</td>
<td>grooved, 3-4</td>
<td>raised teeth</td>
<td>5 5 6</td>
<td>10 10 20</td>
<td>1 1 1,2 smooth</td>
<td>2 protuberances, 1 spine beneath</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calypso</td>
<td>♀</td>
<td>2.9</td>
<td>grooved, 3</td>
<td>raised teeth</td>
<td>6 5 ?</td>
<td>9 7 16</td>
<td>1 1 0 smooth</td>
<td>2 protuberances, 1 spine beneath</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P-708</td>
<td>♀</td>
<td>4.8</td>
<td>grooved, several teeth at random</td>
<td>5 5 8</td>
<td>9 10 19</td>
<td>1 1 0 smooth</td>
<td>2 blunted teeth, 1 spine beneath</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Project Hourglass M</td>
<td>♀</td>
<td>4.8</td>
<td>grooved</td>
<td>5+</td>
<td>5 7,9</td>
<td>8 8 16</td>
<td>1 1 0 smooth</td>
<td>2 protuberances, 1 spine beneath</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Albatross Holotype</td>
<td>♀</td>
<td>5.5</td>
<td>grooved</td>
<td>5,7 5+</td>
<td>10-11 6 8 14</td>
<td>1 1 0</td>
<td>knobs</td>
<td>3 blunted teeth, 1 spine beneath</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P-854</td>
<td>♀</td>
<td>6.0</td>
<td>grooved, several teeth in a row on one, random on other</td>
<td>5+</td>
<td>5 9-10</td>
<td>8 11 19</td>
<td>1</td>
<td>1 (both trifid)</td>
<td>0 1 small knob</td>
<td>2-3 protuberances, 1 spine beneath</td>
<td>2 knobs</td>
<td>–</td>
</tr>
<tr>
<td>P-734</td>
<td>♀</td>
<td>7.9</td>
<td>grooved, 3 raised teeth in a row on one, none on other</td>
<td>5+</td>
<td>5+ 11-14</td>
<td>8 8 16</td>
<td>1 1 1,1</td>
<td>smooth</td>
<td>2 blunted protuberances, 1 beneath</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Oregon 6715</td>
<td>♀</td>
<td>8.2</td>
<td>grooved</td>
<td>5</td>
<td>5+1.5</td>
<td>12,13</td>
<td>9 8 17</td>
<td>1 1 0</td>
<td>smooth</td>
<td>2 blunted protuberances, 1 beneath</td>
<td>2 knobs</td>
<td>–</td>
</tr>
<tr>
<td>Silver Bay 3497</td>
<td>♀</td>
<td>6.2</td>
<td>slightly concave</td>
<td>5+3</td>
<td>6+1</td>
<td>12</td>
<td>10 11 21</td>
<td>2 2 1.2</td>
<td>1 protuberance on each side</td>
<td>smooth</td>
<td>2 blunted teeth, 1 behind</td>
<td>2 knobs</td>
</tr>
<tr>
<td>G-503</td>
<td>♀</td>
<td>9.4</td>
<td>slightly concave</td>
<td>5+1</td>
<td>5+ 10,15</td>
<td>10 15 23</td>
<td>2 1 0</td>
<td>smooth</td>
<td>2 blunted teeth, 1 behind</td>
<td>2 knobs</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>
ble over a range which includes the number of the animal taken by the Calypso (see table 2). The distinct row of larger tubercles on the cheliped of the specimen collected from the Calypso is not apparent in most of the large specimens of C. ornatus. There are a few conspicuous tubercles (occasionally in an irregular line) on the palms of the animals from Trinidad, which suggests that prominent tubercles become less distinct with increased size of the individual. One large C. ornatus (P-734) shows large “double” tubercles arranged in a row on one palm and scattered irregularly on the other, indicating the variability of this character even in the same individual.

The two male specimens of C. ornatus are slightly different from the six females examined. The most apparent difference is in the opercular surface of the palm of P. It is concave but smooth in the males, while in the females there is a distinct longitudinal groove. The tubercles appear more irregular in the females. The inner surface of the palm, near the dorsal margin, is smoother in the females, and the fissures are fairly regular and consistent in number (five). These fissures in the males are irregular and there are as many as eight or nine, although five of them are often deeper or more pronounced than the others. Also, the spines just anterior to the transverse carina on each side of the sixth abdominal tergite are monofid in all the females examined (except one side of one female, P-854). One of the males had both of these bifid, and the other had one bifid.

There are differences between the two male specimens also. Although they have both been identified herein as C. ornatus, the specimen taken by the Silver Bay near Inagua is less like the females than the male captured by the Gerda in the Bahamas. Forest (personal communication) believes the differences are such that it is difficult to consider these the same species. Since the range of variation is not known due to the small amount of material collected, these differences are simply listed here rather than being taken as the basis for the description of a new species. The telson of the male from Inagua is slightly lobed and has spines at the anterolateral margins, one on the left and a bifid spine on the right. The spine just anterior to the transverse carina of the sixth abdominal tergite is bifid on both sides. The spines on the frontal margin of the plate are not projected from a ridge, as are the spines of the other specimens, and they are reduced medially. On the dorsal surface of the protopod, there are spines—a single one on the left and a bifid one on the right. The posterior margin of each protopod has four blunt teeth; there is a heavy spine projecting from beneath with a tiny dorsal denticle. The exopod of the uropod has a strong laterally projecting spine on the dorsal surface near its insertion in the protopod. There is a low rounded protuberance in this position in all other specimens of C. ornatus. The fifth coxal segments are more depressed and thinner mesially in the specimen caught by the Silver Bay. The telson of the animal from the Bahamas is not strongly lobed and has no spines on the margins; there are no spines on the protopod, and the posterior margin has two protuberances with one spine underneath. The left P of the specimen from Inagua is missing, but the propodus of the right P has six distinct lobes, with one subdivided for a total of seven lobes. The lobes of P on other specimens of C. ornatus, while they may occasionally be subdivided, are five in number. The shape and lobation of the carpus of P is also different. The distal part of the propodus of P of the male from Inagua is lobed (four distinct lobes), whereas it is armed with irregular teeth in other individuals. The basal segment of the antennular peduncle of the animal from Inagua lacks the three or four spines on the external rounded projection found in other C. ornatus.

Six of the seven females examined had the pleopods on the left side; the other specimen had them on the right, as did the female taken by the Calypso.

Cancellus ornatus is closely related to the eastern Pacific species, C. tanneri, from which it can be distinguished by the shape of the cheliped, the spination of the sixth abdominal tergite, and the relative proportions of the merus and propodus of P and P. C. tanneri resembles C. spongicola in that the spines are more truncate and fewer than in C. ornatus. Also, the longitudinal groove on the plate is more distinct in C. tanneri. The cardiac plate is wider with respect to length in C. ornatus than in C. tanneri. The carapaces of the C. tanneri examined look like those of C. ornatus, and I could not detect the differences in the "triangular rostral projection" described by Benedict (1901).
**Figure 8.** *Cancellus ornatus* Benedict. Female, sl. 4.8 mm, P-708: a, sixth abdominal tergite and telson; b, left uropod. Male, sl. 6.2 mm, *Silver Bay* Sta. 3497: c, sixth abdominal tergite and telson; d, left uropod. Male, sl. 9.4 mm, G-503: e, sixth abdominal tergite and telson; f, left uropod. Female, sl. 5.5 mm, holotype, *Albatross* Sta. 2405: g, sixth abdominal tergite and telson (setae omitted).
The relationship, as indicated by morphological similarities, between *C. ornatus* and *C. tanneri* of the western Atlantic and eastern Pacific respectively, is far closer than that between *C. spongicola* and *C. parfaiti* of the western and eastern Atlantic, respectively. *C. ornatus* and *C. viridis*, new species, seem to be very closely related also. (See discussion of *C. viridis*.)

3. *Cancellus viridis*, new species

**Figures 9-11**

**Material.**—1 $\delta$, 4.2 mm, cl. 6.7 mm, holotype; P-134, north of Panama; 9°14.6'–9°13.5'N, 80°21.8–80°22.8'W; 48–49 m; in a piece of siliceous sponge; 20 July 1966; 10° otter trawl; USNM 128732.—1 $\delta$, 4.5 mm, paratype collected with holotype; USNM 128733.

**Description of Holotype.**—Cephalothoracic shield only slightly wider than maximum shield length; frontal margin of shield with rounded postorbital indentations, bordered between antennal peduncles by continuous narrow inflated rim, slightly broader behind ocular peduncle, armed at lateral terminations with 2 minute denticles. Rostrum broad, sides slightly concave, exceeding lateral projections. Crescentic transverse depression behind frontal rim, widening behind ocular scales; swelling posterior to apex of rostrum followed by a groove extending posteriorly, separating 2 areas of irregular transverse ridges and grooves. Raised sculpturing on both anterolateral edges of shield extending mesially behind frontal rim to a point behind ocular peduncles. Shield laterally convex, smooth in center, especially smooth in gastric region.

Calculated part of cardiac region approximately as long as wide; rounded posteriorly.

Ocular scales well separated, mesial two-thirds projected anteriorly, armed with two spinules distally. Ocular peduncle approximately two-thirds length of shield, slender, slightly broader proximally. Uneven row of widely spaced tubercles with setae on dorsal surface of ocular peduncle, curved toward inside distally. Cornea slightly inflated with basal emargination dorsally.

Antennular peduncle approximately as long as ocular peduncle when extended. Basal segment with 4 spines anteroventrally.

Fifth article of antennal peduncle reaching about two-thirds length of ocular peduncle. Antennal acicles reaching to one-half length of ocular peduncle. Left antennal acicle with 2 distal spines, one slightly lateral to those, and one on the inner margin (4 spines total). Right antennal acicle with 3 distal spines, one behind those on inner margin and 2 on outer margin (6 spines total). All acicular spines projecting anteriorly.

Ocular peduncle of manus of cheliped tuberculare; tubercles in irregular transverse rows, appearing finer toward central longitudinal concavity. Several tubercles larger than others, but not in distinct row. Depression extending into opercular surface of carpus, bordered posteriorly by a projecting ridge divided into 3 tuberculate lobes with setae on crests; anterior margin of outer carpal lobe serrated with setae on edge. Inner face of manus smoothly reticulate; raised crest at boundary between inner and opercular faces in approximately 6 irregular lobes, determined by small fissures at base between lobes; tubercles obscure lobation. Rounded knob in raised medial area on opercular surface of manus at distal end. Inner face of dactylus with single row of 4 small protuberances with corneous denticles near dorsal ridge and 4 large tufts of setae.

Opercular surface of *P₂* tuberculare, carpus and propodous concave, dactylus flat. Inner dorsal ridge of carpus irregularly toothed; outer ridge divided into 4 or 5 toothed lobes. Inner ridge of propodus with 7 small groups of tubercles and one toothed distal lobe; outer ridge expanded and thin, divided into 5 or 6 overlapping toothed lobes. Inner margin of dactylus with a row of approximately ten tubercles of diminishing height, 2 or 3 of these paired; 5 corneous denticles on ventral border of dactylus, one minute denticle adjacent to dark tip; dorsal margin in approximately nine sections: 4 proximal tuberculate lobes, and 5 groups of tubercles diminishing in size to a single protuberance distally.

Dorsal surface of carpus of *P₃* broadening distally, with several tubercles. Dorsal surface of propodus rough with scattered groups of 2 or 3 setae; 5 or 6 prominent teeth or tubercles on margin, armed with accessory tubercles at base; group of teeth and tubercles at distal end; small corneous tooth on ventral margin of propodus at insertion of dactylus. Dorsal margin of dactylus with a small
**FIGURE 9.** *Cancellus viridis*, new species. Male, sl. 4.2 mm, holotype, P-434: *a*, carapace; *b*, left antennular peduncle, lateral view; *c*, sixth abdominal tergite and telson; *d*, fifth coxal segments; *e*, left uropod. Intersex, sl. 4.5 mm, paratype, P-434: *f*, anterior part of carapace, eyes, acicles (setae omitted); *g*, sixth abdominal tergite and telson.
protuberance with several setae followed by 9 teeth with setae, diminishing in height distally; ventral margin with row of 6 corneous denticles and one minute denticle adjacent to corneous tip.

P_4, with oval pad of corneous granules on face of propodus, slightly longer than wide. Dactylus slender, subcylindrical, extending slightly beyond distal edge of propodus, with row of corneous denticles. No spines on carpus at insertion of propodus.

Dactylus of P_5 slightly more than one-third length of propodus. Corneous pad on propodus extending onto dactylus as double row of corneous granules. Setae on distal part of P_5 directed posteroventrally, not plumose, serrated on distal half.

Fifth coxal segments flattened, with very shallow central depression. Gonopores on male located anterior to depression.

Abdomen spherical; partly calcined transverse plate on anterior and posterior part; no pleopods on male.

Sixth abdominal tergite hexagonal, its length slightly less than three-fourths maximum width. In front of triangular lateral projections of transverse carina on each side, one spine projecting anterolaterally, inserted near lateral margin. Ridge on forward margin armed with groups of irregular blunted teeth, approximately 10 on each side; slight indentation in margin medially. Deep rounded depression medially, anterior to transverse carina. Rounded protuberances scattered over surface of plate. Posterior lobe with shallow longitudinal depression medially. Posterolateral borders serrate. Posterior margin inflated, armed with 3 to 5 small teeth.

Telson irregularly rounded, length approximately three-fourths width; surface with medial swelling, depressed to margins; rounded protuberances symmetrically placed, one on either side of swelling with area of pigmentation around base of seta. Median denticle on posterior margin.

Dorsal face of protopod slightly concave. Posterior projections each with 4 small teeth, more distinct on left side of type-specimen, and one spine underneath. Anterior to these, one rounded protuberance with several setae.

COLOR.—The general color of recently preserved material is green, orange, and brown markings on a cream background. There are large green areas on the central anterior one-third of the shield, on the lateral margins, and just anterior to the gastric pits. Reddish brown markings are scattered in the depressions on each side of the semi-circular sculptured areas of the shield, at the middle of the lateral margins, and around the gastric pits.

The remainder of the shield is pale orange, as are the ocular peduncles, antennal acicles and flagella, and antennules. The ocular scales are pale orange with green patches. The antennal peduncle is light orange with a darker greenish brown band around the middle.

The calcified part of the cardiac and branchial regions have scattered pigmentation.

The chelipeds and ambulatory legs have green and brownish orange markings over a pale orange or cream background. A few reddish brown spots are scattered on the surfaces; one is especially distinct on the inner surface of the dactylus at its insertion. The carpus and merus have more orange color, particularly in depressions and on dorsal margins. Green color forms a band on the distal part of the merus of P_5; the proximal part has brownish orange markings. The green banding is more distinct on the proximal parts of the dactylus, propodus, and carpus of P_5; the merus is green distally and on the outside, but has more orange and brown proximally and on the inner surfaces. The green color is more noticeable on the outer faces of both P_2 and P_3. P_4 and P_5 are pale with scattered orange and green markings.

The coxal segments have green marks on a pale orange background; there are brown areas on the fourth segments; fifth segments are pale orange.

The maxillipeds have pigmentation around the middle of most segments.

Some spots of pigment are in transverse lines across the abdomen; these are associated with the partly calcified plates.

No pigmentation is discernible on the tail fan. All green color fades in preserved specimens; brown areas become red, orange, or pale a year after preservation.

The tips of the fingers of the chelipeds and ambulatory legs are dark brown to black.

TYPE.—The holotype and paratype are in the Division of Crustacea, National Museum of Natural History, Smithsonian Institution, USNM 128732, 128733.

TYPE-LOCALITY.—Southwest Caribbean Sea, north of Panama, P-434.
FIGURE 10.—*Cancellus viridis*, new species, male, sl. 4.2 mm, holotype, P-434: a, left cheliped, lateral view; b, left pereiopod 2, mesial view; c, left pereiopod 3, mesial view.
Figure 11.—Cancellus viridis, new species, male. sl. 4.2 mm, holotype, P-434: a, left pereiopod 2; b, left pereiopod 3; c, left pereiopod 5; d, left pereiopod 4. (All lateral views.)
ETYMOLOGY.—The name is from the Latin *viridis*, referring to the general greenish color of the animal when alive or recently preserved.

DISTRIBUTION.—Known only from the type-locality.

DISCUSSION.—*Cancellus viridis* is closely related to *C. ornatus* of the western Atlantic and *C. tanneri*, the eastern Pacific species. Since *C. viridis* and *C. ornatus* occur in the same general area, it is important to distinguish them. In life, the striking character separating the two is the green color of *C. viridis* as opposed to the purple or brown and cream color of *C. ornatus*.

There are morphological features which can be used to distinguish the two species when the colors have faded after preservation. The frontal rim is semicylindrical in *C. viridis* but flattened in other species (*C. ornatus, C. tanneri, C. spongicola*). The two tiny teeth at the lateral terminations of the frontal carina are not seen on other species (except occasionally on a large *C. ornatus*). The ocular scales have a rounded projection armed with two to four spines in *C. viridis*, while in *C. ornatus, C. tanneri*, and most other described species, there is only one triangular spine on each scale. *C. parfaiti* may have as many as three spines arming the ocular scales, but the three-part form of the frontal rim, granulation on the anterior part of the shield, and lack of spination on the anterior margin of the sixth abdominal tergite prevent confusion of it with *C. viridis*. *C. typus* has two spines on the ocular scale, but a divided frontal rim, hirsute appendages, and a lobed telson serve to separate it from *C. viridis*. The longitudinal groove in the opercular surface of the cheliped is as distinct in the type-specimen of *C. viridis* as it is in the females of *C. ornatus* and much deeper than in the males of *C. ornatus*. A slight concavity in the ventral margin of the cheliped of *C. viridis* makes the general shape of the manus, seen in lateral view, different from that of any other species except the male of *C. tanneri*. There are tubercles on the outer ventral margin of the palm of *C. viridis*, not raised ridges as in *C. ornatus* and *C. tanneri*, nor a patch of striae as in *C. spongicola* and *C. parfaiti*. There is only one row of corneous granules on the inner surface of the dactylus of the cheliped of *C. viridis*, as opposed to two rows on *C. ornatus* and other species. The black corneous tips on the fingers of the cheliped are not as extensive in *C. viridis* as in other species. The ornamentation of the tail fan is different (the spination is less ornate in the typespecimen of *C. viridis*, but the paratype looks very much like *C. ornatus*). Other characters examined in detail (ornamentation of P₃ and P₄, relative size and shape of the cephalothoracic shield, depth of fissures on the inner dorsal margin of the cheliped, nature of the swelling behind the rostrum) show further differences between *C. viridis* and other species. The antennal acicles are slightly longer and thinner in *C. viridis* when animals of the same size are compared, and the eyestalks are relatively longer in *C. viridis* than in *C. ornatus*.

The slightly flattened fifth coxal segments of the holotype of *C. viridis* are intermediate in shape between the large rounded coxae of the male *C. spongicola* and the distinctly depressed coxae of the *C. ornatus* and *C. tanneri* males.

The paratype of *C. viridis*, an intersex (explained below), is nearly the same size as the holotype, but there are differences between the two individuals. The ocular scales of the paratype are armed distally with three and four spines. The rostrum is more triangular than in the type, and there is a rounded spinule at the apex. The depression behind the frontal rim is shallower between the ocular scales, and the swelling behind the rostrum is less distinct. The cornea is noticeably wider than the slenderest part of the ocular peduncle. One of the tubercles on the ocular peduncles is armed with a tiny spine. The left gonopore is on the third coxal segment, and the right one is located on the fifth segment. There are four extremely small, poorly developed pleopods on the right side of the abdomen. These characters suggest an intermediacy between the male and female sex. There was no external evidence of a parasite which might have caused this condition. The spination on the anterior margin of the sixth abdominal tergite is very similar to that in *C. ornatus*, not reduced or truncate like the armature of the holotype.

4. *Cancellus tanneri* Faxon, 1893

**Figures 12-14**

FIGURE 12.—*Cancellus tanneri* Faxon, male, sl. 10.7 mm, *Velero* III Sta. 167-34: a, carapace; b, left antennular peduncle, lateral view; c, sixth abdominal tergite and telson; d, left uropod; e, fifth coxal segments.
Material.—1 ♂, 4.2 mm, holotype; Albatross sta. 3368, off Cocos Island, eastern Pacific; 5°32'24"N, 86°54'30"W, 121 m; rocky bottom, taken in a piece of coral rock; 28 February 1891; indirect examination from camera lucida sketches by B. Stolen; MCZ 4515.—1 ♂, 8.1 mm; Coll. Bovallius, Pa Perlas, Panama, Central America; 11 m; stone and coral bottom; 5 June 1882; Naturhistoriska Riks-museum, Stockholm 50, Everebratatdelningen, No. 5024.—1 ♂ 10.7 mm; Velero III sta. 167-34, Post Office Bay, Charles Island, Galapagos; 1°14'30"S, 90°28'08"W; 27 m; rock; 19 January 1934; Allan Hancock Foundation, to be returned to USNM collection.

Description.—Same as Cancellus ornatus with the following exceptions:

Rostrum barely exceeds lateral projection. Swelling behind rostrum sometimes not present. Depression near lateral margins of shield, curving toward center and widening posteriorly. Gastric pits oval or slitlike.

Calcified portion of cardiac plate longer than wide, rounded posteriorly.

Ocular peduncles shorter than shield, subcylindrical, smooth, broader proximally. Cornea not inflated.

Antennal acicle reaches more than one-third length of ocular peduncle.

Terminal parts of antennal flagella broken off (not present for examination).

Tubercles on chelipeds and ambulatory legs rounded, not denticulate. No longitudinal row of tubercles on opercular surface of manus. Inner margin of dactylus with 6 to 8 corneous denticles in upper row, 4 to 6 in lower row. As many as 10 denticles on ventral margin of dactylus of ambulatory legs. Length of merus and propodus of P2 and P3 approximately twice or less than twice width of these segments.

Several rows of corneous granules on dactylus of P5.

Transverse carina on sixth abdominal tergite with median depression. Spines on anterior margin of tergite reduced or truncate, particularly medial ones. Raised areas and tubercles on surface of plate, but no spines. Teeth on posterior margin not armed with spinules. Propod of uropod with 2 or more rounded tubercles posteriorly; one strong spine projecting from underneath.

Color.—The calcified parts of the test are white, spotted with red. On the eyestalks and legs the spots show a tendency to coalesce in transverse bands” (Faxon, 1895:54). The two preserved specimens examined were completely devoid of color.

Type.—MCZ 4515.

Type-Locality.—Off Cocos Island, eastern Pacific.

Distribution.—Known only from the locations given for the examined material (eastern Pacific and Gulf of Panama). In depths from 11–121 m.

Discussion.—Cancellus tanneri is very closely related to C. ornatus as indicated by morphological similarities; the only character mentioned by Benedict (1901) separating the two was the “triangular rostral projection” of C. ornatus. The triangular rostrum was not apparent in Faxon’s published drawings of C. tanneri. Although the type-specimen was not available to me, Miss Barbara Stolen made camera lucida drawings of it which show the rostrum to be triangular; the two specimens of C. tanneri examined directly also had triangular rostra.

Comparison of the two individuals examined with the specimens of C. ornatus was difficult. The female of C. tanneri has heavy encrustations of barnacles and other epifauna on her chelipeds and ambulatory legs. Her right cheliped is smaller than the left, but both chelipeds are shaped like those of C. ornatus. The spines on the tail fan of the female are strong as in C. ornatus. The male has a tail fan with reduced truncate spines like the type. The fifth coxae are depressed as in C. ornatus, but have a slightly different shape.

These characteristics differing from C. ornatus are found in the two specimens and also in the drawing of the type: the length of the outer face of the merus and propodus of P2 and P3 is barely twice or less than twice the width (in C. ornatus these segments are noticeably longer than twice the width), the calcified portion of the cardiac region is longer than wide, and the ocular peduncles are smooth.

The black or dark brown areas on the fingers of the chelipeds of the specimens from the Galapagos and from Panama cover only the opposing surfaces of the tips of the dactylus and propodus; these areas are more extensive in C. ornatus (except for the specimen from Inagua). The sketch of the type of C. tanneri shows this black area about as in C. ornatus. The extent of the black area was observed.
FIGURE 13.—Cancellus tanneri Faxon, male, sl. 10.7 mm, Velero III Sta. 167-54: a, left cheliped, lateral view; b, left pereiopod 2, mesial view (outer anterior lobe of carpus broken off); c, left pereiopod 3, mesial view.
FIGURE 14.—*Cancellus tanneri* Faxon, male, sl. 10.7 mm, Velero III Sta. 167-34; *a*, left pereiopod 2; *b*, left pereiopod 3; *c*, left pereiopod 4; *d*, left pereiopod 5. (All lateral views.)
in *C. spongicola*, of which many specimens and their molts were available, and the character appeared variable with postmolt wear. Although these corneous surfaces on *C. tanneri* were probably worn down with use, the angle of the base of the area suggests they were never as long as those of *C. ornatus*.

The abdomen of the specimens from the Galapagos and Panama is quite a bit larger than the cephalothoracic part of the animal; the abdomen is generally smaller (shorter) than the cephalothorax in *C. ornatus*. The asymmetry reported for the type was not apparent in either of the individuals examined. Remnants of four tergites are visible on the male as hardened areas with stronger setae than on the rest of the abdomen. On the female, these wide transverse strips are partly calcified near the insertion of the well-developed biramous pleopods on the left side of the abdomen.

The corneous granules making up the pads on the fourth and fifth legs appear to be smaller and more numerous on the specimens from the Galapagos Islands and Panama than on specimens of *C. ornatus* of comparable size. The drawings of the holotype, however, indicate that the granules there are more nearly the size of those on a small *C. ornatus*.

The pad on the exopod of the uropods of *C. tanneri* appears much broader in respect to length than in *C. ornatus*. This is true for the drawing of the type as well as the specimens.

*Cancellus tanneri* can be distinguished easily from other previously described species. It differs from *C. typus* in having the frontal margin of the shield less deeply incised on either side of the rostrum, the posterior margin of the telson straight or rounded but not bilobed, and the fifth coxal segments without the prominent anterior lobe.

*Cancellus tanneri* lacks the patch of striae on the ventral face of the manus of the cheliped and the postorbital depressions in the surface of the frontal rim found in *C. spongicola*, *C. parfaiti*, and *C. typus*; also, the shape of the cheliped and the depressed fifth coxae of the male of *C. tanneri* are different from other species.

According to Faxon (1893), *C. tanneri* is different from *C. canaliculatus* in having a shorter and broader abdomen, lobate marginal crests on the first and second pairs of legs, a more pubescent thorax and abdomen, and short antennae. Faxon probably had access only to Herbst's (1804) paper showing a smooth abdomen, since the abdomen is now missing on the type-specimen of *C. canaliculatus* (see discussion of *C. canaliculatus*). Differences in the frontal rim of the shield, spination on the ocular scales, and the structure of the dorsolateral margin of the chelipeds, prevent confusion of these two distinct species.

### 5. *Cancellus parfaiti* A. Milne Edwards and Bouvier, 1891

**Figures 15-17**


**Material.**—1 $, 5.2 mm; P-275, Annobon; 01°24'S, 05°37'E; 9-69 m; no dwelling taken; 20 May 1965; box dredge; USNM 128736.—1 $, 9.6 mm; 1 $, 10.5 mm; P-282, Annobon; 01°28'S, 05°36'E; 18-37 m; no dwellings taken; 21 May 1965; box dredge, USNM 128735, 128734 (both illus.).

**Description.**—Cephalothoracic shield wider than maximum shield length. Frontal margin of shield with angular postorbital indentations. Subtriangular rostrum projecting slightly beyond blunt lateral projections. Distinct narrow ridge immediately behind and parallel to anterior margin of rostrum, interrupted behind apex and at angles of postorbital indentations but continuing similarly on inner half of lateral projections. Lateral projections with tiny denticles at anteriormost point and all along outer margin. Several (4 or 5) small tubercles at base of rostrum in transverse line, each with approximately 4 setae in center. Transverse channel behind rostrum extending from lateral terminations anteriorly into postorbital notches, and posterolaterally as deep channel delimiting gastric region. Small raised area with many setae in front of each posterolateral extension of groove. Patch of setae at postolateral termination of channel. Anterior one-fourth of shield covered with large distinct tubercles arranged in irregular transverse rows with scattered setae between tubercles. Entire gastric region slightly raised as round area in
FIGURE 15.—Cancellus parfaii A. Milne Edwards and Bouvier. Female, sl. 10.5 mm, P-282: 
a, left uropod; b, sixth abdominal tergite and telson; c, carapace (left antennule and setae on right side omitted). Male, sl. 9.6 mm, P-282: d, left antennular peduncle, lateral view; e, coxal segments.
center of shield. Shallow mediolongitudinal depression extending length of shield; depression deeper on front behind apex of rostrum, terminating posteriorly in tiny group of setae. Other symmetrically placed punctae on surface of shield, usually associated with groups of setae. Posterior gastric pits rounded, elongate. Anterolateral margins with many short and long setae, several longer setae plumose on distal half. Anterior margin with fewer setae. Broad posterolateral indentations in shield with other sculpturing creating three-lobed appearance.

Cardiac region longer than wide, rectangular, calcified, with calcification decreasing posteriorly. Five or 6 patches of setae on anterior margin. Other symmetrically placed setose patches.

Ocular scales almost width of base of ocular peduncle; mesial part projected as large tubercle armed with 2 spinules (occasionally 1 or 3); projection with many fairly long setae, some of them plumose. Several short setae on base of scale. Ocular peduncle shorter than shield length, broader basally and distally, but narrower in middle. Several groups of setae arranged irregularly on inner dorsal margin of ocular peduncle; 3 or 4 groups on the outer dorsal margin. Ocular peduncle smooth except for slightly raised areas at base of setae. Cornea slightly inflated with curved basal emargination.

Antennular peduncle approximately length of ocular peduncle; antennular flagellum composed of about 20 to 22 segments. Basal segment with 4 teeth usually.

Antennal flagellum longer than ocular peduncle. Fifth article of antennal peduncle exceeding one-half length of ocular peduncle. Antennal acicle reaching middle of ocular peduncle, narrowed distally and terminating in two spines; an additional spine on the lateral margin, and one on the inside posterior to these. Lateral spine on basal segment of peduncle a little larger than mesial one. Many groups of setae and scattered setae on acicle, some plumose.

Oперcular surface of chelipeds flattened, barely concave, granular; small protuberances at bases of short setae on surface of palm sometimes in irregular transverse rows. Dorsal margin of carpus raised in a crest divided into lobes; dorsalmost 2 with tufts of setae; usually a total of 4 carpal lobes. Inner margin of propodus slightly raised, divided in about 6 quadrangular lobes by fissures discernible about one-third distance across palm; dorsolateral margin rounded with several tubercles on an otherwise smooth surface; no deep channels on this margin. Broad patch of 8 to 10 regular striae on ventrolateral face of palm; inner surface finely reticulate, smooth. Dactylus with several tubercles on opercular side; on inner margin approximately 3 corneous-tipped tubercles in longitudinal row; two rows of approximately 5 smaller corneous projections beneath these.

Dorsal part of merus of P₂ with deep longitudinal furrow on distal one-third; several ridges with tufts of short bristly setae on lateral face. Dorsolateral margin of carpus divided into 4 separate subrectangular lobes forming a raised ridge; upper edge with bristly setae and several small teeth; inner margin with 5 or 6 shallow indistinct fissures; areas between fissures bristly and lightly toothed on upper edge. Dorsolateral margin of propodus expanded to a ridge in 5 approximately equal lobes, separate at base, but closer at outer edge; crest of lobes with dense patch of bristles, other margins of lobes unarmed; inner edge of propodus rounded, with 5 or 6 fissures; protuberances between fissures with tufts of setae. Dactylus noticeably narrower than more proximal segments; lateral margin with small fissures proximally, short setae on anterior edge of fissures; distal part of outer margin smooth; inner edge with rounded tubercles and tufts of longer setae; 6 to 10 corneous teeth along ventral margin. Opercular surface of dactylus flat, smooth except for raised areas around numerous short setae; opercular surfaces of other segments barely concave. Lateral faces of dactylus and propodus very smooth except for occasional small groups of setae.

Dorsal edge of carpus of P₃ with approximately five lobular projections, distal ones more proterant; upper part of projections covered with dense patch of setae. Dorsolateral margin of propodus forming ridge in 5 lobes with dense bristles on upper edges; inner face with small granular tubercles; lateral face smooth; no distinct inner ridge; several tufts of setae along ventral margin. Dorsal edge of dactylus with irregular protuberances and many setae; ventral margin with about 6 to 9 corneous teeth.

Corneous pad on propodus of P₃ rounded distally, emarginate next to insertion of dactylus. Dac-
Figure 16.—*Cancellus parfittii* A. Milne Edwards and Bouvier. Female, sl. 10.5 mm, P-282: 
a, left pereiopod 3, mesial view; c, left cheliped, lateral view. Male, sl. 9.6 mm, P-282: b, 
left pereiopod 2, mesial view.
tylus tapering distally, armed with 2 corneous teeth, reaching distal margin of propodus. Setae on distal outer margins of both dactylus and propodus. Posteriorly projecting knob at base of propodus. Several protuberances and setae on dorsal surface of carpus; occasionally a tooth near articulation with propodus.

Dactylus of P3 about one-half as long as propodus, with rows of corneous granules. Propodus with suboval pad of corneous granules on palm.

Fifth coxal segment of males rounded, large, with small gonopore on anteromesial margin; setae conspicuous on anteromesial margin and anterolateral margin. Other coxal segments with symmetrically placed patches of setae.

Five partially calcified abdominal plates: the first very small and close to the cardiac region, others evenly spaced along dorsal surface of abdomen. Tiny groups of setae arranged regularly over whole surface of abdomen and on abdominal plates. First abdominal tergite of female indented, calcified; other 4 plates hardened areas, but not calcified—harder on left side at insertion of biramous pleopods. Pleopods with both rami partially segmented; exopod slightly shorter than endopod.

Sixth abdominal tergite, suboval, roughly hexagonal, discontinuous median depression on anterior and posterior sections of plate. Group of setae on triangular lateral projections of transverse carina, another small group mesial to this on anterolateral margin. Raised area with group of setae behind and lateral to median depression in front part of plate. Four major groups of setae on each side of plate along posterior margin; 2 to 4 small teeth between posteriormost groups on posterior margin, 2 small teeth at posterolateral corners, another tiny tooth between anterior 2 groups of setae.

Protopod of uropod smooth, anterolateral corner almost divided off by deep furrow; group of setae on anterior margin, another patch of setae just behind furrow. Posterior projection of protopod with rounded protuberance on inside and tooth and/or group of setae on posterolateral corner. Another distinct tooth beneath setae on posterolateral corner. Groups of setae along all margins, upper surfaces smooth, with few setae.

Telson roughly rectangular; one or two small teeth on the anterolateral corners; depression anteriorly on each side of raised area in center. Small clusters of setae symmetrically arranged on surface. Narrow longitudinal raised area in center of the posterior two-thirds of telson. Setae of various lengths along all posterior margins.

COLOR.—A. Milne Edwards and Bouvier (1900) noted that all the thoracic appendages and carapace were red-orange, except for the branchial areas and the abdomen which were whitish, with several parts less colored or whitish.

The Pilkbury specimens are reddish orange with large areas of pink and white. (Color notes were made a year after preservation in alcohol, and four years later they have faded but little. The general patterns are still easily recognizable).

The red-orange markings on the carapace are concentrated on the anterior one-third of the shield, particularly in the depressions on each side. More orange color appears around the margins of the shield, but the broad smooth areas on the central gastric region and on each side are distinctly pink. The cardiac region is orange. The eyestalks and antennal acicles have pink and orange splotches.

The orange color coalesces in incomplete bands on the ambulatory legs. The opercular surfaces are a more generalized pinkish hue, but this may be due to fading. The other surfaces show the banding; there is an indication of an interrupted band under the palm of the chelifeds; the dactylus has the darker red-orange color on the dorsal and inner faces; the merus has two patches of color on the dorsal surface. Both pairs of ambulatory legs have an indistinct band at the articulation of the dactylus and propodus, two bands on the inside of the propodus, one wide distinct band on the outside of the propodus and carpus proximally, and two obvious dark areas on the dorsal surface that continue down onto the inside but are narrower there. There is a colored area on each of the coxal segments, generally in the center, but more mesial on the fifth coxae. There is a generalized band around the merus of both the fourth and fifth legs.

The uropods are only faintly colored, and the rest of the tail fan is devoid of color except for scattered small round spots of orange and a large orange area on the middle of the posterior margin of the sixth abdominal tergite.

FIGURE 17.—Cancillus perfaiti A. Milne Edwards and Bouvier, male, sl. 9.6 mm, P-282; a, left pereiopod 2; b, left pereiopod 3; c, left pereiopod 5; d, left pereiopod 4. (All lateral views.)
Type-Locality.—Ile du Prince (=Principe), 15 m.

DISTRIBUTION.—Off Dakar, Senegal; Annobon, Principe, and Sao Tome in the Gulf of Guinea; and Angola. In depths from 6-69 m.

REMARKS.—In the paper originally describing the species, A. Milne Edwards and Bouvier (1891) reported that specimens had been taken by the Talisman in the regions of the Cape Verde Islands, and that Parfait had collected that species at the "ile du Prince" and at Annobon. There is some question whether this location is valid, but this cannot be determined on the basis of the literature.

The original descriptive note reported C. parfaiti inhabiting a hole in a piece of stone. Forest (1959, 1961, 1966) reported them in clumps of melobesiid algae. At least one of the Pillsbury specimens was collected in a large piece of coral-line algae (Holthuis, personal communication).

DISCUSSION.—All of the specimens of Cancellus collected and reported from the eastern Atlantic near the west coast of Africa seem to be Cancellus parfaiti; there has never been confusion about the identification of this animal. The divided ridge behind the anterior margin of the carapace, the coarse granules on the anterior third of the cephalothoracic shield, as well as coloration and less obvious characteristics of the ambulatory legs and tail fan serve to separate it from any other described species.

This species is easily distinguished from Cancellus typus Edwards by the ornamentation in the form of quadrangular lobes on the margins of the first pair of legs. Cancellus (Cancer) canaliculatus Herbst is very close to the species which we have, but differs, nevertheless, by the presence of teeth in the area of the quadrangular lobes of which we have spoken.

C. tanneri Faxon is very close to our species, but it lacks the rugose area on the posterior face of the claws, its acicle does not reach the middle of the antennal peduncles, and its abdomen is asymmetrical. (Translated from A. Milne Edwards and Bouvier, 1906.)

As Benedict (1901) observed, C. spongicola appears to be more closely related to C. parfaiti than to any other species. He pointed out that a small specimen of C. parfaiti had more deeply excavated palms, with the inner margins a little more raised and more distinctly cut into lobes; the triangular median projections of the front have a distinct raised margin, and the dactylus of the first pair of ambulatory legs is nearly smooth, not lobed as in C. spongicola. (See discussion of C. spongicola.)

Cancellus parfaiti, although generally similar to C. canaliculatus (Herbst), differs from the latter species in several easily recognizable characters other than those mentioned by A. Milne Edwards and Bouvier (1900): the tuberculate sculpturing on the shield, the patch of striæ on the ventrolateral surface of the chelifed, and the toothed dorsal margin of the dactylus of P₂ and P₃ of C. canaliculatus. Also the relatively smooth dorsolateral margin of the manus of the cheliped on C. parfaiti differs from that of C. canaliculatus with its toothed projections and distal concavity.

Alcock (1905) compared his new species, C. investigatoris, with a specimen of C. parfaiti, and reported that the differences were extremely slight. Thus, although they are distinguishable (see discussion of C. investigatoris), these two may be more closely related than C. parfaiti is to C. spongicola.

According to Faxon (1893), C. parfaiti has longer eyestalks than C. tanneri, a less pubescent thorax and abdomen, and more protuberant coxal segments of the posterior legs. The specimens I compared did not differ appreciably in pubescence and eyestalk length.

6. Cancellus typus H. Milne Edwards, 1836

FIGURES 18-20


MATERIAL.—1 ♂, 10.0 mm; Victoria, Australia; before May, 1908; Grant Collection; Australian Museum No. P334.—1 ♀, 9.1 mm; Coll. Endeavour Expedition; off Davenport and Launceston, Tasmania; before 1923; Australian Museum No. E6670.—1 ♀, 7.8 mm; Coll. Endeavour Expedition; Shoalhaven Bight, NSW, Australia; 15-45 fms; before 1909; Australian Museum No. E283; USNM 71003.
Figure 18.—Cancillus typus H. Milne Edwards. Female, sl. 7.8 mm, E-283: a, left antennular peduncle, lateral view. Male, sl. 10.0 mm, P-334 (not a Pillsbury station): b, carapace (typical antennal acicle from female added on right side, some setae on right side omitted); c, sixth abdominal tergite and telson; d, left uropod; e, fifth coxal segments.
DESCRIPTION.—Cephalothoracic shield slightly wider than long; anterior margin of shield bordered by semicylindrical or flattened ridge in the shape of an obtuse W, with depressions interrupting ridge at postorbital indentations; rostrum armed at apex with spinule, not exceeding blunt lateral projections. Central and lateral depressed areas behind frontal rim connected by narrow channel behind postorbital notches; these areas smooth with scattered setae; central depression extending short distance posteriorly between two raised semicircular areas. Sculpturing on raised semicircles and on anterolateral part of shield consisting of rounded or flattened irregular ridges, generally transverse, or of large tubercles in uneven transverse rows. Heavy sculpturing only on anterior third of shield; central area smooth; many punctae on posterolateral areas of shield. Gastric pits elongate slits. Few setae around margins of shield; greatest number on anterolateral borders. Protuberance behind cervical groove with one or two tubercles armed with several setae.

Cardiac region longer than wide; calcification almost complete except for posterior areas; approximately 5 groups of setae along front border.

Anteromesial area of branchial region calcified with 2 or 3 well-defined groups of setae on forward part.

Ocular scales with inner half projected to a triangle armed with one or two terminal spines; occasionally an additional spine behind the terminal ones; many setae on projection.

Ocular peduncles much shorter than shield length; broader basally and distally; several groups of setae on a slightly raised line along the inner dorsal margin. Cornea not inflated. Base of cornea barely emarginated dorsally.

Antennular peduncle reaching about three-fourths length of eyestalk when extended; basal segment with 2 or 3 teeth; flagellum composed of about 20 segments.

Fifth article of antennal peduncle reaching approximately half or slightly more than half length of ocular peduncle. Antennal flagellum longer than ocular peduncle; flagellum with as many as 24 segments. Antennal acicle reaching one-third to one-half length of ocular peduncle, armed distally with 3 teeth, usually one additional tooth on inner margin behind these; many setae on all parts of acicle.

Ocular peduncle with 2 or 3 well-defined groups of setae on forward part.

Cardiac region longer than wide; calcification almost complete except for posterior areas; approximately 5 groups of setae along front border.

Anteromesial area of branchial region calcified with 2 or 3 well-defined groups of setae on forward part.

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Antennular peduncle reaching about three-fourths length of eyestalk when extended; basal segment with 2 or 3 teeth; flagellum composed of about 20 segments.

Fifth article of antennal peduncle reaching approximately half or slightly more than half length of ocular peduncle. Antennal flagellum longer than ocular peduncle; flagellum with as many as 24 segments. Antennal acicle reaching one-third to one-half length of ocular peduncle, armed distally with 3 teeth, usually one additional tooth on inner margin behind these; many setae on all parts of acicle.

Opercular surface of cheliped flattened, slightly concave, extremely rough and tuberculate with many short strong setae. Dorsal margin of carpus in several raised lobes with setae on outer surfaces and projecting ridge. Inner margin of manus raised, divided into 5 to 7 separate tuberculate sections; tubercles on inner face of distalmost sections with corneous granule or denticle; dorsal-lateral margin rounded, channels between tubercles deeper there, but not extending down on outer face; several regular transverse striae on ventro-lateral area of palm; on ventral margin, several raised areas with several blunt forward-projecting teeth and setae. Lateral surface of fixed finger and dactylus with strong toothlike tubercles on opposing margins; several tufts of long stiff setae on both fingers. Inner face of dactylus with two rows of 4 or 5 corneous granules; similar granules ornamenting inner surface of tubercles along dorsal margin.

Distal one-third of merus of P_2 expanded on dorsal surface with longitudinal furrow. Dorsolateral edge of carpus slightly raised, sometimes in 4 or more distinct lobes, but fissures often very shallow and indistinct. Opercular surfaces of carpus and propodus concave; dactylus flat; all covered with numerous short setae. Outer margin of propodus raised in 5 distinct lobes, their edges seldom touching, short setae on dorsal and forward edges of lobes; 7 or 8 groups of tubercles on inner margin of propodus with tufts of setae from each group. Inner and outer margins of dactylus tuberculate, with many short setae; distinct line of corneous denticles on ventral margin, tufts of setae in rows on either side of line.

Merus of P_3 broad, flat. Carpus with several forward-projecting lobes and setae distally, reduced proximally. Lateral margin of propodus with approximately 5 toothed projections, patches of strong setae on crests and smaller ones on inner and ventral surfaces in several longitudinal rows; denticle on distal ventral margin; some setae on external face. Dorsal margin of dactylus tuberculate with many laterally projecting setae; shorter setae in many clusters on inner face, few on outer face; row of tufts of setae ventrally on either side of line of 4 to 8 corneous denticles.

Round pad of corneous granules covering most of distal surface of propodus of P_4, several tufts of setae on proximal uncovered portion. Dactylus not reaching end of propodus, with a row of granules
FIGURE 19.—*Cancillus typus* H. Milne Edwards. Male, sl. 10.0 mm, P-334 (not a Pillsbury station): a, left pereiopod 2, mesial view; c, left pereiopod 3, mesial view. Female, sl. 7.8 mm, E-283: b, left cheliped, lateral view.
and a few tufts of setae. Carpus with tooth on dorsal distal margin near the articulation with propodus; setae in groups along dorsal margin.

*P*₂ with elongate pad of corneous granules on propodus, one row of granules extending onto fixed finger; dactylus with two irregular rows of granules and setae. Many long setae on all margins.

Female gonopores large, round, mesial on the proximal part of coxae of *P*₃.

Front borders of basis, coxa, and ischium of *P*₄ with heavy fringe of long, plumose setae.

Male gonopores (on inside anterior edge of the forward projection of the coxae of *P*₃) much smaller than those of female; coxal projection expanded and thin anteromesially; broad depression in center of segment; many short setae on front margin on either side of and beneath gonopore.

Four hardened transverse strips across abdomen (remnant of first abdominal tergite close to junction with carapace). Tiny groups of setae arranged evenly over whole surface of abdomen. Females with four well-developed biramous pleopods on one side of abdomen; exopod usually shorter than endopod; anterior pleopods partly calcified.

Sixth abdominal tergite with a shallow median depression in front of transverse carina. Anterior lobe of plate depressed to lateral margins; anterior margin bordered by slight swelling on either side of midline; rounded tooth lateral to the swellings; lateral tooth on each side in front of carina; median longitudinal depression on posterior section; 2 to 4 rounded teeth on each posterolateral margin, several teeth mesially on posterior border. Small clusters of short setae evenly placed over entire surface of plate; several groups of longer setae on posterior margins.

Uropods covered with tiny clusters of setae; protopod smooth; posterior projection armed with only one lateral tooth and large round protuberance mesially. Setae along all margins of exopod and endopod much longer than those covering surface.

Telson with scalloped border creating a bilobed effect. Occasionally a few teeth on anterolateral borders; slight swelling medially with depressed areas anterolaterally. Longer setae on posterior margins.

**Color.**—"The color in spirit specimens is reddish, and especially the limbs are marked with large dark red spots, some of them encircling the legs, forming bands... The pericardial cavity is marked by the branchio-cardial groove as a red shield. The branchial regions are of a pale horny color" (Zietz, 1888:298).

The preserved specimens available for examination had lost all traces of color.

**Type.**—Not in Museum National, Paris. Presumed lost.

**Type-Locality.**—Unknown.

**Distribution.**—Australia: off Port Jackson and Port Phillip, St. Vincent Gulf; and off Devonport, Tasmania; sublittoral.

**Remarks.**—This species is not uncommon just below the low watermark of the southern shores of Australia. It has been included in several popular works under the common names of "miner hermit crab" (Hale, 1927) and "boring hermit" (Dakin, 1952), referring to its alleged habit of drilling its own hole in the stone used for its dwelling. Zietz (1888) said that the animal lived in "self-made burrows in loose stones." He further noted that the collector of his specimens observed that the crabs did not drag their dwelling about with them.

In her magazine articles, Pope (1944, 1947) commented on *C. typus* habit of living in a hole excavated in a stone or, occasionally, in a clinker (a coal cinder). She reported that when the animal moved about, the stone was dragged along too. In a more extensive article, Pope (1953) noted from records of the Australian Museum that one *Cancellus* had extended its burrow so far back into the pebble that it had just broken through on the upper surface of the stone. "The crustacean had discovered the mistake, however, and had begun to turn the end of the burrow slightly downwards, away from the surface." Pope felt that this supported the theory that the crab made the excavation and that it does not merely appropriate a hollow stone left by some previous occupant.

Hale (1941) briefly described and figured an early stage of *C. typus* from juveniles clinging to the abdominal appendages of a female. This and an earlier mention of the same female (Hale, 1927) are the only reports of the young form of a species in the genus *Cancellus* other than an aberrant species, *C. macrothrix*, and indicates that development is direct. Gurney (1939) based his report of direct development in *C. typus* on Hale's (1927) paper.

**Discussion.**—The type-species of the genus *Can-**
Figure 20.—*Cancillus typus* H. Milne Edwards, male, s.l. 10.0 mm, P-334 (not a Pillsbury station): *a*, left pereiopod 5; *b*, left pereiopod 4; *c*, left pereiopod 2; *d*, left pereiopod 3. (All lateral views.)
cellus was described from one male specimen from an unknown location. Dr. L. B. Holthuis confirmed the possibility that H. Milne Edwards could have had material from Australia. It seems that Zietz did not consider the possibility of his new species being a Cancellus when he named Gryllo-pagurus lithodomus. Whitelegge (1889a) indicated that "Grallograpsus lithodomus Zietz" [sic] was the same species as C. typus Milne Edwards. He gave a complete bibliographical reference to Zietz' 1888 paper, and it cannot be demonstrated that this name change was intentional. Thus, Grallagrap-sus is an incorrect subsequent spelling, and, according to the International Code of Zoological Nomenclature, has no nomenclatural status. No commentary accompanied Whitelegge's (1889a) synonymy, and there has been little question since about the name of the Australian species. Alcock (1905) did not treat Cancellus lithodomus, but simply listed it in his table of species, as did Gordan (1956).

The only specific character mentioned in H. Milne Edwards' (1836, 1837) descriptions of C. typus is the wide squamiform structure of the basal article of the last pair of legs which shows up clearly in his illustration. Zietz (1888), too, pointed out a "shovel-shaped prolongation" on the basal article or coxa of the fourth pair of ambulatory limbs. The bilobed nature of the telson is also apparent on Milne Edwards' figure. The frontal rim of the carapace on either side of the rostrum seems to be more deeply indented than in Zietz' (1888) or Hale's (1941) drawing of the anterior margin. In any case, the raised rim is not continuous between the lateral teeth. Actually, H. Milne Edwards' drawing of the rostrum of C. typus looks more like that of C. parfaiti, as does Hale's; Zietz' drawing looks like the rostrum of C. ornatus. All three specimens examined had the frontal rim in three distinct sections.

According to other authors, C. typus can be distinguished from C. parfaiti by the latter species' quadrangular lobation of margins of the first pair of legs (Milne Edwards and Bouvier, 1900), from C. ornatus and C. tanneri by the anterior projection of the fifth coxal segment (Benedict, 1901 and Faxon, 1893), and from C. tanneri also by the notched telson and the deeply incised margin of the carapace (Faxon, 1893).

The external morphology of C. typus is more similar to that of C. parfaiti, the eastern Atlantic species, than to any other Cancellus examined. Some of the characteristics shared by these species are the general shape and lobation of the chelipeds and ambulatory legs and the smooth anterior margin of the sixth abdominal tergite. These two can be distinguished easily, however, by the expanded fifth coxal segments of the male, the lobular telson, and hairy surfaces on the tail fan of C. typus, as opposed to the rounded coxal segments, rectangular telson, and relatively bare tail fan of C. parfaiti.

No other species examined has the numerous clusters of short setae present on C. typus. This character is particularly noticeable on the inner surface of the dactylus of P₃, on the abdomen, and on all parts of the tail fan.

All females reported previously had pleopods on the left side; one of the two females examined here had them on the right.

Among the differences noted between the male and female specimens examined were the expansion of the coxal segments of the male, and the bifid nature of the ocular scales on the females (this scale has a simple, triangular projection in the male). Also, the females had even shorter ocular peduncles than the male.

7. Cancellus canaliculatus (Herbst, 1804)

**Figures 21, 22 (part)**

*Cancer canaliculatus* Herbst, 1804:22, pl. 60: fig. 6.

*Pagurus canaliculatus*—Olivier, 1811:647.—H. Milne Edwards, 1836:287; 1837:244.


**Material.**—1 $\delta$, sl. 6.2 mm, cl. 9.0 mm, sw. 7.7 mm, holotype, Indian Ocean.

**Description of Holotype.**—Cephalothoracic shield shorter than maximum width (sl./sw. = 0.8), laterally convex, frontal margin with angular postorbital indentations. Subtriangular rostrum unarmeed, not projecting beyond blunt lateral projections. Anterior margin between antennal acicles with semicylindrical ridge interrupted by depressions at postorbital indentations. Depressed areas behind lateral extensions of frontal rim connected by narrow transverse channel. Medial swelling anterior to this channel; mediolongitudinal groove
FIGURE 21.—

Cancellus canaliculatus (Herbst). Male, sl. 6.2 mm, holotype, "East Indies":

a, carapace; b, left chelifed, lateral view; c, left pereiopod 2, mesial view; d, left pereiopod 2, lateral view; e, left pereiopod 4, lateral view; f, left antennular peduncle, mesial view. (Apparent length difference between two views of pereiopod 2 is due to illustration angle.)
between two raised sculptured areas. Similar sculpturing laterally on anterior one-fourth of shield. Remainder of shield smoother, with scattered punctae at bases of setae. Indentation on each side of shield just posterior to center of lateral lobe; slight concavity in shield posterolaterally on line between indentation and round gastric pits. Most setae broken off; remnants of some setose fringe on anterolateral margins.

Cardiac region approximately square, corners rounded; calcification appearing complete. Some setae remaining on front border. Punctae indicating scattered setae and groups of setae.

Anteromesial area of branchial region heavily calcified with several groups of setae near anteromesial margin.

Ocular scales with inner half broadly projected, armed with 4 or 5 terminal teeth; projection with setae, especially at termination.

Ocular peduncles and antennules missing on type-specimen.

Antennal acicle armed with one or two teeth distally, 2 teeth anterolaterally and one tooth on inner dorsal margin; basal segment indented and armed with 2 swollen teeth. Setae on all parts of acicle. Antennal peduncle and flagellum missing.

Opercular surface of cheliped slightly concave; evenly tuberculate. Concavity more distinct on opercular surface of carpus, bordered posteriorly by a raised toothed ridge; fissure perpendicular to opercular surface dividing one anterolateral lobe from remainder of carpus; anterior margin of this lobe with small rounded teeth and setae. Dark depressions on lateral and mesial surfaces of all segments, indicating clusters of setae present at one time. Furrows between toothed protuberances on dorsolateral margin of manus more distinct distally, protuberances becoming small overlapping lobes on distal projection of anterolateral corner of manus; concavity in outer surface below lobes accentuating projection. Raised area with scattered small tubercles mesial to projection on opercular surface. No patch of parallel striae on ventrolateral surface of manus. Crest between opercular and inner surfaces of manus raised, divided into 6 or 7 tuberculate lobes, indications of tufts of setae between lobes, several corneous granules on tubercles on inner face of distal lobes. Similar corneous granules on groups of large tubercles on inner dorsal margin of dactylus, another row of tiny granules below tubercles on dactylus. Dorsolateral margin of dactylus with border of larger tubercles than those on opercular surface. Tips of finger eroded away on both chelipeds of holotype.

Opercular surface of P2 flat to slightly concave; finely tuberculate medially, tubercles larger on borders. Distal part of dorsolateral surface of merus expanded with furrow on flat surface. Dorsolateral margin of carpus raised, divided into 4 lobes toothed on upper edge; inner dorsal ridge irregularly toothed. Dorsolateral margin of propodus expanded, divided into 5 distinct lobes, their edges very close, toothed with tufts of setae on dorsal edges; swelling with forward projecting setae near base of some lobes on lateral surface, below this, row of groups of setae, more distinct proximally; inner ridge with several groups of tubercles; tufts of forward-projecting setae on ventral margin. Dorsolateral margin of dactylus in approximately 4 or 5 shallow lobes, lobes finely toothed; inner margin obscured by dried, cemented setae.

Dorsal edge of P3 with several toothed projections, more prominent distally, with tufts of forward-projecting setae. Lateral to projections 3 depressions with clusters of setae in longitudinal row. Dorsal margin of propodus slightly expanded, divided into 5 sections: one proximal toothed projection and 4 distinct toothed lobes with setae; tufts of setae on lateral face below fissures between lobes; inner surface with several groups of setae in irregular longitudinal rows; ventral margin with many large tufts of setae. Dorsal margin of dactylus irregularly toothed, 4 proximal groups almost lobate; tufts of setae between teeth; inner surface with many groups of short and long setae; ventral margin with 4 large tufts of setae and 3 or 4 corneous denticles.

P4 with round pad of corneous granules covering outer distal face of propodus. Dactylus not extending to end of propodus, with terminal corneous denticle and one just proximal to it mesially. No spine on carpus at insertion of propodus.

Type.—Zoologisches Museum Berlin No. 2451.

Type-Locality.—"East Indies."

Distribution.—Known only from the type-locality.

Remarks.—The holotype was dried and glued to paper; many appendages were disarticulated and placed incorrectly on the specimen. Some body parts were missing completely, notably the eye.
FIGURE 22.—*Cancellus canaliculatus* (Herbst), male, sl. 6.2 mm, holotype, "East Indies":
a, left pereiopod 3, mesial view; b, left pereiopod 3, lateral view. *Cancellus macrothrix* Stebbing, female, cl. 21, holotype, Algoa Bay: c, anterior carapace (redrawn from Stebbing, 1924, plate 3); d, sixth abdominal tergite, telson and uropods (redrawn from Barnard, 1950:448, fig. 82, setae on uropods and telson omitted).
stalks, right $P_2$, both $P_5$, antennae, antennules, abdomen, uropods, sixth abdominal tergite, and telson. This substantiates Benedict's (1901) suggestion that Herbst (1804) had added a typical pagurid abdomen to his illustration, since the abdomen was lacking on the type-specimen. In most cases tufts of setae were missing and dark areas or pits served to indicate their position. These were not reconstructed on the illustrations. Although the last pereiopods, $P_5$, were missing entirely, the holotype was a male, determined by the absence of gonopores on the coxae of $P_3$.

**DISCUSSION.**—This species has not been definitely reported since the original description. The note given by Herbst was very brief, and while there is little doubt that the *Cancer canaliculatus* he described and figured was a *Cancellus*, the information he presented is not specific. Beyond describing the general shape of the appendages, Herbst said the hands were concave with toothed margins and the second and third segments on the first pair of legs were concave. The color was described as white with red spots, with the red color forming a band on the legs. The one small drawing of the crab shows the abdomen narrowed posteriorly with several constrictions and dark lines indicating at least five segments. Benedict (1901) commented on this departure from the usual spherical shape of the abdomen: "The abdomen in this genus seems to be even more readily separated from the thorax than in other genera, and this separation had not unlikely taken place in Herbst's specimen and the conventional form may have been added to the figure for the sake of completeness." He added that Herbst had substituted an incorrect part in another well-known work. No location data was given other than "east Indies."

The holotype of *C. canaliculatus* differs in the structure of the cheliped from all other *Cancellus* examined. The toothed projections and the small distal lobe on the dorsolateral margin of the manus are found in no other species. Also, an interrupted frontal rim and transverse sculpturing rather than tubercles on the shield do not occur together on any other species except *C. spongicola*, and the latter species has a patch of striae on the cheliped not present in *C. canaliculatus*. 

*Cancellus canaliculatus* can be distinguished from *C. investigatoris*, the other "east Indian" species, by the following characters: *C. canaliculatus* has the frontal margin inflated and divided into three parts with no depression in the margin behind the rostrum, the basal segment of the antennal acicle armed with two heavy teeth, no distinct denticles at rostral apex or lateral projections (none on holotype; however, these may have been broken off if they were present at one time), and three or four teeth on the basal segment of the antennular peduncle; *C. investigatoris* has a four-part ridge behind the frontal margin, three or more teeth on the basal segment of the acicle, distinct denticles at the rostrum and lateral projections, and only two sharp teeth on the basis of the antennular peduncle. Also, *C. investigatoris* lacks the distinctive toothed projections on the distal, dorsolateral margin of the manus of *C. canaliculatus*, but has the ventrolateral patch of striae that is missing on *C. canaliculatus*.

8. *Cancellus investigatoris* Alcock, 1905

**Figures** 23-25

*Cancellus investigatoris* Alcock, 1905:77-78, 167 [list], pl. 5: fig. 8.—Southwell, 1906:217; 1910:179-184, pls. 1, 2; 6 figs.—Gordan, 1956:305 [list].

**MATERIAL.**—1 ♀, sl. 7.8 mm, cl. 10.0 mm, sw. 8.8 mm; Sagami Bay, Kannon-zuka-dashi, Japan; 62 m; in calcareous rock; 20 January 1959; Biological Laboratory of the Imperial Household (BLIH), No. 9.

**DESCRIPTION.**—Cephalothoracic shield shorter than maximum shield width (sl./sw. = 0.9), laterally convex. Frontal margin with angular postorbital indentations; subtriangular rostrum armed with tiny denticle at apex, not exceeding lateral projections; a single denticle at apex of each lateral projection. Distinct narrow ridge just posterior and parallel to anterior margin of rostrum, interrupted behind apex and at angles of postorbital indentations, but continuing similarly on inner half of lateral projections. Several groups of setae arranged symmetrically in depressed areas behind rostrum and lateral projections; medial depression extending posteriorly, terminating in larger group of setae separating two sculptured semicircular areas. Depressions lateral to raised sculptured areas, also terminating posteriorly in group of setae; smaller groups of setae scattered in depressions and concavities of sculptured surface. Sculpturing
FIGURE 23.—Cancillus investigator Alcock, female, sl. 7.8 mm, BLIH No. 9, Sagami Bay: a, carapace; b, coxal segments; c, left antennular peduncle; d, sixth abdominal tergite and telson; e, left uropod. (Setae on coxal segments, antennular peduncle, and right side of carapace omitted.)
consisting primarily of irregular swellings with upper surface slightly projected like the frontal rim, often forming crescents with concavity anterior. Similar sculpturing anterolaterally; central gastric region relatively smooth, with several punctae at bases of small groups of setae. posterolateral margins slightly concave; anterior to concavity, two channels directed posteromesially from lateral edge of shield. Gastric pits elongate, rounded anteriorly, pointed posteriorly. Anterolateral margins with numerous setae, many of them plumose. Anterior margin with fewer setae.

Cardiac region subrectangular, slightly wider than long. Two wide transverse patches of long setae on anterior margin of plate; several distinct groups of setae in longitudinal row along lateral margins.

Anteromesial area of branchial region calcified with 5 or 6 groups of long setae near anteromesial margin.

Ocular scales broad at base, with inner half projected anteriorly and armed with 3 or 4 teeth distally, several setae on dorsal surface of projections; many long plumose setae on anterior margin.

Length of ocular peduncle about one-half shield length; slightly narrower in middle. Several groups of short setae on dorsal surface; proximal half of inner margin with longitudinal row of projections: the proximal 2 distinct curved teeth, distal ones diminishing to rounded tubercles; groups of strong setae between projections, some plumose. Cornea with slight basalmost emargination, not as wide as distal part of ocular peduncle.

Antennular peduncle when extended not reaching cornea; flagellum with approximately 16 segments. Basal segment with 2 sharp anteriorly projecting teeth and one anteroventral protuberance.

Antennal flagellum only slightly longer than ocular peduncle. Fifth article of antennal peduncle exceeding one-half length of ocular peduncle. Antennal acicle setose, narrowed distally, armed with 2 terminal teeth, the inner longer than the outer; 2 teeth posterior to these: one on outer margin, one on inner. Basal segment with 3 or 4 teeth.

Opercular surface of cheliped flat; evenly covered with denticulate tubercles and short setae. Opercular face of carpus concave; dorsal margin projected into 3 toothed lobes; anterolateral lobe most distinct, fissures between other two not as deep, anteromesial lobe subdivided by several distinct irregular fissures; many short strong setae on projecting edge. Inner margin of manus divided in approximately 6 quadrangular lobes by fissures extending about one-fourth distance across face of palm: middle 4 lobes small, well separated, proximal and distal lobes larger, subdivided by shallower, less distinct fissures; inner surface of distal lobes with many small protuberances with setae, some with small corneous denticles; dorsolateral margin rounded, tubercles with setae extending short distance on lateral face. Ventrolateral surface of palm with rugose area of 9 regular striae; ventral extension of some striae toothed with setae, particularly sixth and ninth striae from distal end; one or more teeth with setae in a group on ventral surface just mesial to distalmost stria; large tufts of setae near corneous tips of propodus and dactylus. Inner face of manus smooth with scattered short setae, sometimes slight swelling at base of seta. Dactylus tuberculate on opercular side; inner dorsal margin with a few bifid corneous denticles on tubercles; below these on inner face, 2 longitudinal rows of 5 or 6 corneous denticles, most of them bifid.

Opercular surface of P2 slightly concave; tuberculate, with short strong setae scattered evenly on surface, many tubercles denticulate. Ventral margin of merus with many small curved teeth. Dorsolateral margin of carpus slightly raised, divided in 4 or 5 lobes, toothed on dorsal edge with tufts of setae; several fissures dividing inner margin in groups of toothlike tubercles. Dorsolateral margin of propodus expanded, divided in 5 well-separated lobes: occasionally one subdivided to form more lobes; dense setae on outer crest and anterior edge of lobes; inner margin with 6 or 7 tufts of setae ventrally; 3 or 4 small teeth on distal margin of lateral face. Dactylus flat, dorsolateral margin irregularly toothed; inner margin with fissures separating 5 to 10 protuberances with setae; 6 or 7 corneous teeth along ventral margin.

Dorsal margin of carpus of P3 with 4 anterodorsal projections: distal one or two lobulate; tufts of setae and several teeth along dorsal margin. Dorsolateral margin of propodus divided into 4 or 5 lobes: distal one larger, proximal one or two smaller; lobes tuberculate with setae on dorsal edge; inner face smooth, with scattered groups of 2 or 3 setae in rows; several teeth on distal margin.
FIGURE 24.—*Cancillus investigatoris* Alcock, female, sl. 7.8 mm, BLIH No. 9, Sagami Bay:
a, left cheliped, lateral view; b, left pereiopod 2, mesial view; c, left pereiopod 3, mesial view.
of lateral face. Dactylus smooth, flat, with longitudinal rows of groups of setae; outer margin irregularly toothed; tufts of setae just lateral to dorsal margin; 3 to 6 corneous denticles and 4 large tufts of setae on ventral margin.

Dactylus of P₅ not extending to distal margin of propodus, terminating in corneous denticle and tufts of setae; 2 or 3 proximal to this on mesial margin. One distinct curved tooth on anterodistal margin of carpus.

Dactylus of P₆ less than one-half length of propodus; row of 2 or 3 corneous granules extending onto dactylus from subrectangular pad of granules on propodus.

Abdomen semispheroidal, 4 transverse strips of clear material across abdomen, partially hardened at insertion of well-developed pleopods on female.

Sixth abdominal tergite suboval, barely hexagonal; lobe of plate anterior to transverse furrow larger than posterior lobe; posterior lobe with medial longitudinal depression; lateral projections of transverse carina rounded, group of setae just anterior to these on each lateral margin; several low tubercles with setae on anterolateral margin; short setae scattered over surface; several rows of setae along posterolateral margins.

Protopod of uropod smooth, groups of short setae on surface; posterolateral projection with rounded protuberance mesially, very weak tooth and group of setae on posterolateral corner; stronger tooth beneath setae. Exopod with 2 large rounded protuberances dorsally near insertion to protopod.

Telson roughly rectangular; dorsal area smaller than that of sixth tergite; anterior part of plate wider than posterior; many groups of short setae arranged symmetrically on surface; a central swelling with depressed areas anterolaterally. Long setae bordering posterolateral and posterior margins; many tufts originating just inside margins. An indentation posterolaterally. Posterior margin concave.

**Type.**—Indian Museum 1629/7. Reported by Dr. B. K. Tikader (personal communication) to be in extremely bad condition.

**Distribution.**—Indian Ocean, off the southeast and west coasts of Ceylon, Gulf of Mannar, shallow water, 13 m; Sagami Bay, Japan, 62 m.

**Discussion.**—The female specimen of *C. investigatoris* from Sagami Bay differs from specimens of *C. parfaiti* in the following characters: *C. investigatoris* has three or four spines on the raised dorsal edge of the antennal acicle (the specimen examined has three spines on the left and four on the right), deflated corneas, ocular peduncles approximately one-half shield length, broad prolongation of the ocular scale, spines on the mesial proximal surface of the ocular peduncles, distinct spinules at the rostrum and lateral projections, two sharp teeth on the anterior margin of the basal segment of the antennal peduncle, one or more low, toothlike protuberances on the anterolateral margin of the sixth abdominal tergite, and no teeth or tubercles at the anterolateral margins of the telson; *C. parfaiti* has only two spines on the dorsal edge of the antennal acicle, inflated corneas, the ocular peduncles two-thirds to three-fourths shield length, narrow prolongation of the ocular scale, smooth ocular peduncles, spines at the rostrum and lateral projections indistinct or lacking, four teeth projecting from the anterolateral margin of the basal segment of the antennal peduncle, the anterior margin of the sixth abdominal tergite smooth, and tubercles or teeth at the anterolateral margins of the telson. These differences are listed to show that *C. investigatoris* and *C. parfaiti* are distinguishable morphologically rather than to discredit the point Alcock (1905) was making by emphasizing their similarities. The two species are quite similar in many characters and are probably more closely related than any other species in the *C. typus* complex. Alcock mentioned that there was no patch of striae on the inner surface of the palm, but he did not describe, nor did his illustration show, the distinct patch on the ventrolateral surface that *C. investigatoris* has in common with *C. parfaiti*. Also the frontal margin appears to be continuous in Alcock's illustration, rather than interrupted at the rostral apex and behind the ocular scales as it is in the specimen from Sagami Bay, as well as in *C. parfaiti*. Although Alcock's description and illustrations were not specific, he noted that the differences between *C. investigatoris* and a specimen of *C. parfaiti* were very slight. This indicates that he had a new species rather than a specimen of *C. canaliculatus* (Herbst), the only other species described from that area. Therefore, although the holotype of *C. investigatoris* could not be examined, it is reasonable to conclude that the specimen described here is indeed *C. investigatoris*. 

**C. parfaiti**
FIGURE 25.—Cancellus investigatoris Alcock, female, sl. 7.8 mm, BLIH No. 9, Sagami Bay: a, left pereiopod 2; b, left pereiopod 3, c, left pereiopod 4; d, left pereiopod 5. (All lateral views.)
A summary of the differences between C. investigatoris and C. canaliculatus appears in the discussion section of the latter species account.

The only other occurrence of C. investigatoris was reported by Southwell (1906). One specimen was taken in shallow water in the Gulf of Mannar (between the west coast of Ceylon and the southern tip of India). Later (1910), Southwell described the modification of the chelipeds to form an operculum for the hole of the crab. He reports:

During a survey of the Ceylon pearl banks this specimen was dredged up, occupying a small cavity on the ventral edge of a flattish lobulated piece of Porites arenosa four inches in diameter. ... The terminal portion of the abdomen could be slightly protruded through a very small hole situated a little nearer the basal centre of the coral, and the specimen could turn completely round in its shelter. The tube appeared to be lined with reddish Nullipore (Lithothamnion).

The location was given as west coast of Ceylon, in 7 fathoms. The indications are that this was the same specimen reported in 1906.

9. Cancellus macrothrix Stebbing, 1924

Cancellus makrothrix Stebbing, 1924:240-241, pl. 3.—Barnard, 1950:447-450, fig. 82.
Cancellus macrothrix.—Gordan, 1956:305 [list].

Material.—None
Description.—Most parts of the body and appendages strongly hirsute. Rostrum broad and very short, but acute and distinct. Frontal margin rather strongly costate, the costa interrupted at the shallow notch between rostrum and the very obtuse submedian points. Behind the costa a transverse crescentic groove, and a short medio-longitudinal groove. Eye-stalks equal to anterior width of carapace (i.e. between the very obtuse anterolateral angles), and extending slightly beyond apex of extended peduncle of ant. 1 (by about length of cornea), slender, dilated at base, but swelling only very slightly distally, setose. Ocular scales L-shaped, apically acute, closely approximate or contiguous. Apex of peduncle of ant. 2 reaching half-way along eye-stalk, acicule reaching nearly to end of last joint of peduncle, acute, 2 spinous tubercles on outer margin, and one on inner margin, with numerous bristly hairs; flagellum about as long as length of anterior (calcified) part of carapace, its joints with whorls of short setules. Chelipeds and 2nd and 3rd legs thickly covered on their anterior surfaces with stiff bristly hairs arranged in tufts, and on the hands of the chelipeds more or less in longitudinal lines. Inner upper margin of hands and fingers with a few blunt (mostly dark-tipped) tubercules, and on the inner surface of the fingers below the upper margin two additional rows of tubercles (4-5 in each row). Inner upper margin of 5th joint of 2nd leg with 7-8 denticles, of 6th joint more or less scalloped owing to the insertion of bristle-tufts. Sixth and 7th joints of 2nd and 3rd legs subequal. Biramous appendages in Q on left side of abdominal segments 2-5 (in the single ♂ specimen the abdomen is missing). Left uropod slightly longer than right; 6th abdominal segment calcified, transversely divided by a deep groove, granulose and setose, its distal margin overhanging base of telson, margin denticulate, a broad quadrangular lobe projecting slightly beyond the postero-lateral corners. Telson about as broad as long, or slightly longer than broad, asymmetrically subcircular, a semicircular shallow groove and a few granules setules on upper surface, margin strongly setose, and (in one specimen) with a few calcified denticles. (Barnard, 1950:447-448.)

Type.—South African Museum No. A1541.
Type-Locality.—Algoa Bay (off South Africa), 18.3 m.

Distribution.—Off South Africa: Cape Morgan, East London, Aloga Bay.

Remarks.—The specimens from East London and Cape Morgan examined by Barnard (1950) were housed in Murex shells. This species has been reported from 18-31 meters.

Discussion.—This species is a very aberrant one, if it is to be regarded as a Cancellus. Both the 2nd and also the 3rd pairs of legs participate with the chelipeds in closing the aperture of the mollusc shell, and in conformity with this unusual habitat the abdomen is spirally coiled to an extent equal to that of any other shell-inhabiting Hermit-crab. The uropods, however, remain nearly symmetrical. The upper distal corner of the wrists of the chelipeds does not project so strongly (knuckle-like) as in more typical species, and the anterior surface of the hand, though flat, is scarcely concave. The carapace is widened posteriorly. The ocular scales are closely approximate, in fact contiguous. (Barnard, 1950:449.)

Cancellus macrothrix can easily be distinguished from the other Cancellus by almost any of the characters just described.

The form of this species may show characters more primitive than those of other members of the genus Cancellus. Certainly the spirally coiled abdomen, slightly asymmetrical tail fan, flattened opercular surface of the cheliped (rather than concave), and only weakly projected carpus are characters intermediate between those of the more typical pagurids and those of Cancellus.

In his opening remarks, Stebbing (1924) noted
that the leading character in the original definition of the genus was the symmetry of the pleon. He then referred to Faxon's (1895) statement about the partial asymmetry of Cancellus tanneri and to Alcock's (1905) remark that the telson was symmetrical "... or nearly so...." It appears that Faxon's specimen is the only asymmetrical Cancellus that had been reported; the tail fans of specimens of C. tanneri examined by this author were symmetrical.

Barnard's (Cancellus-like) description of the rostrum and frontal margin of the carapace do not agree with Stebbing's rough sketch (pi. 3, figure of carapace, redrawn in Figure 22, this paper) which is more like pagurids of other genera.

Barnard (1950) described eight juveniles attached or "adhering" to various parts of the abdomen and sides of the carapace of a female specimen; two were still enclosed in the egg membrane, the other six were free and stated to be in the "glaucothoe stage." He concluded that in C. macrothrix, the free-swimming zoeal stage was suppressed and the larvae developed up to the glaucothoe stage within the mother's dwelling. This agrees with the direct development reported by Hale (1941).

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