

**The Atlantic Gall Crabs,  
Family Cryptochiridae  
(Crustacea: Decapoda: Brachyura)**

**ROY K. KROPP  
and  
RAYMOND B. MANNING**

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 462

## SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

*Smithsonian Contributions to Anthropology*  
*Smithsonian Contributions to Astrophysics*  
*Smithsonian Contributions to Botany*  
*Smithsonian Contributions to the Earth Sciences*  
*Smithsonian Contributions to the Marine Sciences*  
*Smithsonian Contributions to Paleobiology*  
*Smithsonian Contributions to Zoology*  
*Smithsonian Folklife Studies*  
*Smithsonian Studies in Air and Space*  
*Smithsonian Studies in History and Technology*

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams  
*Secretary*  
Smithsonian Institution

The Atlantic Gall Crabs,  
Family Cryptochiridae  
(Crustacea: Decapoda: Brachyura)

*Roy K. Kropp  
and Raymond B. Manning*



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1987



## ABSTRACT

Kropp, Roy K., and Raymond B. Manning. The Atlantic Gall Crabs, Family Cryptochiridae (Crustacea: Decapoda: Brachyura). *Smithsonian Contributions to Zoology*, number 462, 21 pages, 10 figures, 1 table, 1987.—The Atlantic cryptochirids comprise four species in four different genera. One new species and three new genera are named. *Troglocarcinus corallicola* Verrill, 1908, shows an amphi-Atlantic distribution and is a generalist insofar as coral host is concerned. *Pseudocryptochirus hypostegus* Shaw and Hopkins, 1977, is assigned to a new genus, *Opecarcinus*, the only genus known in the Atlantic that also is represented in the Pacific. It ranges from the western Atlantic to Ascension Island and lives on agariciid and siderastreid corals. *Troglocarcinus balssi* Monod, 1956, is assigned to a new genus, *Detocarcinus*. It is restricted to the eastern Atlantic and lives on rhizangiid, oculinid, caryophyllid, and dendrophyllid corals. A new genus and species, *Cecidocarcinus brychius*, is named for specimens taken on dendrophyllid corals from the Valdivia Ridge, southeastern Atlantic, in 512 meters; it is the deepest occurring cryptochirid.

OFFICIAL PUBLICATION DATA is handstamped in a limited number of initial copies and is recorded in the Institution's Annual Report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

---

### Library of Congress Cataloging in Publication Data

Kropp, Roy K.

The Atlantic gall crabs, family Cryptochiridae (Crustacea, Decapoda, Brachyura).

(Smithsonian contributions to zoology ; no. 462)

Bibliography: p.

Supt. of Docs. no.: SI 1.27:462

1. Cryptochiridae—Atlantic Ocean—Classification. 2. Crustacea—Classification. I. Manning, Raymond B., 1934-. II.

Title. III. Series.

QL1.S54 no. 462 591 s 87-600156

[QL444.M33] [595.3'842]



# Contents

	<i>Page</i>
Introduction . . . . .	1
Materials and Methods . . . . .	2
Acknowledgments . . . . .	2
Family CRYPTOCHIRIDAE Paulson, 1875 . . . . .	2
Key to Atlantic Cryptochiridae . . . . .	3
<i>Cecidocarcinus</i> , new genus . . . . .	3
<i>Cecidocarcinus brychius</i> , new species . . . . .	3
<i>Detocarcinus</i> , new genus . . . . .	6
<i>Detocarcinus balssi</i> (Monod, 1956), new combination . . . . .	6
<i>Opecarcinus</i> , new genus . . . . .	9
<i>Opecarcinus hypostegus</i> (Shaw and Hopkins, 1977), new combination . . . . .	10
<i>Troglocarcinus</i> Verrill, 1908 . . . . .	13
<i>Troglocarcinus corallicola</i> Verrill, 1908 . . . . .	14
Literature Cited . . . . .	20

# The Atlantic Gall Crabs, Family Cryptochiridae (Crustacea: Decapoda: Brachyura)

*Roy K. Kropp  
and Raymond B. Manning*

## Introduction

This study is in part an outgrowth of attempts by one of us (R.B.M.) to identify the gall crabs he collected on Ascension Island, South Atlantic Ocean, in 1971. In order to identify those specimens, which proved eventually to belong to two species then unknown outside of the western Atlantic, a review of the Atlantic species was initiated. This remained unfinished for several years until one of us (R.K.K.) began studying the Indo-West Pacific species to satisfy the requirements of a doctoral program. We then decided to collaborate on this review, using it, in part, to define generic characters that could be used to classify the numerous species from the Indo-West Pacific region.

The gall crabs, although long of interest to marine biologists, remain one of the poorest known of all of the marine crab groups. They are so poorly known that their affinities with other brachyuran groups remain unclear. They are adapted to life within galls or in open pits that they form in corals, and among the adaptations are a diminution in size: the largest male we report here has cl 4.2 mm, the largest female has cl 5.8 mm. Males and females as small as cl 1.4 mm can be identified as to sex and species. In addition, the species generally are sexually dimorphic in morphological characteristics and the general facies, especially that of females, can change dramatically with age, making identification of isolated specimens difficult.

In addition to problems involved in the identification of these minute crabs, their classification at the generic level has been highly unsatisfactory. In their monumental work on

Vietnamese species, Fize and Serène (1957) introduced the concept that members of different genera live exclusively on different genera of host corals; they recognized several genera named from the host coral, e.g., *Mussicola* (= living in *Mussa*). This scheme works for some genera of crabs, but not others. One of the species we report here, *Troglocarcinus corallicola* Verrill, 1908, is a generalist that occurs in association with a variety of corals.

More recent studies on the group, mainly by M. Takeda, National Science Museum, Tokyo, have greatly added to our knowledge of these interesting crabs, yet we find that the definition of genera now recognized is so imprecise that it often is difficult to decide in which genus to place a species.

As a prelude to other studies in progress on the classification of the Indo-West Pacific species by one of us (R.K.K.), we introduce here a suite of generic characters, based on the features of adult specimens, that we believe can be used to characterize other genera in the group. We have also tried to refine species descriptions, and present here accounts for males, adult females, and, where applicable, juveniles. As can be seen from the key to genera given below, the Atlantic taxa, at least, can be differentiated by the use of a few, easily seen characters.

The Cryptochiridae comprises the following 12 genera:

*Hapalocarcinus* Stimpson (1859:412)

*Cryptochirus* Heller (1861:19) (with *Lithoscaptus* Milne Edwards (1862:F10) as its synonym)

*Troglocarcinus* Verrill (1908a:427) (with *Mussicola* Fize and Serène (1957:110) as its synonym)

*Pseudocryptochirus* Hiro (1938:150)

*Pseudohapalocarcinus* Fize and Serène (1955:378)

*Favicola* Fize and Serène (1957:84)

*Fungicola* Fize and Serène (1957:122)

*Neotroglocarcinus* Fize and Serène (1957:135)

---

*Roy K. Kropp, Department of Zoology, University of Maryland, College Park, Maryland 20740. Raymond B. Manning, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

*Fizeserenia* Takeda and Tamura (1980a:137)

*Hiroia* Takeda and Tamura (1981:20)

*Utinomia* Takeda and Tamura (1981:23)

With the exception of *Troglocarcinus corallicola*, described from the western Atlantic, none of the species reported here fits into any of these genera. We recognize three new genera below.

Until now, three species had been recorded from the Atlantic: *Troglocarcinus corallicola* Verrill, 1908, and *Pseudocryptochirus hypostegus* Shaw and Hopkins, 1977, both from the western Atlantic, and *Troglocarcinus balssi* Monod, 1956, from the east Atlantic. Each of these is assigned to a separate genus herein, and new genera are recognized for *P. hypostegus* and for *T. balssi*. In addition, a new genus and species is recognized from the southeastern Atlantic. We also have paid particular attention to the host corals of these species; these are summarized under the accounts of each species.

**MATERIALS AND METHODS.**—Most of the material studied here is from the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Included are specimens from the western Atlantic previously discussed by Rathbun (1937); collections made by R.B. Manning et al. at Ascension Island in 1971 and 1976, all of which were detected by H. Zibrowius, Station Marine d'Endoume, Marseille, France, as a result of his examination of the corals; and eastern Atlantic crabs donated by H. Zibrowius, who removed them from host corals he studied. The latter specimens often are badly disarticulated, but most are readily identifiable and provide valuable locality records.

Two other major collections of western Atlantic gall crabs were studied: one from the Indian River Coastal Zone Museum, Fort Pierce, Florida (IRCZM), through Paula Mikkelsen, and the second from Darryl L. Felder, Department of Zoology and Center for Crustacean Research, University of Southwestern Louisiana, Lafayette, Louisiana (USLZ). Additional material was lent by Willard Hartman, Peabody Museum, Yale University, New Haven, Connecticut (YPM); R.W. Ingle, British Museum (Natural History), London, England (BMNH); Torben Wolff, Zoological Museum, Copenhagen, Denmark (ZMC); L.B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RMNH); D. Guinot, Muséum National d'Histoire Naturelle, Paris, France (MP); and Enrique Macpherson, Instituto de Ciencias del Mar, Barcelona, Spain (ICM).

The latitude and longitude for each locality mentioned in the text is given at the first occurrence of that locality in the text. We have enclosed in brackets coordinates not given in the original collection data. These coordinates were determined from gazetteers of the United States Board on Geographic Names or from navigational charts.

Coral host records, if provided in the collection data, are listed. The name listed is the currently accepted name; label name, if different, is included in brackets.

Specimens were measured with an ocular micrometer in a Wild M-5 microscope and are reported to the nearest 0.1 mm.

Measurements are given in the text as carapace length (measured at the midline, not including a median tubercle) × carapace width (measured at the widest part).

Gonopods were examined after preparations modified from Monod and Cals (1970). They were digested in lactic acid, containing a Chlorazol Black/Fast Green mixture (approximately 50:50), for 15 minutes at 150° C. They were drawn with the aid of a camera lucida on a Wild M-20 compound microscope.

In our illustrations, surface setation of carapace and pereopods has been omitted.

Abbreviations for repositories are given above, in the discussion of sources of material. Other abbreviations used in the text are as follows: cl, carapace length; cb, carapace width; juv, juvenile; MXP, maxilliped; ov, ovigerous; P, pereopod; PLP, pleopod.

This report is contribution number 157 from the Smithsonian Marine Station, Fort Pierce, Florida.

**ACKNOWLEDGMENTS.**—We thank all of the individuals named above who lent to us or provided us with material. H. Zibrowius is due special thanks for his efforts to find cryptochirids from a variety of corals and for providing references. We acknowledge with thanks the help of Steven Cairns, Smithsonian Institution, on the names of coral hosts and the coral literature, of Janet Reid in translating from the Portuguese, and of Lilly K. Manning with the illustrations.

We are indebted to John S. Garth, Janet Haig, Geerat J. Vermeij, and Austin B. Williams for their critical reviews of a late draft of this manuscript, and to Darryl L. Felder for providing photographs of crab dwellings.

#### Family CRYPTOCHIRIDAE Paulson, 1875

**LITHOSCAPTES** A. Milne Edwards, 1862:F10. [Vernacular name. Type genus *Lithoscaptus* A. Milne Edwards, 1862, a subjective junior synonym of *Cryptochirus* Heller, 1861.]

**CRYPTOCHIRINAE** Paulson, 1875:72 [page 78 in translation]. [Type genus *Cryptochirus* Heller, 1861.]

**CRYPTOCHIRIDAE**.—Richters, 1880:159.—Kropp and Manning, 1985:954.

**LITHOSCAPTIDAE**.—Richters, 1880:159.

**HAPALOCARCINIDAE** Calman, 1900:3, 49. [Type genus *Hapalocarcinus* Stimpson, 1859.]

**HAPALOGARCINIDAE**.—Coelho and Ramos, 1972:205 [erroneous spelling].

**DEFINITION.**—Mandibular palp absent, cutting edge of mandible lacking processes. MXP-3 with exopod reduced (shorter than lateral margin of ischium) and lacking flagellum or absent, merus much narrower than ischium. Maxilla 2 reduced to finger-like, undivided protopod. Maxilla 1 consisting of undivided protopod and exopod. Gills absent from P-4 and P-5. Adult female larger than male, with 3 pairs of pleopods, occurring on abdominal somites 2 to 4, PLP-4 uniramous. Female with posterior abdomen greatly expanded to form egg brood chamber, visible in dorsal view.

**REMARKS.**—Fize and Serène (1957) based their classification of the cryptochirids on two major points: (1) the coral



hosts of the crabs, and (2) the form of the first two pairs of pleopods in females, whether uniramous or biramous. Our experience with the hosts for *Troglocarcinus corallicola*, discussed below under that species, suggests that they may have relied too heavily on this feature, which may vary from genus to genus. Female gall crabs have pleopods only on abdominal somites two, three, and four. Much of the literature refers to the pleopod found on somite two as the "first" pleopod, followed by the "second" and "third" pleopods, respectively. Here we number the pleopods according to the somite on which they occur. Therefore, the "first" pleopod is that found on somite two, abbreviated PLP-2. McCain and Coles (1979) reported the form of the pleopods in *Utinomia dimorpha* (Henderson, 1906) to vary considerably. They found pleopod two to be uniramous on one side, biramous on the

other, and variable from specimen to specimen. They also mentioned similar variation in two other Indo-West Pacific species. These observations have been confirmed by one of us (R.K.K.) for specimens from Micronesia and in our opinion this diminishes the value of pleopod two as a generic character. The examination of the Micronesian and other specimens has suggested that pleopod three may be useful as a generic character. Pleopod three may be either uniramous or biramous and does not show the variation noted for pleopod one.

Comparisons between Atlantic genera given in the text also hold for the Atlantic species, as each of the Atlantic genera contains but one species.

The Atlantic cryptochirids (genera and species) can be differentiated by using the following key. The key can be used to identify both males and females.

#### Key to Atlantic Cryptochiridae

1. Front deflected anteriorly. (Female PLP-2 uniramous) . . . . . 2  
Front not deflected anteriorly. (Female PLP-2 biramous) . . . . . 3
2. P-1 sternite tuberculate. Pterygostomial region fused to carapace . . . . .  
. . . . . *Opecarcinus hypostegus*, new combination  
P-1 sternite smooth. Pterygostomial region not fused to carapace . . . . .  
. . . . . *Troglocarcinus corallicola*
3. MXP-3 with exopod. P-1 sternite smooth. Cornea lateral . . . . .  
. . . . . *Cecidocarcinus brychius*, new species  
MXP-3 without exopod. P-1 sternite with granules. Cornea terminal . . . . .  
. . . . . *Detocarcinus balsi*, new combination

#### *Cecidocarcinus*, new genus

DEFINITION.—Carapace longer than broad, not deflected anteriorly, widest posteriorly. Pterygostomial region not fused to carapace, separated by distinct suture. Antennule base with lateral projection extending beyond eyestalk; angled lateral lobe present. MXP-3 with exopod; latter oval, longer than half length lateral margin of ischium; anteromesial lobe of ischium extending to merocarpal articulation; merus without distolateral projection; carpus length subequal to length of propodus and dactylus. Sternite of P-1 smooth, of P-4 with partial medial suture. P-1 of female and male visible in dorsal view. Merus of P-2 with prominent mesial expansion; carpus without mesial expansion. PLP-3 of female biramous; female opening longitudinal, oval, with hood. PLP-1 of male sharply curved distally; apex produced into blunt, expanded lobe, directed laterally.

TYPE SPECIES.—*Cecidocarcinus brychius*, new species, by present designation and monotypy.

ETYMOLOGY.—From the Greek *cecis* (gall) plus the generic name *Carcinus*. The gender is masculine.

REMARKS.—Of the Atlantic representatives of the group, *Cecidocarcinus* appears to be most similar to *Detocarcinus*, differing in having an exopod on the third maxilliped, having the sternite of the first pereopod smooth rather than tuberculate,

and having the cornea lateral rather than anterolateral. *Cecidocarcinus* resembles *Detocarcinus* and differs from both *Opecarcinus* and *Troglocarcinus* in having the carapace lined laterally with erect tubercles and in not having the anterior part of the carapace noticeably deflected.

*Cecidocarcinus* is similar to two Indo-West Pacific genera, *Neotroglocarcinus* and *Pseudocryptochirus*. It can be separated from *Neotroglocarcinus* in that the epimeral plates are not fused to the carapace; they are fused in *Neotroglocarcinus*. *Cecidocarcinus* differs from *Pseudocryptochirus* by having an incomplete suture on the sternite of the fourth leg and a biramous second pleopod in the female; in *Pseudocryptochirus* the sternal suture of the fourth leg is complete and PLP-3 is uniramous.

#### *Cecidocarcinus brychius*, new species

FIGURES 1, 2

MATERIAL EXAMINED.—EASTERN ATLANTIC. *Off Namibia*: Valdivia Ridge, 25°38'S, 06°12'E, 512 m, *Valdivia* I sta P-8, 21 May 1982, 1 female (ov), on *Enallopsammia rostrata* (Pourtales, 1878) (holotype, USNM 231662); same data, 1 male, 1 female (ov) (paratypes, ICM); same collection data, 1 male, on *Dendrophyllia* sp. (paratype, USNM 231663).

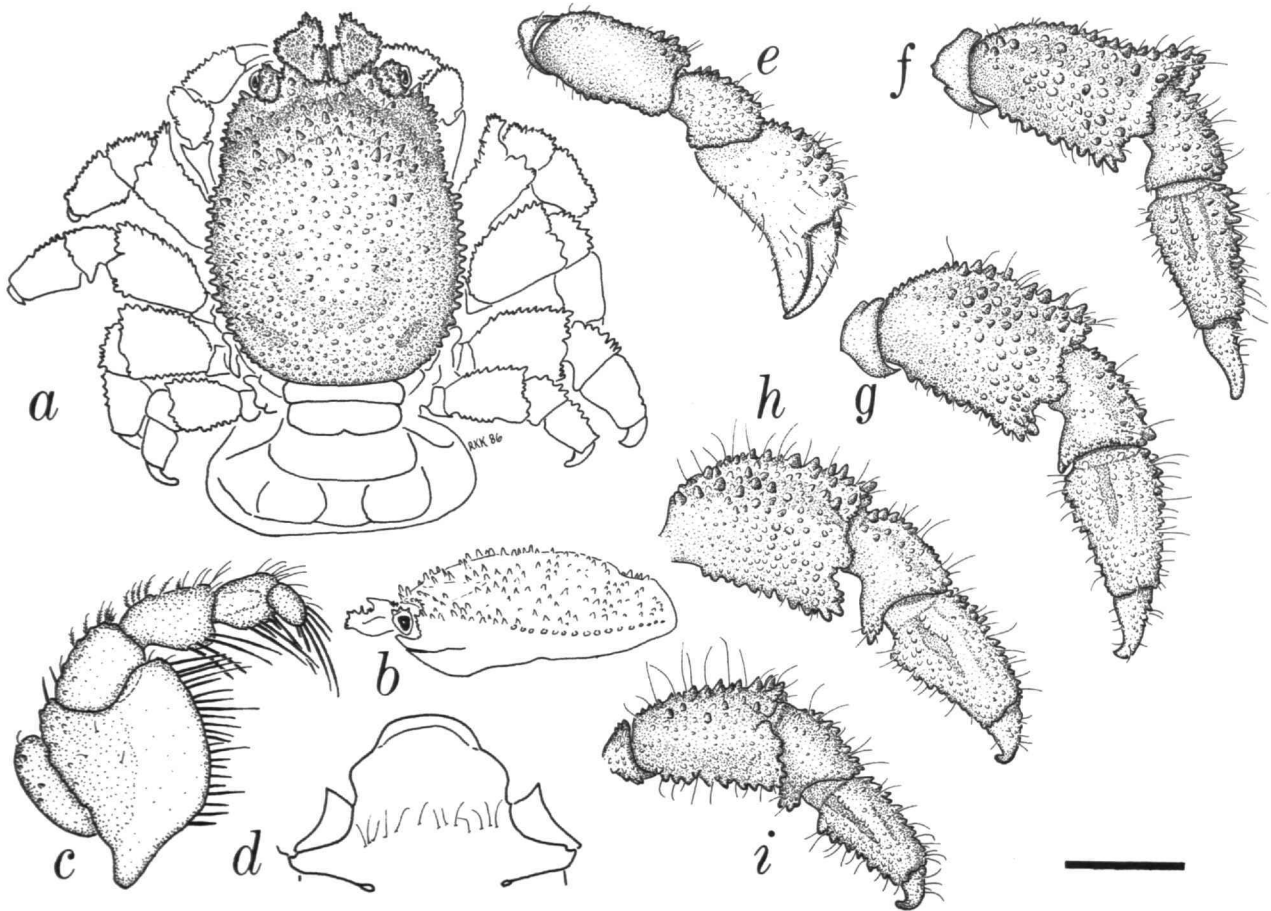


FIGURE 1.—*Cecidocarcinus brychius*, new species: *a*, dorsal view of carapace; *b*, lateral view of carapace; *c*, MXP-3; *d*, P-1 sternite; *e-i*, P-1 to P-5. (*a*, holotype, USNM 231662; *b-i*, paratype, ICM. Scale: *a,d-i* = 1 mm; *b* = 2.1 mm; *c* = 0.5 mm.)

**DESCRIPTION.**—*Adult Female* (Figure 1): Carapace about 1.2 times longer than broad, slightly inflated laterally at branchial regions, narrowing slightly towards front. Surface convex from side to side and front to back, with slight transverse depression anteriorly. Surface completely covered with variously sized, raised granules, some tubercles on anterior, lateral margins, forming distinct border laterally; surface covered with simple setae of length less than largest tubercles, few scattered longer setae not obscuring surface. Inner orbital angle with 1 spine. Anterolateral angle with spine, apex falling short of inner orbital angle. Front concave, tuberculate, with median spine, about  $\frac{1}{4}$  width at anterolateral angles, latter about  $\frac{2}{3}$  greatest carapace width. Orbit broadly U-shaped, margin tuberculate.

Basal segment of antennular peduncle with projection having transverse distal margin; angled lateral lobe extending beyond length of eyestalk; dorsal surface concave, variably armed with low and raised tubercles, distalmost largest. In

ventral view, basal segment broadening anteriorly; surface with many granules. Second segment of antenna with low tubercles and with granules ventrally.

Eye directed anterolaterally, scarcely extending to inner orbital angle. Cornea lateral; in dorsal view, occupying most of lateral part of stalk. Stalk partially covered by carapace dorsally; surface with granules and mesial tubercles, granulate ventrally.

MXP-3 with mesial margin of ischium smooth, convex; surface with few granules distolaterally; exopod with few granules. Merus longer than broad, width less than half that of ischium. Following segments much slenderer, carpus elongate, as long as propodus and dactylus combined. Palp segments with few pappose or simple setae on upper margins.

Chelipeds (P-1) equal, with few scattered simple setae, slightly smaller than P-2; merus not extending to anterolateral angle of carapace. Dactylus as long as dorsal margin of palm; cutting edges of fingers unarmed. Dorsal margin of palm with

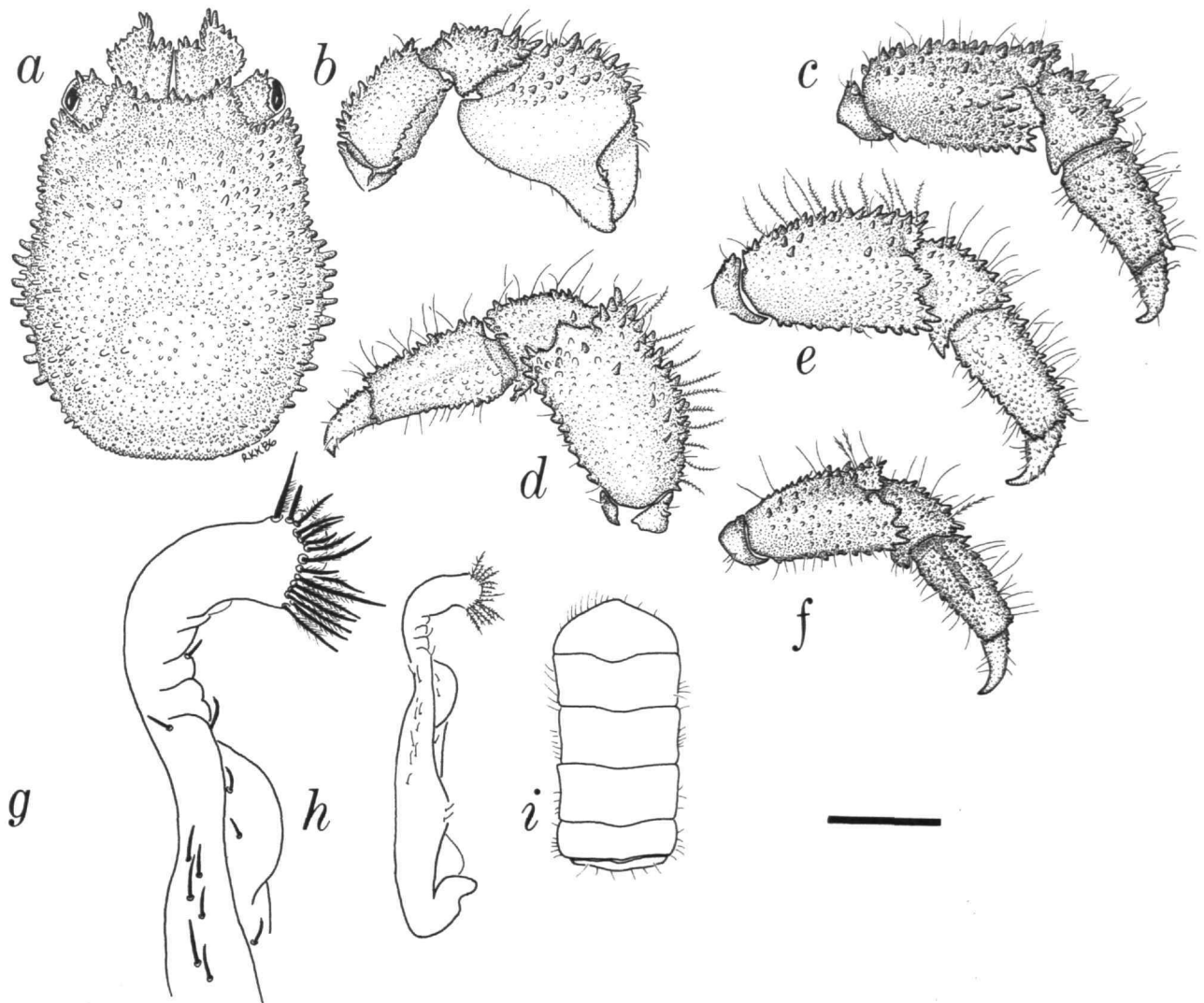


FIGURE 2.—*Cecidocarcinus brychius*, new species, male paratype, ICM: a, dorsal view of carapace; b-f, P-1 to P-5; g, detail of PLP-1; h, PLP-1. (Scale: a-f, i = 1 mm; g = 238  $\mu$ m; h = 95  $\mu$ m.)

line of erect tubercles; dorsal part of outer surface of palm and upper surface of carpus and merus tuberculate.

Walking legs (P-2 to P-5) very stout, with few scattered simple setae; P-3 largest, P-5 smallest; meri of P-2 to P-5 longer than high (Table 1), produced ventrodistally, with 3 tubercles; dorsal and ventral margins cristate, each with line of erect tubercles. Posterior surface of merus, carpus, and propodus of all legs covered with tubercles. Merus of P-2 falling short of anterolateral angles of carapace; pronounced distomesial expansion present. Carpus about as high as long, lacking mesial expansion; carpi of P-4 and P-5 with prominent posterodistal projection. Propodus much longer than carpus, with slight longitudinal depression at lower third; propodi of P-2 to P-5 not progressively shorter. Dactylus much shorter

than propodus, with low tubercles proximally on upper surface; slightly curved, hollowed ventrally. P-5 similar to preceding 2 legs, distinctly smaller than P-4. Proportions of the leg segments of Atlantic cryptochirids are summarized in Table 1.

Abdomen of ovigerous female, in dorsal view, only slightly wider than carapace. Egg size of holotype (in alcohol) 0.6 mm maximum diameter.

**Male** (Figure 2): As in female, slightly smaller, claws proportionally more robust. Palm inflated, with erect tubercles on dorsal surface. Dactylus longer than dorsal margin of palm; cutting edges of fingers with tooth proximally. P-2 lacking mesial projection. Sides of abdomen subparallel; telson suboval. PLP-1 as for genus.

**SIZE RANGE.**—Males, 4.1  $\times$  3.2 mm and 4.2  $\times$  3.3 mm;



TABLE 1.—Length:height ratios for meri and propodi of Atlantic gall crab walking legs (Cb = *Cecidocarcinus brychius*; Db = *Detocarcinus balssi*; Oh = *Opecarcinus hypostegus*; Tc = *Troglocarcinus corallicola*).

Character	Cb	Db	Oh	Tc
Merus				
P 2	1.8	1.5	1.7	1.7
P 3	1.5	1.4	1.5	1.6
P 4	1.6	1.4	1.5	1.6
P 5	1.7	1.6	1.8	1.8
Propodus				
P 2	1.8	1.2	1.2	1.1
P 3	1.7	1.7	1.2	1.3
P 4	1.6	1.9	1.6	1.9
P 5	1.7	2.2	2.4	3.1

ovigerous females, 4.8 × 4.4 mm and 5.2 × 4.2 mm.

ETYMOLOGY.—From the Greek *brychios* (from the deep), in reference to the depth from which this species was collected.

TYPE.—The holotype is an ovigerous female, 5.2 × 4.2 mm, in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., under catalog number USNM 231662; a male paratype also is housed in the Smithsonian. A male and a female paratype are in the collections in the Instituto de Ciencias de Mar, Barcelona.

The type locality is off Namibia, on the Valdivia Ridge, 25°38'S, 06°12'E.

BIOLOGY.—Ovigerous females were collected in May.

Collected at a depth of 512 m, this species is the deepest occurring gall crab known.

No parasites were found on the material examined.

CORAL HOSTS.—*Cecidocarcinus brychius* has been taken on two dendrophyllid corals, *Enallopsammia rostrata* and an unidentified species of *Dendrophyllia*.

The shape of the dwelling opening has not been recorded.

DISTRIBUTION.—Known only from the type locality, on the Valdivia Ridge in the southeastern Atlantic (Figure 9).

### *Detocarcinus*, new genus

DEFINITION.—Carapace longer than broad, not deflected anteriorly, widest behind midlength. Pterygostomial region fused to carapace, not separated by distinct suture. Antennule base with lateral projection extending to eyestalk; angled lateral lobe present. MXP-3 without exopod; anteromesial lobe of ischium extending beyond merocarpal articulation; merus without distolateral projection; carpus length greater than length of propodus and dactylus combined. Sternite of P-1 with granules; of P-4 without medial suture. P-1 of female and male visible in dorsal view. Merus of P-2 with slight mesial expansion; carpus without mesial expansion. PLP-3 of female biramous; female opening transverse, oval, without hood. PLP-1 of male curved distally; apex produced into blunt tip, directed laterally.

TYPE SPECIES.—*Troglocarcinus balssi* Monod, 1956, by present designation and monotypy.

ETYMOLOGY.—The name is derived from the Greek *detos* (bound) plus the generic name *Carcinus*. The gender is masculine.

REMARKS.—*Detocarcinus* is the only Atlantic genus of cryptochirids that lacks an exopod on the third maxilliped. It further differs from both *Opecarcinus* and *Troglocarcinus* in not having the front bent downward, and resembles *Opecarcinus* and differs from both *Cecidocarcinus* and *Troglocarcinus* in having granules on the sternite of the first pereopod. As in *Cecidocarcinus*, the lateral border of the carapace is defined by a line of granules or tubercles.

*Detocarcinus* also shows some resemblance to the genera *Neotroglocarcinus*, *Pseudocryptochirus*, and *Utinomia* from the Indo-West Pacific. *Detocarcinus* lacks an exopod on the third maxilliped, separating it from the first two of these, both of which have an exopod on the third maxilliped. *Detocarcinus* agrees with *Utinomia* in lacking an exopod on the third maxilliped, but females of *Utinomia* have a uniramous PLP-3; the PLP-3 is biramous in *Detocarcinus*.

### *Detocarcinus balssi* (Monod, 1956), new combination

FIGURES 3, 4

*Troglocarcinus corallicola*.—Balss, 1922:87, 99.—Utinomi, 1944:716 [part]. [Not *T. corallicola* Verrill, 1908.]

*Troglocarcinus balssi* Monod, 1956:463, 632, figs. 620–627.—Longhurst, 1958:88.—Gauld, 1960:72.—Monod, 1963:fig. 37.—Crosnier, 1969:535.—Zibrowius, 1976:71; 1980:52, 139, 142.—Takeda and Tamura, 1980b:147.—Zibrowius, 1982:114.

*Neotroglocarcinus Balssi*.—Fize and Serène, 1957:6, 55, 135, 136, 141, 142, 167.

*Troglocarcinus Balssi*.—Fize and Serène, 1957:54, 55, 135, 143.

*Pseudocryptochirus Balssi*.—Fize and Serène, 1957:136.

*Neotroglocarcinus balssi*.—Takeda and Tamura, 1980b:147, 150.—Manning and Holthuis, 1981:251.—Serène, 1966:397.—Zibrowius, 1976:71, 72, plates 19A, 19c, 19g, 19r, 82i; Zibrowius, 1982:118.—Takeda and Tamura, 1986:63, 68.

*Neotroglocarcinus bassi*.—Takeda and Tamura, 1986, fig. 7 [erroneous spelling].

PREVIOUS RECORDS.—*West Africa*: Manning and Holthuis (1981).

*Canary Islands*: Fuertaventura, Punta Morro Jable [= Ponta da Matorra; 28°02'N, 14°20'W], 14 km from Morro (Manning and Holthuis, 1981; Zibrowius, 1982).

*Mauritania*: 21°00'N, 17°22.9'W (Zibrowius, 1982).

*Senegal*: Île du Cap Vert [14°43'N, 17°28'W] (Zibrowius, 1976).

*Gambia*: 12°55.5'N, 17°33'W (Zibrowius, 1976, 1982).

*Guinea*: 10°40'N, 16°44'W; 09°27'N, 14°48'W (Zibrowius, 1976).

*Sierra Leone*: 08°25'N, 14°18'W (Monod, 1956; Longhurst, 1958) [both records based on same specimen]; 07°15.5'N, 12°05'W (Zibrowius, 1976).

*Benin*: 06°07.5'N, 02°04'E (Zibrowius, 1976).

*Ghana*: Off Accra [05°33'N, 00°13'W] (Monod, 1956; Gauld, 1960).

*Ivory Coast*: Off Abidjan [05°19'N, 04°02'W] (Manning

and Holthuis, 1981).

*Congo*: Pointe-Noire [04°48'S, 11°51'E] (Crosnier, 1969).

*São Tomé*: Ilhéu Gago Coutinho [= Ilha das Rolas; 00°01'S, 06°32'E] (Balss, 1922).

In addition to these records for specimens, Zibrowius (1980, 1982) recorded crypts, presumably formed by *D. balssi*, from corals taken off Senegal and Gambia.

**MATERIAL EXAMINED.**—EASTERN ATLANTIC. *West Africa*: No specific locality, A. Longhurst, 1 female (ov) (BMNH).

*Canary Islands*: Fuertaventura, Jandra, Punta Morro Jable [= Punta del Mattorral], 1 km from Morro, 20–25 m, M. Grasshoff/F. Engelhardt, 27 Jan 1975, 1 male, on *Phyllangia mouchezi* (Lacaze-Duthiers, 1897) (MP).

*Mauritania*: 20°00'N, 17°22'30"W, 50–70 m, *Cornide de Saavedra*, Cruise Atlor VII, sta 48, R. Anadon, Nov 1975, 1 female (ov), on *P. mouchezi* (USNM).

*Senegal*: Dakar [14°40'N, 17°26'W], Iles de la Madeleine, main island, south side, 3 m, J. Laborel, 24 Jun 1971, 2 females, on *Schizoculina africana* (USNM) Cap de Naze [14°32'N, 17°06'W], 20 m, 1 female (ov) on *S. africana* (Thiel, 1928) [as *Cladangia gemmans* Chevalier, 1976] (USNM).

*Guinea*: 10°49'N, 16°39'W, 42 m, *Atlantide Expedition*, sta 153, 16 Apr 1946, 1 female (ov) (ZMC).

*Ghana*: Accra, 44 m, R. Bassindale, C85/53, 2 May 1951, 1 female (holotype, BMNH 1957:12.4.21); same data, 1 male (paratype, BMNH 1957:12.4.22); Kpone Bay [05°41'N, 00°04'W], 10 m, J. Laborel, 11 Mar 1970, 1 male, 1 female (with cryptoniscine isopod attached to inside of marsupium), on *S. africana* (USNM).

*Ivory Coast*: Abidjan, 62 m, CRO G8023, radiale 5 sta 8, 23 Aug 1968, 1 female on *Asterosmia marchadi* (Chevalier, 1966) (MP).

*Congo*: Pointe-Noire, 10–40 m, A. Crosnier, 27 Jan 1967, 1 female (ov) (MP).

*Angola*: Ilha de Luanda [08°48'S, 13°13'E], 40–60 m, S. Gofas, 1984, 1 female on *Phyllangia* sp. (USNM). Cabo Ledo [09°41'S, 13°12'E], 10–40 m, dredged, S. Gofas, 1984, 13 females (9 ov) on *S. africana* (USNM); sta data unknown (COR A225), 1 female on *S. fissipara* Milne Edwards and Haime, 1850 [as *Cladangia carvalhoi* Chevalier, 1966] (USNM).

**DESCRIPTION.**—*Adult Female* (Figure 3): Carapace about 1.1 times longer than broad, slightly inflated laterally at branchial regions, narrowing slightly towards front. Surface flattened, slightly convex from side to side and front to back, with shallow depression on each side extending from just behind front to branchial region; surface variably ornamented, completely covered with low, rounded or raised, conical tubercles forming distinct border laterally and with scattered simple, pappose setae of length greater than largest tubercle, not obscuring surface; margin fringed with pappose setae. Inner orbital angle with spine or tubercle. Anterolateral angle with tubercle, apex ahead of inner orbital angle. Front concave, tuberculate, with median tubercle, less than half width at anterolateral angles, latter little more than half carapace width.

Orbit broadly V-shaped, margin tuberculate.

Basal segment of antennular peduncle with distal projection having transverse distal margin, angled lateral lobe shorter than eyestalk; dorsal surface concave, variably tuberculate, lacking spines. In ventral view, basal segment tapering anteriorly, surface with stout, raised granules. Second segment of antenna with few raised granules on ventral surface.

Eyes directed anterolaterally, extending beyond anterolateral angles of carapace. Cornea anterolateral, in dorsal view, less than half length of stalk. Stalk wholly exposed dorsally, with granules, tuberculate distomesially, and covered with granules ventrally.

Ischium of MXP-3 with mesial margin denticulate, convex; surface with raised granules and scattered pappose setae. Merus longer than broad, width less than half that of ischium. Raised granules on merus and on upper margin of carpus. Carpus and propodus with many pappose setae on upper margins.

Chelipeds (P-1) equal, slightly smaller than P-2, with pappose setae on dorsal margins; merus extending about to anterolateral angle of carapace. Dactylus longer than dorsal margin of palm, cutting edges of fingers unarmed. Dorsal margin of palm cristate, tuberculate, tubercles extending about halfway down palm. Merus and carpus tuberculate dorsally.

Walking legs (P-2 to P-4) stout, subequal, P-2 largest; P-5 smallest, longer, slenderer than P-2 to P-4. Posterior and upper surfaces of walking legs variably setose. P-2 to P-5 with meri longer than broad (Table 1), cristate and tuberculate dorsally, produced ventrodistally, with 1 tubercle ventrally; merus, carpus, and propodus each tuberculate on posterior face. Merus of P-2 falling short of anterolateral angle of carapace, with distinct but small distomesial expansion. Carpi broader than long, lacking mesial expansion, with clump of tubercles proximally on lower surface. Propodi longer than respective carpi. Propodus of P-3 to P-5 slenderer than that of P-2 (Table 1). Dactyli shorter than propodi, slightly curved, claw-like, dorsal surface smooth; dactylus of P-5 slenderer than those of P-2 to P-4. Proportions of segments of walking legs are summarized in Table 1.

Abdomen of ovigerous female, in dorsal view, no wider than carapace, up to third somite visible. Egg size (in alcohol) 0.3–0.4 mm maximum diameter.

*Male* (Figure 4): Very similar to female in form, showing typical carapace tuberculation and contour; slightly smaller. Claws proportionally larger; palm inflated. Sides of abdomen subparallel, telson suboval. PLP-1 slightly curved distally.

**SIZE RANGE.**—Males, 4.0 × 3.5 mm to 3.3 × 2.8 mm; females, 1.7 × 1.6 mm to 4.7 × 4.3 mm; ovigerous females, 2.2 × 2.0 mm to 4.7 × 4.3 mm.

**TYPE.**—The holotype is a mature female, 3.5 × 3.0 mm, housed in the British Museum (Natural History), under catalog number 1957:12.4.21. It is less tuberculate than the figured specimen and the tuberculate lateral border of the carapace is not evident. There are no tubercles on the inner orbital angle, front or anterolateral angle of the carapace. The depressions on the carapace match those of the figured specimen. The

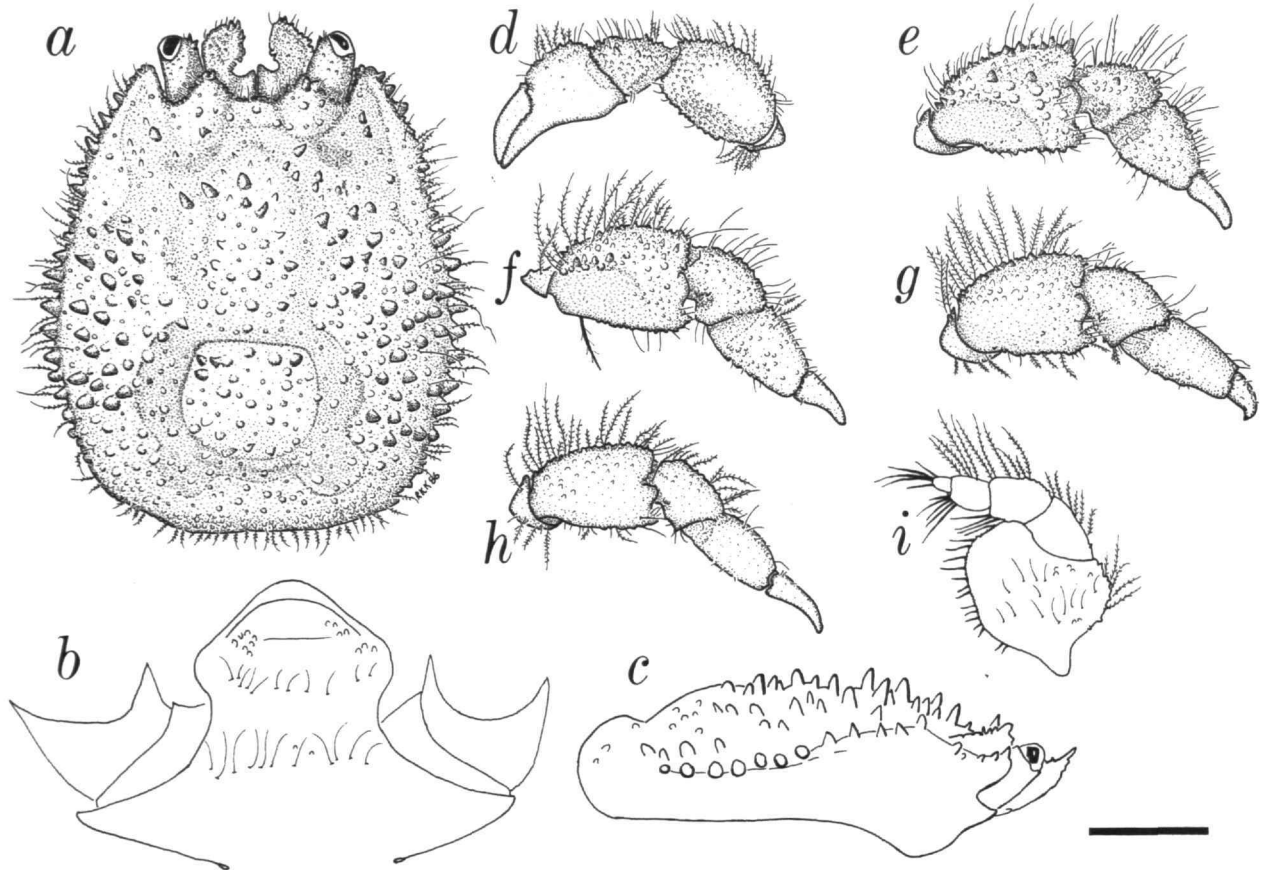


FIGURE 3.—*Detocarcinus balssi* (Monod), female, Angola, USNM 231666: a, dorsal view of carapace; b, P-1 sternite; c, lateral view of carapace; d–h, P-1 to P-5; i, MXP-3. (Scale: a, c–h = 1 mm; b, i = 0.5 mm.)

holotype is missing all pereopods, pleopods, and the abdomen. All mouthparts are present.

The paratype is a mature male, in very good condition, showing the tuberculation and depressions characteristic for the species. All pereopods are present; the pleopods, and left third maxilliped are missing. It, too, is in the collections of the British Museum (Natural History).

The type locality is Accra, Ghana.

**BIOLOGY.**—Ovigerous females have been collected in January (Congo), April (Guinea), and November (Mauritania).

Known from depths of 3 m (present study) to 98 m (Zibrowius, 1976). Longhurst (1958) reported *D. balssi* from a depth of 200 m, but there is some doubt as to the validity of that record (see below).

One female, from Ghana, was infested by a cryptoniscine isopod parasite attached within the abdominal pouch of the crab. No bopyrid isopods were found on the material examined. We found no evidence of a rhizocephalan parasite on this infested female.

**CORAL HOSTS.**—*Detocarcinus balssi* has been found in

association with the following corals:

Rhizangiidae: *Phyllangia mouchezi*, herein; *Phyllangia* sp. by Crosnier (1969).

Oculinidae: *Schizoculina africana*, *S. fissipara*, herein.

Caryophyllidae: *Asterosimilia marchadi*, herein and recorded by Zibrowius (1976, 1980); *Caryophyllia smithii* Broderip, 1828, recorded by Zibrowius (1976, 1980), whose records may have been based on empty crypts.

Dendrophyllidae: *Dendrophyllia*, recorded by Gauld (1960), who reported that his material “probably” occurred on this coral; his observation may have been in error.

As Manning and Holthuis (1981:251) pointed out, Monod’s (1956) record of this species on a sea urchin of the genus *Cidaris* and Longhurst’s (1958) record of its association with the echinoid *Eucidaris*, both based on the same specimen, probably were in error, because no cryptochirid is known to occur with echinoids.

The shape of the dwelling opening has not been recorded, although Zibrowius (1976) has figured gall crab pits attributed to *D. balssi*.



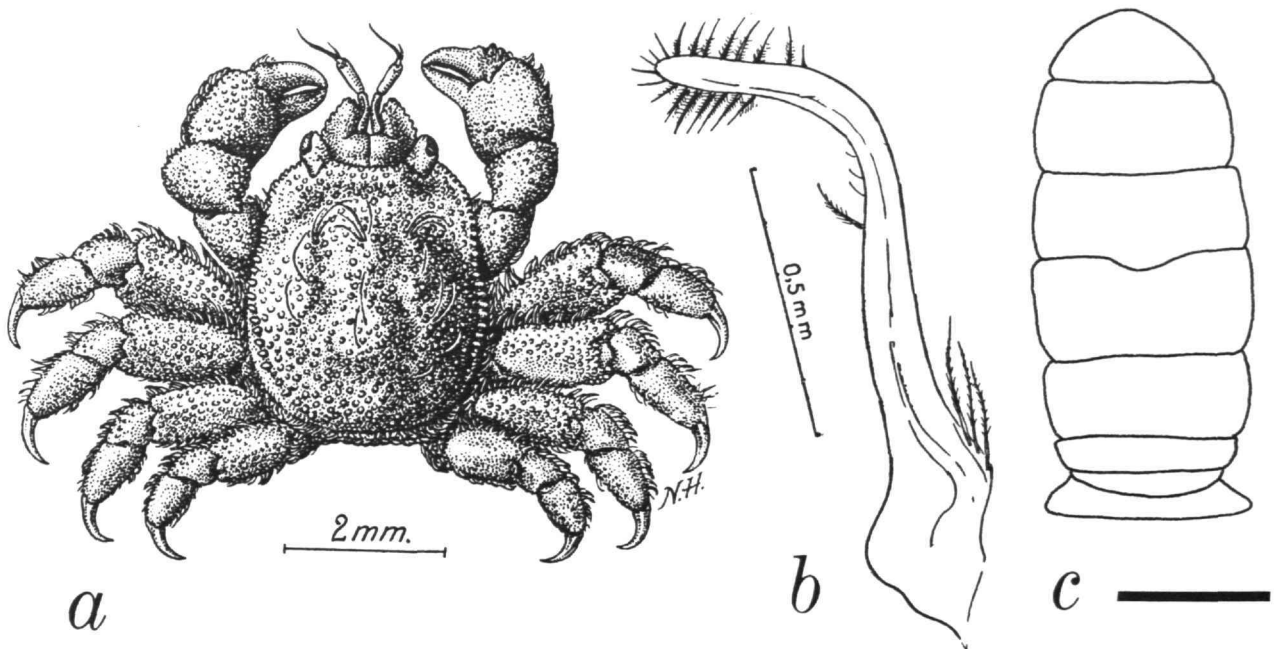


FIGURE 4.—*Detocarcinus balssi* (Monod), male: *a*, dorsal view of paratype; *b*, PLP-1; *c*, abdomen. (*a, b* from Monod, 1956; *c*, Ghana, USNM 231665. Scale: *c* = 0.5 mm.)

DISTRIBUTION.—Eastern Atlantic, off West Africa, from localities between the Canary Islands southward to Angola (Figure 9).

Zibrowius (1982) discussed crypts on corals taken from depths to 635 m in the southwestern Indian Ocean that resembled those attributable to *D. balssi*. However, no crabs were collected so those records are uncertain, especially as *D. balssi* is not known to occur outside the Atlantic.

#### *Opecarcinus*, new genus

DEFINITION.—Carapace longer than broad, deflected anteriorly at about angle of  $40^\circ$ , widest posteriorly. Pterygostomial region fused to carapace, not separated by suture. Antennule base with lateral projection overreaching inner margin of eyestalk; angled lateral lobe present. MXP-3 with elliptical exopod, longer than half length of lateral margin of ischium; merus with distolateral projection; anteromesial lobe of ischium extending beyond merocarpal articulation; carpus length less than length of propodus and dactylus combined. Sternite of P-1 tuberculate, of P-4 with complete medial suture. P-1 of female not visible in dorsal view; visible in male. Merus of P-2 with moderate mesial expansion; carpus with moderate mesial expansion. PLP-3 of female uniramous; female opening longitudinal, oval, without hood. PLP-1 of male slightly curved

distally; apex blunt tipped, directed laterally.

TYPE SPECIES.—*Pseudocryptochirus hypostegus* Shaw and Hopkins, 1977, by present designation.

INCLUDED SPECIES.—*Opecarcinus hypostegus* (Shaw and Hopkins, 1977), from the Atlantic, and *Opecarcinus crescentius* (Edmondson, 1925), from the East and West Pacific. *Pseudocryptochirus* is now restricted to one species, *P. hongkongensis* (Shen, 1936) from the Indo-West Pacific.

ETYMOLOGY.—From the Greek *ope* (opening or hole) plus the generic name *Carcinus*. The gender is masculine.

REMARKS.—*Opecarcinus* resembles *Troglocarcinus* and differs from both other Atlantic genera in having the front of the carapace noticeably deflected ventrally and in having a uniramous PLP-3 in the female; it further differs from *Detocarcinus* in having an exopod on the third maxilliped. *Opecarcinus* differs from *Troglocarcinus* in having distinct tubercles on the sternite of the first pereopod and in having the pterygostomial region fused to the carapace.

Species now assigned to *Opecarcinus* have been assigned to *Pseudocryptochirus* in the past; the latter genus occurs only in the Indo-West Pacific region. Members of *Opecarcinus* can be distinguished from members of *Pseudocryptochirus* by having the pterygostomial region fused to the carapace and by having the front of the carapace deflected anteriorly. The pterygostomial region is not fused to the carapace and the carapace is not deflected anteriorly in *Pseudocryptochirus*.

***Opecarcinus hypostegus* (Shaw and Hopkins, 1977),  
new combination**

FIGURES 5, 6

*Troglocarcinus corallicola*.—Coêlho, 1966:140 [part?] [Not *T. corallicola* Verill, 1908].

*Pseudocryptochirus hypostegus* Shaw and Hopkins, 1977:179, figs. 1, 2a, 3a.—Takeda and Tamura, 1981:14, 15, 20.—Abele and Felgenhauer, 1982:318, fig. on p. 318.—Scott, 1985:345, 347.—Abele and Kim, 1986:68, 727, 728, fig. on p. 729.—Takeda and Tamura, 1986:63, 68, fig. 4.

**PREVIOUS RECORDS.**—*Gulf of Mexico*: Florida Middle Ground, 28°30'49"N, 84°20'30"W, about 137 km west of Tarpon Springs, Florida (Shaw and Hopkins, 1977). Florida (Abele and Kim, 1986).

*Jamaica*: Discovery Bay area, 18°28'N, 77°24'W (Scott, 1985).

*Brazil*: Brazil, northeast coast (Coêlho, 1966), exact localities uncertain, see below under "Coral Hosts."

**MATERIAL EXAMINED.**—WESTERN ATLANTIC. *Florida*: Looe Key Reef, ~4.5 mi SSW of Big Pine Key [24°41'N, 81°21'W], D.L. Felder et al., 2 Jul 1979, 1 female on *Agaricia* (USLZ); same locality, Project Area IV, SCUBA transect sample, study finger # 2, D.L. Felder/J. Goy, 5 Oct 1983, 2 females (ov) (USLZ); Tortugas [24°37'N, 82°57'W], West Lab Dock, 6.1 m, 14 Aug 1930, 1 female on *Agaricia* [as *Agaricina*] (USNM).

*Gulf of Mexico*: Florida Middle Ground, BLM-MAFLA sta 147, 27 m, K. Shaw, 29 Jun 1976, 1 female (ov) on *Agaricia fragilis* Dana, 1848 (holotype, USNM 168532); same data, 1 male (paratype, USNM 168533); Florida Middle Ground, BLM-37, sta 047, 29 Jun 1976, 1 male, 1 female on *Agaricia* (IRCZM 89-5117) [possibly from the type locality, station data as in types, but station number different].

*Mexico*: Veracruz, Isla En Medio [21°29'N, 97°15'W], USLTFE III-B, north side of windward reef-canyon, 12–15 m, D.L. Felder/J.W. Martin, 24 Jun 1978, 1 female (USLZ); same data, 3 males, 3 females (ov) on *Agaricia* (USLZ); same locality, 10–12 m, D.L. Felder/J.W. Martin, 22 Jun 1978, 8 females (4 ov) on *Agaricia* (USLZ).

*Belize*: 16°48.2'N, 88°04.5'W, 36 m, G. Hendler sta 22, 29 Mar 1980, 1 female (juv) (USNM); same locality, 15.2 m, fore reef crest, G. Hendler sta 14, 20 Apr 1981, 1 male, 2 females (juv) (1 with 3 cryptoniscine isopod parasites in abdominal pouch) on *Agaricia* (USNM); same locality, 24.4–27.4 m, forereef dropoff, G. Hendler sta 85, 21 Apr 1981, 4 females (juv); 16°48.2'N, 88°04.6'W, 9.1 m, spur and groove zone, 24 Apr 1981, 1 male, on *Agaricia*; 16°48.1'N, 88°04.8'W, 1–2 m, reef platform (reef crest), G. Hendler sta 40, 41, 42, 25 Apr 1981, 1 immature, 2 females on *Agaricia*.

*Jamaica*: Discovery Bay, Jul 1983, B. Feifarek, 1 male, 2 females on *Agaricia* (USNM).

*Puerto Rico*: La Parguera [17°58'N, 67°04'W], Playa Rosada, V.A. Capriles, 22 Jul 1972, 2 females on *Agaricia* (USNM); Joyuda, Cabo Rojo [17°56'N, 67°12'W], 1.2–1.8 m, J.A. Rivero, 21 Aug 1948, 5 females on *A. agaricites* (Linnaeus, 1758) (USNM); same locality, J.A. Rivero, 5 Aug

1948, 1 male, 2 females on *A. agaricites* (USNM).

**CENTRAL ATLANTIC.** *Ascension Island* [7°57'S, 14°22' W]: English Bay, north end at rocky point, sta RBM Asc-15, R.B. Manning et al., 22 May 1971, 1 female (USNM).

**DESCRIPTION.**—*Adult Female* (Figure 5): Carapace about 1.6 times longer than wide, slightly inflated laterally at branchial regions, narrowing slightly towards front. Anterior third of carapace deflected at angle of up to 40°, angle similar at all sizes. Carapace with transverse depression confined to protogastric region; posterior surface slightly convex side to side. Surface variably ornamented with tubercles, some spines; tubercles more numerous, larger at midcarapace; posterior carapace with granules decreasing in size posteriorly, smoother than anterior. Anterolateral angle without prominent spine or tubercle; adjacent lateral margins with tubercles, not forming distinct border. Surface variably setose; setae simple, sparse, most shorter, some longer than largest tubercles, not obscuring surface. Inner orbital angle slightly swollen, having distinct spine larger than adjacent tubercles, extending almost to apex of anterolateral spine of carapace. Front slightly concave, tuberculate, with larger median tubercle; width about half that at anterolateral angles, latter about  $\frac{3}{5}$  greatest carapace width. Orbit broadly V-shaped, margin with few tubercles.

Basal segment of antennular peduncles with distal projection overreaching eyestalk, projection with apex of angled lateral lobe at tip of eyestalk; dorsal surface flat, variably ornamented with spines and tubercles, marginal spines longest. In ventral view, basal segment broadening anteriorly; surface with numerous granules. Second segment of antenna with granules on ventral surface, distal margin granulate.

Eyes directed anterolaterally, extending beyond anterolateral angle. Cornea anterolateral; in dorsal view, occupying less than half lateral length of stalk. Stalk wholly exposed dorsally; surface mostly smooth, tuberculate distomesially, ventral surface with granules.

Ischium of MXP-3 with mesial margin minutely denticulate, straight; surface of ischium and exopod with many prominent, raised granules. Merus as broad as long, width half that of ischium; lateral three-fourths with many prominent, raised granules. Following segments decreasing in length and size distally. Propodus and dactylus with pappose setae on upper margins, setae longer than carpus width.

Sternite of first pereopods with transverse row of tubercles and with smaller tubercles posteriorly.

Chelipeds (P-1) equal, merus not extending beyond anterolateral angle of carapace. Dactylus shorter than dorsal margin of palm, with proximal tubercle on dorsally; cutting edges of fingers unarmed. Dorsal margin of palm variably tuberculate, with pappose setae; outer surface of palm flat, smooth, clean. Merus and carpus tuberculate dorsally; carpus with pappose setae.

Walking legs (P-2 to P-4) stout, decreasing in size posteriorly to P-4, P-2 largest. P-5 longer, slenderer than P-4. Merus of P-2 to P-4 each with blunt, rounded tubercles dorsally

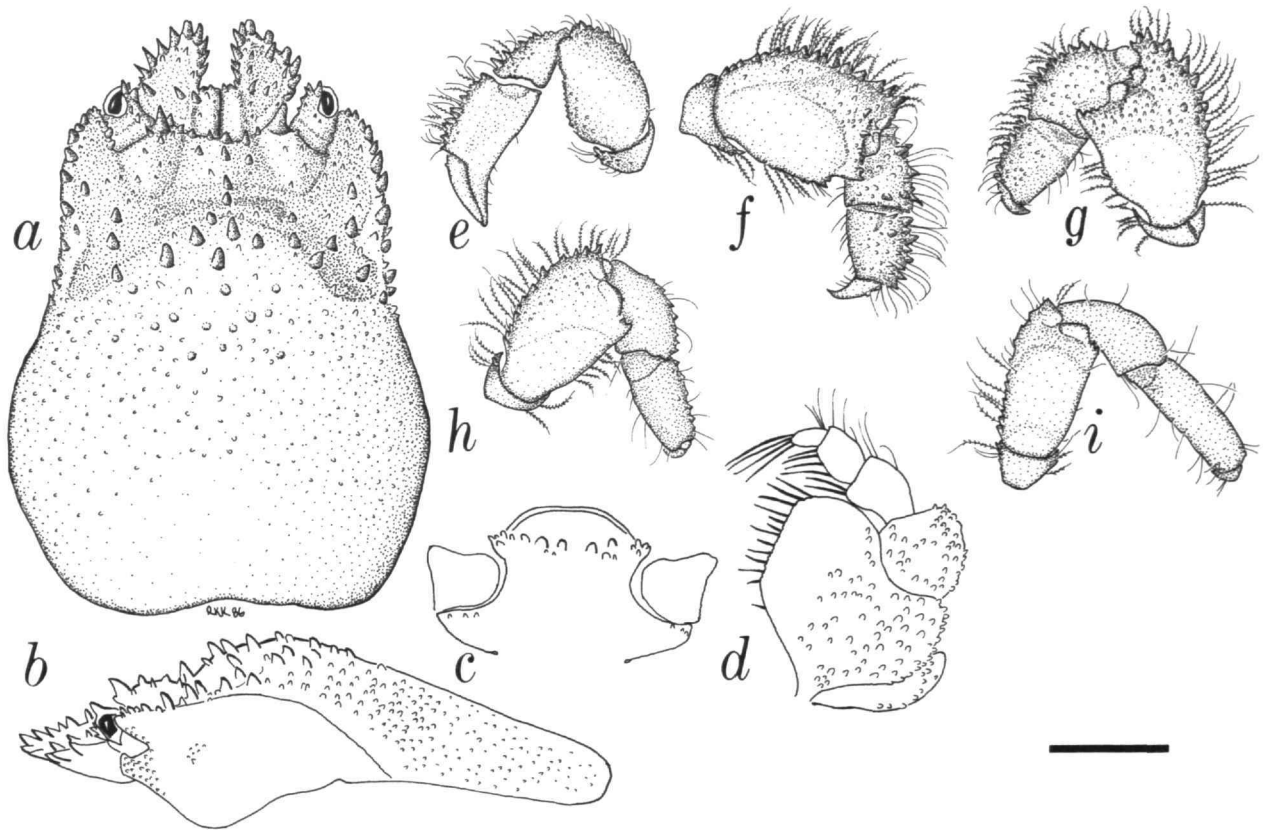


FIGURE 5.—*Opecarcinus hypostegus* (Shaw and Hopkins), female holotype, USNM 168532: a, dorsal view of carapace; b, lateral view of carapace; c, P-1 sternite; d, MXP-3; e-i, P-1 to P-5. (Scale: a-c, e-i = 1 mm; d = 0.5 mm.)

and produced ventrodistally, with 1 tubercle; dorsal surface with pappose setae; merus of P-2 falling short of anterolateral angle of carapace. Carpus about as broad as long, not produced ventrodistally, carpus of P-3 with proximal clump of tubercles on lower surface; carpus and propodus subequal in length. Dactylus of P-2 shorter than propodus, slightly curved, claw-like; dactyli of P-2 to P-3 with tubercles proximally on dorsal margin, of P-4 and P-5 rotated anteriorly  $\sim 90^\circ$  with respect to merus. Meri of P-2 to P-5 decreasing in size posteriorly from P-2 to P-5, propodi increasing in length posteriorly from P-2 to P-5, becoming slenderer (Table 1).

Abdomen of ovigerous females, in dorsal view, up to half again as wide as carapace; up to part of fourth somite visible. Egg size (in alcohol) 0.4–0.6 mm maximum diameter.

**Adult Male** (Figure 6): Similar to female, smaller; carapace smoother. Chelae proportionally more robust than in female; dactylus shorter than dorsal margin of palm, cutting edge may have proximal tooth. Dactyli of P 2–5 more slender than female.

**Juveniles:** Not significantly different from adults.

**SIZE RANGE.**—Males, 1.4 × 1.3 mm to 3.4 × 2.6 mm; females 1.6 × 1.3 mm to 5.8 × 3.5 mm; ovigerous females, 2.1 × 1.4 mm to 5.4 × 3.4 mm.

**TYPES.**—The holotype is an adult female, 3.8 × 3.3 mm, in the collections of the National Museum of Natural History, Smithsonian Institution (USNM 168532). It is ovigerous, with depressions on the protogastric and hepatic regions. The margin of the front is without a larger median tubercle. The specimen is mostly disarticulated, the the right cheliped, P-3, and right third maxilliped missing. The sternite of P-4 is punctured ventrally.

The male paratype, also in the collections of the Smithsonian, is mostly disarticulated, missing the left P-5, and with the left P-2 to P-4 missing various segments; the mouthparts are present, but the abdomen and pleopods are missing.

Two specimens in the collection of the Indian River Coastal Zone Museum, Fort Pierce, Florida, may also be paratypes. They show the same locality and date as the holotype, but a different station number.

Other types reported by Shaw and Hopkins (1977) are in the



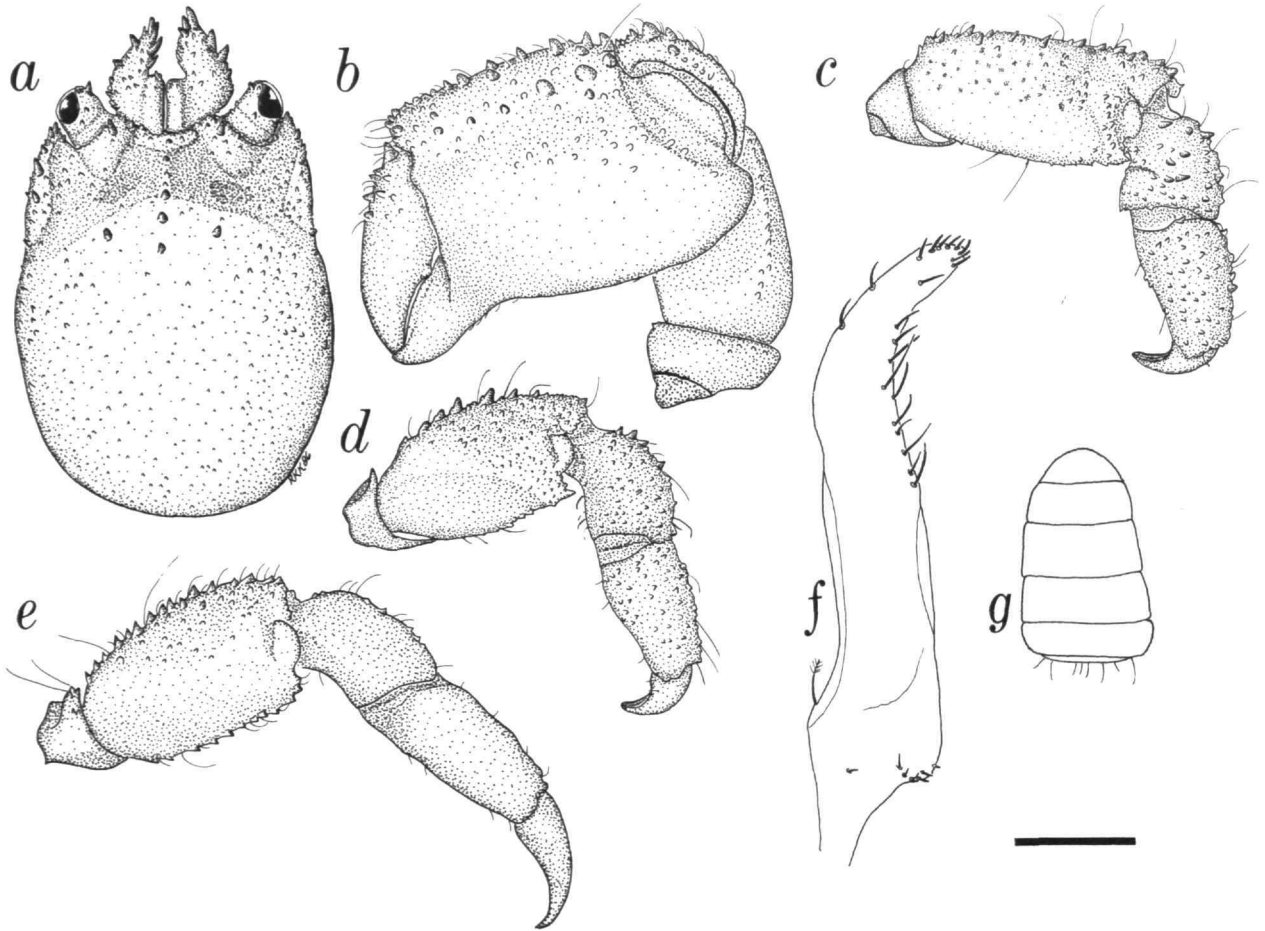


FIGURE 6.—*Opecarcinus hypostegus* (Shaw and Hopkins), male: *a*, dorsal view of carapace; *b–e*, P-1 to P-4; *f*, PLP-1; *g*, abdomen. (*a–e*, paratype, USNM 168533; *f*, Florida Middle Ground, IRCZM 89:5117; *g*, Isla En Medio, Mexico, USLZ 2708. Scale: *a* = 0.8 mm; *b,e,g* = 0.5 mm; *c,d* = 1 mm; *f* = 238  $\mu$ m.)

collections of the Dauphin Island Sea Lab, Dauphin Island, Alabama. John Garth and Janet Haig pointed out to us that paratype material is also in the collections of the Allan Hancock Foundation, Los Angeles, California. These were not listed by Shaw and Hopkins. We did not examine either set of material.

The type locality is the Florida Middle Ground, west of Tarpon Springs, in the Gulf of Mexico.

**BIOLOGY.**—Ovigerous females have been taken in June (Florida Middle Ground, Shaw and Hopkins, 1977, and herein; Mexico, herein) and October (Florida, herein).

This species has been collected in depths between 0 and 27 m.

One juvenile female, from Belize, was infested by three cryptoniscine isopod parasites, all attached within the abdominal pouch of the crab. We found no evidence of a rhizocephalan parasite on this infected female.

None of the material examined was infested by bopyrid

isopod parasites.

**CORAL HOSTS.**—*Opecarcinus hypostegus* has been recorded from relatively few coral hosts, having been taken only on members of the following two families:

**Agariciidae:** *Agaricia* sp. and *A. agaricites* (Linnaeus, 1758), herein; *A. fragilis* Dana, 1848, reported by Shaw and Hopkins (1977) and herein; *A. lamarcki* Milne Edwards and Haime, 1851; and *A. grahamae* Wells, 1973, listed by Scott (1985).

**Siderastreidae:** *Siderastrea siderea* (Ellis and Solander, 1786) listed by Scott (1985).

Coelho listed gall crabs from Brazil as being collected on mussid and agariciid corals. However, *T. corallicola* is not known to occur on agariciids. Because *O. hypostegus* is the only Atlantic gall crab known to live on agariciids, we tentatively include part of Coelho's records here.

The dwelling of *O. hypostegus* (Figure 10e) has been

described as a canopy-shaped tunnel (Shaw and Hopkins, 1977) resulting from the combined effects of the host coral growth and movement of the crab. Bak et al. (1977) found that experimentally damaged *Agaricia* colonies repaired lesions by forming a dome-shaped skeletal roof over the affected area. These domes took a long time to close completely, and ultimate closure could be delayed by a foreign substance such as algae. Therefore it seems likely that the gall crab is living in a dwelling resulting from crab-caused irritation and coral regenerative processes. The opening of the dwelling is crescent-shaped (Figure 10d).

REMARKS.—*Opecarcinus hypostegus* differs from the Pacific *O. crescentus* by having fewer, smaller tubercles on the carapace and pereopods. In *O. crescentus* the anterior depression of the carapace is deeper and better defined than in *O. hypostegus*. The eyestalk of the former is partially covered dorsally and extends only to the level of the anterolateral angle of the carapace, whereas in the latter species, the eyestalk is wholly exposed and extends beyond the anterolateral angle. The third maxilliped is much more heavily granular and the anteromesial lobe of the ischium more pronounced in *O. hypostegus* than in *O. crescentus*.

DISTRIBUTION.—Western and Central Atlantic, from northern Mexico, the Gulf of Mexico, Florida, Jamaica, Puerto Rico, Ascension Island, and probably Brazil (Figure 9).

#### *Troglocarcinus* Verrill, 1908

*Troglocarcinus* Verrill, 1908a:427. [Type species *Troglocarcinus corallicola* Verrill, 1908, by monotypy. Gender masculine.]

*Mussicola* Fize and Serène, 1957:10, 55, 110. [Published as *Troglocarcinus* (*Mussicola*). Type species *Troglocarcinus corallicola* Verrill, 1908, by present designation. Gender masculine.]

DEFINITION.—Carapace longer than broad, deflected anteriorly at angle of about 60°, widest posteriorly. Pterygostomial region not fused to carapace, separated by suture. Antennule base with lateral projection extending to or slightly beyond eyestalk, lacking angled lateral lobe. MXP-3 with oval exopod, slightly longer than half lateral margin of ischium; merus with distolateral projection; anteromesial lobe of ischium extending beyond merocarpal articulation; carpus length less than combined length of propodus and dactylus. Sternite of P-1 smooth, of P-4 with complete medial suture. P-1 of adult female not visible in dorsal view, visible in male. Merus of P-2 with prominent mesial expansion; carpus with prominent mesial expansion. PLP-3 of female uniramous; female opening longitudinal, oval, lacking hood. PLP-1 of male slightly curved; apex broadly pointed, directed slightly laterally.

REMARKS.—The genus *Troglocarcinus* was established by Verrill, 1908a, with *T. corallicola*, from Bermuda and Dominica, as its type species. Edmondson (1933:5) assigned *T. corallicola* to *Cryptochirus* Heller, 1861 (type species *Cryptochirus coralliodytes* Heller, 1861, by monotypy), and this was accepted by Shen (1936), Rathbun (1937), Garth and

Hopkins (1968), and Fausto-Filho (1974).

Hiro (1938:149) named the genus *Pseudocryptochirus*, then monotypic, containing *P. viridis* Hiro, 1938, from Japan. Utinomi (= Hiro) (1944) disagreed with Edmondson, and considered *Troglocarcinus* Verrill, 1908, and his genus *Pseudocryptochirus* to be congeneric. He erroneously used the junior synonym for the genus, noting (p. 724): "For the same group VERRILL'S *Troglocarcinus* greatly precedes the latter [*Pseudocryptochirus*]; but this is not preferable since it conveys a somewhat inadequate conception about the generic distinction of this group." In this action, Utinomi was followed by Shaw and Hopkins (1977) and Scott (1985).

Monod (1956:466) commented on Utinomi's action, "Paireille raison justifie-t-elle l'abandon de nom du genre ayant une indubitable priorité? On peut en douter." In a footnote on page 466, Monod noted that Utinomi (in litt.) had accepted the synonymy of *Pseudocryptochirus* with *Troglocarcinus*.

Fize and Serène (1957:9) noted that Utinomi had written on a reprint of his 1944 paper, "the name *Troglocarcinus* should be used instead of my name for the genus" [*Pseudocryptochirus*].

Later, Serène (1962:30, footnote) remarked that "Utinomi uses *Pseudocryptochirus* as the name of the genus, but *Troglocarcinus* has priority." Curiously, Serène (1966:396) noted that "La remarque de Monod (1956, page 466) au sujet de la priorité du nom *Troglocarcinus* Verrill 1908 sur *Pseudocryptochirus* Hiro 1938 n'était valable que parce qu'Utinomi (1944) considérait les deux genres comme identiques, synonymes."

Fize and Serène (1957) recognized four subgenera in the genus *Troglocarcinus*: *Troglocarcinus* proper and three new subgenera, *Favicola*, *Fungicola*, and *Mussicola*. They incorrectly assigned the type species of *Troglocarcinus*, *T. corallicola*, to their new subgenus *Mussicola*, along with two other species. No type species was designated. In a later paper, Serène (1966:396) regarded *Mussicola* as a synonym of *Troglocarcinus* and placed the species originally assigned to *Troglocarcinus* (*Troglocarcinus*) by Fize and Serène (1957:10, 55, 56) to *Pseudocryptochirus* Hiro, 1938. McNeill (1968:87) also recognized *Mussicola* as a synonym of *Troglocarcinus*, but took no corrective action.

Takeda and Tamura (1980a:138) recognized that this action by Fize and Serène was incorrect, but apparently did not realize that *Mussicola* could be used as a generic name by the designation of one of the other species assigned to it as its type species; they recognized a new genus, *Fizesereneia* (type species *Troglocarcinus heimi* Fize and Serène, 1955, one of the three species originally assigned to *Mussicola*), for a new species and the two other species originally assigned to *Mussicola* by Fize and Serène in 1957.

The present designation of *Troglocarcinus corallicola*, one of the three species originally assigned to *Mussicola*, as the type species of *Mussicola*, removes *Mussicola* as a potential senior synonym of *Fizesereneia* and makes it a harmless junior

synonym of *Troglocarcinus* Verrill, 1908.

*Troglocarcinus* agrees with *Opecarcinus* and differs from both *Cecidocarcinus* and *Detocarcinus* in having the front of the carapace strongly deflected ventrally, in having the PLP-3 uniramous in the female, and in lacking a distinct line of tubercles marking the lateral edge of the carapace. *Troglocarcinus* differs from *Opecarcinus* in having the sternum of the first pereopod smooth and in having a free epimeral plate; in *Opecarcinus* the epimeral plate is fused to the carapace.

*Troglocarcinus* has been confused with *Pseudocryptochirus* of the Indo-West Pacific in the past. It can be distinguished from that genus by having the front deflected anteriorly; it is not deflected in members of *Pseudocryptochirus*.

### *Troglocarcinus corallicola* Verrill, 1908

FIGURES 7, 8

*Troglocarcinus corallicola* Verrill, 1908a:427, figs. 48, 49a-c, pl. 28: fig. 8; 1908b:291, fig. 3.—Edmondson, 1933:5.—Shen, 1936:21.—Hiro, 1937:140, 142 [discussion].—Utinomi, 1944:697, 698, 699, 713, 716 [part], 718–719, 721–723, fig. 14.—Fize and Serène, 1955:378; 1957:6, 8, 9, 22, 53, 54, 55, 66, 68, 110 136, 153, 154.—Serène, 1966:396, 397.—Coelho, 1966:140.—Garth and Hopkins, 1968:40.—McNeill, 1968:87.—Coelho, 1970:234 [no material].—Coelho and Ramos, 1972:205 [no material].—Zibrowius, 1976:71.—Takeda and Tamura, 1980a:137, 138.—Markham and McDermott, 1981:1272.—Scotto and Gore, 1981:486 p.p., figs. 1–6.—Reed et al., 1982:761 p.p., fig. 7.—Van Dover, 1982:212, fig. 1F.—Zibrowius, 1982:119.—Gore et al., 1983:141, 143, 147, figs. 2d, 3d.—Kropp, 1986:377.—Hines, 1986:450, 458.—Takeda and Tamura, 1986:63, 68, fig. 3.

*Troglocarcinus corallicola*.—Edmondson, 1925:35 [erroneous spelling].

*Cryptochirus corallicola*.—Edmondson, 1933:5.—Shen, 1936:22.—Rathbun, 1937:262, fig. 47, pl. 78: figs. 5–8.—Ekman, 1953:51.—Garth and Hopkins, 1968:40.—Fausto-Filho, 1974:13, 22, 25, 28 [no material].—Shaw and Hopkins, 1977:178.

*Troglocarcinus corallicola*.—Utinomi, 1944:688 [erroneous spelling].

*Pseudocryptochirus corallicola*.—Utinomi, 1944:698, 701, 706, 707, 709, 710, 711, 712, 713, 715, 724, 726, 728, figs. 11g, 12d, 14a, 15d, 16g–i, 17, pl. 4: figs. 11–14, pl. 5: fig. 4.—Shaw and Hopkins, 1977:178, 179, 181, 182, figs. 2b, 3b.—Scout, 1985:345, 347.—Abele and Kim, 1986:68, 727, 728, fig. on p. 729.

*Troglocarcinus (Mussicola) corallicola*.—Fize and Serène, 1957:55, 68, 110, 115, 121, 136, 163, 165 [discussion].

*Pseudocryptochirus corallicola*.—Shaw and Hopkins, 1977:177 [erroneous spelling].

**PREVIOUS RECORDS.**—*Bermuda*: [32°18'N, 64°45'W] (Verrill, 1908a,b; Markham and McDermott, 1981).

*Florida*: South of Pepper State Park, St. Lucie County, 27°29.6'N, 80°17.3'W (Scotto and Gore, 1981). Off central east Florida, ~0.6 km off Fort Pierce [27°28'N, 80°16'W]; 7 miles east of St. Lucie Inlet [27°10'N, 80°08'W] (Reed et al., 1982). Dry Tortugas (Rathbun, 1937; Utinomi, 1944; Shaw and Hopkins, 1977). Florida Middle Ground (Shaw and Hopkins, 1977). Florida (Abele and Kim, 1986).

*Jamaica*: Discovery Bay area (Scott, 1985).

*Dominica*: Dominica [15°30'N, 61°20'W] (Verrill, 1908a,b).

*Brazil*: Atoll das Rocas [03°52'S, 33°49'W]. Fernando de Noronha [03°51'S, 32°25'W]. San Luiz, Maranhão [02°31'S,

44°16'W]. Recife [08°03'S, 34°54'W] and Tamandaré [08°45'S, 35°06'W], Pernambuco. Macéio, Alagoas [09°40'S, 35°45'W]. Mar Grande, Bahia [12°57'S, 38°37'W] (Coelho, 1966, 1970; Coelho and Ramos, 1972)

In addition to these records, Utinomi (1944:731) recorded galls attributed to this species, based on accounts in the coral literature, from the following localities: Bermuda, Florida, West Indies, and Bahia, Brazil.

**MATERIAL EXAMINED.**—WESTERN ATLANTIC. *Bermuda*: In hole in coral, A.E. Verrill, 1901, 1 female (lectotype, YPM 7162). Castle Harbour Causeway [32°21'N, 64°40'W], Savazzi, Aug 1982, 1 female on *Isophyllia* sp. (USNM).

*Florida*: Monroe County: Tortugas, off east side of Loggerhead Key [24°38'N, 82°56'W], W.L. Schmitt, 18 Jul 1931, 2 females, on probably *Diploria* [as *Meandrina*] (USNM). Off north end of Loggerhead Key, in stomach of fish #280, *Apogon maculatus* (Poey, 1861) [as *A. sellicauda* Evermann and Marsh, 1900], W.L. Schmitt, 9 Jun 1925, 1 male (USNM). West side of Loggerhead Key, sta 33, C.R. Shoemaker, 26 Jul 1930, 3 males, 10 females (7 ov) (USNM). Bush Key Reef [24°38'N, 82°52'W], sta 29, 23 Jul 1930, Mr. Visscher, 3 females (ov), on *Diploria* [as *Meandrina*] (USNM); H. Boschma, Jul/Aug 1925y, 4 males, 10 females (3 ov), on *Manicina areolata* (USNM). Fort Jefferson [24°38'N, 82°53'W], sta 3, C.R. Shoemaker, 17 Jul 1926, 2 females (ov) (USNM). Bush Key Reef, sta 21, C.R. Shoemaker, 14 Aug 1926, 1 male, 6 females (2 ov) (USNM). Bush Key Reef, sta 22, C.R. Shoemaker, 16 Aug 1926, 4 males, 8 females (4 ov) (USNM); W.H. Longley, Aug 1927, 1 female (ov) (USNM). St. Lucie County: Pepper State Park, 1.4 m, J. Reed, 25 May 1979, 1 female on *Oculina* sp. (IRCZM 89-4835); same locality, 6.1 m, 25 Jan 1977, J. Reed, 2 males, 1 female (ov), 1 female (juv) (IRCZM 89-5116); same locality, 4.5 m, J. Reed/K.D. Cairns, 11 Jul 1979, 2 females (IRCZM 89-5114). Collier County: Sanibel Is. [26°26'N, 82°10'W], EJ-80-29, ~X sta K, R/V *Hernan Cortez*, D.K. Camp et al., 31 Jul 1980, 1 female (ov) (USLZ).

*Mexico*: Tamaulipas [23°03'N, 97°46'W], off Barra del Tordo, 12.8 m, D.L. Felder, 17 Aug 1979, 1 female (ov) on *Siderastrea siderea* (USLZ). Veracruz, Isla En Medio, in channel of windward reef, USLTFE III-B, ~6 m, D.L. Felder et al., 22 Jun 1978, 2 females (ov) (USLZ). Off city of Veracruz, Bird Reef, USLTFE I-B, 9 Jan 1977, 1 female (ov) (USLZ).

*Belize*: W of Twin Keys [16°50'N, 88°05'W], *Thalassia* grassflat, 1 m, J.E. Miller, 21 Mar 1981, 1 female (ov) on *Manicina areolata* (Linnaeus, 1758) (IRCZM).

*Panama*: Portobelo [09°33'N, 79°39'W], H. Lasker, 9/10 Dec 1975, 7 males, 5 females (juv) on *Montastrea cavernosa* (Linnaeus, 1767) (IRCZM 89-2985), males free-living on the coral surface.

*Puerto Rico*: Southwestern coast, V.A. Capriles, 1 male, 4 females (2 ov) on *Diploria strigosa* (Dana, 1848), *Isophyllia sinuosa* (Ellis and Solander, 1786), *Micetophyllia* sp. (USNM).

*Curaçao*: Piscadera Baai [12°08'N, 68°59'W], 0–0.5 m,

L.B. Holthuis, 25 Jan 1957, 1 male, 28 females (23 ov) (RMNH).

CENTRAL ATLANTIC. *Saint Paul Rocks* [00°56'N, 29°22'W]: SW of Belmonte Islet, 14-2b, 20 Sep 1983, 1 male on *Polycyathus* sp. (RMNH).

*Ascension Island*: Shelly Beach, in tide pool, sta RBM Asc-18, R.B. Manning et al., 23 May 1971, 1 female (USNM). Turtle Shell Beach, tide pool, sta RBM Asc-23, R.B. Manning/K. Double, 25 May 1971, 2 females (ov) (USNM). North East Bay, tide pool, sta RBM Asc-5, R.B. Manning et al., 19 May 1971, 1 male, 1 female (ov) (USNM). MacArthur Pt., Jones et al., 12 Jul 1976, 1 male, 1 female (ov) on *Favia* (USNM). Collyer Pt., Jones et al., 14 Jul 1976, 1 female (juv) (USNM). South West Bay, C85/53, 1978:52, Nov 1972, 2 males, 8 females (7 ov) (BMNH).

*St. Helena* [15°55'S, 05°43'W]: James Bay, between landing steps and Munden's Pt. (northwestern coast), sta 15, 1-6 m, J.C. den Hartog, 19 Jun 1983, 5 females (4 ov) on *Sclerhelia hirtella* (Pallas, 1766) (RMNH). James Bay, sta H 2-67, 8-9 m, A. Edwards/C. Glass, 18 Jul 1983, 1 male, 7 females on *S. hirtella* (RMNH).

EASTERN ATLANTIC. *Gabon*: Cap Esteiras [00°37'N, 09°20'E], 4-8 m, J. Laborel, 27 Jan 1971, 4 females on *F. gravidia* (USNM).

*São Tomé Island* [00°12'N, 06°39'E]: São Tomé, S. Gofas, Nov 1983, Jun 1984, 2 females on *Favia gravidia* Verrill, 1868 (RMNH, USNM).

*Pagalú Island* [= Annobon; 01°25'S, 05°36'E]: Between village and San Pedro, 3-9 m, J. Laborel, 18 Jan 1971, 5 females on *F. gravidia* (USNM). On right side of village (Nizery sta 2), 3-8 m, J. Laborel, 18 Jan 1971, 9 females on *F. gravidia* (USNM).

**DESCRIPTION.**—*Adult Female* (Figure 7): Carapace about 1.3 times longer than broad, slightly inflated laterally at branchial regions, narrowing slightly towards front. Anterior part of carapace strongly deflected, at angle of up to 60°, greatest amount of deflection in older (larger) specimens, and with well-defined depression covering protogastric regions; posterior surface slightly convex side to side. Surface variably ornamented with tubercles and some spines, tuberculation increasing anteriorly, with granules decreasing posteriorly; posterior fourth may be smooth but pitted. Larger spines on dorsal surface variable, usually 3-4 occurring on mesogastric swelling, several on anterolateral margin. Inner orbital angle with 1 spine, slightly swollen. Surface of carapace variably setose, setae simple, distally curved; deflected part of front may be completely obscured by setae longer than longest spines. Anterolateral angle with spine, apex extending to or exceeding apex of inner orbital spine. Front concave, with few tubercles and with median spine or tubercle occasionally missing); front about 2/5 width at anterolateral angles, latter about 3/5 greatest carapace width. Lateral margins of carapace lacking distinct border of tubercles, but with some tubercles present behind anterolateral angles. Orbit broadly U-shaped, margin with few tubercles.

Basal segment of antennular peduncle with distal projection extending to or slightly beyond eyestalk; dorsal surface flat, variably armed with spines and tubercles, distal spines usually largest; lateral margin deflected ventrally. In ventral view, basal segment tapering sharply anteriorly; surface with granules proximally and mesially. Second segment of antenna with raised granules on distal half.

Eyes directed anteriorly, extending beyond anterolateral angle. Cornea anterolateral, in dorsal view occupying more than distal half of stalk. Stalk partially covered dorsally, finely tuberculate, especially mesially; smooth ventrally.

Ischium of MXP-3 with mesial margin minutely denticulate, convex; surface of ischium and exopod with few scattered granules. Merus as broad as long, width half that of ischium, with few granules laterally. Following segments decreasing in length and size distally. Proximal 3 palp segments with scattered pappose setae of length greater than carpus width.

Chelipeds (P-1) equal, merus not extending beyond anterolateral angle of carapace. Dactylus longer than dorsal margin of palm, usually with low tooth in basal fourth; smooth dorsally. Dorsal margin of palm variably tuberculate, with simple setae; outer surface of palm flat, largely smooth, clean. Merus and carpus tuberculate, spinose dorsally; dorsal margins with simple setae.

Anterior two walking legs (P-2 and P-3) stout, P-4 and P-5 slenderer; legs decreasing in size posteriorly, first (P-2) distinctly largest. P-2 to P-5 each with merus tuberculate dorsally, variably ornamented, usually sparsely, with simple, distally-curved setae. Merus of P-2 extending almost to anterolateral angle of carapace, distomesial expansion most prominent in larger specimens; inner margin of merus matching carapace edge in contour. Meri of P-2 to P-4 with ventrodistal tubercle. Carpus of P-2 about as broad as long; carpi of P-2 to P-4 with clump of tubercles proximally on outer surface; meral and carpal expansions variably spined and tuberculate, largest spines on mesial lobes. Propodus slightly shorter than carpus, tapering distally, becoming more slender from P-2 to P-5 (Table 1); propodi of P-2 to P-5 shorter than respective meri. Dactylus slenderer than propodus, shorter, curved, claw-like; dorsal margin smooth. Dactyli of P-4 and P-5 rotated -90° to longitudinal plane of merus. Outer and upper surfaces of leg variably tuberculate and setose. P-5 shortest, smallest, slenderest, and smoothest of walking legs.

Abdomen of ovigerous females, in dorsal view, as wide as to half again as wide as carapace, somites separate, up to fourth somite visible. Egg size (in alcohol) 0.3-0.5 mm maximum diameter.

*Adult Male* (Figure 8): As in female but smaller, carapace and pereopods less tuberculate, front much less deflected. Chelipeds proportionally larger than in female, visible in dorsal view, part of carpus extending beyond anterolateral angle of carapace. Dactylus longer than dorsal margin of palm, with basal tooth; palm inflated. Walking legs (P-2 to P-5) slenderer, less tuberculate; merus of P-2 with slight mesial projection distally. Abdomen margins convex, telson broadly rounded.



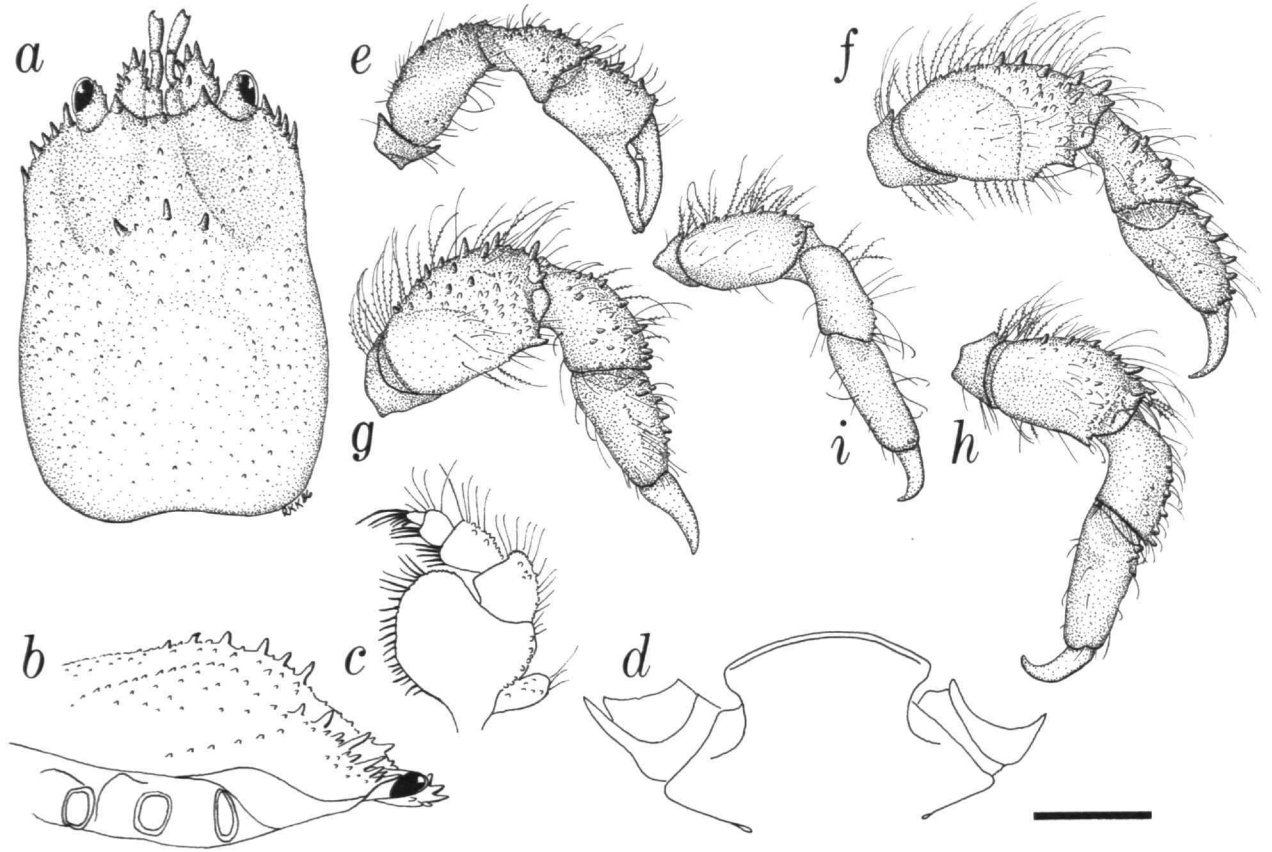


FIGURE 7.—*Troglodarcinus coralicola* Verrill, female, Tortugas, USNM 59964: a, dorsal view of carapace; b, lateral view of carapace; c, MXP-3; d, P-1 sternite; e-i, P-1 to P-5. (Scale: a, b = 0.8 mm; c, d = 0.5 mm; e-i = 1 mm.)

PLP-1 simple, as for genus.

**Juveniles** (Figure 8b): Carapace with slight deflection anteriorly, often with anterior, submedian shallow depressions. Chelipeds equal, small, palm of chela not inflated. Walking legs very slender, elongate, P-2 merus, carpus lacking expanded lobes mesially. P-2 to P-5 largely smooth, with some dorsal tubercles only and few scattered long setae, not obscuring surface.

**SIZE RANGE.**—Males, 1.6 × 1.4 mm to 3.1 × 2.6 mm; females, 1.4 × 1.3 mm to 5.2 × 3.9 mm; ovigerous females, 2.5 × 1.9 mm to 5.2 × 3.9 mm. Verrill (1908a) reported a female 7.0 × 4.0 mm.

**TYPE.**—Verrill (1908a) did not originally designate a holotype. He reported on specimens from Bermuda and Dominica. Rathbun (1937) gave the type locality as Dominica, but did not designate a lectotype albeit reporting a type in the Peabody Museum. Shaw and Hopkins (1977) reported a holotype collected on *Mussa* from Dominica in the Yale Peabody Museum under catalog number 7612. The only specimen collected by Verrill we have found in the Peabody

Museum is from Bermuda, with the designation holotype on the label, under catalog number 7162. No coral host is mentioned on the label. This specimen is herein designated the lectotype as no holotype was originally specified. It is a preovigerous female, 2.4 × 1.8 mm, having an abdomen not fully expanded to form the typical marsupium. The specimen is missing the left P-2, the distal three segments of the left P-3, the dactylus of the right P-5, and the left cheliped. The carapace has been punctured at the mesogastric region. The lectotype shows other typically juvenile features as mentioned above. The lectotype does not resemble any of the specimens shown in Verrill's (1908a) figure 49.

By the lectotype designation herein, the type locality becomes Bermuda.

**BIOLOGY.**—Ovigerous females have been collected in January (Florida, Mexico, Curaçao, all herein), March (Belize, herein), May (Florida, Scotto and Gore, 1981; Ascension Island, herein), June (Florida Middle Ground, Shaw and Hopkins, 1977; Mexico, St. Helena; both herein), July (Florida, Ascension Island, both herein), August (Florida, Mexico, both

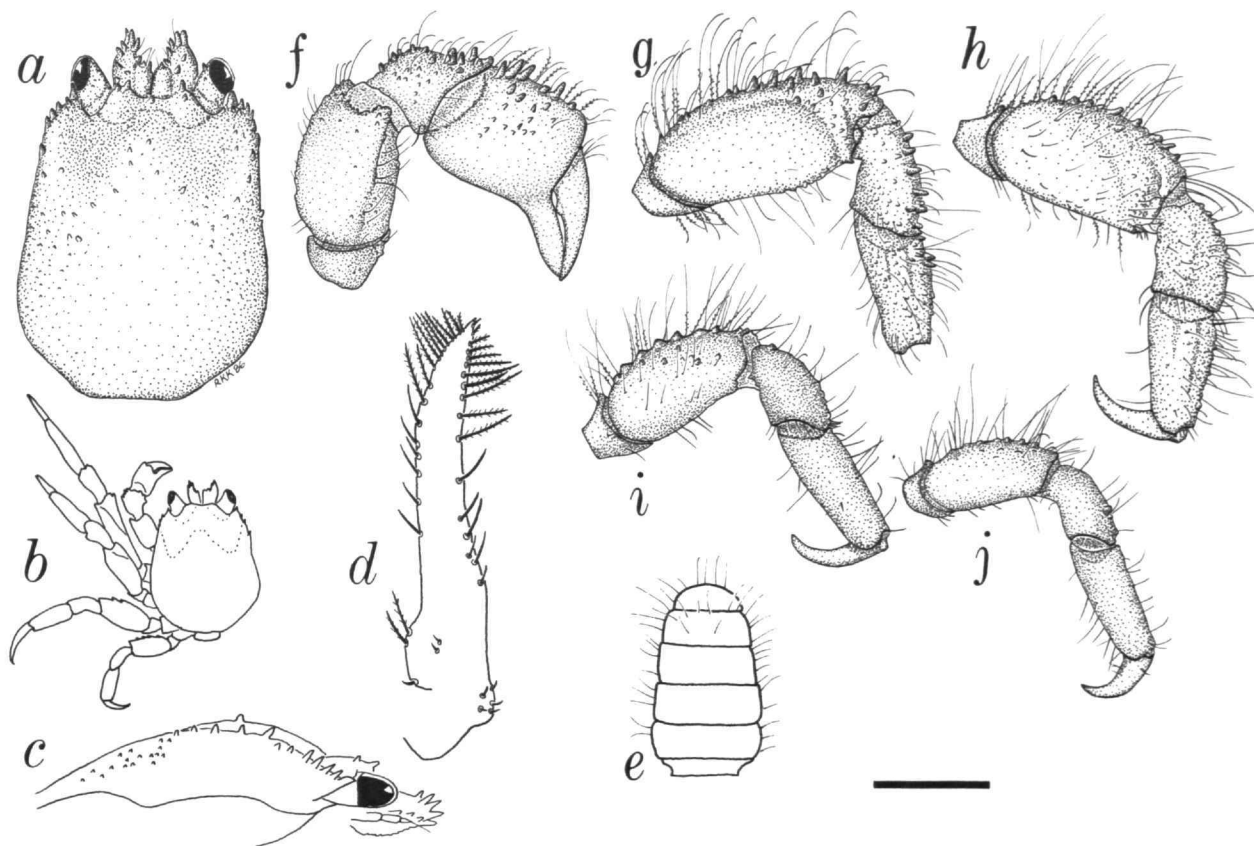


FIGURE 8.—*Troglorcarinus corallicola* Verrill, male: *a*, dorsal view of carapace; *b*, dorsal view of juvenile (right pereopods omitted); *c*, lateral view of carapace; *d*, PLP-1; *e*, abdomen; *f*–*j*, P-1 to P-5. (*a*, *c*, *f*–*j*, Tortugas, USNM 59964; *b*, Panama, IRCZM 89-2985; *d*, Tortugas, USNM 77365 (cl = 2.9 mm); *e*, off Pepper State Park, IRCZM 89-5116 (cl = 3.6 mm). Scale: *a* = 0.8 mm; *b* = 2.1 mm; *c*, *e*, *g*–*j* = 1 mm; *d* = 238  $\mu$ m; *f* = 1.3 mm.)

herein), and November (Ascension Island, herein).

Lasker noted on his collection labels that males were found free-living on the coral colonies he examined in Panama. This observation may indicate that the male found in the stomach of an apogonid fish from the Tortugas was not picked from out of a dwelling by the fish, but rather taken from the surface of the coral. Schmitt's field notes (archived in the USNM) indicate the fish was collected by dynamiting the reef.

This species has been recorded from 0–0.5 m (present study) to 75 m (Coelho, 1970). Most records are from shallower water.

No parasites were found on the material examined.

**CORAL HOSTS.**—*T. corallicola* shows the least degree of host specificity yet known for any gall crab, Atlantic or Pacific (R.K.K., unpublished; also see Fize and Serène, 1957). Because of this, we feel that host coral group should not be used as a character defining genera, as has been used in the past.

**Astrocoeniidae:** *Stephanocoenia michelinii* Milne Edwards and Haime, 1848, listed by Scott (1985).

**Siderastreidae:** *Siderastrea siderea*, herein.

**Faviidae:** *Diploria clivosa* (Ellis and Solander, 1786), by Scott (1985); *D. strigosa*, by Scott (1985) and herein; *Favia grandidieri*, herein; *Manicina areolata*, by Shaw and Hopkins (1977), Scott (1985), and herein; *Montastrea annularis*, by Scott (1985) and herein; *M. cavernosa*, herein.

**Oculinidae:** *Oculina varicosa* Lesueur, 1820, by Scotto and Gore (1981) and Reed et al. (1982); *Oculina* sp., herein; *Sclerhelia hirtella*, herein.

**Meandrinidae:** *Dichocoenia* sp., by Shaw and Hopkins (1977:179), but not listed in their material examined.

**Mussidae:** *Isophyllia sinuosa*, by Scott (1985) and herein; *Mussa angulosa* (Pallas, 1766), by Shaw and Hopkins (1977:179), but not in their material examined; *Mussismilia hispida tenuisepta* (Verrill, 1901), by Coelho (1966) as *Mussismilia* cf. *tenuisepta*; *Mycetophyllia* sp., herein; *Scolymia lacera* (Pallas, 1766), by Shaw and Hopkins (1977).

**Caryophylliidae:** *Polycyathus* sp., herein.

The dwelling of *T. corallicola* is a cylindrical pit that may

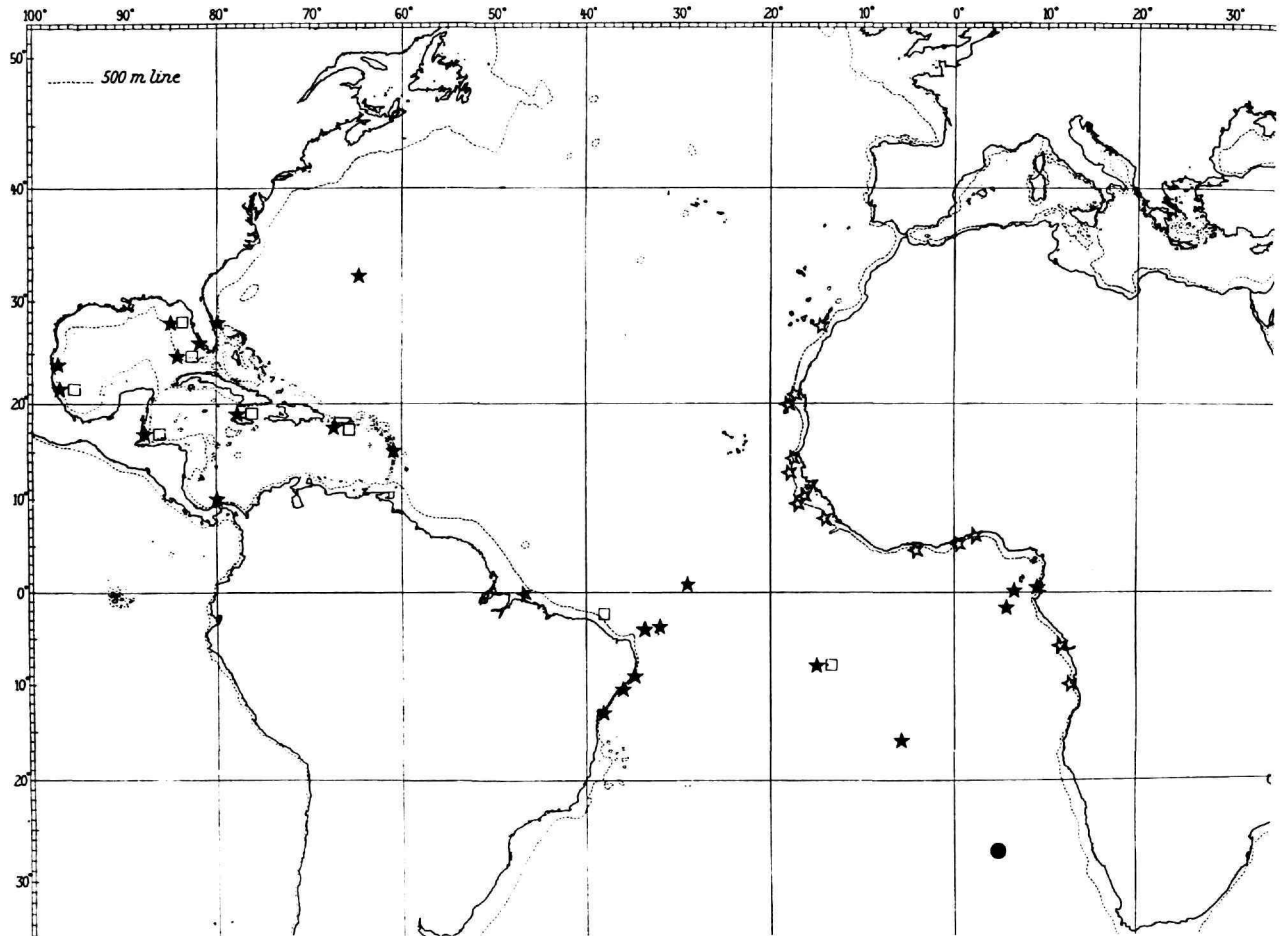


FIGURE 9.—Distribution of Atlantic gall crabs based on material reported here and on previous literature records. (Key: solid circle = *Cecidocarcinus brychius*, new species; star = *Detocarcinus balssi* (Monod); square = *Opecarcinus hypostegus* (Shaw and Hopkins); solid star = *Troglocarcinus corallicola* Verrill.)

be of considerable length (Figure 10a). Dwelling openings are suboval (Figure 10b,c).

**DISTRIBUTION.**—Amphi-Atlantic (Figure 9). *Troglocarcinus corallicola* is the most widely distributed of the Atlantic cryptochirids. In the western Atlantic it has been taken at

localities between Bermuda and southeastern Florida to Brazil. In the central Atlantic it occurs on St. Paul Rocks, Ascension Island, and at St. Helena. In the eastern Atlantic it is known from the islands of São Tomé and Pagalu (= Annobon), and off Gabon.

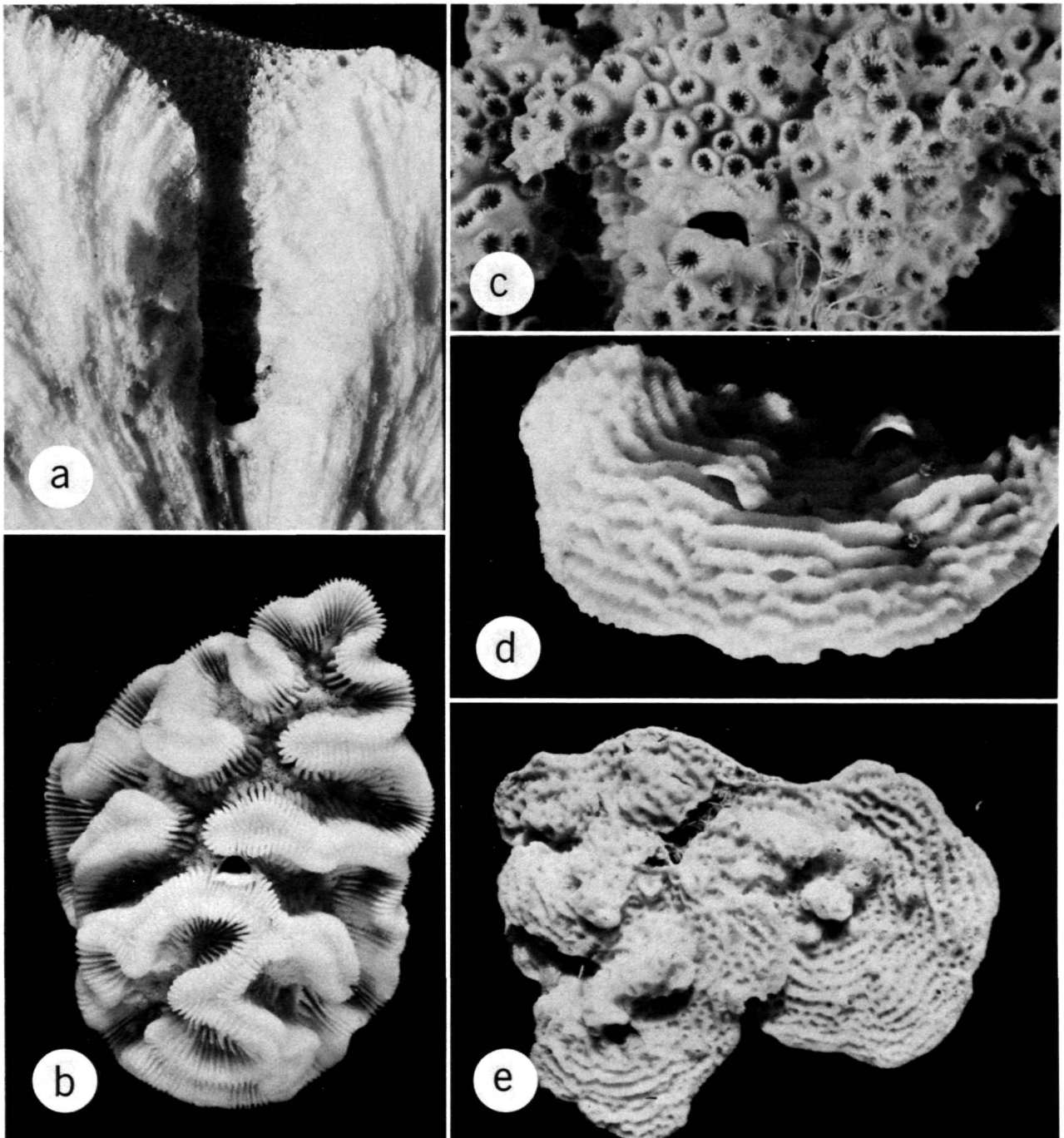


FIGURE 10.—Dwellings of *Troglodactylus corallicola* (a–c) and *Opecarcinus hypostegus* (d,e): a, longitudinal section of pit, Isla En Medio, Mexico; b, opening of dwelling in *Manicina areolata*, Twin Keys, Belize; c, opening of pit in *Oculina varicosa*, Pepper State Park, Florida; d, opening of tunnel in *Agaricia*, Isla En Medio, Mexico; e, tunnels on *Agaricia*, Isla En Medio, Mexico. (a,d,e by D.L. Felder.)



## Literature Cited

- Abele, L.G., and B.E. Felgenhauer  
1982. Decapoda. In S.P. Parker, editor, *McGraw-Hill Synopsis of Living Organisms*, 2:296–326, 14 unnumbered figures. New York: McGraw-Hill Book Company, Inc.
- Abele, L.G., and W. Kim  
1986. An Illustrated Guide to the Marine Decapod Crustaceans of Florida [Parts 1 and 2]. *Florida Department of Environmental Regulation, Technical Series*, 8(1):1–326 [Part 1], 327–760 [Part 2].
- Bak, R.P.M., J.J.W.M. Broun, and F.M.L. Heys  
1977. Regeneration and Aspects of Spatial Competition in the Scleractinian Corals *Agaricia agaricites* and *Montastrea annularis*. *Proceedings of the Third International Coral Reef Symposium, Miami*, 1:143–148.
- Balss, H.  
1922. Decapoda Brachyura (Oxyrhyncha und Brachyrhyncha) und geographische Übersicht über Crustacea Decapoda: Crustacea, VII. In W. Michaelsen, *Beiträge zur Kenntnis der Meeresfauna Westafrikas*, 3(3):70–110, figures 1–5. Hamburg.
- Calman, W.T.  
1900. On a Collection of Brachyura from Torres Straits. *The Transactions of the Linnean Society of London*, second series (Zoology), 8(1):1–50, plates 1–3.
- Coelho, P.A.  
1966. Alguns decápodos novos para Pernambuco e estados vizinhos na Coleção Carcinológica do Instituto Oceanográfico da Universidade Federal de Pernambuco...Segunda lista. *Ciencia e Cultura* (São Paulo), 18(2):139–140.  
1970. A distribuição dos Crustáceos Decápodos Reptantes do Norte do Brasil. *Trabalhos Oceanográficos, Universidade Federal de Pernambuco (Recife)*, 9/11:223–238, figure 1.
- Coelho, P.A., and M.A. Ramos  
1972. A Constituição e a distribuição da fauna de decapodos do litoral leste da América do Sul entre las latitudes 5°NE 39°S. *Trabalhos Oceanográficos, Universidade Federal de Pernambuco (Recife)*, 13:133–236, figures 1–4.
- Crosnier, A.  
1969. Sur quelques Crustacés Décapodes ouest-africains: Description de *Pinnotheres leloeuiffi* et *Pasiphaea ecarina* spp. nov. *Bulletin du Muséum National d'Histoire Naturelle* (Paris), series 2, 41(2):529–543, figures 1–36.
- Edmondson, C.H.  
1925. Marine Zoology of the Tropical Central Pacific: Crustacea. *Bernice P. Bishop Museum Bulletin*, 27:3–62.  
1933. *Cryptochirus* of the Central Pacific. *Bernice P. Bishop Museum Occasional Papers*, 10(5):3–23, figures 1–6, plates 1–4.
- Ekman, S.  
1953. *Zoogeography of the Sea*. xiv + 417 pages, figures 1–121. London: Sidgwick and Jackson.
- Fausto-Filho, J.  
1974. Stomatopod and Decapod Crustaceans of the Archipelago of Fernando de Noronha, Northeast Brazil. *Arquivos de Ciências do Mar*, 14(1):1–35, figure 1.
- Fize, A., and R. Serène  
1955. Note préliminaire sur huit espèces nouvelles, dont une d'un genre nouveau, d'*Hapalocarcinidae*. *Bulletin de la Société Zoologique de France*, 80(5–6):375–378, figures 1, 2.  
1957. Les hapalocarcinidés du Viet-Nam. *Archives du Muséum National d'Histoire Naturelle* (Paris), series 7, 5:1–202, figures 1–44, plates 1–18.
- Garth, J.S., and T.S. Hopkins  
1968. *Pseudocryptochirus crescentus* (Edmondson), a Second Crab of the Corallicolous Family Hapalocarcinidae (Crustacea, Decapoda) from the Eastern Pacific with Remarks on Phragmosis, Host Specificity, and Distribution. *Bulletin of the Southern California Academy of Sciences*, 67:40–48, figures 1–2.
- Gauld, D.T.  
1960. Brachyura: An Annotated Check-List of the Crustacea of Ghana, IV. *Journal of the West African Science Association*, 6(1):68–72.
- Gore, R.H., L.E. Scotto, and J.K. Reed  
1983. Early Larval Stages of the Indo-Pacific Coral Gall-forming Crab *Hapalocarcinus marsupialis* Stimpson, 1859 (Brachyura, Hapalocarcinidae) Cultured in the Laboratory. *Crustaceana*, 44(2):141–150, figures 1–3.
- Heller, C.  
1861. Synopsis der im rothen Meere vorkommenden Crustaceen. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft, Wien*, 11:1–32.
- Hines, A.H.  
1986. Larval Patterns in the Life Histories of Brachyuran Crabs (Crustacea, Decapoda, Brachyura). *Bulletin of Marine Sciences*, 30(2):444–466, figures 1–6.
- Hiro, F.  
1937. *Hapalocarcinus* and *Cryptochirus*: Studies on the Animals Inhabiting Reef Corals, I. *Palao Tropical Biological Station Studies*, 1(1):137–154, figures 1–8, plates 4–6.  
1938. A New Coral-inhabiting Crab, *Pseudocryptochirus viridis* gen. et sp. nov. (Hapalocarcinidae, Brachyura). *Zoological Magazine* (Tokyo), 50:149–151.
- Kropp, R.K.  
1986. Feeding Biology and Mouthpart Morphology of Three Species of Coral Gall Crabs (Decapoda: Cryptochiridae). *Journal of Crustacean Biology*, 6(3):377–384, figures 1–2.
- Kropp, R.K., and Raymond B. Manning  
1985. Cryptochiridae, the Correct Name for the Family Containing the Gall Crabs (Crustacea: Decapoda: Brachyura). *Proceedings of the Biological Society of Washington*, 98(4):954–955.
- Longhurst, A.R.  
1958. An Ecological Survey of the West African Marine Benthos. *Colonial Office, Fishery Publications*, 11:1–102, figures 1–11.
- Manning, Raymond B., and L.B. Holthuis  
1981. West African Brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, 306:1–379, figures 1–88.
- Markham, J.C., and J.J. McDermott  
1981. A Tabulation of the Crustacea Decapoda of Bermuda. *Proceedings of the Biological Society of Washington*, 93(4):1266–1276.
- McCain, J.C., and S.L. Coles  
1979. A New Species of Crab (Brachyura, Hapalocarcinidae) Inhabiting Pocilloporid Corals in Hawaii. *Crustaceana*, 36:81–89, figures 1–3, plate 1.
- McNeill, F.A.  
1968. Crustacea, Decapoda & Stomatopoda. *Scientific Reports, Great Barrier Reef Expedition, 1928–29*, 7(1):1–98, figures 1–2, plates 1–2.

- Milne Edwards, A.  
1862. Faune carcinologique de l'Île de la Réunion, Annexe F de l'ouvrage intitulé: Notes sur l'Île de la Réunion par L. Maillard. In L. Maillard, *Notes sur l'Île de la Réunion (Bourbon)*, pages F1-F16, plates 17-19. Paris.
- Monod, Th.  
1956. Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut Français d'Afrique Noire*, 45:1-674, figures 1-884.  
1963. *Notice sur les titres et travaux scientifiques de Théodore Monod*. 127 pages, 73 figures, 2 plates. Macon.
- Monod, Th., and Ph. Cals  
1970. VI. Sur une espèce nouvelle de crevette cavernicole: *Typhlatya galapagensis* (Decapoda Natantia; Atyidae). *Mission Zoologique Belge aux Îles Galapagos et en Ecuador (N. et J. Leleup, 1964-1965)*, 2:57-103, figures 1-67.
- Paulson, O.  
1875. *Podophthalmata and Edriophthalmata (Cumacea): Studies on Crustacea of the Red Sea with Notes Regarding Other Seas, Part I*. xiv + 144 pages, plates 1-21. Kiev. [Original in Russian. Reprinted 1961, with different pagination, by the Israel Program for Scientific Translations, Jerusalem, 164 pages.]
- Rathbun, M.J.  
1937. The Oxystomatous and Allied Crabs of America. *United States National Museum Bulletin*, 166:vi + 278 pages, figures 1-47, plates 1-86.
- Reed, J.K., R.H. Gore, L.E. Scotto, and K.A. Wilson  
1982. Community Composition, Structure, Areal and Trophic Relationships of Decapods Associated with Shallow- and Deep-water *Oculina varicosa* Coral Reefs: Studies on Decapod Crustacea from the Indian River Region of Florida, XXIV. *Bulletin of Marine Science*, 32:761-786, figures 1-11.
- Richters, F.  
1880. Decapoda. In K. Möbius, *Beiträge zur Meeresfauna der Insel Mauritius und der Seychelles*, pages 139-178, plates 15-18.
- Scott, P.J.B.  
1985. Aspects of Living Coral Associates in Jamaica. *Proceedings of the Fifth International Coral Reef Congress, Tahiti*, 5:345-350.
- Scotto, L.E., and R.H. Gore  
1981. The Laboratory Cultured Zoeal Stages of the Coral Gall-forming Crab *Troglocarcinus corallicola* Verrill, 1908 (Brachyura: Haplocarcinidae) and Its Familial Position: Studies on Decapod Crustacea from the Indian River Region of Florida, XXIII. *Journal of Crustacean Biology*, 1(4):486-505, figures 1-6.
- Serène, R.  
1962. Species of *Cryptochirus* of Edmondson 1933 (Haplocarcinidae). *Pacific Science*, 16:30-41, figures 1-5.  
1966. Note sur la taxonomie et la distribution géographique des Haplocarcinidae (Decapoda-Brachyura). *Proceedings of the Symposium on Crustacea held at Ernakulam, 12-15 Jan 1965, Marine Biological Association of India*, 1:395-398.
- Shaw, J.K., and T.S. Hopkins  
1977. The Distribution of the Family Haplocarcinidae (Decapoda, Brachyura) on the Florida Middle Ground with a Description of *Pseudocryptochirus hypostegus* New Species. *Proceedings of the Third International Coral Reef Symposium, Miami*, 1:177-183, figures 1-3.
- Shen, C.J.  
1936. Notes on the Family Haplocarcinidae (Coral-infesting Crabs) with Descriptions of Two New Species. *Hong Kong Naturalist Supplement*, 5:21-26, plates 1-2.
- Stimpson, W.  
1859. [*Haplocarcinus marsupialis*, a Remarkable New Form of Brachyurous Crustacean on the Coral Reefs at Hawaii]. *Proceedings of the Boston Society of Natural History*, 6:412-413. [Untitled.]
- Takeda, M., and Y. Tamura  
1980a. New Genus *Fizesereneia*: Coral-inhabiting Crabs of the Family Haplocarcinidae from Japan, III. *Bulletin of the National Science Museum (Tokyo)*, series A (Zoology), 6(3):137-146, figures 1-5.  
1980b. Genus *Neotroglocarcinus*: Coral-inhabiting Crabs of the Family Haplocarcinidae from Japan, IV. *Bulletin of the National Science Museum (Tokyo)*, series A (Zoology), 6(3):147-151, figures 1-2.  
1981. Genus *Pseudocryptochirus* and Two New Genera: Coral-inhabiting Crabs of the Family Haplocarcinidae from Japan, VIII. *Bulletin of the Biogeographical Society of Japan*, 36(3):14-27, figures 1-3, plates 1-4.  
1986. Biogeographical Distribution: Coral-inhabiting Crabs of the Family Haplocarcinidae from Japan, XI. *Bulletin of the Biogeographical Society of Japan*, 41(8):61-70, figures 1-9. [In Japanese, with English abstract.]
- Utinomi, H.  
1944. A Revision of the Family Haplocarcinidae (Brachyura), with Some Remarks on Their Morphological Peculiarities: Studies on the Animals Inhabiting Reef Corals, III. *Palao Tropical Biological Station Studies*, 2(4):687-731, figures 1-17, plates 3-5.
- Van Dover, C.L.  
1982. Reduction of Maxillary Endites in Larval Anomura and Brachyura. *Crustaceana*, 43(2):211-215, figure 1.
- Verrill, A.E.  
1908a. Brachyura and Anomura: Their Distribution, Variations, and Habits: Decapod Crustacea of Bermuda, I. *Transactions of the Connecticut Arts and Sciences*, 13:299-474, figures 1-68, plates 9-28.  
1908b. Geographical Distribution; Origins of the Bermudian Decapod Fauna. *American Naturalist*, 42:289-296, figures 1-7.
- Zibrowius, H.  
1976. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. 302 pages, 105 plates. Thesis, L'Université d'Aix-Marseille.  
1980. Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut Océanographique*, Monaco, 11:1-284, plates 1-107.  
1982. Deep-water Scleractinian Corals from the South-western Indian Ocean with Crypts Excavated by Crabs, Presumably Haplocarcinidae. *Crustaceana*, 43(2):113-120, plates 1-2.



## REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

**Manuscripts** intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

**Review** of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

**Copy** must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

**Front matter** (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

**First page of text** should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

**Center heads** of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

**Tabulations** within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

**Formal tables** (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

**Taxonomic keys** in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

**Synonymy** in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

**Text-reference system** (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "... Jones (1910:122)." If bibliographic

footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

**Footnotes**, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

**Bibliography**, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number): pagination: "10(2):5-9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

**Legends** for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

**Illustrations** must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

**Some points of style:** Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun." etc. Omit space between initials of a personal name: "J.B. Jones."

**Arrange and paginate sequentially every sheet of manuscript** in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.



