ABSTRACT

Title of Dissertation: Biology and Systematics of Coral Gall
Crabs (Crustacea: Cryptochiridae)
Roy Karl Kropp, Doctor of Philosophy, 1988
Dissertation directed by: Dr. Geerat J. Vermeij, Professor,
Department of Zoology

The family name of the coral gall crabs was corrected from Hapalocarcinidae Calman, 1900 to Cryptochiridae Paulson, 1875.

Study of the feeding biology of three species of gall crabs, *Favicola rugosa*, *Hapalocarcinus marsupialis*, and *Utinomia dimorpha*, falsified the previous hypothesis that gall crabs were filter feeders on minute plankton. Gall crabs were found to have feeding appendages suitable for gathering coral mucus, not straining food from the water column. Observations of feeding behavior showed that crabs collected coral mucus for food and on occasion snipped off pieces of coral tissue to ingest.

In a review of the Atlantic gall crabs three new genera, *Cecidocarcinus*, *Detocarcinus*, and *Opecarcinus*, and one new species, *C. brychius* were described. Two Atlantic genera, *Detocarcinus* and *Troglocarcinus*, showed little host specificity.

Reexamination of four previously described species clarified some taxonomic confusion. *Cryptochirus*

hongkongensis Shen was shown to be a senior synonym of *Neotroglocarcinus monodi* (Fize and Serène), *Lithoscaptus paradoxus* Milne Edwards was removed from the synonomy of *Cryptochirus coralliodytes* Heller which was redefined, and *Cryptochirus granulatus* Shen was reestablished and transferred to *Opecarcinus*.

The genus *Opecarcinus* from the Pacific was reviewed and found to be comprised of seven species, five of which were new, *O. aurantius*, *O. lobifrons*, *O. peliops*, *O. pholeter*, and *O. sierra*. The genus occured on agariciid and siderastreid corals and was one of two genera reaching the eastern Pacific.

The genera of cryptochirids occurring in the Pacific were reviewed. *Fizesereneia* Takeda and Tamura was determined to be based on a misidentified type species and the situation referred to the International Commission on Zoological Nomenclature. Four new genera were established, *Dacryomaia*, *Pelycomaia*, *Sphenomaia*, and *Xynomaia*. Each genus is diagnosed and a list of known species and hosts for each is included.

Cladistic techniques were used to determine possible relationships of the gall crabs. These results were then compared to the relationships of the coral hosts. A trend was discovered that showed the evolution of the cryptochirids has been toward colonization of hosts providing increasinly safe palces to live. The most ancestral crabs occur on relatively nonaggressive corals, whereas derived crabs live on relatively predator and competition resistant hosts.

BIOLOGY AND SYSTEMATICS
OF CORAL GALL CRABS
(CRUSTACEA: CRYPTOCHIRIDAE)

by

Roy K. Kropp

Dissertation submitted to the faculty of the Graduate
School of the University of Maryland in partial
fulfillment of the requirements for the
degree of Doctor of Philosophy
1988

Advisory Committee:

Professor Geerat J. Vermeij
Associate Professor David W. Inouye
Associate Professor Marjorie L. Reaka
Associate Professor Charles Mitter
Adjunct Professor Raymond B. Manning

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PROLOGUE

Since the first gall crab, *Hapalocarcinus marsupialis*, was described by Stimpson (1859) biologists have been fascinated with the peculiar lifestyle of these diminutive crustaceans. Most gall crabs are small. One species, in which mature females only reach about 3 mm in carapace length, may replace a pea crab as the smallest known brachyuran crab (Bell, 1987). Gall crabs live as obligate symbionts of scleractinian corals. The crabs reside in modifications of the host skeleton that result from activities of the crab. These range from the totally enclosed gall inhabited by *H. marsupialis*, which has only a few small openings to allow for water exchange, to simple cylindrical pits inhabited by a variety of gall crabs (Hiro, 1938).

Although the exact relationship of gall crabs to other brachyurans is not known, the family itself is well-defined. This attribute, in addition to the obligatory (from the crab point of view) nature of the symbiosis make the relationship between corals and the gall crabs desirable to study.

The present study was undertaken to: (1) establish a nutritional basis for the symbiosis, i. e., the crabs depend on the hosts for nutriment in addition to shelter; (2) restructure the taxonomic arrangement of the family using morphological characters; (3) correct errors made by previous taxonomists; and (4) reconstruct a hypothetical phylogeny of the family and compare that phylogeny to the relationships of the hosts in order to investigate the distribution of the symbionts on the hosts.

Each chapter is written addressing a particular problem concerning the biology and systematics of the coral gall crabs and is designed to be ready for publication, hence each has its own abstract, methods, reference sections, and so on.

The first chapter reestablishes the name of the family as the Cryptochiridae Paulson, 1875, which has priority over the more familiar Hapalocarcinidae Calman, 1900.

The second chapter addresses the feeding biology of three species of gall crabs, testing the old hypothesis that the crabs were filter feeders on plankton. In this chapter a nutritional basis for the symbiosis between crabs and corals is established.

The third through eighth chapters are concerned with a series of taxonomic problems, which include an evaluation of some species that have for many years been considered synonyms of other species. Also included are separate revisions of the genera of gall crabs occurring in the Atlantic Ocean and those occurring in the Pacific Ocean. The only genus of gall crabs that is found in both the Atlantic and Pacific is reviewed and found to consist of eight species, five of which were previously unknown to science.

The final chapter presents a suite of morphological characters that are used to construct a hypothetical phylogeny of the family. The results of the cladistic analyses are compared to probable relationships of the host corals, in addition to other attributes such as host commonness and level of aggression, in an attempt to determine the factors contributing to the distribution of the symbionts on the host taxa.

This dissertation is not a valid publication for formal taxonomic purposes and the names of new taxa described herein are not available.

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Stimpson, W. 1859. [*Hapalocarcinus 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].

Chapter 1

Cryptochiridae, the Correct Name for the Family Containing the Gall Crabs (Crustacea: Decapoda: Brachyura)

Abstract.--Cryptochiridae Paulson, 1875, is shown to be a senior synonym of Hapalocarcinidae Calman, 1900.

Until now, most authors have assigned the gall crabs, members of the genera *Cryptochirus* Heller, 1861, *Hapalocarcinus* Stimpson, 1859, *Troglocarcinus* Verrill, 1908, and several others, to the family Hapalocarcinidae Calman, 1900. Manning and Holthuis (1981:250), who summarized the names applied to families of marine brachyuran crabs, cited Calman as author of the family name.

However, a different family group name was used by at least three different authors prior to 1900. O. Paulson (1875:78) introduced the subfamily Cryptochirinae within the family Pinnotheridae for the genus *Lithoscaptus* A. Milne-Edwards, 1862, now a synonym of *Cryptochirus* Heller, 1861. Paulson, who may not have been aware that Heller's account was published before that of Milne-Edwards, actually considered *Cryptochirus coralliodytes* Heller to be a junior synonym of *Lithoscaptus paradoxus*, whereas the reverse is true. Later, F. Richters (1880:159) cited the family Cryptochiridae. He recognized that *Lithoscaptus paradoxus* A. Milne-Edwards, 1862 was a synonym of *Cryptochirus* *coralliodytes* Heller, 1861 and synonymized the former. He erroneously attributed the family name Lithoscaptidae to A. Milne-Edwards. As pointed out by Manning and Holthuis (1981:250), Milne-Edwards used a name in the French vernacular for the family.

E. von Martens, in the *Zoological Record* for 1880, cited the "Cryptochiridae" on p. 30, and noted that Richters had proposed the family but had not characterized it.

Calman (1900:48) recognized that Paulson had used the family group name Cryptochirinae, and, on p. 49, noted "we can only regard these two genera [*Cryptochirus* and *Hapalocarcinus*] as forming a family for the present *incertae sedis*, for which the name Hapalocarcinidae will have to replace Milne-Edwards's "Lithoscaptes", the latter being based on a synonym of *Cryptochirus*."

The synonymy for the family Cryptochiridae Paulson, 1875, is as follows:

Lithoscaptes A. Milne-Edwards, 1862:F10 [vernacular name; type-genus *Lithoscaptus* A. Milne-Edwards, 1862].

Cryptochirinae Paulson, 1875:77 [type-genus *Cryptochirus* Heller, 1861].

Hapalocarcinidae Calman, 1900:49 [type-genus *Hapalocarcinus* Stimpson, 1859].

The superfamily name (see Bowman and Abele, 1982 for a summary of crustacean classification to the family level) becomes Cryptochiroidea Paulson, 1875.

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Chapter 2

Feeding Biology and Mouthpart Morphology of Three Species of Coral Gall Crabs (Decapoda: Cryptochiridae)

ABSTRACT

This study refutes the long-standing hypothesis that coral gall crabs are filter feeders. *Hapalocarcinus marsupialis* collected mucus by fanning the third maxillipeds or by scratching the coral with the legs. *Utinomia dimorpha* used chelipeds to collect mucus and other debris, or to snip pieces of coral tissue. *Favicola rugosa* used mouthparts and chelipeds to make a mucous ball and sweep it along the coral surface to pick up mucus and debris. SEM photographs of the mouthparts of each species show setae illsuited for filter feeding, but useful for collecting coral mucus.

Coral gall crabs have been known for over 100 years, yet cryptochirid feeding biology is poorly known. Stimpson (1859) described *Hapalocarcinus marsupialis* as free-living, but feeding on coral polyps. Verrill (1867) considered the crabs parasitic on corals. Henderson (1906), finding live polyps in the gall, discounted Stimpson's idea that *Hapalocarcinus* fed on coral tissue. Potts (1915) presumed that gall crabs fed on nannoplankton drawn through the holes in the gall by the respiratory currents of the crabs.

Potts' ideas have been cited frequently (Hiro, 1937; Marshall and Orr, 1960; Patton, 1967; Castro, 1976; Barnes, 1980; McLaughlin, 1982).

There are indications that Potts' ideas are not valid. Patton (1976) briefly mentioned that *Hapalocarcinus* picked at coral tissue with its chelipeds and passed the material to its mouthparts. Reed *et al*. (1982) listed *Troglocarcinus corallicola* as an obligate coral mucus-feeder.

Here I clarify cryptochirid feeding biology by using anatomical studies to determine the food gathering apparatus available to the crabs, and behavioral studies to describe feeding activities. These studies showed that the crabs do not filter feed, but collect food from their host corals.

MATERIALS AND METHODS

Collection Data.--I collected crabs on their host corals at Apra Harbor, Luminao, and Agana Bay, Guam during 1979-1981 and 1984. Crabs and corals were kept in the laboratory in large, flow-through seawater tanks. I collected *Hapalocarcinus marsupialis* Stimpson, 1859 on *Pocillopora damicornis* and *P. eydouxi*; *Utinomia dimorpha* (Henderson, 1906) on *P. eydouxi*; and *Favicola rugosa* (Edmondson, 1933) on *Leptoria phyrgia*.

Feeding Behavior.--I used a dissection microscope to observe crabs feeding in their dwellings on small pieces of the host coral placed in a dish of sea water. Light from the microscope illuminator did not appear to affect crab behavior. It was necessary to remove the growing edge of *Hapalocarcinus* galls to observe the crabs feeding, but not necessary to alter dwellings of the other crabs. Feeding was observed for at least 14 twenty-minute periods per species. To test the results of feeding motions, I put a few drops of a carmine suspension in seawater onto the coral surface adjacent to the crab dwelling. Carmine rapidly coagulated into the mucous strings permitting observation of mucus movement patterns.

Scanning Electron Microscopy.--Crabs collected in 1984 were fixed in 3% Glutaraldehyde and stored in 70% ETOH. I removed feeding appendages from these crabs and cleaned the appendages by brushing them with a fine brush. The gastric mill was removed from crabs, cut lengthwise along the ventral surface, and cleaned by gentle water currents created by passing a brush above the mill. Structures were dehydrated in a graded ethanol series, air dried, sputter coated with gold-palladium, and observed with a Cambridge S-100 or S-250 scanning electron microscope at accelerating voltages of 10-20 kv.

RESULTS

Crab Dwellings

Hapalocarcinus lives enclosed in a coral skeleton gall. Water circulates through the gall via small holes along the suture line between gall halves. The inside of the gall is lined with living coral tissue.

Utinomia lives in a pit in the coral skeleton. Surrounding the pit is a narrow border zone of dead coral in which brown, flocculent debris accumulates and in which filamentous algae may occur. Coral verrucae next to the zone are eroded.

A narrow border zone of dead coral surrounds pits inhabited by *Favicola*. The host calice wall completely surrounds the pit with the long axis of each septum perpendicular to the pit.

Feeding Behavior

Hapalocarcinus used chelipeds to grab coral tissue and pull it to the mouth, to pick mucous flocs off the coral, and to scoop material along the coral surface toward the buccal area. After such motions, the setae of the palp of the third maxillipeds wiped accumulated mucus from the chelipeds. Alternate or simultaneous third maxilliped fanning episodes, usually less than 30-s long, drew carmine-marked mucus to the mouth. The legs assisted feeding by vigorously shaking in a plane perpendicular to the coral surface, thus actively scratching the dactylus on polyps causing mucus to accumulate on the hooked setae of the dactylus. The chelipeds then picked the material off the dactylus and transferred it to the mouth. Usually only one leg shook at a time. Sometimes, after a shaking episode, the dactyli of two adjacent legs rubbed together casting accumulated material into the water near the crab. Fanning of the third maxillipeds pulled this debris to the mouth.

Utinomia used chelipeds to pick debris from its body or the wall of the pit and to grab debris from the border zone around the pit. Crabs snipped and ingested small pieces of tissue from the coenosteum fringing the border zone or from polyps. The chelipeds also probed the border zone or adjacent coral tissue then flexed rapidly toward the mouth. Occasionally the claw squeezed coral tissue, then flexed toward the mouth. This scooping motion, followed by maxilliped fanning, moved mucous strings that had accumulated in the border zone to the mouth. Rarely, the chelipeds pulled mucus into a bolus that was eventually carried to the mouth and manipulated by the maxillipeds. This was similar to that described in detail for *Favicola*. Sometimes the third maxillipeds fanned independently of any cheliped action. The results of this fanning were unclear, but did not pull mucus to the mouth.

Favicola, other than one instance when a crab ingested a piece of coral tissue, used only one method to gather food. The chelipeds or maxillipeds pulled mucus into a bolus. One cheliped then clutched the bolus, swept it along the edge of the pit and back to the starting point, then transferred it to the other cheliped which repeated the action. After 2-31 repetitions of this criss-cross pattern, the bolus was taken to the mouth where it was rotated by the third maxillipeds while being vigorously probed by setae of the second maxilliped exopod. The crab grabbed the bolus with a claw and repeated the criss-cross pattern or expelled the bolus and formed a new one. Mucous strings, moved to the pit by coral ciliary action, were incorporated into the bolus being swept along the pit border by the criss-cross action of the claws.

Feeding Structures

Setal terminology is based on Kunze and Anderson (1979).

Maxillipeds.--The third maxillipeds (Fig. 1a) are similar in all three species. The inner margin of the ischium has few relatively short, simple setae along its entire length and also has scattered serrate setae on its upper half (Fig. 1b). The palp of the third maxilliped has clumps of serrate setae on the carpus, dactylus, and along the inner margin of the propodus. Serrate setae may have distal setules forming a slight spoon (Fig. 1c), or setules terminating proximal to the sharply-pointed tip (Fig. 1d). Spoon-tipped setae are more numerous in each cluster.

The endopod of the second maxilliped has sharply-pointed serrate setae distally on the dactylus, whereas spoon-tipped serrate setae occur on the dactylus and propodus upper margins (Fig. 1e). *Favicola* has fewer setae than the other two species.

The basipodite of the first maxilliped has serrate setae on the inner margin (Fig. 1f).

Maxillae.--The second maxilla is a finger-like process with simple setae distally (Fig. 1g). The protopodite of the first maxilla is undivided and has serrate setae on the inner margin in *Hapalocarcinus* and *Utinomia* (Fig. 1g). These setae are longer dorsally, decreasing in length ventrally. *Favicola* has multiple rows of conate tubercles along the inner margin and two serrate setae and one simple seta dorsally (Fig. 1h).

Gastric Mill.--Only the urocardiac and zygocardiac ossicles are present. All three species have similar median teeth, each consisting of two lateral rows of setiform projections separated by a narrow region of shorter projections or scales (Fig. 2a). The lateral teeth are entirely setiform in *Favicola*; mostly setiform, but with bluntly-rounded papillae in *Hapalocarcinus* (Fig. 2d); and mostly setiform with rounded "cusps" in *Utinomia* (Fig. 2c).

DISCUSSION

None of the cryptochirid species studied has the classical filter-feeding setal net described by Marshall and Orr (1960). Filtering nets found among decapods include the plumose third maxillipeds of porcellanids (Nicol, 1932; Caine, 1975), the plumose antennae of *Paguritta* (see Schuhmacher, 1977), or the plumose net on the chelae of *Atya* (see Felgenhauer and Abele, 1983b). The only feeding structures of gall crabs are the pincer-like chelae and the third maxillipeds which have simple or serrate setae.

Plumose nets may be used for deposit feeding by porcellanids (Kropp, 1981) or atyids (Felgenhauer and Abele, 1983b), but most deposit-feeding decapods use a nonplumose feeding structure. Ocypodid crabs have spoon-shaped setae on the first and second maxillipeds (Miller, 1961; Vogel, 1984) and hermit crabs have simple or serrate setae on maxillipeds (Kunze and Anderson, 1979). Farmer (1974) suggested that simple and serrate setae may be used for gripping food. The maxillipeds of gall crabs are appropriate for gathering soft detrital material such as coral mucus. These maxillipeds are similar to those of *Trapezia*, also a mucus-feeder (Knudsen, 1967).

The teeth of the gastric mills of the three cryptochirid species differ from those of other crabs. For example, the typically brachyuran lateral teeth of *Trapezia* consist of two to three anterior cusps and a posterior series of transverse, flattened ridges (Fig. 2b), whereas gall crabs have mostly setiform lateral teeth. This contrast may support the idea that phylogeny determines mill structure more than diet (Felgenhauer and Abele, 1983a). However, cryptochirids show a range of variation from lateral teeth having what may be remnant cusps and setiform projections (*Utinomia*) to teeth lacking cusps altogether (*Favicola* and *Hapalocarcinus*). *Utinomia* has a high likelihood of having some coarse particles in its diet, and has relatively robust lateral teeth. However, *Favicola* may also ingest coarse material, but has setiform lateral teeth. The relative role of relationship or diet to the structure of the gastric mill remains unclear in this case.

My observations show that gall crabs collect food, including coral mucus and tissue, from the surface of the host. No filter feeding was observed, but it is possible that maxilliped fanning could have been misinterpreted by others as filter feeding. Fanning did not pull particles from the water column, but drew mucous strings to the mouth.

Many animals feed on living corals, some inflicting serious damage (Chesher, 1969; Moyer et al., 1982). Coral mucus is an important food item for organisms such as bacteria (Ducklow and Mitchell, 1979b), zooplankton (Johannes, 1967; Richman *et al.*, 1975), molluscs (Robertson, 1970), crustaceans (Knudsen, 1967), and fish (Benson and Muscatine, 1974).

Uncontaminated mucus consists primarily of acidic mucopolysaccharides (Goreau, 1956) and wax esters (Benson and Muscatine, 1974; Benson *et al.*, 1978). Daumas and Thomassin (1977) and Ducklow and Mitchell (1979a) found glycine, serine, glutamic acid, and aspartic acid to be the most abundant amino acids in coral mucus. Krupp (1982) cautioned that pure coral mucus may be a poor nutrient source, at least in the case of *Fungia scutaria*. However, coral mucus rapidly becomes contaminated with organic material resulting in a mucus high in nitrogen and phosphorus (Coles and Strathmann, 1973; Benson, *et al.*, 1978; Ducklow and Mitchell, 1979a). *Utinomia* and *Favicola* feed on contaminated mucus from border zones. Therefore, studies of purified mucus or of mucus taken from whole colonies do not accurately estimate the dietary intake of these mucus-feeders. Coral mucus may represent a detrital food pathway along which the products of photosynthesis by coral-associated zooxanthellae can be transferred to other members of the reef community.

Because gall crabs feed on their hosts it is tempting to consider them as parasites. Corals, however, continuously exude mucus as part of a sediment rejection system (Abe, 1938). Therefore ingestion of mucus by cryptochirids does not represent a metabolic drain on the host. Other effects of gall crabs on corals are unknown and represent future research possibilities.

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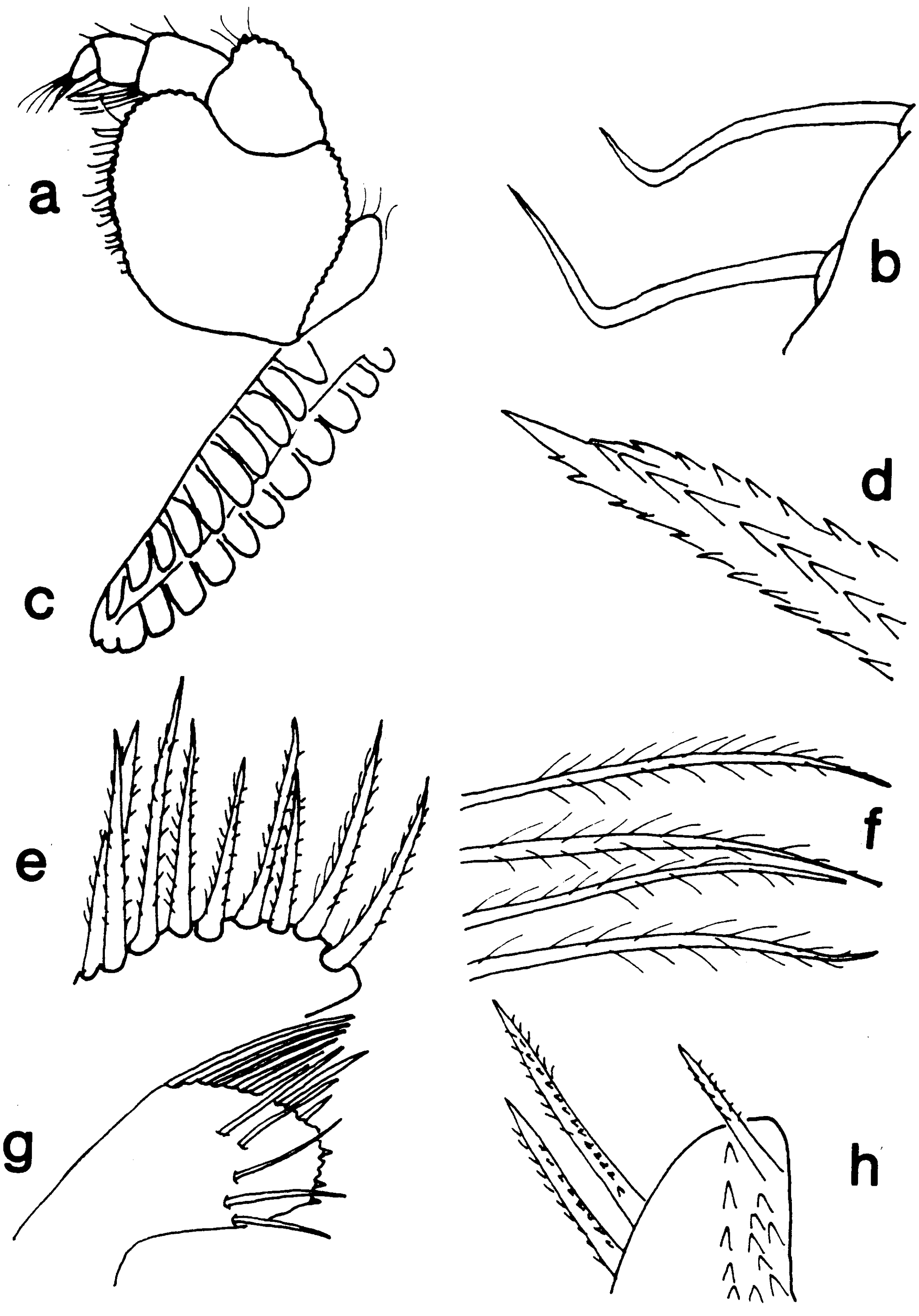
Fig. 1. Selected mouthpart morphology. a, *Favicola rugosa*, third maxilliped; b, *F. rugosa*, setae on inner lower margin of third maxilliped; c, *Hapalocarcinus marsupialis*, seta on palp of third maxilliped; d, *Utinomia dimorpha*, setae on palp of third maxilliped; e, *U. dimorpha*, setae on endopod of second maxilliped; f, *U. dimorpha*, setae on endopod of first maxilliped; g, *U. dimorpha*, first maxilla (upper) and second maxilla (lower); h, *F. rugosa*, upper part of first maxilla. Scales: a = 200 um; b, h = 20 um; c, d = 5 um; e, f = 50 um; g = 100 um.

Fig. 2. Lateral and median teeth of the gastric mill. a, *Favicola rugosa*, median tooth; b, *Trapezia ferruginea*, right lateral tooth; c, *U. dimorpha*, left lateral tooth; d, *Hapalocarcinus marsupialis*, left lateral tooth. Scales: a, = 100 um; b-d = 50 um.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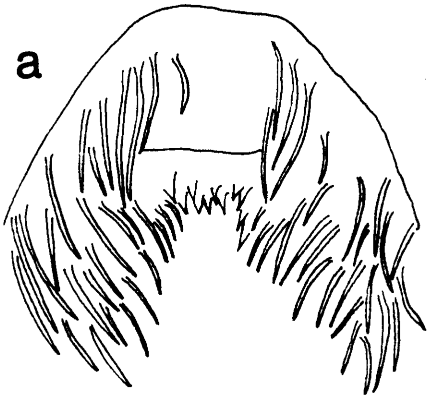

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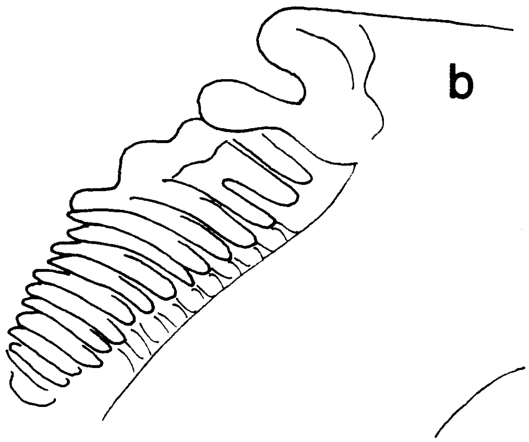

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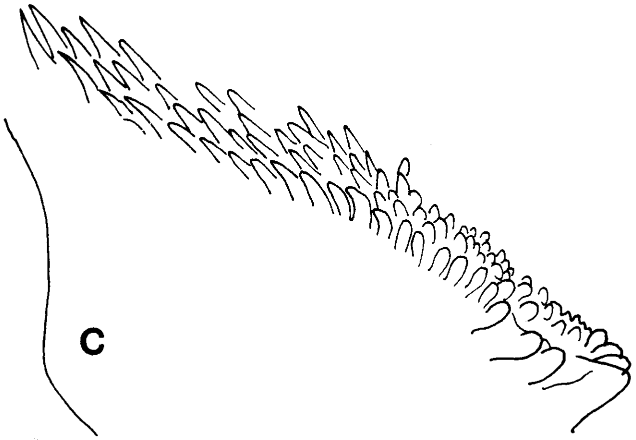

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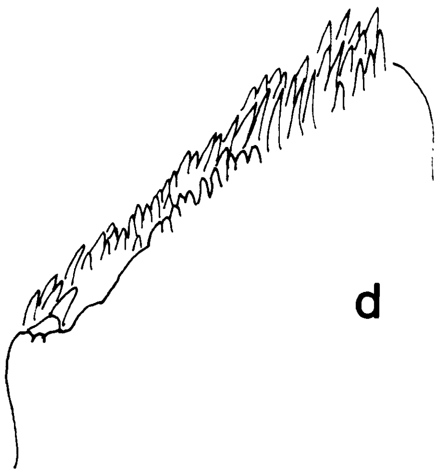

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Chapter 3

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

ABSTRACT

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. *Pseudocrytochirus 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, caryophylliid, and dendrophylliid 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.

Introduction

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 these adaptations are a diminution in size: the largest male I 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 lived 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 I report here, *Troglocarcinus corallicola* Verrill, 1908, is a generalist, and 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 I 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, I introduce here a suite of generic characters, based on the features of adult specimens, that I believe can be used to characterize other genera in the group. I 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 few, easily seen characters.

The Cryptochiridae comprises the following 12 genera:

Hapalocarcinus Stimpson (1859:412)
Cryptochirus Heller (1861:19) [with *Lithoscaptus* Milne Edwards (1862:362) as its synonym]
Troglocarcinus Verrill (1908:427) [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)
Fizesereneia 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 fit into any of these genera. I 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. I 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 loaned 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. I have enclosed in brackets coordinates not given in the original collection data. These coordinates were determined from gazeteers 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 within 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) x 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 my 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.--I thank all of the individuals named above who lent to me or provided me with material. H. Zibrowius is due special thanks for his efforts to find cryptochirids from a variety of corals and for providing references. I acknowledge with thanks the help of Steven Cairns, Smithsonian Institution, with 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.

I am 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.--Coêlho 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. Gastric mill with only lateral and median teeth. 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. My 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 I 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. I have confirmed these observations for specimens from Micronesia and in my opinion this diminishes the value of pleopod one 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 balssi*, 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 the second pleopod is uniramous.

Cecidocarcinus brychius, new species

Figures 3, 4

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).

Description.--*Adult Female* (Figure 3): 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 1/4 width at anterolateral angles, latter about 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. Fingers as long as dorsal margin of palm; cutting edges unarmed. Dorsal margin of palm with 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 more slender than that of previous leg. 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 summarized in Table 1.

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

Male (Figure 4): 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 meral projection. Sides of abdomen subparallel; telson suboval. PLP-1 as for genus.

Size Range.--Males, 4.1 x 3.2 mm and 4.2 x 3.3 mm; ovigerous females, 4.8 x 4.4 mm and 5.2 x 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 x 4.2 mm, in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., under catalogu 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 dendrophylliid 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 11).

Detocarcinus, new genus

Definition.--Carapace longer than broad, not deflected anteriorly, widest posteriorly. 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 resmblance 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 5, 6

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, 19I, 82I; 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 between 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 *Asterosmilia 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 5): 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 projection with 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. Fingers longer than dorsal margin of palm, cutting edges 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; 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 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 6): 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 x 3.5 mm to 3.3 x 2.8 mm; females, 1.7 x 1.6 mm to 4.7 x 4.3 mm; ovigerous females, 2.2 x 2.0 mm to 4.7 x 4.3 mm.

Type.--The holotype is a mature female, 3.5 x 3.0 mm, housed in the British Museum (Natural History), under catalogue 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 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. I found no evidence of a rhizocephalan parasite on this infected female.

Coral Hosts.--*Detocarcinus balssi* has been in association with the following corals:

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

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

Caryophylliidae: *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.

Dendrophylliidae: *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 was in error, as this species is not 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*.

Distribution.--Eastern Atlantic, off West Africa, from localities between the Canary Islands southward to Angola (Figure 11).

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°, 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* *crescentus* (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 western Atlantic genera in having the front of the carapace noticeably deflected ventrally and in having a uniramous second pleopod 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 7, 8

Troglocarcinus corallicola.--Coêlho, 1966:140 [part?] [Not *T. corallicola* Verrill, 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* [= *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, fore reef 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 7): 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 carapace width at anterolateral angles, latter about 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 tubercules, with smaller tubercles posteriorly.

Chelipeds (P-1) equal, merus not extending beyond anterolateral angle of carapace. Fingers shorter than dorsal margin of palm, cutting edges unarmed; dactylus with proximal tubercle on dorsal margin. 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 and produced ventodistally, 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 ca. 90° 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 8): Similar to female, smaller; carapace smoother. Chelae proportionally more robust than in female; fingers shorter than dorsal margin of palm, cutting edge of dactylus may have proximal tooth. Dactli of P 2-5 more slender than female.

Juveniles: Not significantly different from adults.

Size Range.--Males, 1.4 x 1.3 mm to 3.4 x 2.6 mm; females, 1.6 x 1.3 mm to 5.8 x 3.5 mm; ovigerous females, 2.1 x 1.4 mm to 5.4 x 3.4 mm.

Types.--The holotype ia an adult female, 3.8 x 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 on by Shaw and Hopkins (1977) are in the collections of the Dauphin Island Sea Lab, Dauphin Island, Alabama. John Garth and Janet Haig pointed out to me that paratype material is also in the collection of the Allan Hancock Foundation, Los Angeles, California. I 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, 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. I 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).

Coêlho lists 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, I tentatively include part of Coêlho's records here.

The dwelling of *O. hypostegus* 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 along time to close completely and ultimate closure could by 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 the usual coral regenerative process.

Remarks.--*Opecarcinus hypostegus* differs from the Pacific *O. crescentus* by having fewer, smaller tubercules 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, probably Brazil, and from Ascension Island (Figure 11).

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, "Pareille 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'etait valable que parce qu'Utinomi (1944) considerait 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* 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 second pleopod 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 9, 10

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.--Coêlho, 1966:140.--Garth and Hopkins, 1968:40.--McNeill, 1968:87.--Coêlho, 1970:234 [no material].--Coêlho 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, figs. 1-6.--Reed et al., 1982:761, 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.

Troglacarcinus coralliocola.--Edmonson, 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.

Trogrocarcinus 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.--Scott, 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].

Pseudocryptochirum 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] (Coêlho, 1966, 1970; Coêlho 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, VIII-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, *A. maculatus* (Poey, 1861) [as *Apogon 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 1925, 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) (USNM).

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), *Mycetophyllia* sp. (USNM).

Curacao: 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 female 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 19835 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. gravida* (USNM).

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

Pagalu 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. gravida* (USNM). On right side of village (Nizery sta 2), 3-8 m, J. Laborel, 18 Jan 1971, 9 females on *F. gravida* (USNM).

Description.--*Adult Female* (Figure 9): 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. Fingers longer than dorsal margin of palm. Dactylus usually with low tooth in basal fourth; dorsal margin smooth. 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) much the 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 10): 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. Fingers longer than dorsal margin of palm, with basal tooth on dactylus; 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. PLP 1 simple, as for genus.

Juveniles (Figure 10b): 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 x 1.4 mm to 3.1 x 2.6 mm; females, 1.4 x 1.3 mm to 5.2 x 3.9 mm; ovigerous females, 2.5 x 1.9 mm to 5.2 x 3.9 mm. Verrill (1908a) reports a female 7.0 x 4.0 mm.

Type.--Verrill (1908a) did not originally designate a holotype. He reported on specimens from Bermuda and Dominica. Rathbun (1937) reported 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 I 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. It is a preovigerous female, 2.4 x 1.8 mm, having an abdomen not fully expanded to form the typical marsupium. The specimen in 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, Curacao, 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 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 (Coêlho, 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 Serene, 1957). Because of this, I 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 gravida*, 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 Coêlho (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 be of considerable length. Dwelling openings are suboval.

Distribution.--Amphi-Atlantic (Figure 11). *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.

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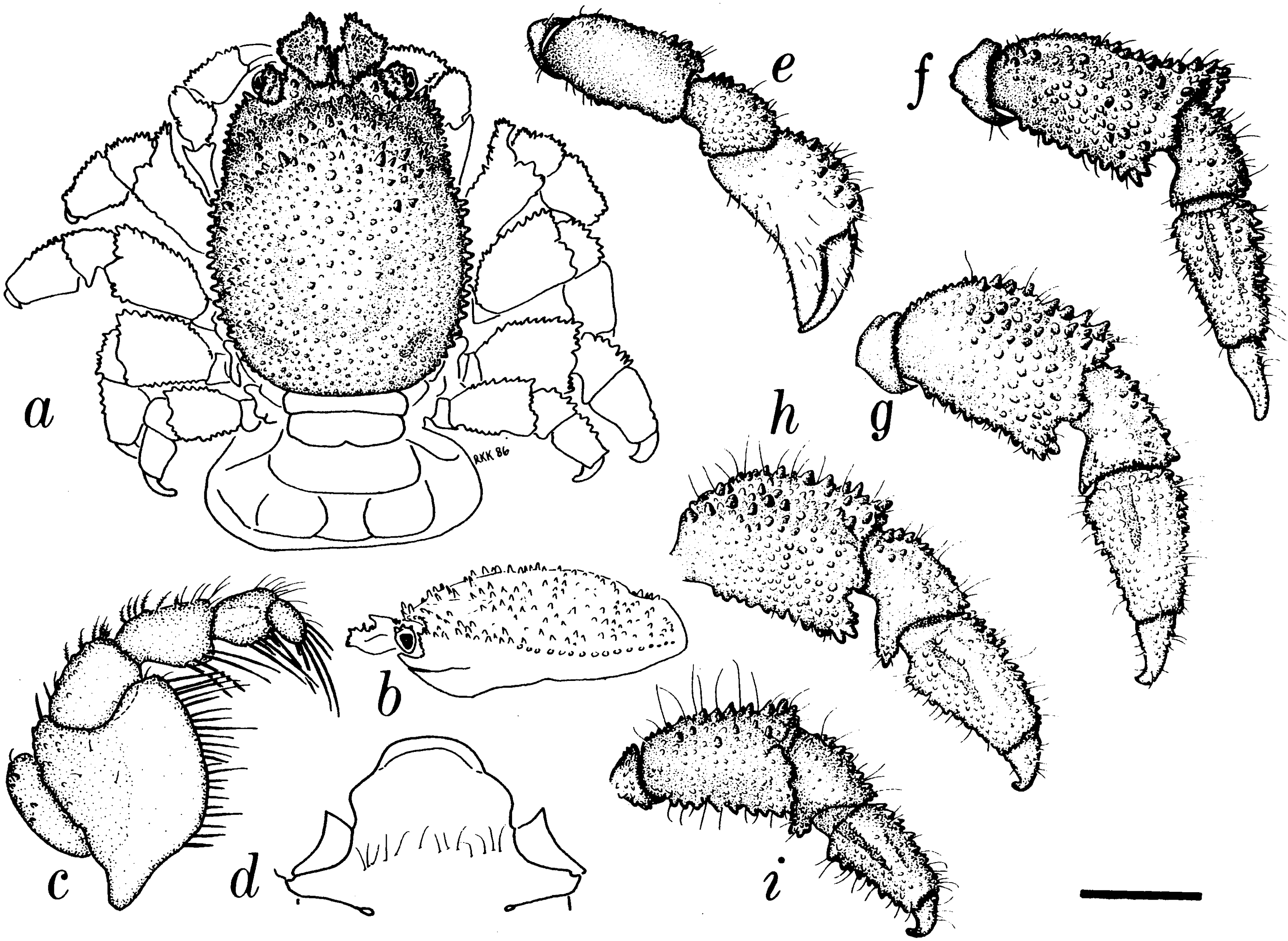
Table 1. Length:height ratios for meri and propodi of Atlantic gall crab walking legs. Cb = *Cecidocarcinus brychius*; Db = *Detocarcinus balssi*; Oh = *Opecarcinus hypostegus*; Tc = *Troglocarcinus corallicola*.

	Cb	Db	Oh	Tc
Merus				
P 2	1.6	1.5	1.7	1.7
P 3	1.6	1.4	1.5	1.6
P 4	1.4	1.4	1.5	1.6
P 5	1.5	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	1.8	1.9	1.6	1.9
P 5	1.6	2.2	2.4	3.1

Figure 3. *Cecidocarcinus brychius*, new species, female. *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.)

Figure 4. *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 um; *h* = 95 um.)

Figure 5. *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.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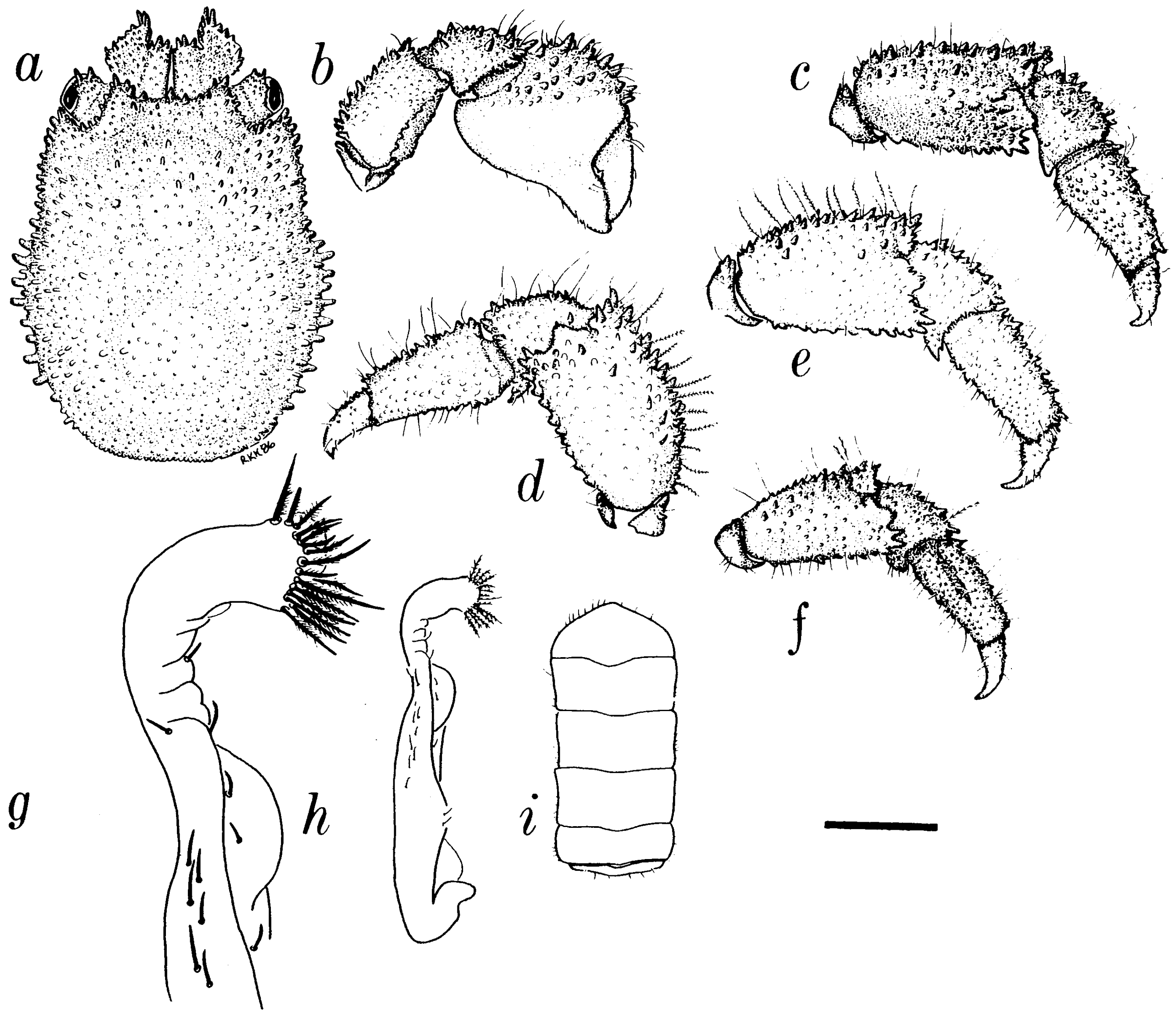
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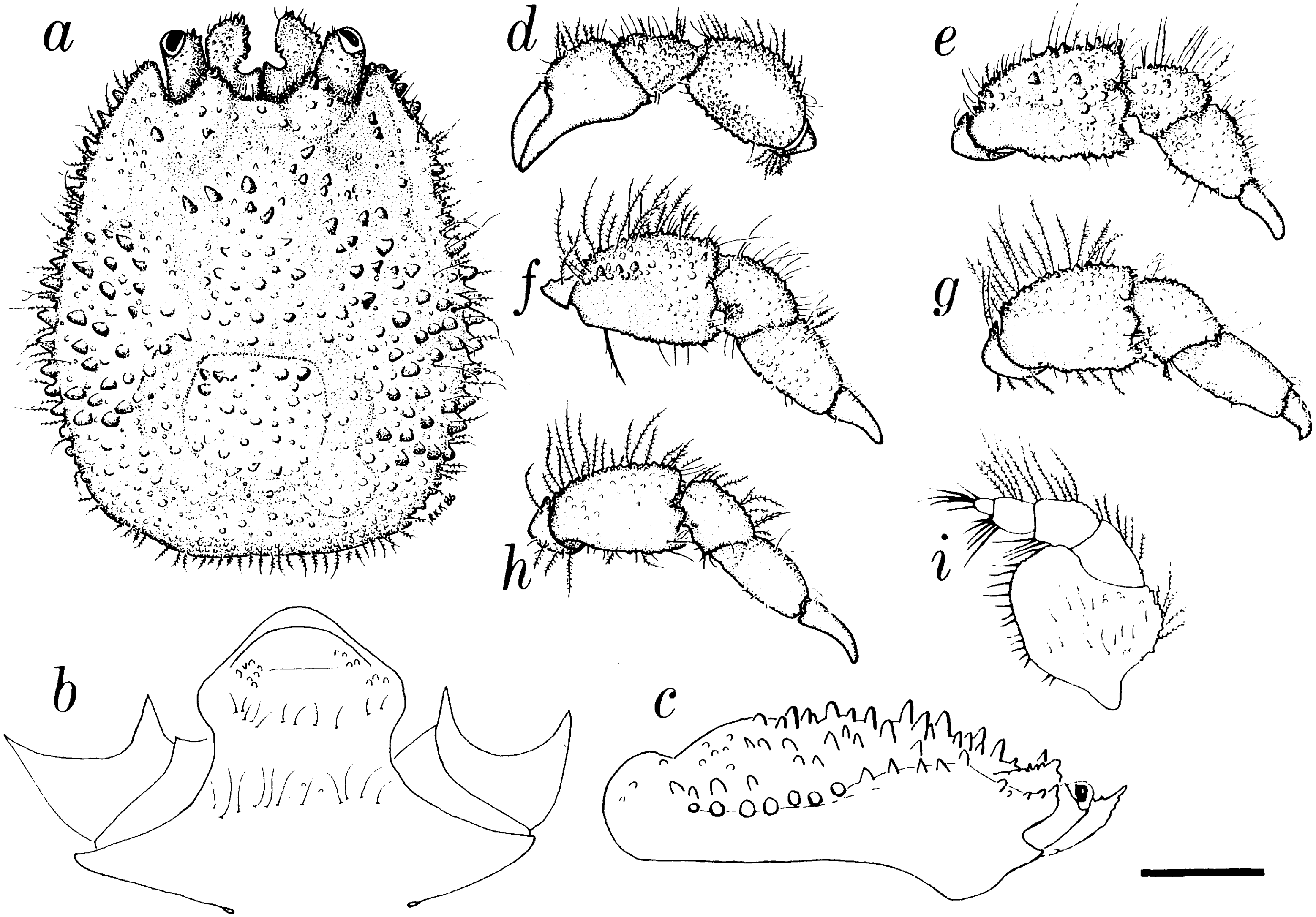
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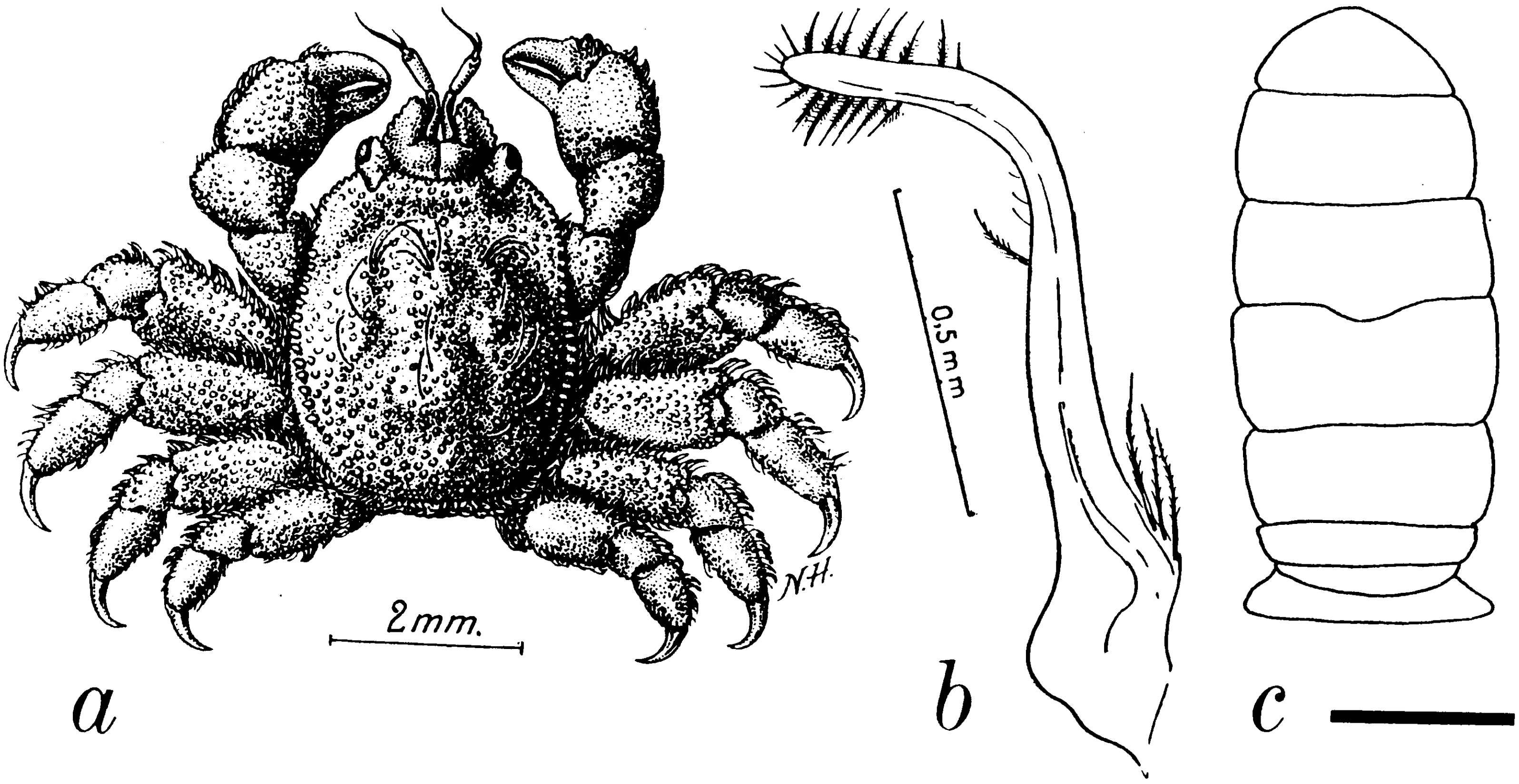
Figure 6. *Detocarcinus balssi* (Monod), male. *a*, dorsal view of paratype; *b*, PLP-1; *c*, abdomen. (*a,b* from Monod, 1956; *c*, Ghana, USNM 231665. Scale: *c* = 0.5 mm.)

Figure 7. *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.)

Figure 8. *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*, USLZ 2708. Scale: *a* = 0.8 mm; *b,e,g* = 0.5 mm; *c,d* = 1 mm; *f* = 238 um.)

Figure 9. *Troglocarcinus corallicola* 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.)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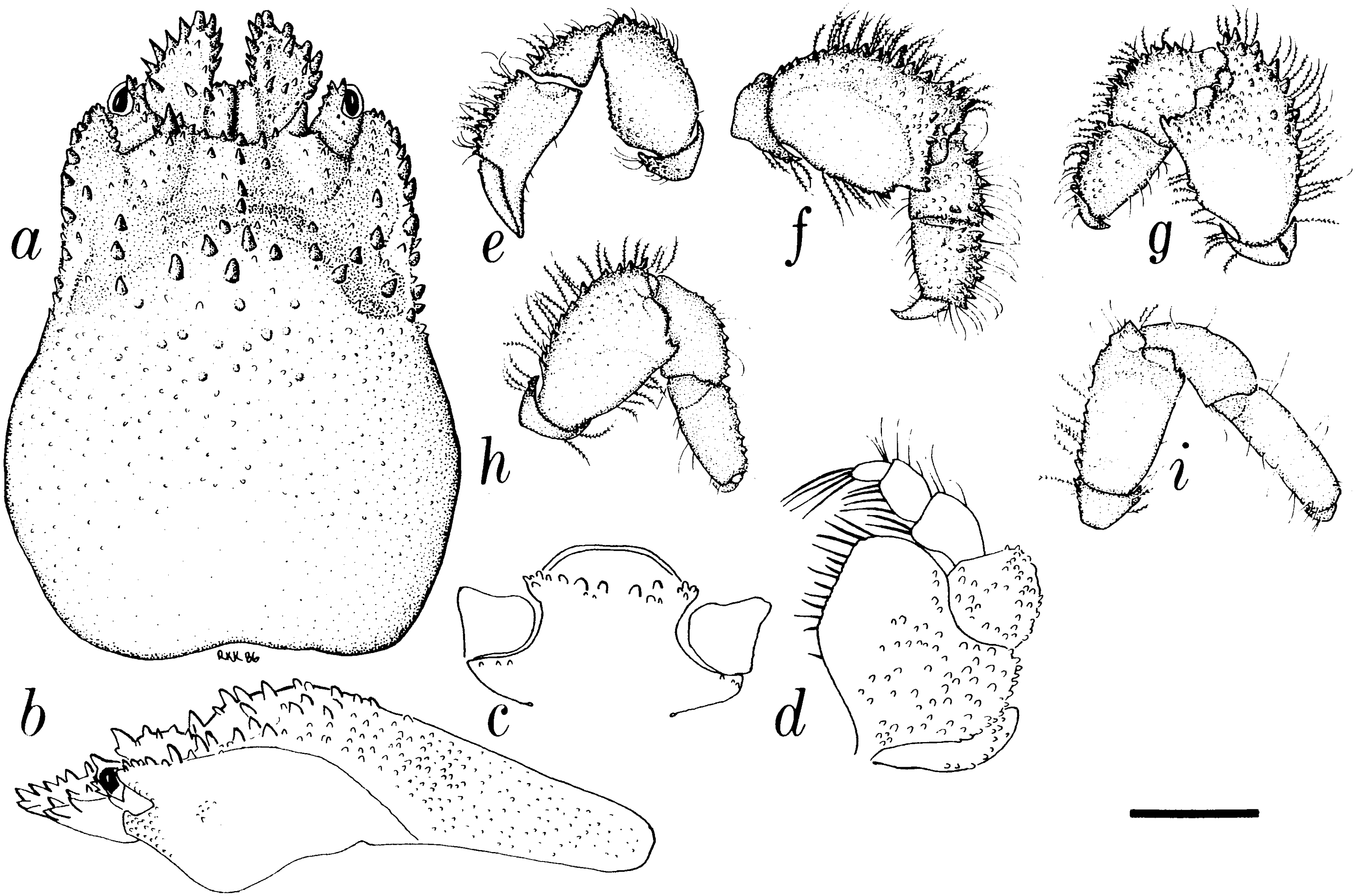
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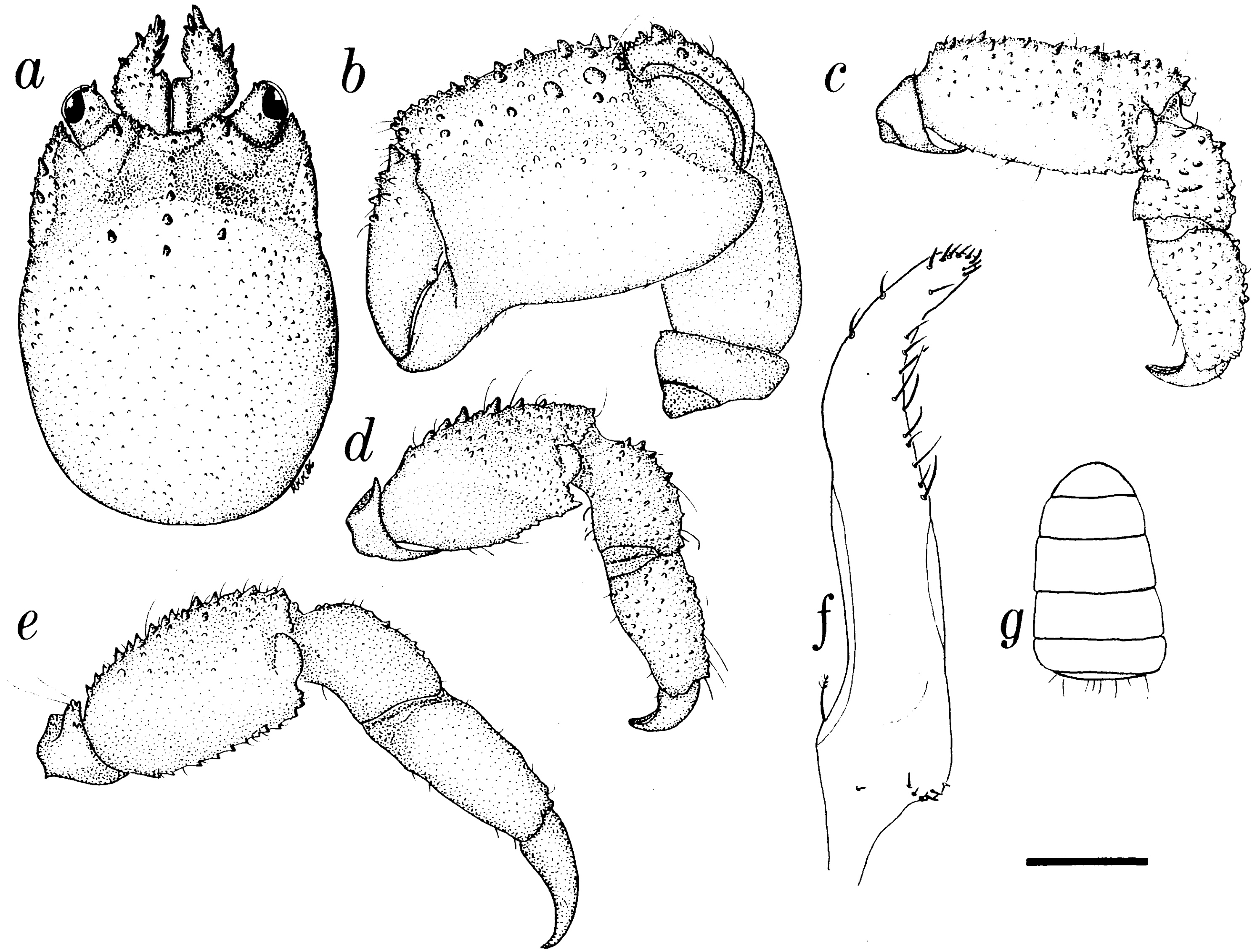
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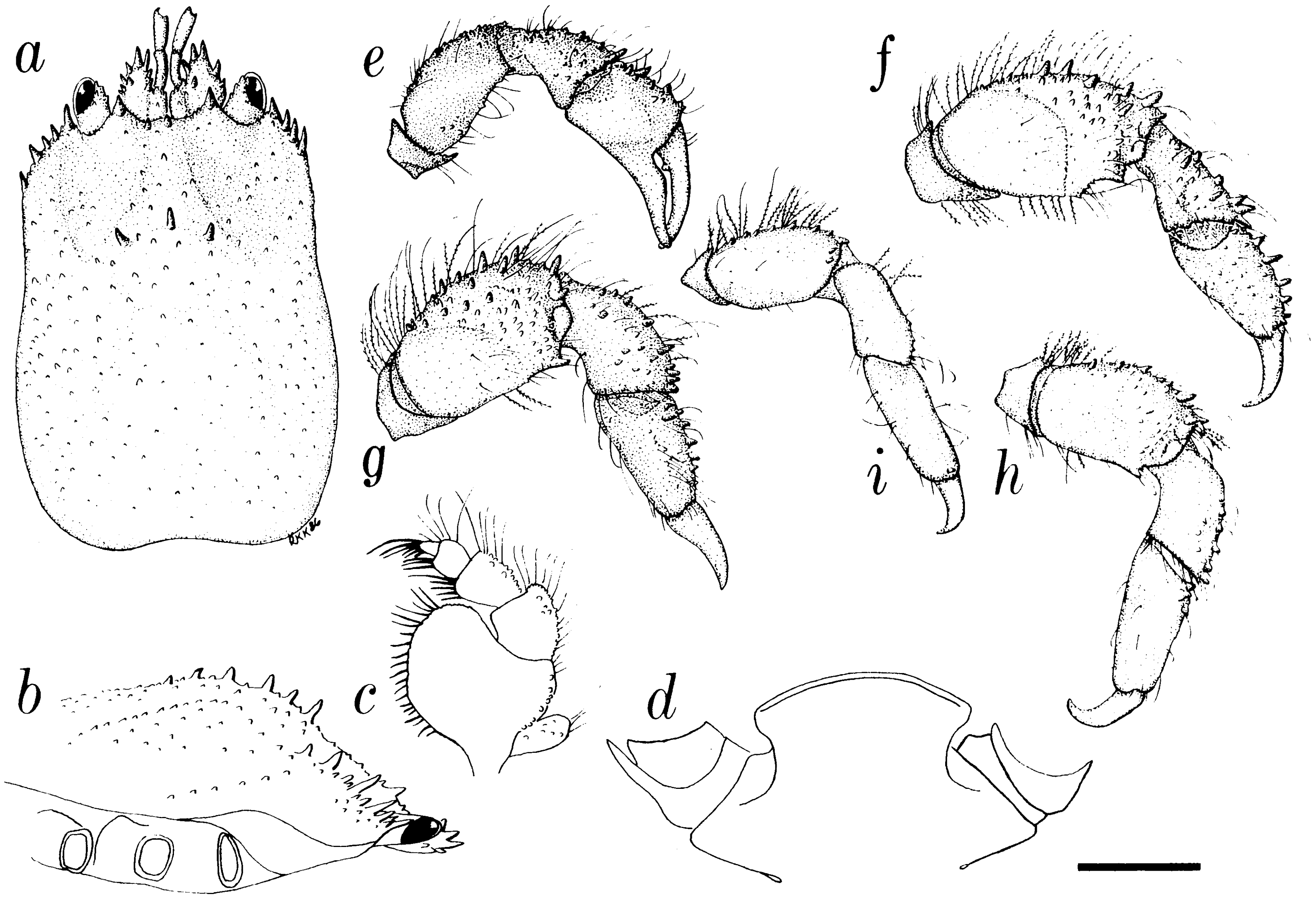
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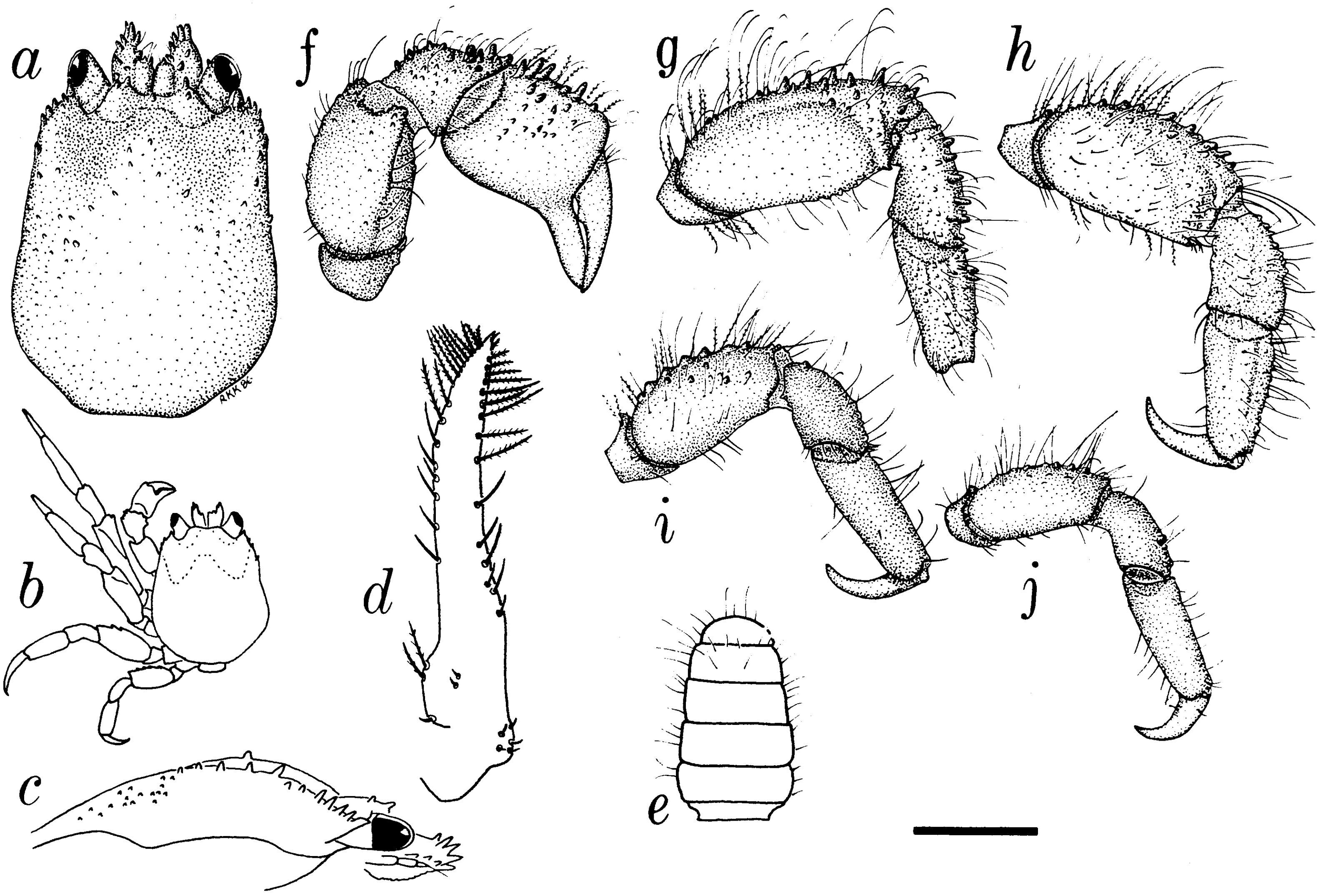
Figure 10. *Troglocarcinus corallicola* Verrill, male. *a*, dorsal view of carapace; *b*, dorsal view of juvenile (right pereopods omitted); *c*, lateral view of carapace; *d*, PLP-1; *e*, abdomen; *f-j*, P-1 to P-5. (*a,c,f-j*, Tortugas, USNM 59964; *b*, Panama, IRCZM 89-2985; *d*, Tortugas, USNM 77365 (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 um; *f* = 1.3 mm.)

Figure 11. 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.)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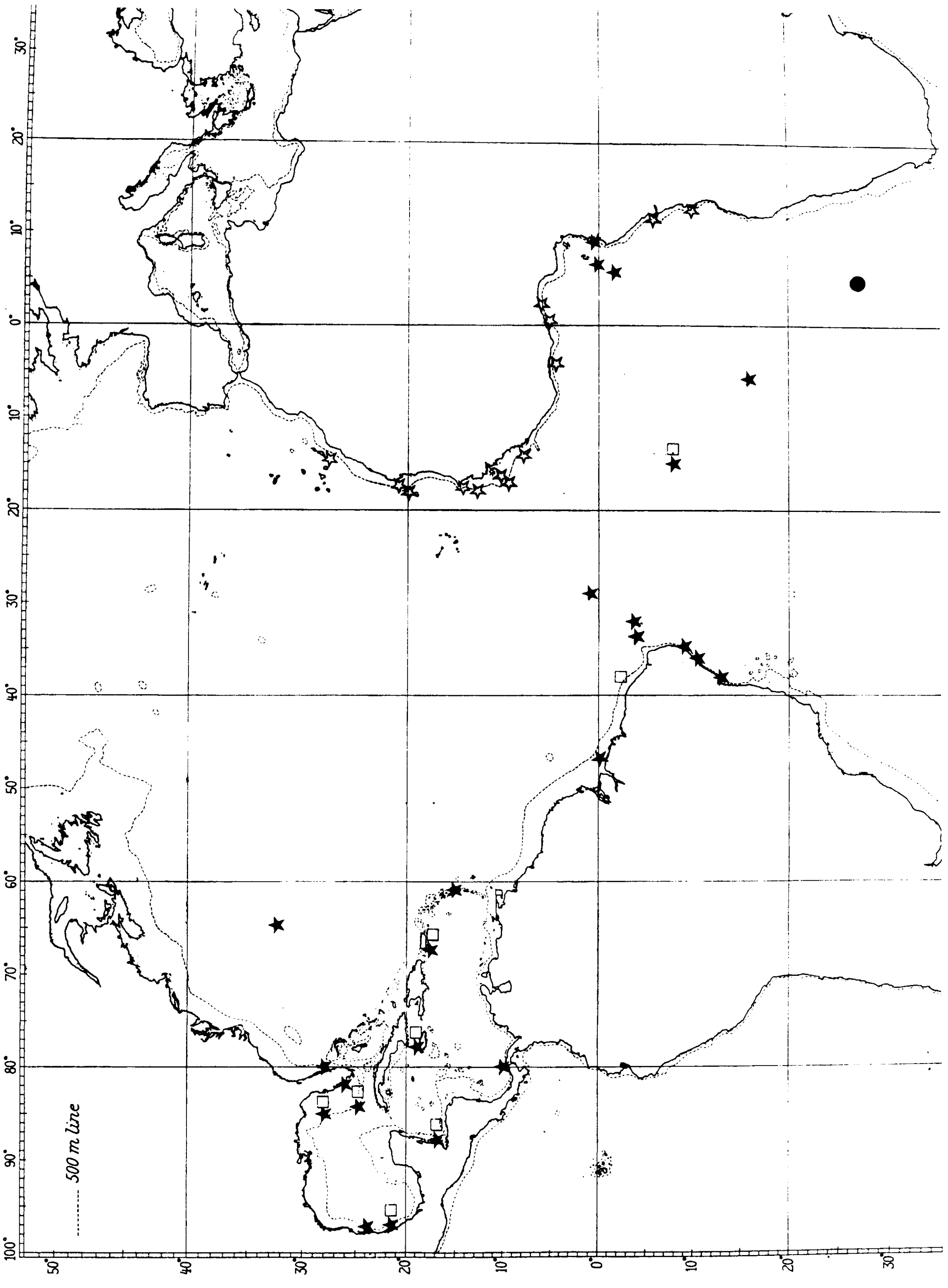
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Chapter 4

The Status of *Cryptochirus hongkongensis* Shen, 1936 (Brachyura: Cryptochiridae)

Abstract.--Morphological differences in the extent of the inner orbital angle, the length of the dactylus of the claw, and the shape of the abdomen are presented that support the removal of *Pseudocryptochirus viridis* Hiro from the synonymy of *Cryptochirus hongkongensis* Shen. This evidence also indicates that *C. hongkongensis* should be transferred to *Neotroglocarcinus* and considered a subjective senior synonym of *N. monodi* Fize and Serène.

In a short paper, Shen (1936) described two new species of the coral gall crab genus *Cryptochirus*. One of these, *C. granulatus*, was synonymized with *C. crescentus* Edmondson, 1925 [now *Opecarcinus crescentus*, see Kropp and Manning (1987)] by Utinomi (= Hiro, 1944), an action followed by all subsequent authors. The status of *C. granulatus* is under review and will be discussed in a subsequent manuscript on the genus *Opecarcinus* in the Indo-Pacific.

The second species described by Shen was *C. hongkongensis*. Utinomi (1944) transferred it to his genus *Pseudocryptochirus* as a subjective senior synonym of *P. viridis* Hiro, 1938, but erred by continuing to use the latter as the valid name for the taxon. This mistake was followed by Fize and Serène (1957), but corrected by Takeda and Tamura (1981). Both of the major works on Indo-West Pacific gall crabs published since Utinomi have upheld the synonymy (Fize and Serène, 1957; Takeda and Tamura, 1981). Both noted apparent discrepencies between Shen's account and the morphology of *P. viridis*, but neither disputed the synonymy of the two.

Here, I discuss the discrepencies mentioned by Fize and Serène and Takeda and Tamura and present additional evidence supporting the argument for the dissolution of the synonymy between *P. viridis* and *C. hongkongensis*. Furthermore, I argue that *C. hongkongensis* is a subjective senior synonym of *Troglocarcinus monodi* Fize and Serène (1955), the type species of *Neotroglocarcinus* Fize and Serène (1957).

Types

I have not been able to locate the type specimen of *Cryptochirus hongkongensis* Shen, 1936. Contrary to the assertion of Fize and Serène (1957:59), the type is probably not in the British Museum (Natural History), London (BMNH). Dr. Raymond B. Manning (Smithsonian Institution, Washington, D. C.), in 1984 and 1987, examined the gall crab collection in the British Museum and did not see any type specimen for the species although he did find the type of *C. granulatus*. Shen (1936) did not report the disposition of the type of *C. hongkongensis*. Although relatively crude, his figures and description do provide enough information by which comparisons to other species can be made. The types for

Neotroglocarcinus monodi (Fize and Serène, 1955) are also not available, however material identified by Serène is available from the BMNH and the Muséum National d'Histoire Naturelle, Paris (MNHN). Additional material examined was collected by the author in Micronesia (HAP and PHAP denote my collection numbers) and is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM).

A series of morphological features that were easily interpreted was selected from the figures and description of *C. hongkongensis* published by Shen (1936). This series was compared among the species in question. As the type description of Shen's species is based on a male, only males were used in the comparisons. The results are presented below in the form of brief comparative diagnoses, based on males only, for each species. I have reproduced Shen's figures of *C. hongkongensis* and provided comparative figures of *P. viridis* and *N. monodi*. Abbreviations used in the text are: km, kilometers; m, meters; ov, ovigerous; P, pereopod. Size ranges of material examined are given in millimeters as carapace length (cl) x width.

At the first occurrence in the text of collection localities in the Caroline Islands, locality names are given as the new orthographic spelling (Motteler, 1986) followed parenthetically by the former spelling.

Systematic Account

Pseudocryptochirus viridis Hiro, 1938

Fig. 12 a-c; 13 a-d

Material.--VIETNAM; Nhatrang [12°14'N, 109°12'E]: Rocher Noir; Rte. 1643; on *Turbinaria* sp.; 1 + (ov), 1 o; BMNH. GUAM: Toguan Bay [13°17'N, 144°39'E]; reef front south of river channel; 6 m; 27 May 1984; HAP 229; on *T. stellulata* (Lamarck, 1816); 1 + (ov), 1 o; USNM. Cocos Lagoon [13°14'N, 144°39'E]; southwest corner of lagoon just inside barrier reef; 1 m; 6 Mar, 3 Oct 1984; HAP 155, 272; on *Turbinaria stellulata*; 3 + (2 ov), 1 o; USNM. BELAU (Palau): Ngeruktabel (Urukthapel) Is. [07°15'N, 134°24'E]; north shore, west end of rock islands; 2 m; 22 Jul 1984; PHAP 166; on *T. reniformis* Bernard, 1896; 2 + (ov); USNM. Same locality; 2 m; 23 Jul 1984; PHAP 193, 199; on *T.* cf. *patula* (Dana, 1846), *T. reniformis*; 3 + (2 ov); USNM. POHNPEI (Ponape): Main lagoon, inside barrier reef about 1.6 km north of Main Passage [07°00'N, 158°13'E]; 2 m; 14 Nov 1984; PHAP 244; on *T.* cf. *mesenterina* (Lamarck, 1816); 1 + (ov), 2 o; USNM. Ant Atoll [06°47'N, 157°58'E]; reef front off Imwinyap Is., 100 m west of pass; 8 m; 17 Nov 1984; PHAP 284; on *T. reniformis*; 1 +, 1 o; USNM.

Size Ranges.--Females, 1.8 x 1.6 to 3.3 x 2.8; smallest ovigerous female, 1.8 x 1.6; males; 1.6 x 1.3 to 2.1 x 1.8.

Diagnosis.--Anterior third of carapace slightly depressed, not sharply set off from posterior carapace, latter lacking grooves or depressions; internal orbital angle greatly exceeding anterolateral angle of carapace. Basal segment of antennule with mesial margin straight, dorsal surface with longitudinal row of spines near mesial margin. Width of abdominal somite 6 about 1/2 that of somite 3. Dactylus of cheliped (P-1) longer than dorsal margin of palm, latter with spines along entire length. Propodus of P-3 about 1.4 times longer than high, dorsal margin with tubercles. Gonopod tapering sharply, mesial, and lateral margins with plumose setae originating just proximal to midlength.

Neotroglocarcinus monodi (Fize and Serène, 1955)

Fig. 12 g-i; 13 i-l

Material.--VIETNAM; Nhatrang: Rte. 1590; on *T. peltata* (Esper, 1797); 1 + (ov), 1 o; MNHN. Bai Miew; 11 Apr 1956; Rte. 1637; on *T. peltata*; 1 o; BMNH. Rocher Noir; 8 May 1956; Rte. 1643; on *T. peltata*; 1 + (ov); BM(NH).

Size Ranges.--Females, 3.2 x 2.7 to 4.6 x 4.1; smallest ovigerous female, 3.2 x 2.7; males, 3.2 x 2.9 to 3.8 x 3.4.

Diagnosis.--Anterior third of carapace markedly depressed, sharply set off from posterior carapace, latter with series of shallow, longitudinal depressions; internal orbital angle slightly exceeding anterolateral angle of carapace. Basal segment of antennule with mesial margin convex, dorsal surface with scattered tubercles, lacking longitudinal row of spines near mesial margin. Width of abdominal somite 6 about 3/4 that of somite 3. Dactylus of P-1 shorter than dorsal margin of palm, latter with few tubercles proximally. Propodus of P-3 about 1.8 times longer than high, dorsal margin entire. Gonopod not tapering sharply, mesial, and lateral margins with plumose setae originating at about midlength.

Cryptochirus hongkongensis Shen, 1936

Fig. 12 d-f; 13 e-h

From Shen (1936).

Size.--Male, 2.3 x 2.0.

Diagnosis.--Anterior third of carapace markedly depressed, sharply set off from posterior carapace, surface of latter uncertain; internal orbital angle slightly exceeding anterolateral angle of carapace. Basal segment of antennule with mesial margin convex, dorsal surface with scattered tubercles, lacking longitudinal row of spines near mesial margin. Width of abdominal somite 6 about 3/4 that of somite 3. Dactylus of P-1 shorter than dorsal margin of palm, latter with few tubercles proximally. Propodus of P-3 about 1.7 times longer than high, dorsal margin entire. Gonopod tapering sharply, mesial, and lateral margins with simple setae originating near or distal to midlength.

Discussion

From the above comparisons and the figures provided, it is clear that *C. hongkongensis* is quite different from *P. viridis*, and further, that *C. hongkongensis* strongly resembles *N. monodi*. These relationships are most strongly supported by features such as the relative extent of the internal orbital angle compared to the anterolateral angle of the carapace, the relative demarcation between the anterior and posterior parts of the carapace, the relative length of the dactylus of the P-1, and the shape of the abdomen as indicated by the relative widths of somite 3 and 6.

Some evidence is equivocal. Setation on the dorsal margins of the walking legs (Fig. 13) allies *C. hongkongensis* more closely to *P. viridis* than to *T. monodi*. However, I have noticed that setation can be variable within gall crab species. Also, setules on walking leg setae are often difficult to see and may have been missed by Shen. The gonopod figured by Shen is problematic. It tapers, as does the gonopod of *P. viridis*. Yet, the setation differs between the two, both in type (plumose in *P. viridis*, simple in *C. hongkongensis*) and position of origin (proximal to midlength in *P. viridis*, midlength or just distal in *C. hongkongensis*). Shen may have erred in figuring the gonopod. Shen's figures and descriptions of the mouthparts and antenna of *C. hongkongensis* are too general to be of use in resolving the affinities of each taxon.

The evidence presented by Utinomi (1944) for synonymizing *P. viridis* with *C. hongkongensis* is weak. He noted (p. 702) the antennule of "*hongkongensis* seems akin to *viridis*" and (p. 703) the third maxilliped of *hongkongensis* "shows close similarity to that of *viridis*." He further argued (p. 725) that the probable identity of the two was supported by "distributional evidences that both forms have been recorded together from neighboring seas."

Fize and Serène (1957:142) noted in particular the differences in the relative extent of the internal orbital angle and the relative length of the dactylus of the P-1 among the three taxa that I have mentioned. However, they did not ally *C. hongkongensis* with *T. monodi*, stating that Shen described the carapace as having "petites épines" a feature they attribute to *P. viridis*, not *T. monodi*. This is not true. Shen (p. 23) describes the carapace as "finely granulate", not as having spinules.

Takeda and Tamura (1981:16) noted the same two discrepencies mentioned above and the relative demarcation between the anterior and posterior carapace regions. They declared that these differences are "too small" to warrant separation of the two species. I disagree. Differences of the magnitude presented here are enough to separate species of gall crabs.

The evidence presented here supports the restoration of *Pseudocryptochirus viridis* Hiro to valid status. This evidence further indicates that *Cryptochirus hongkongensis* Shen is a subjective senior synonym of *Troglocarcinus monodi* Fize and Serène, the type species of *Neotroglocarcinus* Fize and Serène. Shen's species should now be known as *Neotroglocarcinus hongkongensis* (Shen).

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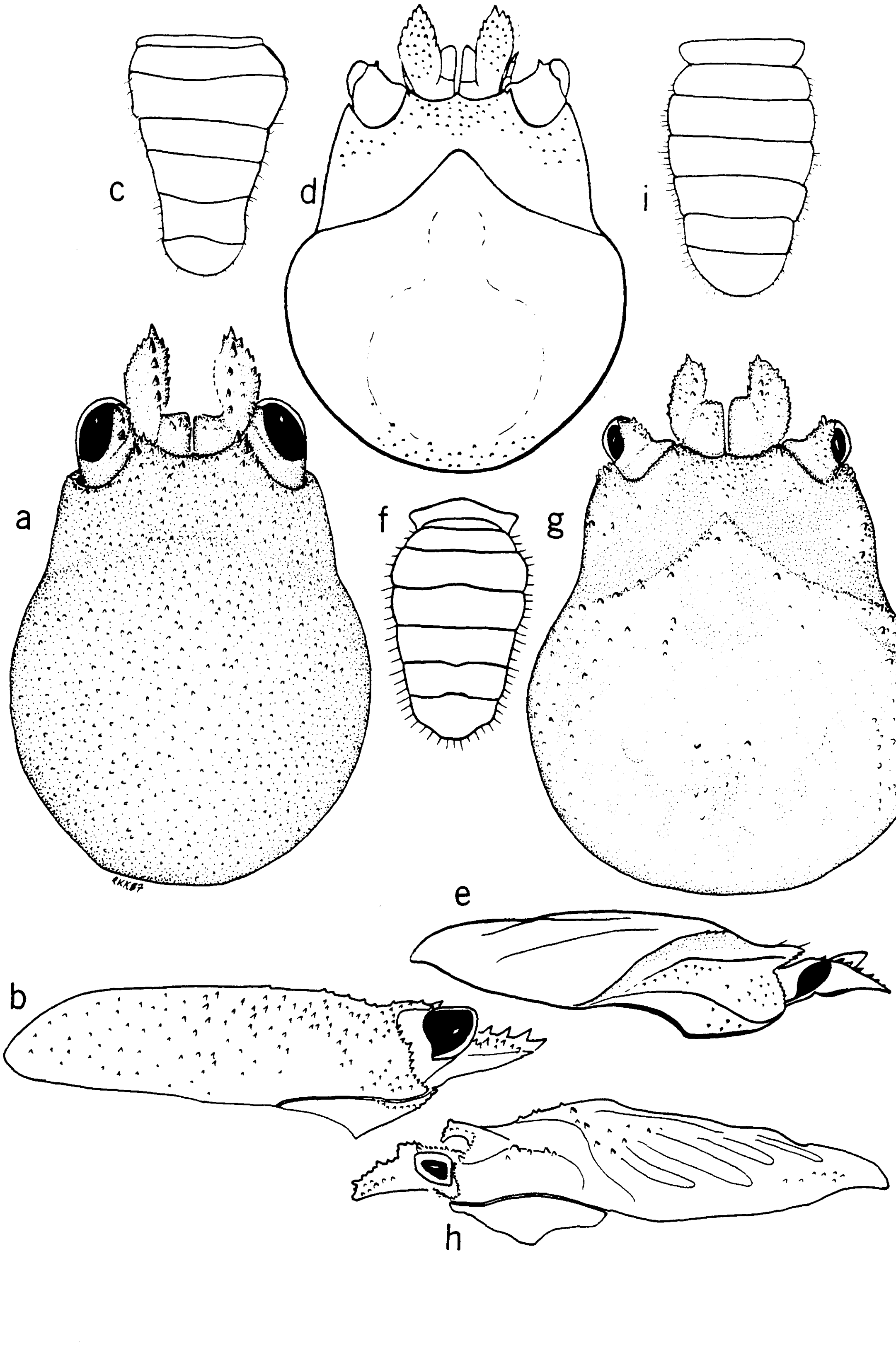
Fig. 12. Dorsal, lateral views of carapace, and abdomen. (a-c), *Pseudocryptochirus viridis*, Pohnpei, USNM, cl = 1.9 mm; (d-f), *Cryptochirus hongkongensis*, from Shen (1936), cl = 2.3 mm; (g-i), *Neotroglocarcinus monodi*, Vietnam, MNHN B-18762, cl = 3.8 mm. All males. Not to scale.

Fig. 13. Pereopods 1 and 3, antennule, and gonopod. (a-d), *Pseudocryptochirus viridis*, USNM; (e-h), *Cryptochirus hongkongensis*, from Shen (1936); (i-l), *Neotroglocarcinus monodi*, MNHN B-18762. All males. Not to scale.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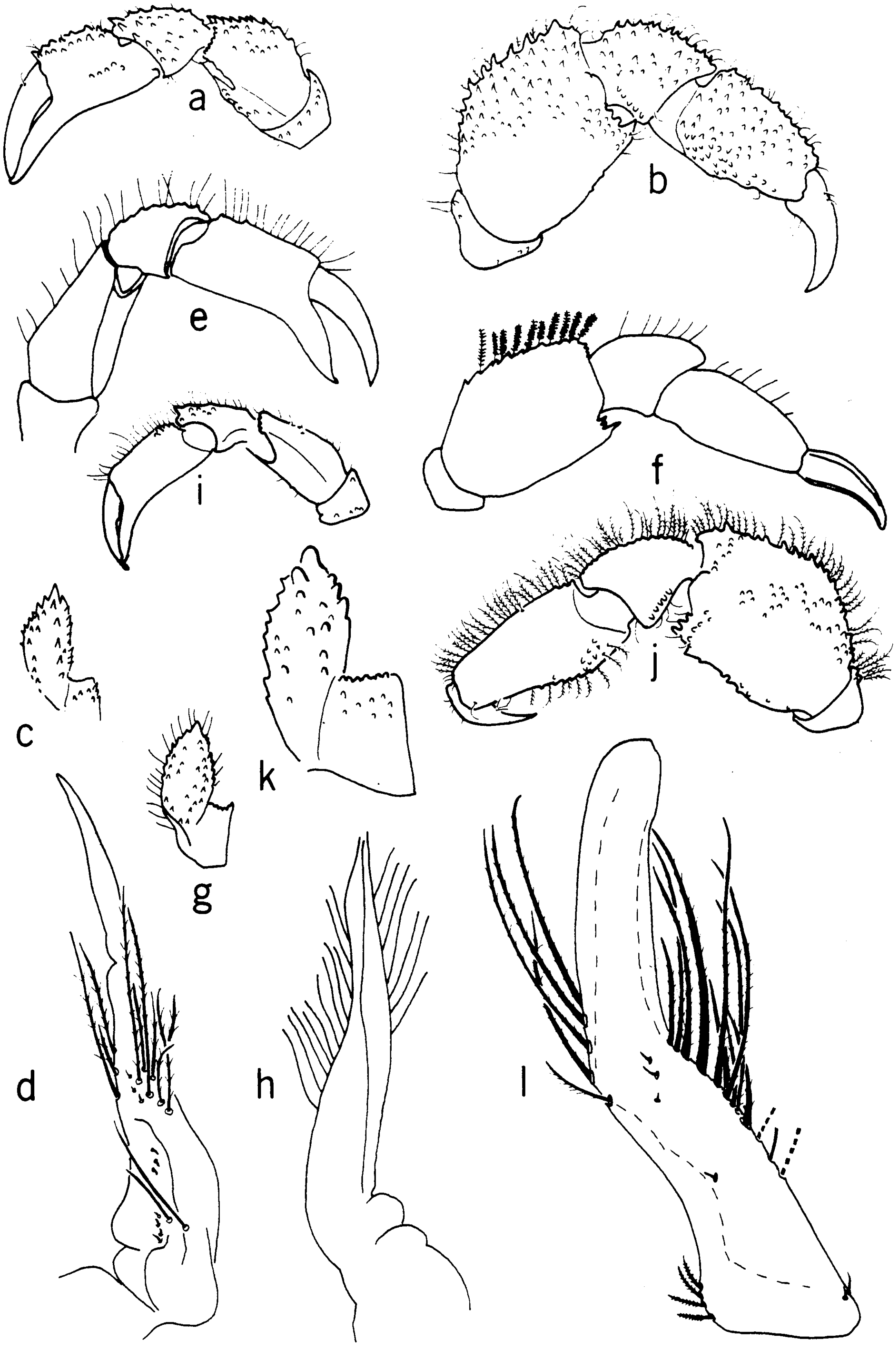
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Chapter 5

The Status of *Cryptochirus coralliodytes* Heller and *Lithoscaptus paradoxus* Milne Edwards (Brachyura: Cryptochiridae)

Abstract.--The types of *Cryptochirus coralliodytes* Heller and *Lithoscaptus paradoxus* Milne Edwards were examined and found to differ in sculpture of the carapace, the epistome, and relative lengths of the carpus and merus of the fifth pereopod among other features. Therefore, the latter is removed from the synonymy of the former. The type of *Cryptochirus rugosus* Edmondson was examined and found to be indistinguishable from *C. coralliodytes*; thus, *C. rugosus* is placed in synonymy with *C. coralliodytes*. The available data suggest that *Cryptochirus bani* Fize and Serène is synonymous with *L. paradoxus*. Lectotypes are designated for *C. coralliodytes* and *L. paradoxus* and are described and figured.

Two years after the description of the first known coral gall crab, *Hapalocarcinus marsupialis* Stimpson, 1859, the second recorded species, *Cryptochirus coralliodytes*, was described by Heller (1861:19). Milne Edwards (1862:F10) followed this with the description of a third species, *Lithoscaptus paradoxus*. All three species were rather incompletely described, probably because they were reasonably different from most other brachyurans known at the time. Although this inadequacy has not been a problem for the first species it has resulted in some misunderstanding regarding the latter two species.

The problem regarding the identities of *C. coralliodytes* and *L. paradoxus* can be traced to the failure of authors to examine type specimens or carefully consider information provided in the original descriptions that should have been useful in separating the two species. Paulson (1875) was the first to place the two in synonymy, but did so by erroneously considering *L. paradoxus* a senior synonym of *C. coralliodytes*. He did not justify his action. Richters (1880) agreed, but did correct the order of synonymy. Rathbun (1897) also noted Paulson's error. After Calman (1900) followed Paulson's action, all authors up until the review of the family by Fize and Serène (1957) attributed the synonymy of the two species to Paulson and/or Calman without question or examination of the types (e. g. Edmondson, 1933; Shen, 1936; Utinomi, 1944). Fize and Serène (1957) discussed *Cryptochirus* in detail and examined the syntypes of *Lithoscaptus* and *Cryptochirus* that are in the collection of the Muséum National d'Histoire Naturelle, Paris. In spite of doing so, they upheld the synonymy of the two species. More recently, Takeda and Tamura (1980) reviewed *Cryptochirus*, but did not alter the status of the two species.

I examined the syntypes of *C. coralliodytes* and *L. paradoxus* and determined that they are not synonymous.

Herein I designate lectotypes for each species and conclude that Heller's species is a subjective senior synonym of *Cryptochirus rugosus* Edmondson, 1933. Because *C. rugosus* is the type species of the genus *Favicola* Fize and Serène, 1957, the latter should now be considered a subjective junior synonym of *Cryptochirus* Heller, 1861.

Materials and Methods

I examined the male and female syntypes of *Cryptochirus coralliodytes* Heller housed in the Muséum National d'Histoire Naturelle, Paris (MNHN) and Naturhistorisches Museum, Vienna (NMW), respectively; the syntypes of *Lithoscaptus paradoxus* Milne Edwards in the MNHN; and the holotype of *Cryptochirus rugosus* Edmondson held in the B. P. Bishop Museum, Honolulu (BPBM). Additional material examined came from the BPBM and my own collections (denoted as HAP and PHAP) made in Micronesia in 1984. The Micronesian material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington D. C. (USNM). Place names for collection sites in the Caroline Islands are from Bryan (1971). At the first occurrence in the text of each locality, the new orthographic spelling (Motteler, 1986) is given followed parenthetically by the former spelling. Subsequently, only the new spelling is used.

Some of the Micronesian material was used in the preparation of the figures and for study by Scanning

Electron Microscopy (SEM). In preparation for SEM, specimens were dissected and cleaned by gentle mechanical agitation, and brushing with a fine paint brush. Specimens were then transfered to 100% ethanol via a graded series and air-dried overnight. Dried specimens were mounted on stubs and sputter-coated with gold-palladium and viewed with a Cambridge Stereoscan-100 microscope at an accelerating voltage of 10 kv.

Drawings were made with a camera lucida mounted on a Wild M-5 microscope. The cheliped was drawn so that the outer surface of the manus is in the plane of the printed page. This distorts the relative proportions of the other segments, particularly the merus. Male pleopods were prepared for illustration by lactic acid digestion and staining using methods described in Kropp and Manning (1987), except acid fuchsin was substituted for fast green.

The carapace length and width of each specimen were measured to the nearest 0.1 mm with an ocular micrometer on a Wild M-5 microscope and are reported in mm as length x width. Abbreviations used in the text are: m, meters; MXP, maxilliped; ov, ovigerous; P, pereopod; PLP, pleopod; and TL, type locality.

In the systematic account, I have restricted the generic synonymies to the original usage of a name for each taxon. For each nominal species the type locality and the location of the type specimen are included.

Systematic Account

Cryptochirus Heller, 1861

Cryptochirus Heller, 1861a:19 [type species: *Cryptochirus coralliodytes* Heller, 1861a:19 by monotypy; gender masculine].

Favicola Fize and Serène, 1957:84 [type species: *Cryptochirus rugosus* Edmondson, 1933:6 subsequent designation by Serène (1966:396); gender masculine (see Remarks)].

Remarks.--The International Code of Zoological Nomenclature (ICZN, 1985) specifies that a genus-group name ending in a noun of variable gender, such as -*icola*, should be treated as masculine unless its author specifies that it is feminine or treats it as feminine by the use of feminine species-group names [Article 30 (a) (i)]. Serène (1966) was the first to use *Favicola* as a distinct generic name and did so with masculine species-group names. Therefore, the gender of *Favicola* is masculine.

Cryptochirus coralliodytes Heller

Figures 14-16

Cryptochirus coralliodytes Heller, 1861a:19 [TL: Red Sea; lectotype NMW, paralectotype MNHN]; 1861b:370, plate IV, figures 33-39.

Cryptochirus corralliodytes Heller, 1861a:19 [incorrect original spelling].

Cryptochirus rugosus Edmondson, 1933:6, figure 1, plate 1 [TL: Line Islands, Teraina [= Washington Island]; holotype BPBM S3668].

Types.--Two syntypes of *C. coralliodytes* are extant. The female syntype is ovigerous, 6.6 x 4.5 mm, and housed in the Naturhistorisches Museum, Vienna. It is herein designated the lectotype. The specimen is disarticulated, with the carapace being detached from the thorax which is missing. The right P-3 to P-5, mouthparts, antennae, and antennules are missing. The abdomen is detached, in poor condition, some pleopods are present. The male syntype, 5.0 x 3.0 mm, is in good condition having all pereopods, mouthparts, and pleopods present. It is housed in the Muséum National d'Histoire Naturelle, Paris, and is herein designated the paralectotype. I examined the holotype of *C. rugosus* at the BPBM in 1984, but have not been able to re-examine it as it is now missing (B. Burch personal communication to R. B. Manning, 1987). It is a female and agrees with the lectotype of *C. coralliodytes*.

Material Examined.--RED SEA [no specific locality]: lectotype, female, 6.6 x 4.5, (NMW); paralectotype, male, 5.0 x 3.0, (MNHN 198-63). CAROLINE ISLANDS: Belau (Palau): Ngerekebesang (Arakabesan) Is. [07° 21'N, 134° 27'E]; north side of cove on west side of island; PHAP 078; 4 m; 7 Jul 1984; on *Platygyra lamellina* (Ehrenberg, 1834); 2 + (1 ov), 1 o. Pohnpei (Ponape): Sokehs Passage [07° 00'N, 158° 11'E]; patch reef bordering west side of reef; PHAP 270; 2 m; 16

Nov 1984; on *P. daedalea* Ellis and Solander, 1786; 2 +. MARIANA ISLANDS: Guam: Double Reef [13°36'N, 144°50'E]; shoreward side of main patch reef; HAP 125; 9 m; 24 Feb 1984; on *Platygyra* sp.; 1 +, 1 o. LINE ISLANDS: Teraina (= Washington Is.) [04°43'N, 160°24'W]: 1 + (BPBM S3668, holotype of *Cryptochirus rugosus* Edmondson).

Description.--Lectotype female (Fig. 14, 15, NMW), except mouthparts, antenna, antennule, and epistome (based on material from Micronesia). Carapace about 1.5 times longer than broad, widest near midlength. Anterior carapace with inverted "V"-shaped depression, anterior gastric region slightly inflated; mid carapace with clusters of prominent, rounded tubercles on posterior gastric, anterior and posterior epigastric regions; posterior surface with scattered pointed and rounded tubercles. Regions of posterior half of carapace set off by series of well-formed grooves, epigastric region divided into anterior, posterior portions by distinct groove. Anterolateral margin of carapace spinous.

Anterolateral angle of carapace with single tubercle, apex exceeding inner orbital angle, latter swollen, with tubercle. Front concave, with few tubercles just behind margin; width about 1/2 that at anterolateral angles, latter about 2/5 greatest carapace width. Orbit deeply "V"-shaped.

Epistome with subparallel longitudinal ridges laterally, median area produced anteriorly into longitudinal ridge subequal in thickness to lateral ridges; anterior margin with few tubercles, slightly sinuous, with scant median indentation.

Basal segment of antennular peduncle with elliptical projection extending beyond length of eyestalk, apex spine-tipped, no angled lateral lobe. Dorsal surface flat, with few pointed tubercles. Mesial margin spinous. Ventral surface of second antennal segment with scattered granules, distal margin toroidal (Fig. 15c).

Eye directed anterolaterally, extending beyond anterolateral angle; cornea subterminal, occupying distal third of stalk in dorsal view. Stalk mostly exposed, broadening proximally; ventral surface with few granules.

MXP-3 with exopod, mesial margin of ischium convex; outer surface with distally-raised granules. Merus longer than broad, width less than half that of ischium. Carpus shorter than length of propodus and dactylus combined.

Endopod of MXP-1 triangular, mesial margin about 2/3 length of lateral margin, anterior margin with sharp curve occurring mesially, lined with stout simple setae.

Chelipeds (P-1) with few scattered simple, pappose setae on upper margins. Dactylus longer than dorsal margin of palm, cutting edges of fingers entire. Dorsal margin of palm entire, outer and upper surfaces with few granules proximally. Manus slightly smaller than merus.

Dorsal margin of merus of P-2 with spines distally, fringed with pappose setae of length > 2 times that of spines; outer surface flat, with granules dorsodistally, ventrally; ventral margin relatively straight, with few tubercles, fringed with pappose setae; ventrodistal angle with prominent tubercles (tubercles worn on lectotype). Merus height < 2 times that of carpus. Dorsal margins of carpus and propodus with robust spines, simple setae; outer surfaces with tubercles dorsally, ventrally; carpus subequal in length to propodus. Dactylus with proximal tooth dorsally; tip with subterminal pore. P-3, P-4 similar in form to P-2, stockier, P-4 less setose. P-5 elongate, smooth; carpus longer than other segments; propodus, dactylus directed anteriorly.

Sternite of P-1 with few granules, that of P-4 with median suture. Female opening longitudinal, oval, with hood; PLP-2 biramous, PLP-3 uniramous.

Variations.--May have spines instead of tubercles at inner orbital angles, anterolateral angles, and on anterior surface of carapace. Spines vary as to number and sharpness. The width and depth of the grooves on the carapace varies considerably. The proximal tooth on the dorsal surface of the dactylus of P-2 may be missing. Smaller females may have a deeper depression on the anterior carapace, may be less spiny, and have a more elongate projection of the antennule base than larger females. The carapace length:width ratio ranged from 1.2 to 1.7 with most crabs within 1.4 to 1.6.

Paralectotype male (Figure 16).--Similar to, smaller than female. Carapace regions distinctly marked as female, spines, rounded tubercles less pronounced. Projection of antennule base more elongate, pointed. P-1 robust, palm inflated, with tubercles; dactylus slightly longer than dorsal margin of palm. Abdominal somites 5-7 narrower than somites 3-4; telson broadly rounded. PLP-1 reaching middle of sternite of P-1; slightly curved, apex sharply pointed, directed slightly laterally; lateral margin with stout setae.

Variations.--P-1 much less robust in smaller males, with the dactylus relatively longer than paralectotype. Regions of carapace may have fewer tubercles.

Lithoscaptus Milne Edwards, 1862

Lithoscaptus Milne Edwards, 1862:F10 [type species: *Lithoscaptus paradoxus* Milne Edwards, 1862:F10, by monotypy; gender masculine].

Lithoscaptus paradoxus Milne Edwards

Figures 17-19

Lithoscaptus paradoxus Milne Edwards, 1862:F10 [TL: Reunion; lectotype, MNHN].

Cryptochirus coralliodytes var. *rubrolineata* Fize and Serène, 1957:40, figure 5D, plate 14, figures E-H [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus coralliodytes var. *cubrolineata*.--Fize and Serène, 1957:201 [erroneous spelling].

Cryptochirus coralliodytes var. *fusca* Fize and Serène, 1957:40, figure 5B [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus coralliodytes var. *parvulus* Fize and Serène, 1957:40, figure 5C [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus bani Fize and Serène, 1957:44, figures 5F, 6, plates 1, figure 7 [TL: Nhatrang, Viet-Nam; location of type unknown].

Type.--Two specimens are in the vial from the MNHN labelled *Lithoscaptus paradoxus* "TYPE". One is a nonovigerous female that is herein designated the lectotype. The carapace of this female is somewhat misshapen, but still recognizable. Both P-2 are missing, but the remaining pereopods are present as are all mouthparts. The pleopods are present and are uniramous. The second specimen is *Cryptochirus coralliodytes* Heller. Milne Edwards indicated which specimen on which he based his description by his reference to uniramous female pleopods (1862:F12). For this reason that the larger female is selected as the lectotype.

Material examined.--INDIAN OCEAN: Reunion Island [20°18'S, 57°29'E]: lectotype, 1 + 6.4 x 5.3, (MNHN). PACIFIC OCEAN: CAROLINE ISLANDS: Belau: Ngeruktabel Is.; patch reef among rock islands on northeast shore; PHAP 045; 2 m; 2 Jul 1984; on *Goniastrea pectinata* (Ehrenberg, 1834); 2 + (1 ov), 1 o. MARIANA ISLANDS: Guam: Luminao Reef [13°28'N, 144°39'E]; reef flat toward Magundas; HAP 315; 1

m; 13 Oct 1984; on *P. daedalea*; 2 + (ov), 1 o. COOK ISLANDS: Rarotonga [21° 14'S, 159° 46'W], Ararua; Wilder and Parks; Jun-Jul 1929; [no host]; 13 + (ov) (BPBM S3221).

Description.--Female, based on lectotype in conjunction with a Guam female (Figure 17, 18 USNM). Carapace about 1.2 times longer than broad, widest just posterior to midlength. Anterior carapace with broadly "W"-shaped depression having scattered spines; anterior gastric region slightly inflated; median gastric with 2 depressions; mid to posterior carapace with many rounded tubercles, regions of carapace not well defined; cardio-intestinal region rimmed anteriorly, laterally with depression. Anterolateral margin of carapace spinous.

Anterolateral angle of carapace with single spine, apex exceeding inner orbital angle, latter swollen, with subterminal spine. Front concave, entire, width about 1/2 that at anterolateral angle, latter 2/5 greatest carapace width. Orbit "V"-shaped.

Epistome with subparallel longitudinal ridges laterally; median area swollen, lacking ridge; anterior margin entire, straight, with scant median indentation.

Basal segment of antennular peduncle with suboval projection extending slightly beyond eyestalk, rounded distally, no angled lateral lobe; dorsal surface flat, without tubercles; entire margin with subequal spines. Ventral surface of second antennal segment with few granules, distal margin with few raised granules.

Eye directed anterolaterally, extending just beyond anterolateral angle; cornea subterminal, occupying distal quarter of stalk dorsally. Stalk mostly exposed, not broadening proximally; ventral surface smooth.

MXP-3 with exopod, mesial margin of ischium slightly convex, outer surface with many distally-raised granules. Merus longer than broad, width less than half that of ischium. Carpus shorter than length of propodus and dactylus combined.

Endopod of MXP-1 subquadrate, mesial margin about 3/5 length of lateral margin; anterior margin with sharp median curve, lined with stout simple setae.

Chelipeds (P-1) with many scattered simple setae on upper margins. Dactylus longer than dorsal margin of palm; cutting edge with low tooth proximally. Dorsal margin of palm with few tubercles proximally, outer surface smooth. Manus much smaller than merus.

Dorsal margin of merus of P-2 with spines distally, fringed with pappose setae of length > 2 times that of spines; outer surface flat, with tubercles distally; ventral margin convex, with few tubercles, fringed with pappose setae. Merus height > 2 times that of carpus. Dorsal margins of carpus, propodus with spines, simple setae; outer surfaces with few tubercles; carpus longer than propodus. Dactylus lacking proximal tooth dorsally, tip with subterminal pore. P-3, P-4 similar in form to P-2; outer surfaces of carpi, propodi with longitudinal row of rounded tubercles near upper margins, upper margins with simple, pappose setae. P-5 elongate, with tubercles dorsally on proximal 3 segments; merus and carpus subequal in length, each longer than propodus; propodus, dactylus directed anteriorly.

Sternite of P-1 smooth, that of P-4 with median suture. Female opening longitudinal, oval, with anterior hood; PLP-2, PLP-3 uniramous.

Variations.--Relative sculpture of the carapace variable, particularly the median gastric area which may have depressions from two to four in number which may vary from very obvious to faintly detectable. The extent of the depression on the anterior carapace varies from occuping the entire surface between the anterolateral margins to somewhat less. The size and number of spines and/or tubercles is highly variable. The carapace length:width ratio ranged from 1.2 to 1.5 with most crabs within 1.3 to 1.4. In some specimens the lateral projection of the antennule base is more elongate than described. Also, the anterolateral angles of the carapace may extend only slightly beyond the inner orbital angles.

Male (Figure 19).--Based on specimens from Micronesia. Similar to, smaller than female. Carapace detail similar to females, spines proportionally smaller. Projection of antennule base elongate, with apical spine. P-1 robust, palm inflated, with few tubercles; dactylus longer than dorsal margin of palm. Abdominal somites 3-7 similar in width, telson broadly rounded. PLP-1 slightly curved, apex sharply pointed, directed slightly laterally; reaching posterior of sternite of P-1; lateral margin with stout setae.

Variations.--Smaller males have relatively smooth carapace, with the anterior depressions more distinct. The inner orbital angle may equal or exceed anterolateral angle of the carapace.

Remarks.--The original description of *Cryptochirus bani* by Fize and Serène (1957) did not provide information necessary to distinguish it from *Lithoscaptus paradoxus*. Serène (1962), in a discussion of some material from Rarotonga sent to him by Edmondson, alluded that *C. bani* might be synonymous with *C. coralliodytes*. Serène thought that this material was very similar to *C. bani*. I have examined material from the same collection (BPBM S3221) and found them to be *L. paradoxus*. Without examination of the type of *C. bani*, there is some uncertainty, but it is likely that *C. bani* is a subjective junior synonym of *L. paradoxus*. Fize and Serène (1957) named three varieties of *C. coralliodytes* based primarily on color differences, giving no substantial morphological data by which to distinguish them. The varieties, *rubrolineata*, *fusca*, and *parvulus* are therefore considered subjective junior synonyms of *L. paradoxus*.

Discussion

Paulson (1875) felt that many taxonomists of the period were not making useful contributions to systematics as a science, and that their research "provides only a useless ballast." He was particularly critical of Heller and A. Milne Edwards. Yet careful consideration of the original species descriptions by Heller and Milne Edwards and comparisons of those with material at hand might have prevented Paulson's confusion of *C. coralliodytes* with *L. paradoxus*. Heller's original species account (1861a:19) was scanty, but the generic description included a characterization of the endopod of the first maxilliped that is useful. This was supported by his later (1861b), more detailed, account which included an accurate figure of the appendage (1861b, plate IV, figure 39). The endopod of the first maxilliped is quite different in *L. paradoxus*, (triangular in *coralliodytes* versus subquadrate in *paradoxus*, compare Fig. 2d and 5d herein). Heller's figure of the female type (1861b: plate IV, figure 33) shows enough carapace detail, despite Edmondson's (1933:4) complaint, to distinguish the two species.

Milne Edwards also gave information sufficient to separate the two species by referring to the uniramous condition of the female pleopods (1862:F12). Although female PLP-2 form is often not a reliable character (McCain and Coles, 1979; Kropp and Manning, 1987), in this case it is applicable because among the specimens of either species that I have examined, the PLP-2 is consistently uniramous in *L. paradoxus* and consistently biramous in *C. coralliodytes*.

Several features other than the above information from the original literature allow separation of the two species. The most obvious difference is that the regions of the carapace of *C. coralliodytes* are well defined whereas those of *L. paradoxus* are not. Additionally, in the former, the epistome has a median ridge, and leg P-5 is smooth, with the carpus longer than the other segments whereas there is no median epistomal ridge and leg P-5 is tuberculate dorsally, with the carpus and merus subequal in length in *L. paradoxus*. Leg P-2 permits the two species to be distinguished because the merus is larger relative to the carpus in *Lithoscaptus* than in *Cryptochirus*.

The changes made here have a bearing on the other species presently included in *Cryptochirus* and *Favicola*. I am reviewing these species and will clarify their status as a part of a revision of the genera of cryptochirids.

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(BPBM), and R. Ingle (BMNH). The corals I collected in Micronesia were identified by R. H. Randall. R. B. Manning and G. J. Vermeij reviewed the manuscript and provided encouragement. Financial support was provided in part by the University of Maryland's Department of Zoology and Graduate School and a grant to G. J. Vermeij by the Biological Oceanography Section of the National Science Foundation. This is from a dissertation to be submitted to the Graduate School, University of Maryland, in partial fulfillment of the requirements for the Ph. D. degree in Zoology and is Contribution No. 250 of the University of Guam Marine Laboratory.

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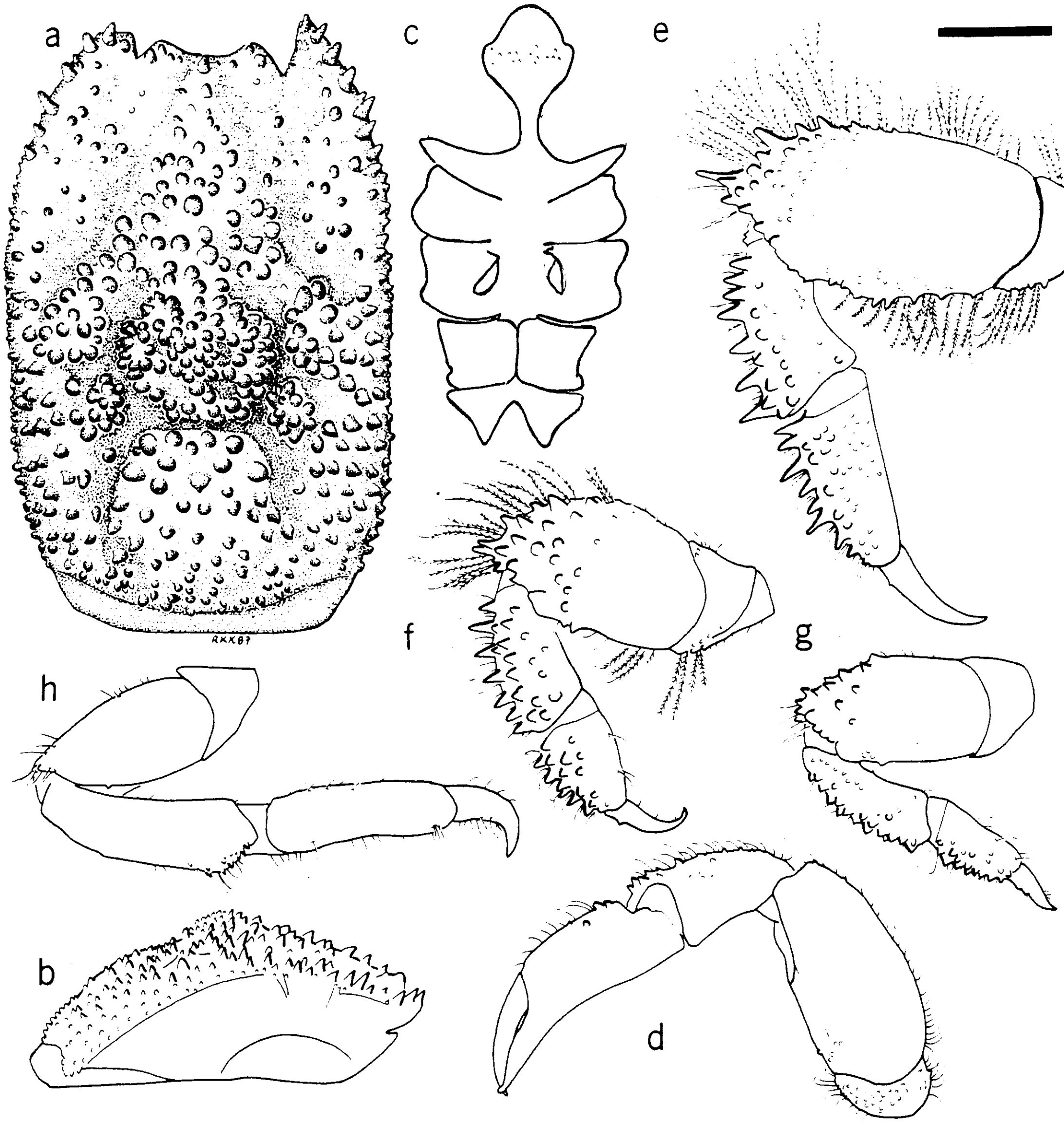
Fig. 14. *Cryptochirus coralliodytes*, +. (a, b, d-h from lectotype, c from Guam +, USNM): a, carapace (dorsal view); b, carapace (lateral view); c, thoracic sternites; d-h, P-1 to P-5. Scale: a = 0.8 mm; b = 2.1 mm; c-h = 1 mm. [Setae on surface of carapace and pereopods not shown].

Fig. 15. *Cryptochirus coralliodytes*, +. (Guam, SEM micrographs): a, epistome; b, MXP-3 (outer view); c, antenna (ventral view); d, endopod of MXP-1 (outer view). Scale: a, c = 0.3 mm; b = 0.5 mm; d = 0.2 mm.

Fig. 16. *Cryptochirus coralliodytes*, o. (a-d from paralectotype, e from Guam o, USNM): a, carapace (dorsal view); b, abdomen; c, left P-1; d, right P-2; e, PLP-1 (outer view). Scale: a = 0.9 mm; b-d = 1 mm; e = 0.1 mm.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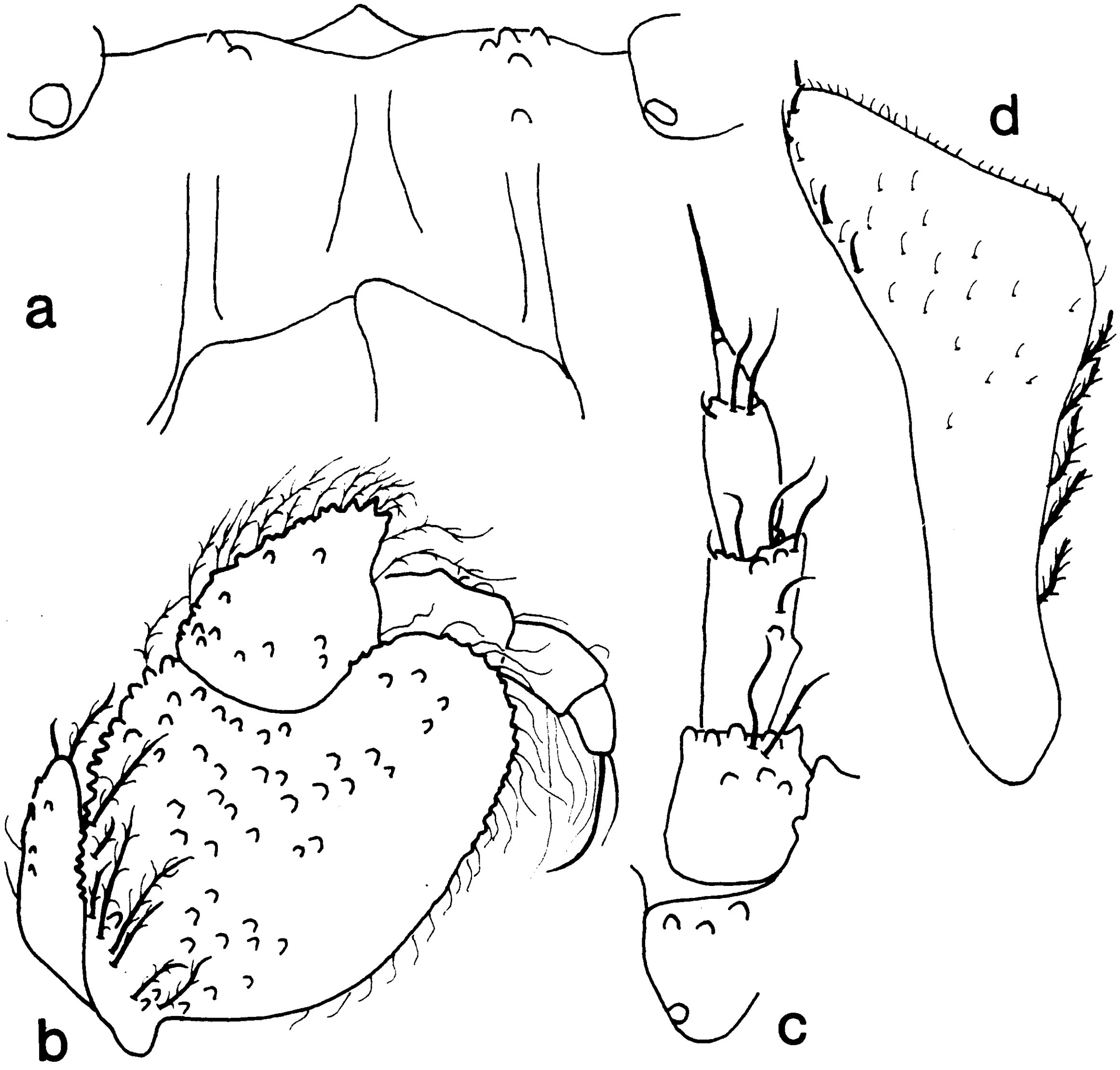
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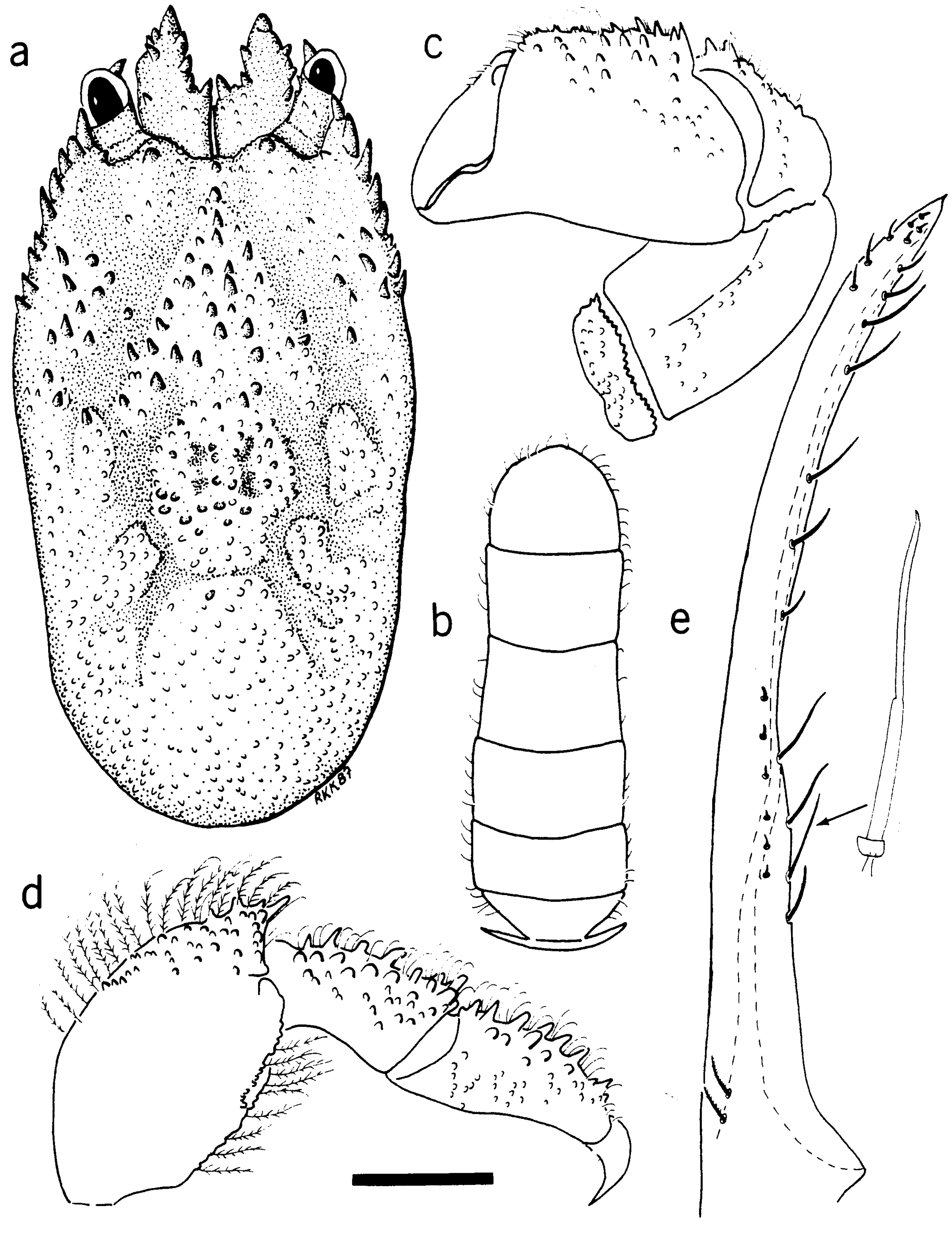
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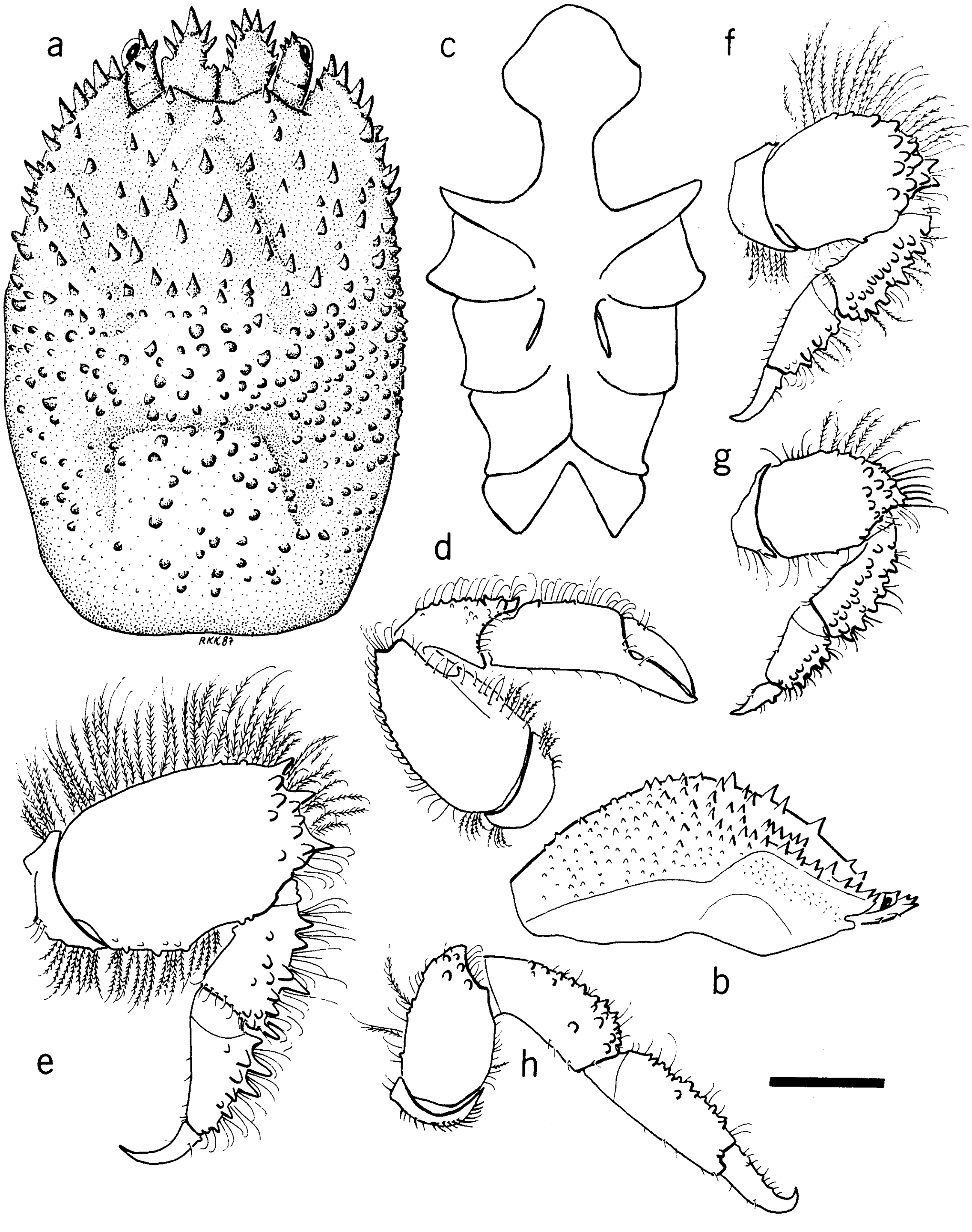
Fig. 17. *Lithoscaptus paradoxus*, +. (Guam, USNM): a, carapace (dorsal view); b, carapace (lateral view); c, thoracic sternites; d-h, P-1 to P-5. Scale: a = 0.8 mm; b = 2.1 mm; c-h = 1 mm. [Setae on surface of carapace and pereopods not showm].

Fig. 18. *Lithoscaptus paradoxus*, +. (Guam, SEM micrographs): a, epistome; b, MXP-3 (outer view); c, antenna (ventral view); d, endopod of MXP-1 (outer view). Scale: a = 0.4 mm; b = 0.6 mm; c = 0.3 mm; d = 0.2 mm.

Fig. 19. *Lithoscaptus paradoxus*, o. (Guam, USNM): a, carapace (dorsal view; b, abdomen; c-d, right P-1, P-2; e, PLP-1 (outer view). Scale: a-d = 1 mm; e = 0.1 mm.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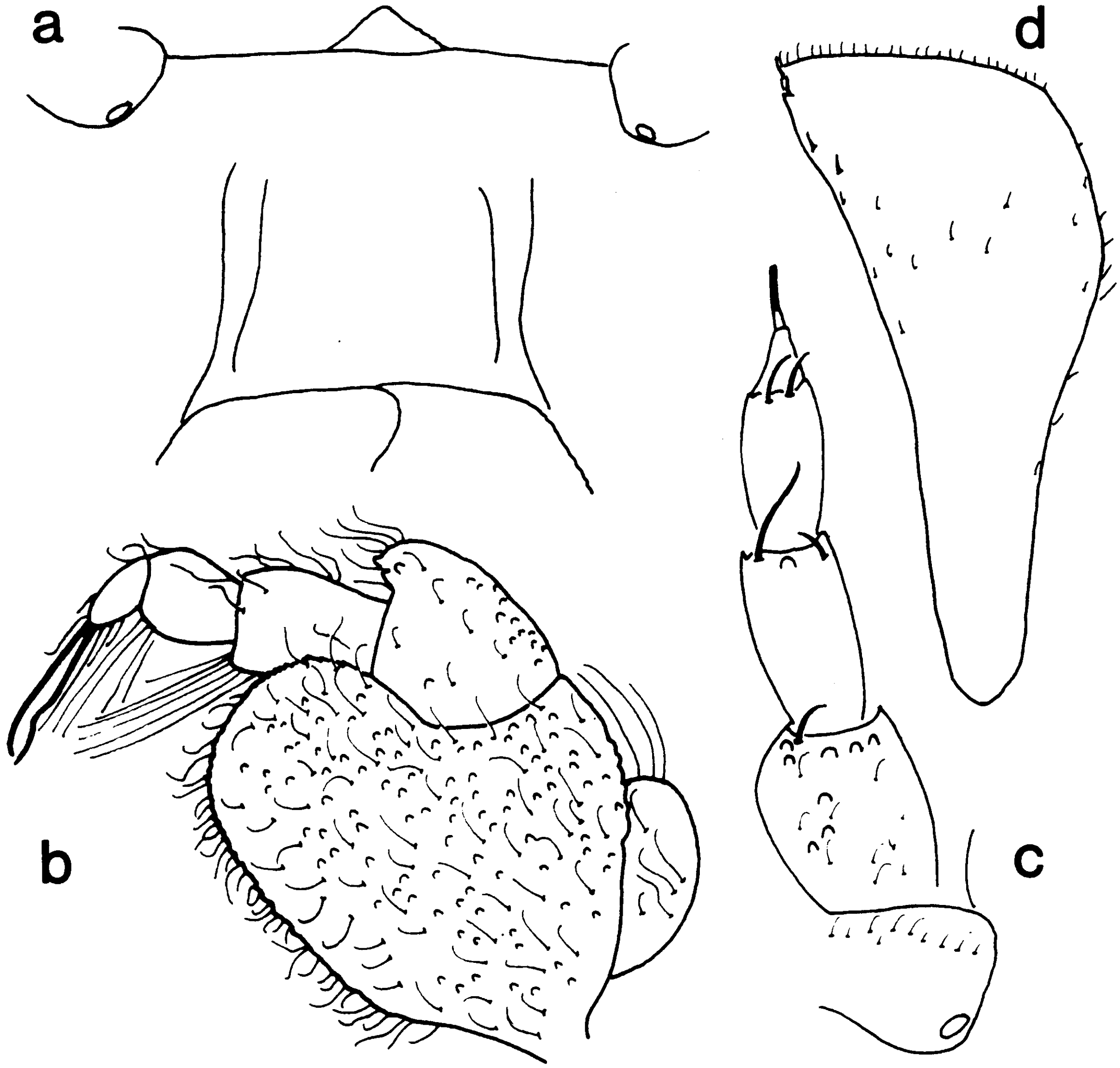
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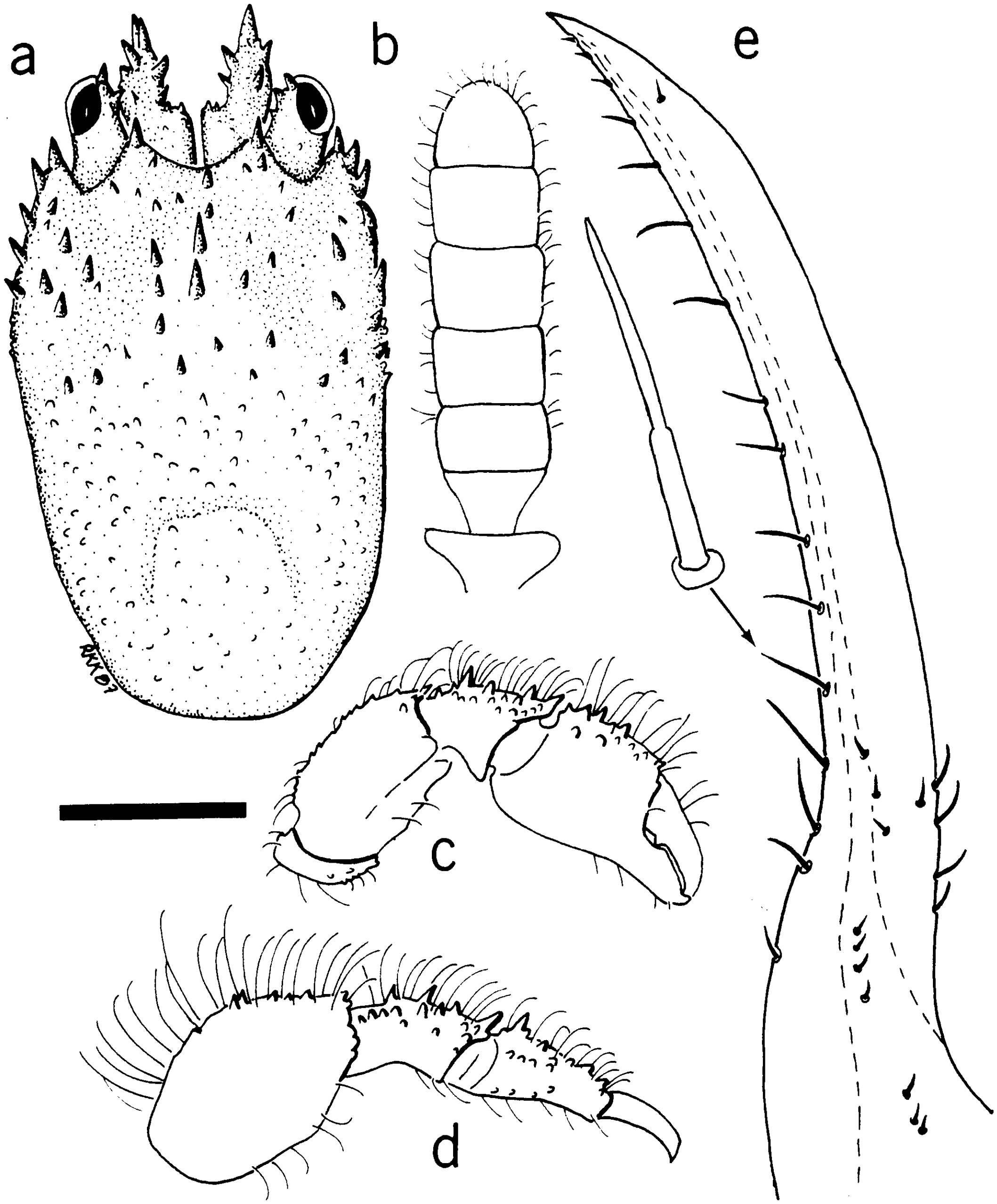
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Chapter 6

A Revision of the Pacific Species of Gall Crabs, Genus *Opecarcinus* (Crustacea: Cryptochiridae)

ABSTRACT

Pacific species of the gall crab genus *Opecarcinus* are reviewed. *O. granulatus* (Shen), by having a much less ornate carapace and having the cornea situated anterolaterally on the eyestalk, differs from *O. crescentus* (Edmondson), which has a carapace ornamented with numerous tubercles and the cornea situated terminally on the eyestalk, and is removed from the synonymy of *O. crescentus*. Five new species are described: *O. aurantius*, having a very elongate antennular peduncle; *O. lobifrons*, having the internal orbital angle exceeding the anterolateral angle of the carapace; *O. peliops*, living specimens having a blue-black cornea; *O. pholeter*, having 3 longitudinal depressions on the posterior carapace; and *O. sierra*, having a convex carapace with many larger, subequal, conical tubercles. All of these species were found on agariciid corals. The genus is known from the eastern Indian Ocean, the Pacific Ocean from Asia to Baja California, and from the Atlantic Ocean. A key to all species of the genus is provided.

The cryptochirid genus *Opecarcinus* was defined by Kropp and Manning (1987) to include two species, *O. hypostegus* (Shaw and Hopkins, 1977) found in the Atlantic Ocean and *O.*

crescentus (Edmondson, 1925) found in the Pacific Ocean. Species in this genus occur on agariciid and siderastreid corals, where they usually live in tunnels on the coral surface or in crescent-shaped pits in the corallum.

I collected a large suite of material of *Opecarcinus* in the course of research on coral symbionts in Micronesia. Among the crabs collected were many specimens not fitting within the definitions of the two presently known species. These are herein recognized as five new species. Additionally, I examined the type of *Cryptochirus granulatus* Shen, 1936 and found evidence for its removal from the synonymy of *O. crescentus*. A key to all known species of *Opecarcinus* is provided.

Materials and Methods

I obtained the type specimens of *Cryptochirus granulatus* Shen from the British Museum (Natural History), London, England (BMNH), the type of *Cryptochirus crescentus* Edmondson from the B. P. Bishop Museum, Honolulu, Hawaii (BPBM), and the type of *Pseudocryptochirus hypostegus* Shaw and Hopkins from the National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM). Specimens of *C. crescentus* were obtained from the BMNH, the Allan Hancock Foundation, Los Angeles, California (AHF), the Muséum National d'Histoire Naturelle, Paris, France (MNHN), Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RMNH), and the Zoological Museum, Copenhagen, Denmark (ZMC). The remainder of the material examined was collected by me (collection numbers denoted by HAP and PHAP) in Micronesia during 1984 and L. G. Eldredge at Johnston Atoll in 1983.

Drawings were made with a camera lucida mounted on a Wild M-5 or M-20 microscope. The cheliped was drawn so that the outer surface of the manus is parallel to the plane of the printed page which distorts the other segments somewhat. Setae on the surfaces of the carapace and pereopods are not shown. The carapace length and width of each specimen were measured to the nearest 0.1 mm with an ocular micrometer on a Wild M-5 microscope and are reported in mm as length x width. Abbreviations used in the text are: ALA, anterolateral angle of carapace; IOA, internal orbital angle of carapace; km, kilometers; m, meters; MXL, maxilla; MXP, maxilliped; ov, ovigerous; P, pereopod; and PLP, pleopod.

In this study I use the term tubercle to describe several cuticular projections in which the basal width is about 1/2 or more than the height; conical tubercles are those having a relatively acute apex (see Fig. 21b); rounded tubercles have a broadly rounded apex (see Fig. 21c); and angled tubercles the height of which is much less than the basal width (see Fig. 20g). Other cuticular projections include spines, in which the basal width is much less than 1/2 the height (see Fig. 29a), and granules, generally small, round slightly raised structures (see Fig. 20c). Orbits are defined as deep, in which the depth is greater than half the width, and shallow, in which the depth is much less than half the width (see Fig. 20a, 24a, respectively). The lateral margin of the female gonopore of some species has a mesial expansion at the anterior end that I refer to as a hood (see Fig 20d). Setal terminology follows that of Kunze and Anderson (1979).

The degree of ornamentation of the carapace varies within species. Many individuals, particularly juveniles, are smoother than others. For this reason degree of tuberculation and granulation are not useful in separating species. Degree of setation on the carapace also seems variable, with a few exceptions. Species accounts are based on the holotype or a representative specimen. Variations occurring among the other material examined are placed within brackets where appropriate. Some proportions appear to be useful in characterizing certain species. These are given for the primary specimen, with the range of variation occurring among the other material examined included within brackets.

Color is based on freshly collected material from Micronesia.

At the first occurrence of a collection locality in the text, the latitude and longitude are given. For some localities new orthographic spellings have been advocated (Motteler, 1986). At the first occurrence of these localities in the text the new orthography is given followed parenthetically by the former spelling. Subsequently, only the new spelling is given. Specific locality names in Micronesia (except Guam) are from Bryan (1971). Guam names are from a United States Geological Survey topographic map. Geographic records from the literature are given in brackets in the synonymies.

Key to the species of *Opecarcinus*

(based on females)

1. Cornea anterolateral..................................2

   Cornea terminal......................................4

2. Distal margin of antennule longer than lateral margin
   (ventral view).......................................3

   Distal margin of antennule shorter than lateral margin
   (ventral view)......................... *O. hypostegus*

3. P-5 carpus smooth.......................... *O. pholeter*

   P-5 carpus tuberculate dorsally........... *O. granulatus*

4. Sternite of P-2 smooth laterally; antennule base
   oblique..5

   Sternite of P-2 tuberculate laterally; antennule base
   transverse...6

5. IOA extends beyond ALA; distal margin of antennule
   shorter than lateral margin............... *O. lobifrons*

   IOA not extending beyond ALA; distal margin of antennule
   longer than lateral margin............... *O. aurantius*

6. Dorsal margin of P-2 notched distally; dorsal margin of
   cornea irregularly sinuous................. *O. peliops*

Dorsal margin of P-2 not notched distally; dorsal margin of cornea evenly concave.............................7

7. Carapace strongly convex; anterior depression restricted to protogastric region...................... *O. sierra*

Carapace relatively flat; anterior depression extending to epibranchial region.................. *O. crescentus*

Systematic Account

Opecarcinus crescentus (Edmondson, 1925)

Fig. 20, 21

Cryptochirus crescentus Edmondson, 1925:33, Fig. 6a-i, Pl. IB-C [Johnston Atoll]; 1933a:16, Pl. 4C-D [Teraina = Washington Is.]; 1933b:233 [Hawaii].--Shen, 1936:23.--Hiro, 1937:142; 1938:149.--Utinomi, 1944:688.--Edmondson, 1946:273 [Hawaii].--Fize and Serène, 1957:9 [Vietnam].--Serène, 1962:30.--Garth, 1974:398.--Takeda and Tamura, 1980b:138; 1980c:46.

Pseudocryptochirus crescentus.--Utinomi, 1944:701, Figs. 5D, 6D, 7C, 7F, 10, 11H, 12C, 14B, 15C, 15G, 16C, 16D, 17.--Serène, 1966:396.--Garth and Hopkins, 1968:41.--Garth, 1974:401.--Serène et al., 1974:20 [Indonesia].--Shaw and Hopkins, 1977:179.--Monod and Serène, 1976:26.--McCain and Coles, 1979:85.--Takeda and Tamura, 1980a:57; 1980b:138; 1980c:47; 1981:14, Fig. 1, Pl. 2 [Japan]; 1983:1; 1986:63, Fig. 4.

Troglocarcinus crescentus.--Fize and Serène, 1957:5, Figs. 10, 11C, 11D, 12B, Pl. 3 Figs. 4-7, Pl. 5 Fig. 2.--Serène, 1962:31.--Garth and Hopkins, 1968:41 [Mexico].--Maragos, 1977:186.

Opecarcinus crescentus.--Kropp and Manning, 1987:9.

Material examined.--Holotype: JOHNSTON ATOLL; "Tanager" 1923; on *Pavona duerdeni* Vaughan, 1907; + (ov); BPBM S1805. Other material: VIETNAM: Nhatrang [12°14'N, 109°12'E]; Rte. 1588; [no specific locality or host recorded]; 1 o; Rte. 1644 (Bai Suot); 31 Mar 1956; [no host recorded]; 1 + (ov); BMNH 1958.10.20.3-4. THAILAND: Ko Kaeo [07°45'N 98°18'E], Phuket; 12 Nov 1972; Coll. Serène and Lundøer; [no host recorded]; 6 + (ov), 3 o; ZMC. INDONESIA: Moluccas; Expedition Rumphius I; 11 Jan 1973; CB 307; [no host recorded]; 1 + (ov), 1 o; MNHN B.12667. BELAU (Palau): Ulong (Aulong) Is. [07°16'N, 134°17'E]; fringing reef on west coast of island; 1 m; 28 Jun 1984; PHAP 035; on *Pavona venosa* (Ehrenberg, 1834); 1 + (ov), 3 o; USNM 234254. Ngeruktabel (Urukthapel) Is. [07°15'N, 134°24'E]; patch reef in bay on northeast coast, facing Ngemelachel (Malakal) Pass; 1 m; 5, 20 Jul 1984; PHAP 068, 071, 141; on *P. cactus* (Forskal, 1775), *P. venosa*; 13 + (7 ov), 5 o; USNM 234255, BPBM. Ngeruktabel Is.; north shore, at west end of rock islands; 2 m; 22 Jul 1984; PHAP 165; on *P. explanulata* (Lamarck, 1816); 1 + (ov), 1 o; USNM 234256. Ngemelachel Is. [07°20'N, 134°28'E]; south of Marine Mariculture Demonstration Center (MMDC); 2 m; 18 Jul 1984; PHAP 126; on

P. explanulata; 3 + (ov); BMNH. GUAM: Double Reef [13°36'N, 144°50'E]; fringing reef; 3 m; 7 Feb 1984; HAP 073; on *P. varians* Verrill, 1864; 2 + (ov), 1 o; MNHN; from main patch reef; 6 m; 24 Feb 1984; HAP 121; on *P. duerdeni*; 2 + (1 ov, 1 with cryptoniscine isopod attached to inside of abdominal pouch), 1 o; USNM 234257. Agaña Bay [13°29'N, 144°46'E]; reef front off Alupat Is.; 8 m; 20 Feb 1984; HAP 108; on *P. duerdeni*; 1 +, 1 o; RMNH; reef flat north of boat basin channel; 1 m; 5 Mar 1984; HAP 145; on *P. venosa*; 2 + (1 ov), 1 o; AHF. Piti Bay [13°29'N, 144°42'E]; north side of bay at mid reef flat; 1 m; 26 Jan 1984; HAP 038; on *P. decussata* (Dana, 1846); 5 + (3 ov); USNM 234258. Luminao Reef [13°28'N, 144°39'E]; reef flat; 1 m; 13, 27 Oct 1984; HAP 319, 361; on *P. varians*, *Pavona* sp.; 6 + (ov), 2 o; BMNH. Calalan Bank [13°27'N, 144°38'E]; reef front near Magundas; 10 m; 16 Oct 1984; HAP 334; on *P. duerdeni*; 2 + (ov); RMNH. Apra Harbor [13°27'N, 144°38'E]; patch reef at Western Shoals; 21 m; 15 Mar 1984; HAP 170; on *P. divaricata* (Lamarck, 1816); 3 + (2 ov); USNM 234259. Agat Bay [13°24'N, 144°39'E]; 0.8 km north of Nimitz Beach; reef front; 14 m; 29 Mar 1984; HAP 186; on *Gardineroseris planulata* (Dana, 1846); 4 + (3 ov), 2 o; MNHN; reef flat; 1 m; 29 Mar 1984; HAP 187; on *Pavona* sp.; 3 + (1 ov), 1 o; RMNH. Fouha Bay [13°18'N, 144°39'E]; south wall of channel; 8 m; 26 Apr 1984; HAP 214; on *P. explanulata*; 1 + (ov); AHF. TRUK: off Moen Is. [07°26'N, 151°52'E]; 11 Apr 1981; HAP 084; on *P. maldiviensis* (Gardiner, 1905); 1 + (ov); USNM

234260. JOHNSTON ATOLL: Pres. R. Gurney; on *P. duerdeni*; 1 +, 1 o; BMNH 1949.v.4.1-2; East, North Islands; 1 m; 24 Oct 1983; HAP 052, 053; Coll. L. G. Eldredge; on *Pavona* sp.; 4 + (ov); USNM 234261. HAWAII: Oahu; Waikiki [21°17'N, 157°50'W]; reef off Waikiki Aquarium; 1.5 m; 18 Dec 1984; HAP 429; on *P. varians*; 2 + (1 ov); USNM 234262. MEXICO: Baja California; El Tule Ranch, 6 km east of Cabo San Lucas [22°53'N, 109°54'W]; Jun 1965; Coll. G. F. Crozier; [host not recorded, but listed as *P. gigantea* Verrill, 1869 by Garth and Hopkins (1968)]; 2 + (1 ov); AHF 2776-01.

Size Range.--Females, 1.4 x 1.2 to 4.4 x 3.8; ovigerous females, 2.1 x 1.8 to 4.0 x 3.3; males, 1.5 x 1.2 to 3.6 x 2.9.

Type data.--Holotype: + (ov), 2.1 x 1.8; BPBM S1805. Type locality: Johnston Atoll [16°45'N, 169°32'W]. Other types: Edmondson (1925) only designated a "type specimen", the holotypic female. He also described males, but the whereabouts of these specimens is not known. The BMNH material (a male and female) from Johnston Atoll listed among the material examined is accompanied by a note reading "may be type material!", but Edmondson did not mention depositing any types in the BMNH. That the material was deposited in 1949 reduces the likelihood that these specimens are types.

Description.--Adult female (Holotype, Fig. 20): Carapace 1.2 [1.1-1.3] times longer than wide. Anterior 1/3 of carapace moderately deflected, not sharply set off from posterior carapace, with transverse depression extending from frontal margin, across protogastric region, to anterolateral angles (ALA) and epibranchial margin of carapace. Posterior 2/3 of carapace with elongate H-shaped depression extending from gastric to cardio-intestinal region. Transverse section of carapace at midlength convex overall, median 1/3 slightly [markedly] concave, with few conical tubercles, scattered setae longer [much longer] than tubercles. Carapace surface ornamented with many rounded and conical tubercles, largest, most numerous at midlength, diminishing slightly in size and number posteriorly. Anterolateral margins of carapace with few conical tubercles, ALA lacking prominent tubercle. Inner orbital angles (IOA) marked with tubercle, slightly inflated, totally elevated above level of and extending to or just beyond apex of ALA. Front concave with few smaller tubercles, lacking prominent median tubercle, width 0.5 [0.4-0.5] that of carapace at ALA, latter 0.7 [0.5-0.7] that of greatest carapace width. Orbit deep, broadly V-shaped, margin with few tubercles.

Basal segment of antennular peduncle transverse, slightly inflated mesially, with distal projection having apex of angled lateral lobe extending beyond eyestalk; dorsal surface concave with few scattered smaller tubercles; margin with 6-10 subequal spines. In ventral view, basal segment broadening distally, length 2.2 [2.0-2.5] times width; distal margin shorter than lateral margin; surface convex with scattered granules.

Eyestalk partially exposed dorsally. Cornea terminal, in dorsal view, occupying about 1/2 length of stalk, dorsal margin evenly concave, lateral margin just reaching ALA.

Mesial margin of ischium of MXP-3 coarsely crenulated; lateral margin of merus strongly produced distally, mesial margin with 2 plumo-denticulate setae. Mesial margin of MXL-1 with 4 stout simple setae, lower margin with 1 stout simple seta; outer surface with 1 serrate seta, not extending beyond mesial margin.

Sternite of cheliped (P-1) with transverse row of 7 [5-8] rounded [conical] tubercles at midlength, none posteriorly. Sternite of first walking legs (P-2) smooth, with tubercles at lateral margin. Gonopore elliptical, lateral margin having [lacking in some specimens] anterior hood.

Manus of P-1 1.8 [2.1-2.3] times longer than high. Dactylus subequal in length to dorsal margin of palm, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with few scattered conical tubercles along entire length, few rounded tubercles; outer surface of palm flat with few granules proximally. Dorsal margin of carpus lacking [present in some specimens] prominent tubercle distally. Merus shorter, taller than manus, ventral margin granular.

Merus of P-2 1.2 [1.3-1.4] times longer than high; dorsal margin moderately convex with larger conical tubercles on distal half; ventral margin convex, tuberculate, moderately emarginate distally; distoventral angle produced into prominent tubercle; outer surface with many larger rounded tubercles on distodorsal half, with elevated transverse row of rounded tubercles distoventrally. Propodus 1.0 [1.1] times longer than high, dorsal margin as long as that of carpus.

Merus of last walking leg (P-5) 1.4 [1.7-1.9] times longer than high; dorsal margin with tubercules along entire length; ventral margin straight, with few angled tubercles; distoventral angle formed into blunt tubercle; outer surface with many tubercles dorsodistally. Dorsal margin of carpus with few tubercles. Propodus 1.6 [2.5-2.9] times longer than high; dorsal margin entire.

Adult male (Vietnam, BMNH 1958.10.20.3, Fig. 21): Carapace ornamentation similar to female; posterior carapace with slight median H-shaped depression. IOA marked with tubercle, extending to or just exceeding ALA. Eyestalk similar to female; cornea terminal, lateral margin extending just beyond ALA. P-1 slightly more robust than female, manus length 1.7 times height. Dorsal margin of dactylus with few conical tubercles proximally, cutting edge with low tooth proximally, dactylus slightly shorter than dorsal margin of palm, latter with subequal conical tubercles along entire margin; ventral margin of palm entire. Dorsal margin of merus of P-2 convex, with conical tubercles on distal half; ventral margin scarcely convex, with few angled tubercles at midlength. Dorsal margin of merus of P-5 with angled tubercles; ventral margin with few tubercles distally; dorsal margin of carpus with few tubercles. Sternite of P-1 with 7 conical tubercles at midlength, 12 granules posteriorly. PLP-1 (Guam, USNM) with plumose seta at proximomesial angle.

Color.--Adult female: Carapace overall off-white; posterior carapace with 4 longitudinal black bands, similar transverse band at apex of carapace; anterior depression red-brown. Cornea dark red, may have white spot.

Comparisons.--See "Discussion" section.

Hosts/habitats.--Agariciidae: *Pavona cactus*, *P. duerdeni*, *P. venosa*, *P. explanulata*, *P. varians*, *P. divaricata*, *P. maldiviensis*, *P. decussata*, and *Gardineroseris planulata*. Material on which this report is based was collected at depths of < 1 m to 14 m from a variety of reef habitats ranging from the open coast to protected embayments.

Several literature host records need to be clarified. Four species listed by Fize and Serène (1957) are now recognized as junior synonyms of species listed above (Veron and Pichon, 1980). These are *P. venusta* Dana, *P. formosa* Dana, and *P. praetorta* Dana (misspelled as *proetorta* by Fize and Serène), all of which are synonyms of *P. cactus*. Fize and Serène listed *P. muelleri* Milne Edwards and Haime as a possible synonym of *P. cactus*, but I have not been able to verify this. Also listed is *P. lata* Dana, a synonym of *P. decussata*. Veron and Pichon (1980) also listed *P. duerdeni* as a synonym of *P. clavus* Dana. Other coral taxonomists prefer to separate the two (Randall and Myers, 1983) and I have done so in order to avoid obscuring the host records. Takeda and Tamura (1983) recorded *O. crescentus* as occurring on corals of the genus *Coscinastrea* of the family Agariciidae. Their record is uncertain because the name *Coscinastrea* is actually a printing error for *Coscinarea* Milne Edwards and Haime of the family Siderastreidae (see Veron and Pichon, 1980). The genus *Opecarcinus* occurs on siderastreid corals in the Atlantic (Scott, 1985; 1987).

Distribution.--Known from Vietnam to Baja California.

Opecarcinus granulatus (Shen, 1936),
new combination

Fig. 22, 23

Cryptochirus granulatus Shen, 1936:23, Pl. 2 [Christmas Is., Indian Ocean].--Utinomi, 1944:688.--Fize and Serène, 1957:54.

Pseudocryptochirus granulatus.--Takeda and Tamura, 1981:14.

Material examined.--Holotype: CHRISTMAS IS. (Indian Ocean); 45 fathoms (82 m); no host recorded; Pres. R. Kirkpatrick; o; BMNH 1911.8.15.2. Other material: GUAM: Fouha Bay; south wall of channel; 8 m; 26 Apr 1984; HAP 215; on *Leptoseris* sp.; 1 + (ov), 1 o; USNM 234263. Cetti Bay

[13°19'N, 144°39'E]; patch reef in middle of bay; 13-14 m; 30 Nov 1984; HAP 407, 410; on *Gardineroseris planulata*, *Pavona explanulata*; 2 +; USNM 234264/5.

Size range.--Females, 1.9 x 1.6 to 2.4 x 2.2; ovigerous female, 2.4 x 2.2; males 1.9 x 1.7 to 2.2 x 2.0.

Type data.--Holotype: o, 2.2 x 2.0; BMNH 1911.8.15.2. Type locality: Christmas Island (Indian Ocean) [10°30'S, 105°40'E]. No other types were described.

Description.--Adult female (Guam, USNM 234263, Fig. 22): Carapace 1.1 [1.2] times longer than wide. Anterior 1/3 of carapace slightly deflected, sharply set off from posterior carapace, with transverse depression extending from frontal margin, across protogastric region, to ALA and epibranchial regions. Posterior 2/3 of carapace with broad, shallow inverted U-shaped central depression. Transverse section of carapace at midlength angularly convex overall, median 1/3 slightly concave, with scattered variously sized tubercles, moderately setose with unequal setae longer than tubercles. Carapace surface ornamented with various granules and conical tubercles, largest at midlength, diminishing considerably in size and number posteriorly. Anterolateral margins of carapace having conical tubercles, ALA lacking prominent tubercle. IOA marked with tubercle, inflated, totally elevated above level of and extending to apex of ALA. Front concave with subequal tubercles, lacking prominent median tubercle, width 0.5 that of carapace at

ALA, latter 0.7 greatest carapace width. Orbit deep, broadly V-shaped, margin granulate.

Basal segment of antennular peduncle slightly oblique, scarcely inflated mesially, with distal projection having apex of angled lateral lobe not reaching tip of eyestalk; dorsal surface flat with few scattered granules; margin with 8-9 spines, those of distal margin larger than those of mesial margin. In ventral view, basal segment tapering anteriorly, length 2.3 [2.6] times width; distal margin longer than lateral margin; surface convex with scattered granules.

Eyestalk mostly exposed dorsally. Cornea anterolateral, in dorsal view, occupying 1/2 length of stalk, dorsal margin evenly concave, lateral margin not extending beyond ALA.

Mesial margin of ischium of MXP-3 coarsely crenulated; lateral margin of merus strongly produced distally, mesial margin with 2 plumo-denticulate setae. Mesial margin of MXL-1 with 3 stout simple setae, lower margin with 3 stout simple setae; outer surface without setae.

Sternite of P-1 with transverse row of 9 conical tubercles, 4 smaller, rounded tubercles at midlength, 1 granule posteriorly. Sternite of P-2 smooth, lacking tubercles at lateral margin. Gonopore oval, lateral margin lacking anterior hood.

Manus of P-1 2.3 times longer than high. Dactylus subequal in length to dorsal margin of palm, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with conical tubercles along entire length; outer surface of palm flat with few granules proximally. Dorsal margin of carpus with prominent tubercle distally. Merus shorter, taller than manus, ventral margin with few tubercles.

Merus of P-2 1.7 [1.5] times longer than high; dorsal margin convex proximally, straight distally, having various acute conical tubercles, largest on distal 1/2, ventral margin convex, with angled tubercles, moderately emarginate distally; distoventral angle produced into prominent tubercle; outer surface with many granules, tubercles on distodorsal 1/2, with elevated transverse row of tubercles distoventrally. Propodus 1.2 [1.3] times longer than high, dorsal margin as long as that of carpus.

Merus of P-5 1.4 [1.3] times longer than high; dorsal margin with angled tubercles along entire length; ventral margin convex, with few angled tubercles; distoventral angle with 2 tubercles; outer surface with few smaller conical tubercles dorsally. Dorsal margin of carpus with rounded tubercles. Propodus 1.6 [1.5] times longer than high; dorsal margin entire.

Adult Male (Holotype, Fig. 23): Similar to female in general form. Carapace smoother, but showing same pattern of depressions. IOA lacking prominent tubercle, extending to level of ALA. Eyestalk proportionally larger than in female, cornea anterolateral, lateral margin just exceeding

ALA. P-1 more robust than in female; manus length 1.6 times height. Dorsal margin of dactylus with few conical tubercles proximally; cutting edge with low tooth proximally; dactylus longer than dorsal margin of palm, latter with several sharp tubercles on proximal half; ventral margin of palm entire. Dorsal margin of merus of P-2 relatively straight with variously sized conical tubercles along entire length; ventral margin convex, entire. Dorsal margin of merus of P-5 bearing tubercles along entire length; ventral margin entire; carpus having tubercles on dorsal margin. Sternite of P-1 with 10 various granules. PLP-1 with plumose setae on proximomesial angle.

Color.--Adult female: Carapace opaque, covered with many small black chromatophores posteriorly, with much larger black chromatophores anteriorly, latter overlain with white, giving a gray hue. Eyestalk clear with black chromatophores, cornea red-orange. Meri of P-2 to P-5 opaque with fine orange line network. Distal merus, carpus, and propodus of P-2 and P-3 grayish with scattered bright blue spots. Male: Generally similar to female, cornea more orange, some fine red chromatophores on P-1.

Comparison.--See "Discussion" section.

Remarks.--Utinomi (1944) synonymized this species with *Cryptochirus crescentus* because the two were fairly similar and they were found in the same locality. The latter argument was based on the type locality of *granulatus* being

Christmas Island and Edmondson (1933) having recorded *crescentus* from Christmas Island. However, Edmondson was referring to Christmas Island (now = Kiritimati) in the Pacific, whereas the type locality for *granulatus* is Christmas Island in the Indian Ocean. Shen (1936) did not specify the ocean of the type locality for *granulatus*, but the label with the holotype reads "Xmas Island, Indian Ocean." Fize and Serène (1957) asserted that the relative lack of carapace ornamentation in Shen's *granulatus*, as compared to male *Q. crescentus* that they observed, could be attributed to differences in size, smaller specimens generally being less ornate. However, the male *Q. crescentus* figured herein (Fig. 23) is about the same size as the holotype of *Q. granulatus* (carapace lengths--2.1 and 2.2 mm, respectively) and shows quite different carapace ornamentation. Other differences, including the position of the cornea on the eyestalk, anterolateral in *Q. granulatus* versus terminal in *Q. crescentus* and the pattern of depressions on the posterior carapace, inverted "U"-shaped in *Q. granulatus* versus "H"-shaped in *Q. crescentus*, would not seem to be size related and strengthen the argument for separation of the two species.

Hosts/Habitats.--Agariciidae: *Gardineroseris planulata*, *Leptoseris* sp., and *Pavona explanulata*. Host of the holotype was not recorded. On Guam this species was collected from embayments, habitats of relatively high productivity. It has been collected at depths of 8-82 m.

Distribution.--Known from Christmas Island (Indian Ocean) and Guam.

Opecarcinus aurantius, new species

Fig. 24, 25

Material examined.--Holotype: GUAM: Cetti Bay; reef on south side of bay; 6 m; 30 Nov 1984; HAP 412; on *Pavona minuta* Wells, 1954; + (ov); USNM 234266. Paratypes: GUAM: Fouha Bay; south wall of channel; 7, 9 m; 6, 26 Apr 1984; HAP 194, 212; on *P. minuta*; 2 +; BPBM, BMNH. Cetti Bay; same collection data as holotype; 3 + (ov); USNM 234267. POHNPEI (Ponape): Ant Atoll [06°47'N, 157°58'E]; in lagoon on patch reef on northeast side of channel at Matenpita; 4.5 m; 23 Nov 1984; PHAP 349; on *P. minuta*; 1 +, 1 o; USNM 234268.

Size range.--Females, 2.0 x 1.7 to 3.4 x 2.9; ovigerous females, 2.5 x 2.0 to 3.4 x 2.9; male, 2.9 x 2.2.

Type data.--Holotype: + (ov), 3.3 x 2.7; USNM 234266. Type locality: Cetti Bay, Guam [13°19'N, 144°39'E]. Paratypes: Several females and males as listed in material examined.

Description.--Adult female (Holotype, Fig. 24): Carapace 1.2 [1.2-1.3] times longer than wide. Anterior 1/3 of carapace moderately deflected, not sharply set off from posterior carapace, with transverse depression extending from frontal margin, across protogastric region, to ALA, not extending to epibranchial margin of carapace. Posterior carapace with shallow H-shaped depression at cardio-intestinal region. Transverse section of carapace at midlength evenly convex overall, with many subequal conical tubercles, sparse setae subequal and shorter than tubercles. Carapace surface ornamented with many conical, rounded tubercles and granules, largest at midcarapace, diminishing markedly posteriorly. Anterolateral margins of carapace having conical tubercules much smaller than those on anterior carapace, ALA lacking prominent tubercle. IOA marked with tubercle, barely inflated, partially elevated above ALA, not reaching apex of latter. Front concave, granulate, having prominent median tubercle, width about 0.5 [0.4-0.5] that at ALA, latter about 0.5 [0.5-0.7] that of greatest carapace width. Orbit shallow, broadly V-shaped, margin tuberculate.

Basal segment of antennular peduncle oblique, not inflated mesially, with distal projection having apex of angled lateral lobe not reaching tip of eyestalk; dorsal surface slightly concave, covered with rounded tubercles and granules; margin with 7-8 [5-8] spines, those of distal margin larger than those of mesial margin. In ventral view, distal projection tapering sharply anteriorly, length 3.0 [2.9-3.0] times width; distal margin subequal in length to lateral margin; surface concave with many granules.

Eyestalk mostly exposed dorsally. Cornea terminal, in dorsal view, occupying 2/5 length of stalk, dorsal margin evenly concave, lateral margin extending to or just beyond level of ALA.

Mesial margin of ischium of MXP-3 coarsely crenulated; lateral margin of merus weakly produced distally, mesial margin with 4-5 plumo-denticulate setae. Mesial margin of MXL-1 with 3 stout simple setae, lower margin with 2 stout simple setae; outer surface lacking setae.

Sternite of P-1 with transverse row of 13 [8-13] conical tubercles at midlength, with few granules posteriorly. Sternite of P-2 smooth, lacking tubercles at lateral margin. Gonopore oval, lateral margin lacking anterior hood.

Manus of P-1 2.8 [2.4-2.8] times longer than high. Dactylus shorter than dorsal margin of palm, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with conical tubercles along entire length, larger on proximal half; outer surface of palm flat with few granules proximally. Dorsal margin of carpus with prominent tubercle distally. Merus shorter, taller than manus, ventral margin densely granulate.

Merus of P-2 1.5 [1.4-1.6] times longer than high, dorsal margin evenly convex, entire length with conical tubercles, slightly larger distally; ventral margin straight, with few angled tubercles, moderately emarginate distally; distoventral angle produced having 1 larger, 2 smaller tubercles, outer surface with various conical, rounded tubercles on distodorsal 1/3, lacking elevated transverse row of tubercles distoventrally. Propodus 1.0 [0.9-1.1] times longer than high; dorsal margin shorter than that of carpus.

Merus of P-5 1.7 [1.4-1.9] times longer than high, dorsal margin slightly concave with fine tubercles proximally, convex with larger tubercles distally; ventral margin relatively straight, entire; distoventral angle obtuse, lacking tubercle. Dorsal margin of carpus entire. Propodus 2.3 [2.0-2.4] times longer than high, dorsal margin entire.

Adult male (Fig. 25): Similar in form to female, carapace lacking larger tubercles, having many smaller tubercles and granules. IOA lacking prominent tubercle, extending beyond ALA. Eyestalk longer than in female; cornea terminal, lateral margin extending beyond ALA. P-1 more robust than in female; manus length 1.7 times height. Dorsal margin of dactylus with many angled tubercles proximally, cutting edge with low tooth proximally; dactylus slightly shorter than dorsal margin of palm, latter with larger conical tubercles on proximal 1/2, many smaller tubercles distally; ventral margin of palm with serrations. Dorsal margin of merus of P-2 straight, with various conical tubercles along entire length; ventral margin straight with many subequal angled tubercles along entire length. Dorsal margin of merus of P-5 with many smaller tubercles; ventral margin with few tubercles; dorsal margin of carpus with tubercles. Sternite of P-1 with 10 rounded tubercles. PLP-1 with stout simple setae at proximomesial angle.

Color.--Adult female: Anterior carapace white, rest opaque with scattered whitish areas, with overall light orange tint. ALA, IOA red-orange. Eyestalk opaque with red-orange tint; cornea bright rust, may have black line proximally. Antennule base rust. Dorsal P-2 matches anterior carapace, eyestalk, and antennules. Color of some specimens may have more orange than holotype. Male: Similar to female, anterior carapace bright white, posterior carapace red-orange.

Comparison.--See "Discussion" section.

Etymology.-- From the Latin *aurantium*, meaning "orange," in reference to the prevalent color found on these crabs.

Hosts/habitats.--Agariciidae: *Pavona minuta*. Collected at depths to 9 m from habitats of relatively high productivity; river embayments at Guam and an atoll lagoon at Pohnpei.

Distribution.--Known from Guam and Pohnpei.

Opecarcinus lobifrons, new species

Fig. 26, 27

Troglocarcinus (Troglocarcinus) crescentus--Garth, 1965:8, figs. 3-6 [Clipperton Is.].

Pseudocryptochirus crescentus--Garth and Hopkins, 1968:41 (in part).

Material examined.--Holotype: GUAM; Tanguisson Pt.; reef front; 3 m; 25 May 1984; HAP 226; on *Gardineroseris planulata*; 1 +; USNM 234269. Paratypes: GUAM; Tanguisson Pt.; same collection data as holotype; 1 +; USNM 234270. Tanguisson Pt.; reef front; 2 m; 7 Feb 1984; HAP 067; on *G. planulata*; 1 +, 1 o; USNM 234271; 2 + (ov); BPBM. Agaña Bay; 300 m north of boat basin channel; reef front; 9 m; 3 Feb 1984; HAP 061; on *G. planulata*; 1 +, 1 o; BMNH. Agat Bay; 0.9 km north of Facpi Pt. [13° 20'N, 144° 38'E]; reef front; 7 m; 8 Mar 1984; HAP 161; on *G. planulata*; 2 + (ov), 1 o; MNHN. CLIPPERTON IS. [10° 17'N, 109° 13'W]; NE Transect; 78 ft [24 m]; 27-VIII-1958; Coll. C. Limbaugh; [host not recorded]; 1 +; AHF 2777-01.

Size range.--Females, 2.4 x 1.9 to 4.6 x 3.8; ovigerous females, 2.4 x 1.9 to 2.6 x 2.0; males, 2.1 x 1.6 to 2.4 x 1.9.

Type data.--Holotype: +, 2.9 x 2.3; USNM 234269. Type locality: Tanguisson Pt., Guam [13° 33'N, 144° 49'E]. Paratypes: several males and females as listed in material examined.

Description.--Adult female (Holotype, Fig. 26): Carapace length 1.2 [1.2-1.3] times width. Anterior 1/4 of carapace slightly deflected, not sharply set off from posterior carapace, with transverse depression restricted to protogastric region. Posterior carapace with inverted U-shaped depression at cardio-intestinal region. Transverse section of carapace at midlength evenly convex overall with scattered variously sized conical tubercles, moderately setose with setae subequal, slightly longer than tubercles. Carapace surface with scattered rounded and conical tubercles, largest just anterior to midlength, decreasing sharply in size posteriorly to fine granules; posterolateral margins rounded. Anterolateral margins with few larger conical tubercles, ALA lacking prominent tubercle. IOA marked with tubercle, inflated, entirely elevated above level of and extending beyond ALA. Front concave, lacking prominent prominent tubercle, with many rounded tubercles; width 0.4 [0.4-0.5] that of carapace at ALA, latter 0.6 [0.7] greatest carapace width. Orbit shallow, broadly J-shaped, margin tuberculate.

Basal segment of antennular peduncle oblique, not inflated mesially, with distal projection having apex of angled lateral lobe not reaching tip of eyestalk; dorsal surface scantly concave with many smaller tubercles; margin with 7-8 [7-8] spines, those of distal margin larger than those of mesial margin. In ventral view, basal segment tapering anteriorly, length 2.3 [2.4-2.6] times width; distal margin shorter than lateral margin; surface convex with scattered granules, most near mesial margin.

Eyestalk partially exposed dorsally. Cornea terminal, in dorsal view, occupying 2/5 length of stalk, dorsal margin evenly concave, lateral margin extending just beyond ALA.

Mesial margin of ischium of MXP-3 coarsely crenulated; lateral margin of merus weakly produced distally, mesial margin with 1 plumo-denticulate seta. Mesial margin of MXL-1 with 3 stout simple setae, lower margin with 2 stout simple setae; outer surface with 1 stout serrate seta not exceeding mesial margin.

Sternite of P-1 with transverse row of 12 [8-13] rounded [conical] tubercles at midlength, none posteriorly. Sternite of P-2 smooth, lacking tubercles at lateral margin. Gonopore oval, lateral margin lacking anterior hood.

Manus of P-1 2.1 [1.8-2.1] times longer than high. Dactylus slightly shorter than dorsal margin of palm, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with conical tubercles along entire length, largest on proximal 1/2; outer surface of palm flat with few rounded tubercles proximally. Dorsal margin of carpus with prominent tubercle distally. Merus shorter, taller than manus, ventral margin irregularly tuberculate.

Merus of P-2 1.6 [1.4-1.6] times longer than high; dorsal margin slightly convex, with various conical tubercles, largest on distal 1/4; ventral margin relatively straight, with several angled tubercles, gently emarginate distally; distoventral angle produced into prominent tubercle; outer surface with many granules, rounded tubercles on distodorsal 1/3, with elevated transverse row of tubercles distoventrally. Propodus 1.1 [1.0-1.1] times longer than high, dorsal margin shorter than dorsal margin of carpus.

Merus of P-5 1.9 [1.6-2.1] times longer than high; dorsal margin with smaller angled tubercles along entire length, with few larger conical tubercles distally; ventral margin straight, entire; distoventral angle with small tubercle; outer surface smooth. Dorsal margin of carpus with few smaller tubercles distally. Propodus 2.5 [1.8-2.2] times longer than high; dorsal margin entire.

Adult male (Fig. 27): Similar in form to female, depression on anterior carapace extends to epibranchial regions; carapace relatively flat with fewer tubercles. IOA marked with spine, not inflated, extending beyond level of ALA. Eyestalk stockier than in female; cornea terminal, lateral margin extending to or just falling short of ALA. P-1 manus more robust than in female, 1.5 times longer than high. Dorsal margin of dactylus with few conical tubercles dorsally, cutting edge with low tooth proximally; dactylus shorter than dorsal margin of palm, latter with few larger tubercles proximally, many rounded tubercles distally; ventral margin of palm entire. Dorsal margin of merus of P-2 scarcely convex, with various conical tubercles; ventral margin scarcely convex with few angled tubercles. Dorsal margin of P-5 convex with smaller angled tubercles on distal 3/4; ventral margin straight, entire. Sternite of P-1 with 6-8 tubercles. PLP-1 with plumose setae at proximomesial angle.

Color.--Adult female: Anterior carapace bright white, posterior carapace with clear band laterally having many fine black chromatophores and overall red-orange hue. Eyestalks clear with red-orange tint, corneas red. Antennule base red-orange around margin, brownish mesially. P-2 clear with fine white lines becoming densely packed distally. P-3 to P-5 clear dorsally with irregular orange lines, thicker distally. Male: Anterior carapace white, posterior brownish with blue spots near anterior edge of brown area. Corneas pink.

Comparison.--See "Discussion" section.

Remarks.--Garth (1965) noticed that the Clipperton specimen differed from typical specimens of *O. crescentus*. This material was examined by Serène who (in Garth, 1965) stated that the differences were age-related. I disagree. The main features separating *O. lobifrons* from *O. crescentus*, the extent of the IOA beyond the ALA and the restricted anterior depression, are consistent among all of the specimens of the two species that I have examined, regardless of size. However these features are exaggerated in the Clipperton specimen of *O. lobifrons*. I have not seen the dried specimens discussed and figured by Garth (1965:10, fig. 4-6).

Etymology.--From the Latin "lobus", elongated projection, in combination with "frons", forehead, in reference to the extension of the front of the carapace beyond the level of the anterolateral angles of the carapace; a noun in apposition.

Hosts/habitats.--Agariciidae: *Gardineroseris planulata*. On Guam, collected from open water reef front areas to a depth of 9 m. The host of the Clipperton Island specimen, collected at 24 m, was not recorded. The coral fauna of Clipperton Island does not seem to be well documented. Two species of *Pavona*, *P. gigantea* Verrill and *P. explanulata* were listed by Durham and Barnard (1952). Of interest is the record of *P. ponderosa* Gardiner at Cocos Island (Durham, 1962). *P. ponderosa* is now considered a junior synonym of *G. planulata* (see Veron and Pichon, 1980), thus the known host of *O. lobifrons* occurs in eastern Pacific waters.

Distribution.--Known from Guam and Clipperton Island.

Opecarcinus peliops, new species

Fig. 28, 29

Material examined.--Holotype: POHNPEI: Pakin Atoll; reef front south of Mant Is.; 3 m; 19 Nov 1984; PHAP 302; on *Pavona duerdeni*; +; USNM 234272. Paratypes: Same location and host species as holotype; 3-6 m; 19 Nov 1984; PHAP 299, 303; 1 + (ov), 1 o; USNM 234273/4.

Size range.--Females, 2.1 x 1.8 to 3.3 x 2.9; ovigerous female, 2.1 x 1.8; male, 2.0 x 1.6.

Type data.--Holotype: + (ov), 3.3 x 2.9; USNM 234272. Type locality: Pakin Atoll, Pohnpei [07° 04'N, 157° 48'E]. Paratypes: One female (ov), one male as listed in material examined.

Description.--Adult female (Holotype, Fig. 28): Carapace 1.2 times longer than wide. Anterior 1/3 of carapace moderately deflected, not sharply set off from posterior carapace, with shallow transverse depression extending from frontal, across protogastric region, to ALA, not reaching epibranchial margin of carapace. Posterior carapace with central H-shaped depression. Transverse section of carapace at midlength evenly convex overall with many subequal conical tubercles, moderately setose with setae subequal, much longer than tubercles. Carapace surface ornamented with erect conical tubercles, largest at midcarapace, smaller tubercles anteriorly; posterior half of carapace with round granules diminishing in size and number posteriorly. Anterolateral margins with few erect conical tubercles, ALA lacking prominent tubercle. IOA marked with tubercle, slightly inflated, elevated above and extending to apex of ALA. Front slightly concave, with larger median tubercle, width 0.4 that of ALA, latter 0.6 that of greatest carapace width. Orbit shallow, broadly U-shaped, margin with few tubercles.

Basal segment of antennular peduncle transverse, not inflated mesially, with distal projection having apex of angled lateral lobe extending beyond eyestalk; dorsal surface slightly concave with few granules; margin with 7-9 [11] subequal spine. In ventral view, basal segment broadening anteriorly, length 2.1 times width; distal margin shorter than lateral margin; surface flat with scattered granules.

Eyestalk mostly exposed dorsally. Cornea terminal; in dorsal view, occupying 1/3 length of stalk, dorsal margin irregularly sinuous, lateral margin of cornea extending beyond ALA.

Mesial margin of ischium of MXP-3 coarsely crenulated; lateral margin of merus weakly produced distally, mesial margin with 4 stout plumo-denticulate setae. Mesial margin of MXL-1 with 3 stout simple setae, lower margin with 1 stout simple seta; outer surface with 1 pappose seta, exceeding mesial margin.

Sternite of P-1 with transverse row of 6 rounded tubercles at midlength, few smaller tubercles along anterolateral margins, 2-3 rounded tubercles posterolaterally. Sternite of P-2 smooth, with tubercles at lateral margins. Gonopore oval, lateral margin lacking anterior hood.

Manus of P-1 1.8 [1.9] times longer than high. Dactylus slightly longer than dorsal margin of palm, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with erect conical tubercles on proximal 1/2, smaller rounded tubercles distally; outer surface of palm flat with few granules proximally. Dorsal margin of carpus lacking larger tubercle distally. Merus as long as, taller than manus.

Merus of P-2 1.5 times longer than high; dorsal margin convex with transverse notch distally and rounded tubercles proximal to notch, prominent blunt tubercles distal to notch; ventral margin convex with few conical tubercles, abruptly emarginate distally; distoventral angle produced into 3 subequal tubercles; outer surface with few scattered tubercles on distodorsal 1/3, lacking elevated transverse row of tubercles distoventrally. Propodus 1.1 times longer than high, dorsal margin shorter than that of carpus.

Merus of P-5 (from paratype) 1.7 times longer than high; dorsal margin with few smaller tubercles; ventral margin convex, entire; distoventral angle with small tubercle; outer surface smooth. Dorsal margin of carpus entire. Propodus 1.7 times longer than high; dorsal margin entire.

Adult male (Fig. 29): Carapace similar to female, much less tuberculate. IOA marked with spine, slightly exceeding apex of ALA. Eyestalk as in female; cornea terminal, lateral margin exceeding ALA. P-1 more robust than female, manus 1.4 times longer than high. Dorsal margin of dactylus with few tubercles proximally, cutting edge entire; dactylus about as long as dorsal margin of palm, latter elevated above level of joint with dactylus, with few smaller tubercles; ventral margin of palm entire. Dorsal margin of merus of P-2 straight with larger conical tubercles along entire length; ventral margin slightly convex with angled tubercles on distal 1/2. Dorsal margin of merus of P-5 slightly convex with few angled tubercles; ventral margin relatively straight with few angled tubercles. Sternite of P-1 with 4 tubercles. PLP-1 with long simple seta at proximomesial angle.

Color.--Adult female: Carapace white with two curved longitudinal opaque bands posteriorly; with fine, irregular fluorescent orange and black lines on most of carapace; may have black, orange, and blue spots; transverse groove opaque; external orbital angle red-orange. Eyestalk opaque with red-orange tint; cornea with black outer ring, bright, light blue center. Carpus of P-1 similar to eyestalk, dorsal margin of manus yellow-white with light blue spots. P-2 similar to carapace. Male: Carapace bright white, transverse groove opaque. Eyestalk opaque with irregular black marks and red-orange tint; cornea bright blue.

Comparison.--See "Discussion" section.

Etymology.--From the Greek "pelios", black and blue, in combination with "ops", eye, in reference to the peculiar eye color of the females.

Hosts/Habitat.-- Agariciidae: *Pavona duerdeni*. Collected from areas of rich coral growth at depths of 3-6 m in nutrient-poor reef front waters off small atolls.

Distribution.--Known only from Pohnpei.

Opecarcinus pholeter, new species

Fig. 30, 31

Material examined.--Holotype: GUAM: Cetti Bay; on isolated patch reef in middle of bay; 14 m; 30 Nov 1984; HAP 410; on *Pavona explanulata*; + (ov); USNM 234275. Paratypes: BELAU: Ngeruktabel Is.; patch reef between Ngeruktabel and rock island directly south of MMDC; 3 m; 2 Jul 1984; PHAP 041; on *P. explanulata*; 1 + (ov), 1 o; USNM 234276; 2 m; 3 Jul 1984; PHAP 057; on *P. explanulata*; 1 + (ov), 1 o; RMNH. Ngeruktabel Is.; north shore, cove at west end of main rock island group; 3 m; 23 Jul 1984; PHAP 195; on *Leptoseris yabei* (Pillai and Scheer, 1976); 2 o; USNM 234277; PHAP 196; on *P. explanulata*; 1 +; NMNH. GUAM: Agat Bay; Taleyfac Channel; north wall of channel; 3-4 m; 20 Mar 1984; HAP 178, 179; on *P. explanulata*; 1 + (ov); AHF; 3 + (2 ov); BPBM. Fouha Bay; south side of bay on wall of channel; 6 m; 6 Apr 1984; HAP 193; on *P. explanulata*; 1 +, 1 o; AHF; 8 m; 26 Apr 1984; on *P. explanulata*; 1 o; NMNH. Cetti Bay; same collection data as holotype; 1 + (ov), 2 o; BMNH.

Size range.--Females, 2.4 x 2.1 to 5.6 x 4.6; ovigerous females, 3.9 x 3.4 to 5.6 x 4.6; males, 1.4 x 1.2 to 4.2 x 3.4.

Type data.--Holotype, + (ov), 5.6 x 4.6; USNM 234275. Type locality: Cetti Bay, Guam [13° 19'N, 144° 39'E]. Paratypes: Several females and males as listed in material examined.

Description.--Adult female (Holotype, Fig. 30): Carapace 1.2 [1.1-1.3] times longer than wide. Anterior 1/3 of carapace slightly deflected, not sharply set off from posterior carapace, with transverse depression extending from frontal area, across protogastric region, to ALA and epibranchial regions. Posterior carapace with 3 longitudinal depressions extending from gastric to cardiac region, covered with round granules decreasing in size posteriorly. Transverse section of carapace at midlength relatively flat overall, each 1/3 slightly concave, with scattered variously sized conical tubercles, moderately dense unequal setae mostly shorter than tubercles. Carapace surface covered with conical tubercles, largest at midlength. Anterolateral margins with few conical tubercles, ALA lacking prominent tubercle. IOA with spine, slightly inflated, totally elevated above level of and extending to apex of ALA. Front concave lacking larger median tubercle, with few granules, width 0.5 [0.4-0.5] that of carapace at ALA, latter 0.6 times greatest carapace width. Orbit deep, broadly V-shaped, margin with few tubercles.

Basal segment of antennular peduncle slightly oblique, not inflated mesially, with distal projection having apex of lateral lobe reaching apex of eyestalk; dorsal surface scarcely concave with scattered conical tubercles; margin with 6-7 [5-8] spines, those of distal margin larger than those of mesial margin. In ventral view, basal segment tapering anteriorly, length 2.6 [2.5-2.7] times width; distal margin longer than lateral margin; surface flat with scattered granules.

Eyestalk partially exposed dorsally. Cornea anterolateral, in dorsal view, occupying 1/4 length of stalk, dorsal margin evenly concave, lateral margin not reaching ALA.

Mesial margin of ischium of MXP-3 finely crenulated; lateral margin of merus strongly produced distally, mesial margin with 6 plumo-denticulate setae. Mesial margin of MXL-1 with 5 stout simple setae, lower margin with 4-5 stout simple setae; outer surface with 2 stout serrate setae, not exceeding mesial margin.

Sternite of P-1 with transverse band of 22 [15-20] rounded tubercles of various sizes at midlength, several rounded tubercles postero-laterally. Sternite of P-2 granular [smooth], with tubercles at lateral margin. Gonopore elliptical, lateral margin having anterior hood.

Manus of P-1 2.5 [2.1-2.5] times longer than high. Dactylus shorter than dorsal margin of palm, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with few conical tubercles on proximal 1/2, smaller tubercles distally. Dorsal margin of carpus with prominent spine distally. Merus shorter, taller than manus, ventral margin densely covered with angled tubercles.

Merus of P-2 1.6 [1.4-1.7] times longer than high; dorsal margin slightly convex, having various conical tubercles, largest on distal 1/4; ventral margin convex, with angled tubercles, gently emarginate distally; distoventral angle produced into single ventral tubercle with 3 smaller tubercles dorsal to it; outer surface with many rounded tubercles on distodorsal 1/2, with elevated transverse row of tubercles distoventrally. Propodus 1.2 [1.1-1.2] times longer than high, dorsal margin shorter than that of carpus.

Merus of P-5 1.6 [1.4-1.8] times longer than high; dorsal margin convex, with smaller angled tubercles along entire length; ventral margin relatively straight, entire; distoventral angle with small tubercle; outer surface smooth with few tubercles near dorsal margin. Dorsal margin of carpus entire. Propodus 2.1 [1.9-2.2] times longer than high; dorsal margin entire.

Adult male (Fig. 31): Carapace overall similar to female, showing similar pattern of depressions, generally less tuberculate, those present smaller than in female. IOA with blunt tubercle, exceeding apex of ALA. Basal segment of antennule relatively shorter than in female. Eyestalk as in female; cornea anterolateral, lateral margin extending to or just beyond ALA. P-1 proportionally more robust than in female, manus 1.6 times longer than high. Dorsal margin of dactylus with many angled tubercles proximally, cutting edge with low tooth proximally; dactylus slightly shorter than dorsal margin of palm, latter with smaller tubercles along entire length, lacking larger tubercles; ventral margin of palm entire. Dorsal margin of merus of P-2 slightly convex with larger conical tubercles on distal 1/2; ventral margin straight with few angled tubercles. Dorsal margin of merus of P-5 convex with smaller angled tubercles along entire length; ventral margin relatively straight, entire. Sternite of P-1 with transverse band of 20 variously sized conical, rounded tubercles. PLP-1 with plumose setae at proximomesial angle.

Color.--Adult female: Anterior carapace off-white, transverse groove dark amber. Posterior carapace opaque with alternating bands of amber, infused with fine, irregular black spots, and bands of white chromatophores (8 white, 9 amber bands). Eyestalk opaque to off-white; cornea red-brown. Walking legs opaque proximally with fine black-line network and amber tint, rimmed with off-white. Male: Similar to female.

Comparisons.--See "Discussion" section.

Etymology.--From the Greek "pholeter", one who lurks in a hole; a noun in apposition.

Hosts/habitat.--Agariciidae: *Pavona explanulata* and *Leptoseris yabei*. All were collected at depths of 2-14 m from areas of relatively high productivity. The Belau specimens were collected in the lagoon next to a high island (Ngeruktabel). The Guam specimens were collected from embayments into which nutrient-laden rivers empty.

Distribution.--Known from Guam and Belau.

Opecarcinus sierra, new species

Fig. 32

Material examined.--Holotype: GUAM: Agat Bay; Taleyfac Channel, from wall on north side of channel; 3 m; 20 Mar 1984; HAP 177; on *Pavona varians*; + (ov); USNM 234278. Paratypes: GUAM: Luminao Reef; mid reef flat; 1 m; 20, 27 Oct 1984; HAP 350, 366; on *P. divaricata*, *P. venosa*; 2 + (ov); MNHN. Apra Harbor; Hotel Reef; 1 m; 31 Jan 1984; HAP 046; on *P. venosa*; 2 + (ov); RMNH. Apra Harbor; Sasa Bay [13° 27'N, 144° 41'E]; harbor side of large patch reef; 2.5 m; 15 Mar 1984; HAP 166; on *P. varians*; 1 + (ov); USNM 234279. Apra Harbor; Western Shoals; [13° 27'N, 144° 39'E]; west slope of shoals; 21 m; 15 Mar 1984; HAP 169; on *P. divaricata*; 1 + (ov); BMNH. Agat Bay; same collection data as holotype; 4 + (ov); MNHN, BMNH, BPBM. Cocos Lagoon; southwest corner of lagoon just inside barrier reef; 1.5 m; 6 Mar 1984; HAP 148; on *P. venosa*; 2 + (ov); USNM 234280.

Size range.--Ovigerous females, 2.2 x 1.9 to 3.5 x 2.8.

Type data.--Holotype: + (ov), 2.3 x 1.8; USNM 234278. Type locality: Agat Bay, Guam [13° 24'N, 144° 39'E]. Paratypes: Several females as listed in material examined.

Description.--Adult female (Holotype, Fig. 32): Carapace 1.3 [1.2-1.4] times longer than wide. Anterior 1/4 of carapace strongly deflected, not sharply set off from posterior carapace, with transverse depression restricted to protogastric region. Posterior carapace with H-shaped depression at cardio-intestinal region. Transverse section of carapace at midlength convex overall with many conical tubercles, moderately dense setae subequal, shorter than tubercles. Carapace surface with many conical tubercles anteriorly, largest at midlength, posterior surface with rounded tubercles diminishing in size and number posteriorly. Anterolateral margins with few larger tubercles, ALA lacking prominent tubercle. IOA marked with tubercle, inflated, entirely elevated above and extending to apex of ALA. Front concave, margin with many subequal conical tubercles, lacking prominent median tubercle; width 0.5 that of ALA, latter 0.6 [0.6-0.7] that of greatest carapace width. Orbit deep, broadly V-shaped, margin tuberculate.

Basal segment of antennular peduncle transverse, not inflated mesially, with distal projection having apex of angled lateral lobe extending beyond tip of eyestalk; dorsal surface slightly concave, with few rounded tubercles, margin with 11-12 [9-14] subequal spines. In ventral view, basal segment broadening distally, length 2.5 [2.2-2.5] times width; distal margin shorter than lateral margin; surface convex, covered with granules.

Eyestalk mostly exposed dorsally. Cornea terminal, in dorsal view, occupying 1/3 length of stalk, dorsal margin evenly concave lateral margin extending to or just beyond apex of ALA.

Mesial margin of ischium of MXP-3 coarsely crenulated; lateral margin of merus strongly produced distally, mesial margin with 2 plumo-denticulate setae. Mesial margin of MXL-1 with 5, lower margin with 4, stout simple setae; outer surface lacking setae.

Sternite of P-1 with 7 [7-10] larger conical tubercles in single row at midlength, with 10 [0-9] granules posteriorly. Sternite of P-2 smooth, with tubercles at lateral margin. Gonopore oval, lateral margin lacking anterior hood.

Manus of P-1 2.3 [2.3-2.6] times longer than high. Dactylus shorter than dorsal margin of manus, with proximal tubercle dorsally; cutting edges of fingers entire. Dorsal margin of palm with smaller conical tubercles along entire length, slightly larger proximally; outer surface of palm flat with several granules proximally. Dorsal margin of carpus lacking prominent spine distally. Merus shorter, taller than manus; ventral margin with few tubercles.

Merus of P-2 1.3 [1.3-1.5] times longer than high; dorsal margin evenly convex, with conical tubercles along entire length, largest on distal 1/2; ventral margin relatively straight, with angled tubercles, moderately emarginate distally; distoventral angle produced into tubercle; outer surface with many rounded tubercles on distodorsal 1/2, with elevated transverse row of tubercles distoventrally. Propodus 1.0 [1.0] times longer than high, dorsal margin as long as that of carpus.

Merus of P-5 1.5 [1.4-1.6] times longer than high; dorsal margin lined with subequal angled tubercles; ventral margin straight, entire; distoventral angle produced into tubercle; outer surface with few rounded tubercles distally near dorsal margin. Dorsal margin of carpus entire. Propodus 2.3 [1.9-2.4] times longer than high; dorsal margin entire.

Male: Unknown.

Color.--Adult female: Posterior carapace off-white, posterior branchial regions solid brown with mix of orange and brown; or with 7 longitudinal black bands. Anterior carapace off-white, anterior depression dark brown. Cornea dark red.

Comparisons.--See "Discussion" section.

Etymology.--From the Spanish "sierra", mountains with a craggy skyline, in reference to the appearance of the carapace in transverse section; a noun in apposition.

Hosts/Habitats.--Agariciidae: *Pavona varians*, *P. divaricata*, and *P. venosa*. Collected from relatively high productivity areas such as river embayments, lagoons, and from a barrier reef flat at depths to 21 m.

Distribution.--Known only from Guam.

Discussion

Comparisons.--Orientation of the cornea on the eyestalk can be used to separate the species of *Opecarcinus* into two groups. The cornea is oriented anterolaterally in *O.*

hypostegus, *O. granulatus*, and *O. pholeter*, whereas it is terminal in *O. crescentus*, *O. aurantius*, *O. lobifrons*, *O. peliops*, and *O. sierra*. Among the first three species, *O. hypostegus*, an Atlantic species, can be distinguished from the other two by having the distal margin of the basal segment of the antennule longer than the lateral margin; the opposite is true for *O. granulatus* and *O. pholeter*. The latter two species can be differentiated by the condition of the dorsal margin of the carpus of leg P-5; it is tuberculate in *O. granulatus* and smooth in *O. pholeter*. Also, the posterior carapace of *O. pholeter* has 3 longitudinal depressions as compared to the broad, inverted U-shaped depression of *O. granulatus*.

Among species having a terminally situated cornea, the orientation of the basal segment of the antennule, oblique in *O. aurantius* and *O. lobifrons*, as compared to transverse in *O. crescentus*, *O. peliops*, and *O. sierra*, divides those species into two groups. The extent of the IOA separates *O. lobifrons*, in which it extends beyond the apex of the ALA, from *O. aurantius* in which it does not exceed the apex of the ALA. *O. peliops* has a notch distally on the dorsal margin of the merus of leg P-2 and the dorsal margin of the cornea is irregularly sinuous, thereby distinguishing it from *O. crescentus* and *O. sierra* in which the dorsal margin is not notched and the dorsal margin of the cornea is evenly concave. The latter two species can be separated by the marked convexity of the carapace and restriction of the anterior depression from the epibranchial region in *O. sierra* versus the relatively flat carapace and the extension of the anterior depression to the epibranchial region in *O. crescentus*.

Color pattern is useful in distinguishing the species. Cornea color is distinctive for three species; black and blue in *O. peliops*, bright rust in *O. aurantius*, and red-orange in *O. granulatus*. The other four Pacific species of *Opecarcinus*, in which the dominant cornea color is red, can be distinguished by color patterns of the carapace. *O. lobifrons* has a bright white carapace with a red-orange hue posteriorly, but lacks dark bands. The remaining three have off-white carapaces; *O. crescentus* has four black longitudinal bands posteriorly, *O. sierra* has seven black bands (or may be solid brown) posteriorly, and *O. pholeter* has nine amber bands posteriorly. Live color has not been reported for *O. hypostegus*.

Hosts.--The Pacific species of *Opecarcinus* may be restricted to corals of the family Agariciidae. All of the material examined here, for which the host was recorded, occurred on agariciid corals. All literature records for the Pacific species list agariciid corals as hosts, except the questionable record of Takeda and Tamura (1983) as mentioned previously. *Opecarcinus hypostegus* occurs on siderastreid, as well as agariciid, corals in the Atlantic (Kropp and Manning, 1987).

Of the five extant genera of agariciid corals in the Pacific, species of *Opecarcinus* occur on three; *Gardineroseris* Scheer and Pillai, *Leptoseris* Milne Edwards and Haime, and *Pavona* Lamarck. The absence of *Opecarcinus* on *Coeloseris* Vaughan may be an artifact of collection bias. *Coeloseris* is known from Nicobar to New Caledonia (Veron and Pichon, 1980), a region from which there are few gall crab records. That *Opecarcinus* has not yet been found on *Pachyseris* Milne Edwards and Haime is noteworthy. *Pachyseris* is widespread, occurring from Madagascar to Samoa (Ditlev, 1980), and has affinities with two gall crab-inhabited genera, *Gardineroseris* and *Pavona* (Veron and Pichon, 1980). It occurs in Guam (Randall and Myers, 1983) where it is fairly common (pers. obs.). During my field studies in Micronesia I examined over 100 colonies of *Pachyseris* for the presence of gall crabs and did not find any. Reasons for the absence of gall crabs on *Pachyseris* are not immediately obvious.

Two species of *Opecarcinus*, *O. aurantius* on *Pavona minuta* and *O. peliops* on *P. duerdeni*, each may be restricted to a single host species. Each of the other species of *Opecarcinus* occurs on several host coral species.

Distribution.--*Opecarcinus* is the only cryptochirid genus known to have representatives in the three major ocean basins. *O. hypostegus* occurs from the western to central Atlantic (Kropp and Manning, 1987). *O. granulatus* occurs in the easternmost Indian Ocean and in the western Pacific.

The absence of *Opecarcinus* from the main Indian Ocean basin may be a result of a collection deficiency as gall crabs are not well-represented in general decapod collections. Two species (*O. crescentus* and *O. lobifrons*) occur in the eastern as well as the western Pacific, thus having distributions not interrupted by the purported East Pacific Barrier (discussed by Vermeij, 1978). All gall crab species known from the eastern Pacific, *Hapalocarcinus marsupialis* Stimpson is the third, also occur in the western Pacific. Four species of *Opecarcinus*, *O. aurantius*, *O. peliops*, *O. pholeter*, and *O. sierra*, occur only on the Pacific Plate or the islands on its western margin. However, all are newly described and may not represent true Pacific Plate species (see Springer, 1982), as further studies may increase their known distributional ranges.

Acknowledgments

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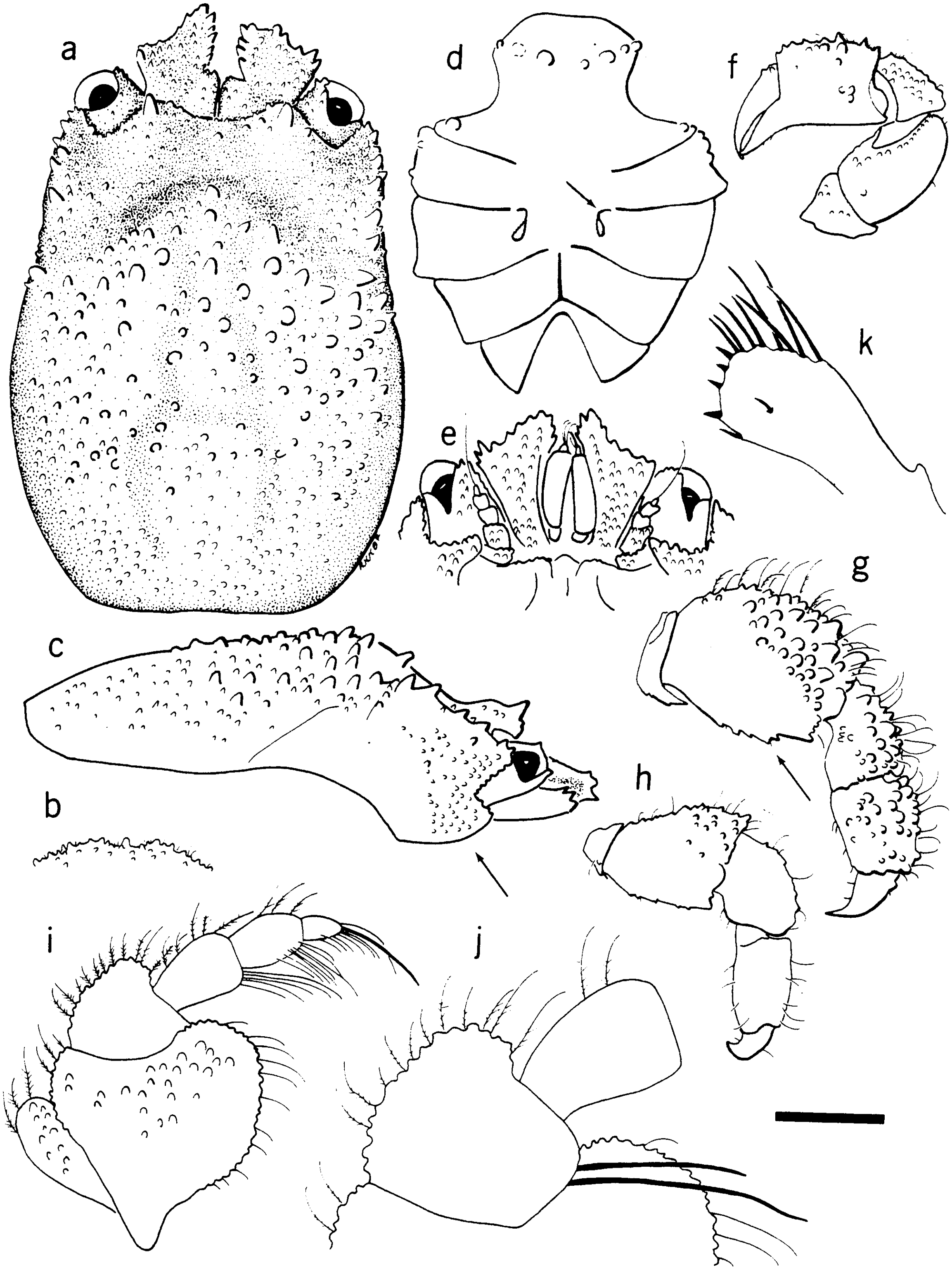
Fig. 20. *Opecarcinus crescentus* (Edmondson), +, Holotype. (Johnston Atoll: BPBM S1805): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view, arrow points to granules); d, thoracic sternites (arrow points to gonopore hood); e, eyes, antennules (ventral view); f, left P-1; g, right P-2 (arrow points to angled tubercles); h, right P-5; i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a, c-h = 0.5 mm; b = 1 mm; i, k = 0.3 mm; j = 0.2 mm.

Fig. 21. *Opecarcinus crescentus* (Edmondson), o. (Vietnam: BMNH 1958.10.20.3-4): a, carapace (dorsal view); b, left P-1 (arrow points to conical tubercles); c, left P-2 (arrow points to rounded tubercles); d, right P-5; e, PLP-1 (outer view). Scale: a-d = 0.5 mm; e = 0.2 mm.

Fig. 22. *Opecarcinus granulatus* (Shen), +. (Guam: USNM 234263): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view); d, thoracic sternites; e, eyes, antennules (ventral view); f-h, right P-1, P-2, P-5; i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a, c, d, f-h = 0.5 mm; b = 0.8 mm; e, j = 0.4 mm; i = 0.3 mm; k = 0.2 mm.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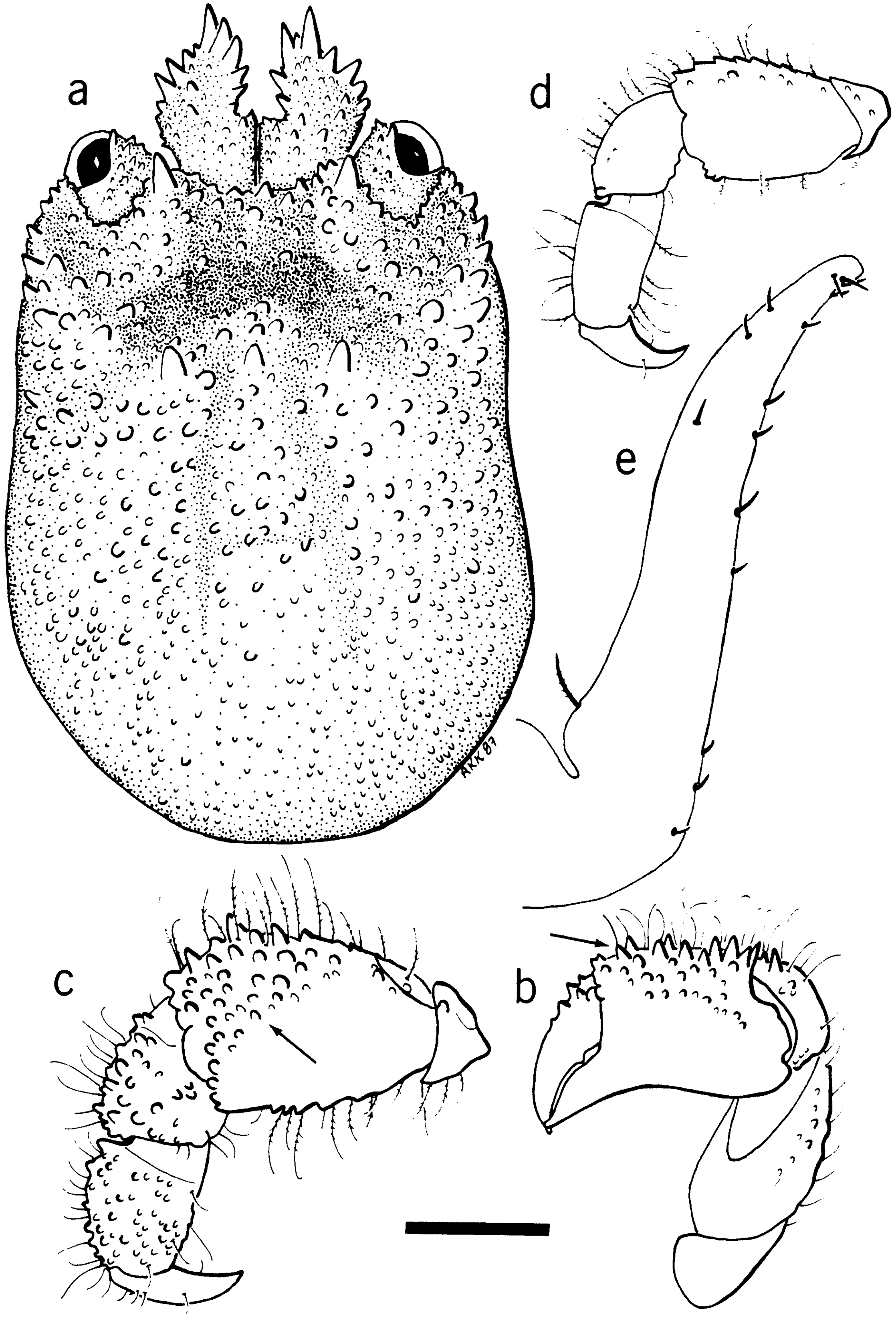
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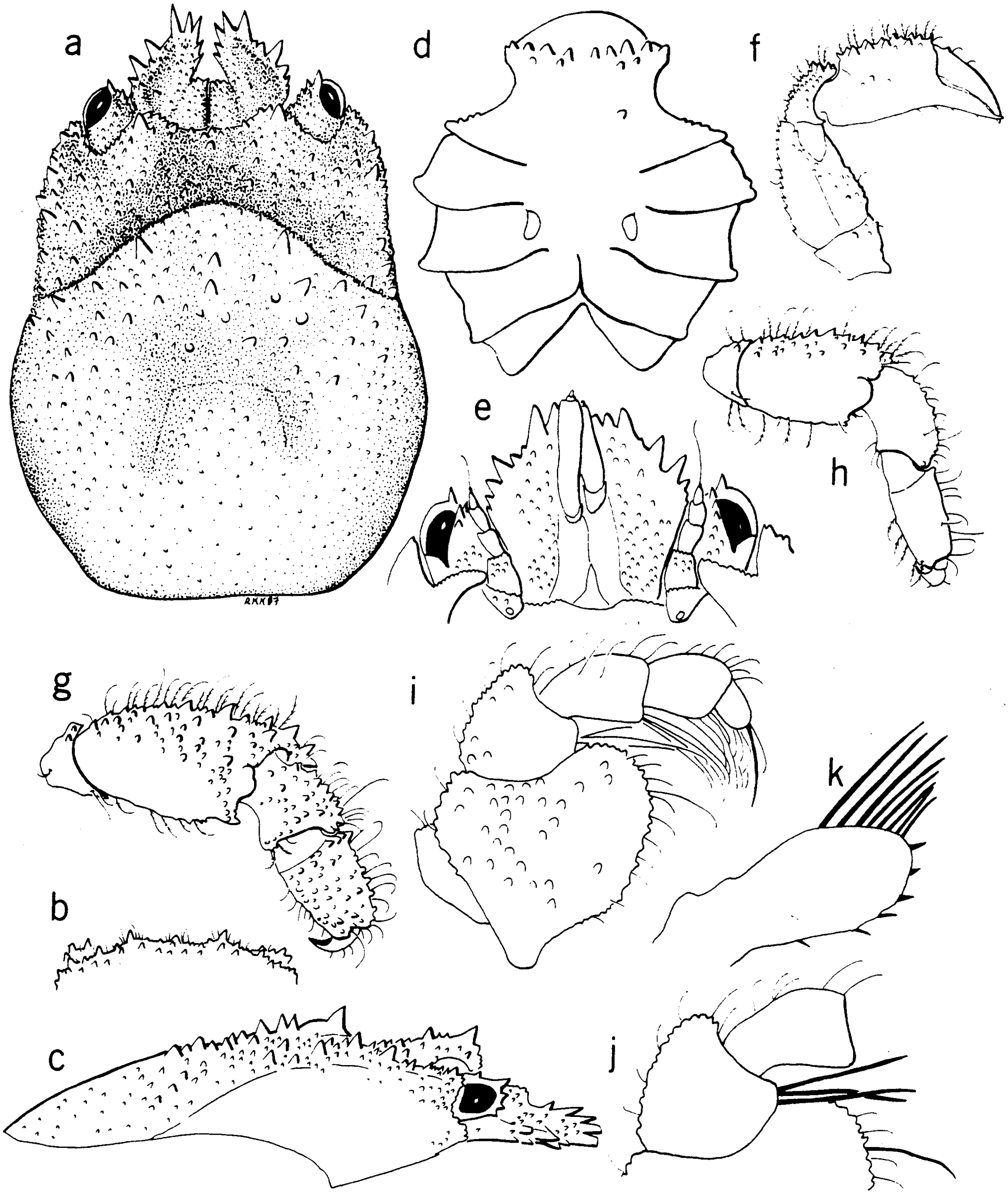
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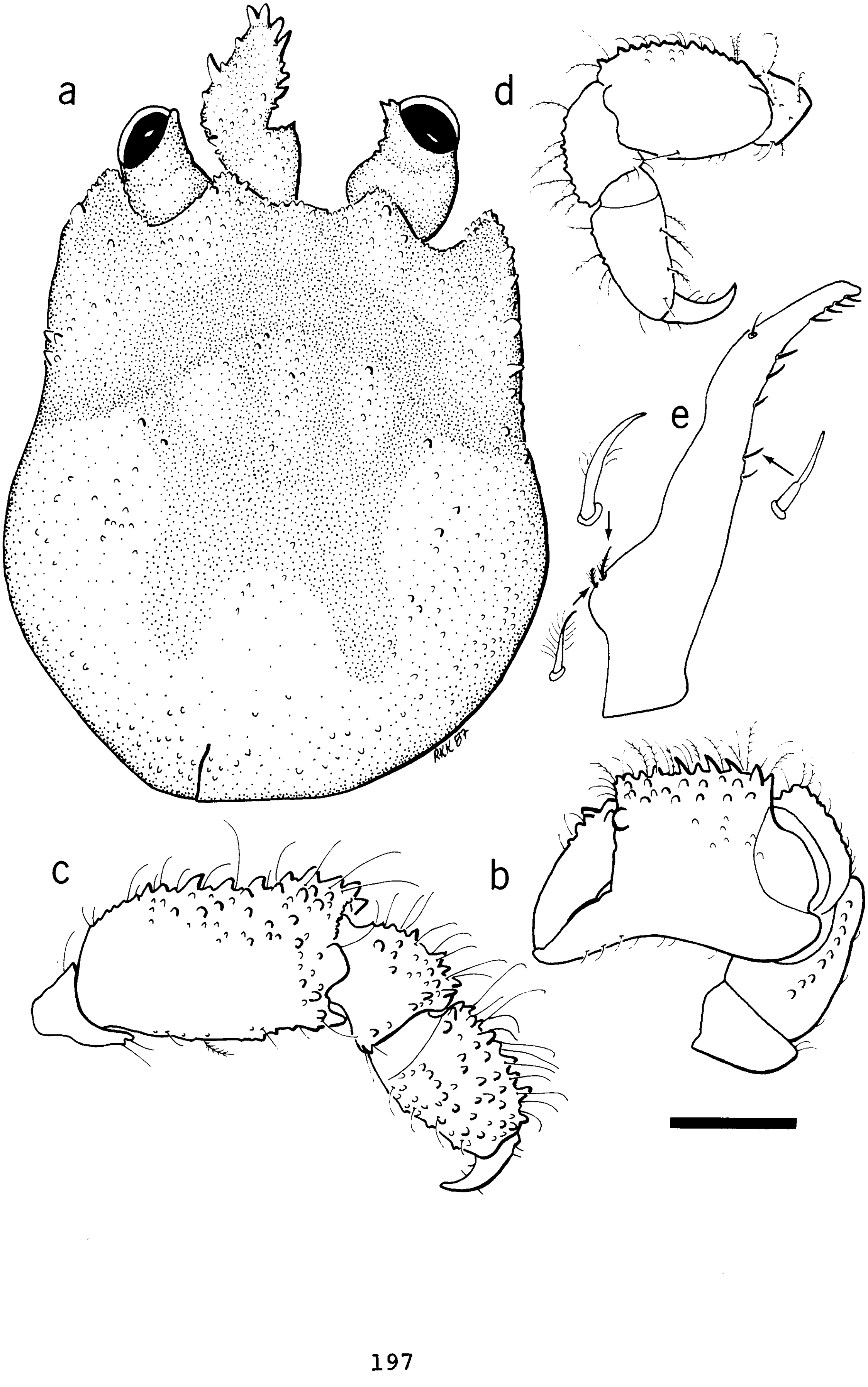
Fig. 23. *Opecarcinus granulatus* (Shen), o, Holotype. (Christmas Island: BMNH 1911.8.15.2): a, carapace (dorsal view); b, left P-1; c, right P-2; d, left P-5; e, PLP-1 (outer view). Scale: a-d = 0.5 mm; e = 0.3 mm.

Fig. 24. *Opecarcinus aurantius*, new species, +, Holotype. (Guam: USNM 234266): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view); d, thoracic sternites; e, eyes, antennules (ventral view); f-h, right P-1, P-2, P-5; i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a, c-d = 1 mm; b = 1.3 mm; e = 0.6 mm; f-h = 0.8 mm; i-j = 0.5 mm; k = 0.2 mm.

Fig. 25. *Opecarcinus aurantius*, new species, o, Paratype. (Pohnpei: USNM 234268): a, Carapace (dorsal view); b-d, Right P-1, P-2, P-5; e, PLP-1 (outer view). Scale: a-d = 0.5 mm; e = 0.2 mm.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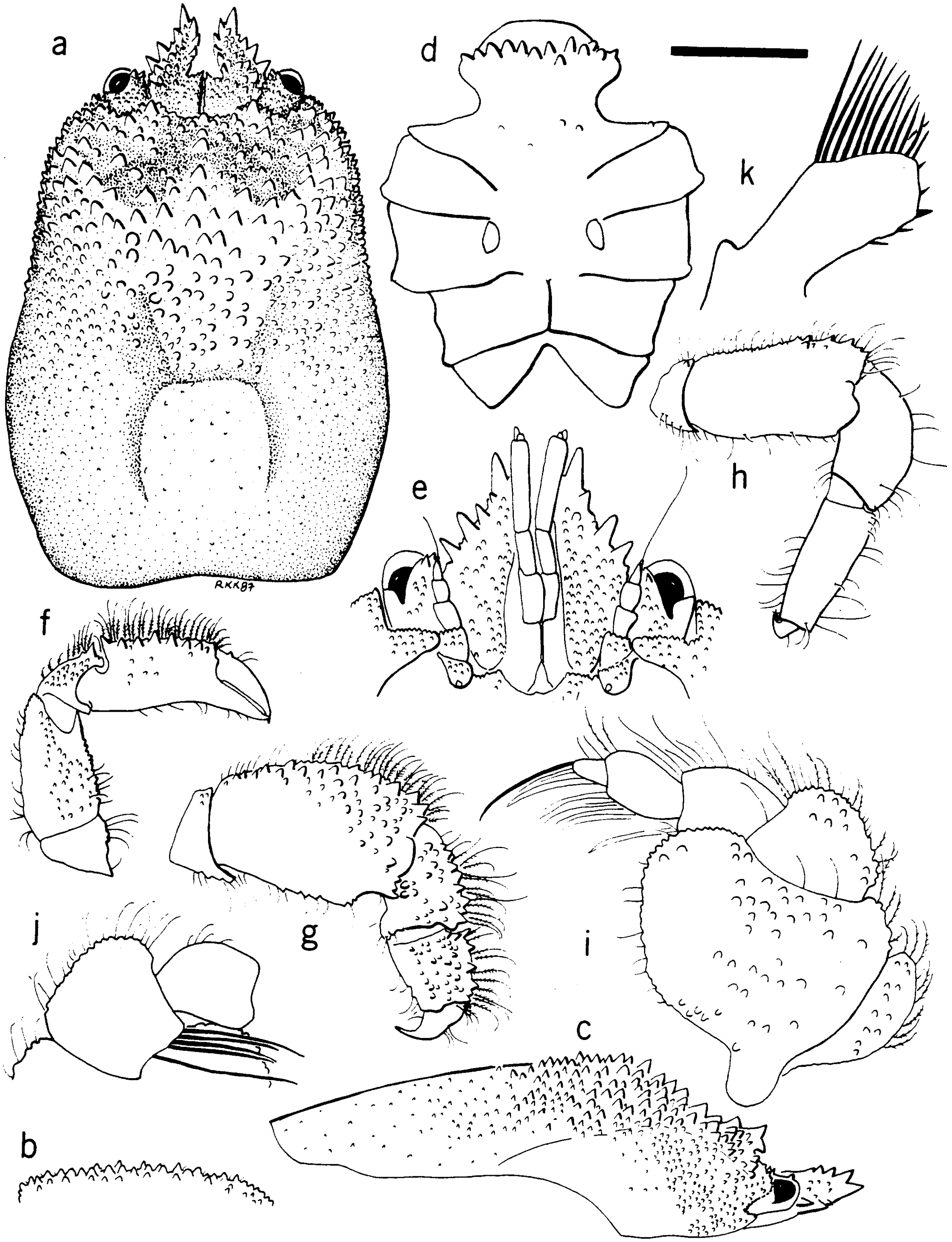
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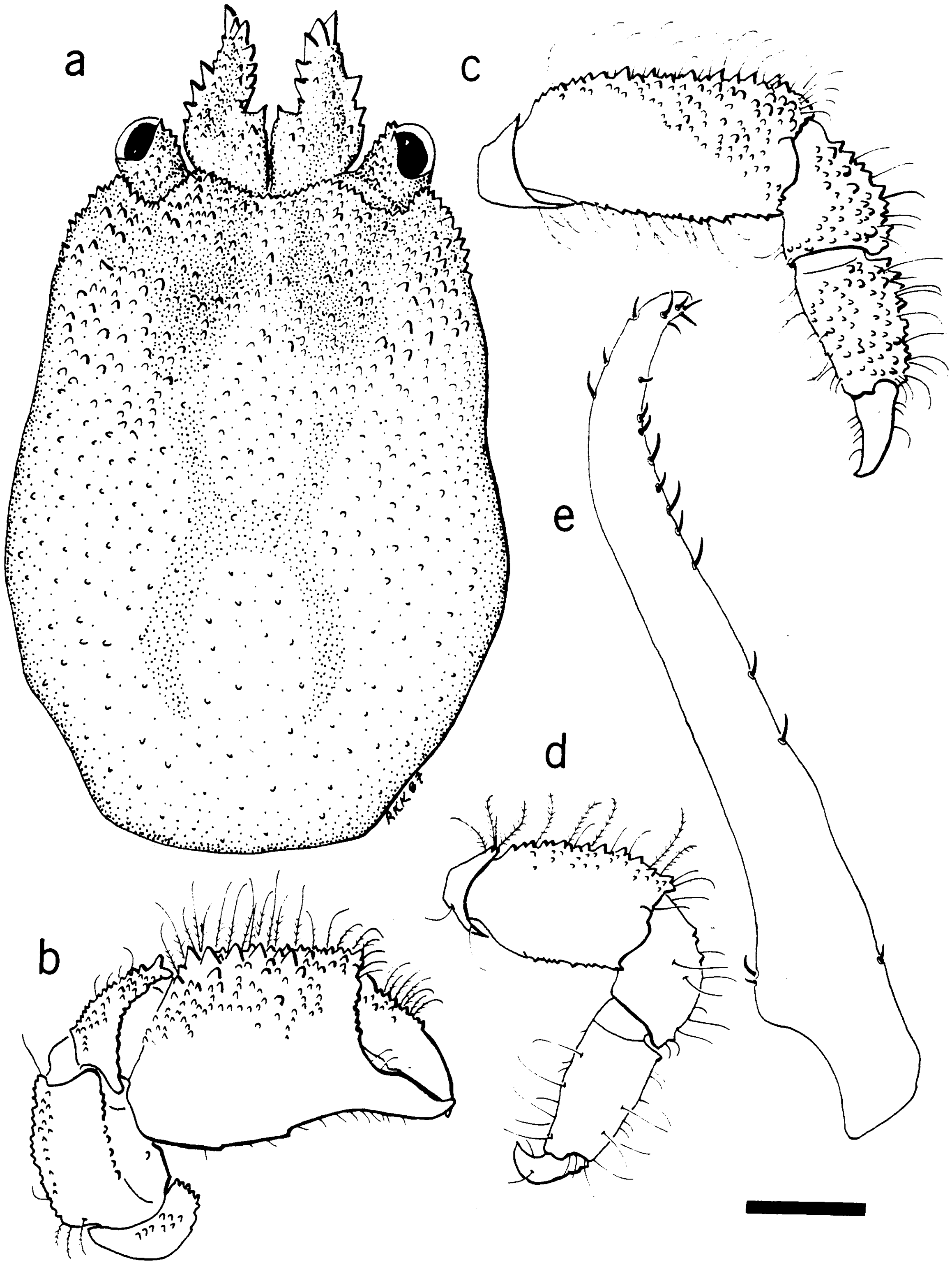
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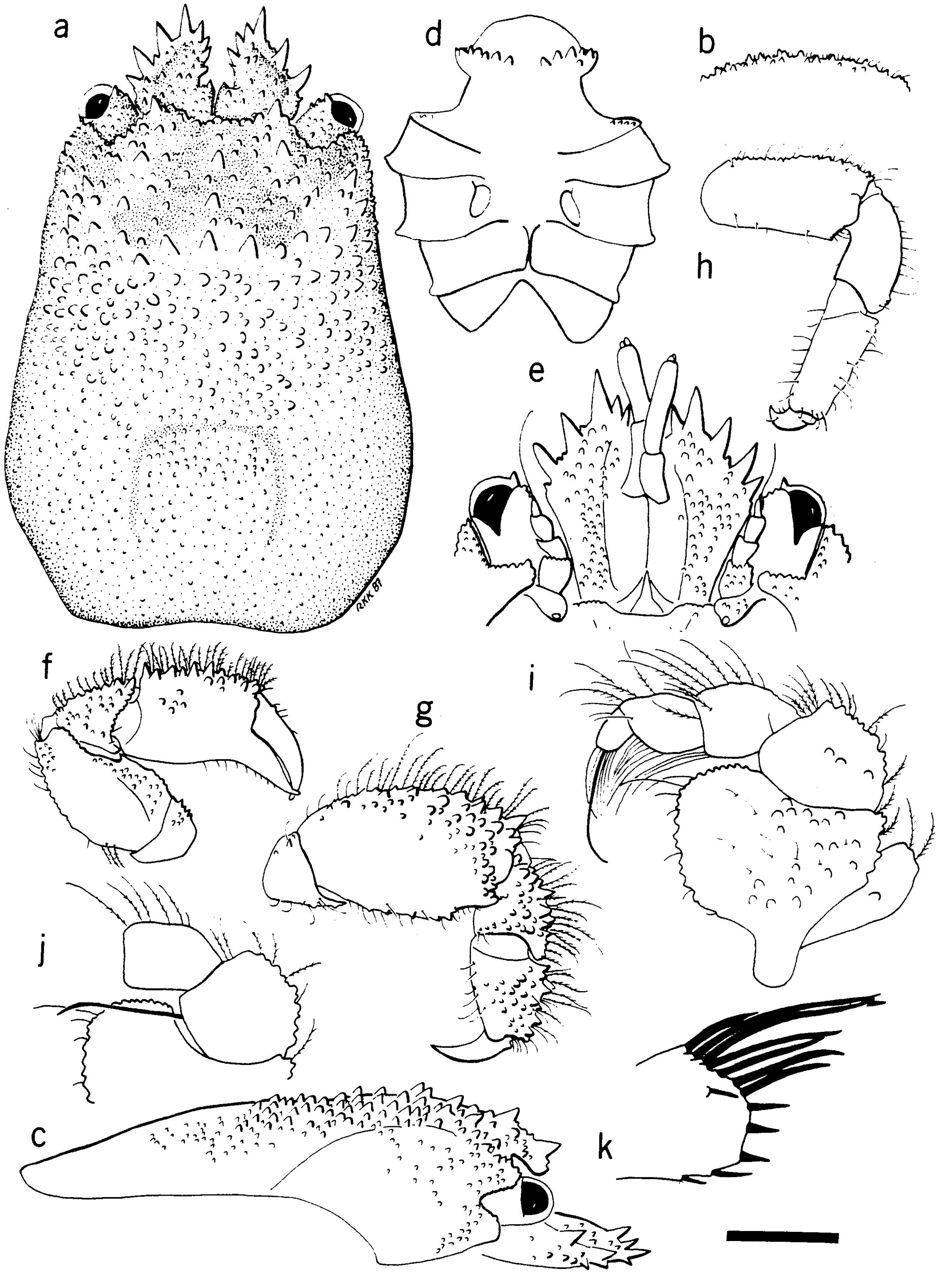
Fig. 26. *Opecarcinus lobifrons*, new species, +, Holotype. (Guam: USNM 234269): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view); d, thoracic sternites; e, eyes, antennules (ventral view); f-h, right P-1, P-2, P-5; i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a, c, f-h = 0.6 mm; b = 1 mm; d = 0.8 mm; e = 0.5 mm; i, j = 0.3 mm; k = 0.1 mm.

Fig. 27. *Opecarcinus lobifrons*, new species, o, Paratype. (Guam: USNM 234271): a, carapace (dorsal view); b-d, right P-1, P-2, P-5; e, PLP-1 (outer view). Scale: a-d = 0.5 mm; e = 0.2 mm.

Fig. 28. *Opecarcinus peliops*, new species, +, Holotype. (Pohnpei: USNM 234272): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view); d, thoracic sternites; e, eyes, antennules (ventral view); f-g, left P-1, P-2; h, right P-5 (from paratype); i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a, c-h = 0.5 mm; b = 1 mm; i, j = 0.3 mm; k = 0.2 mm.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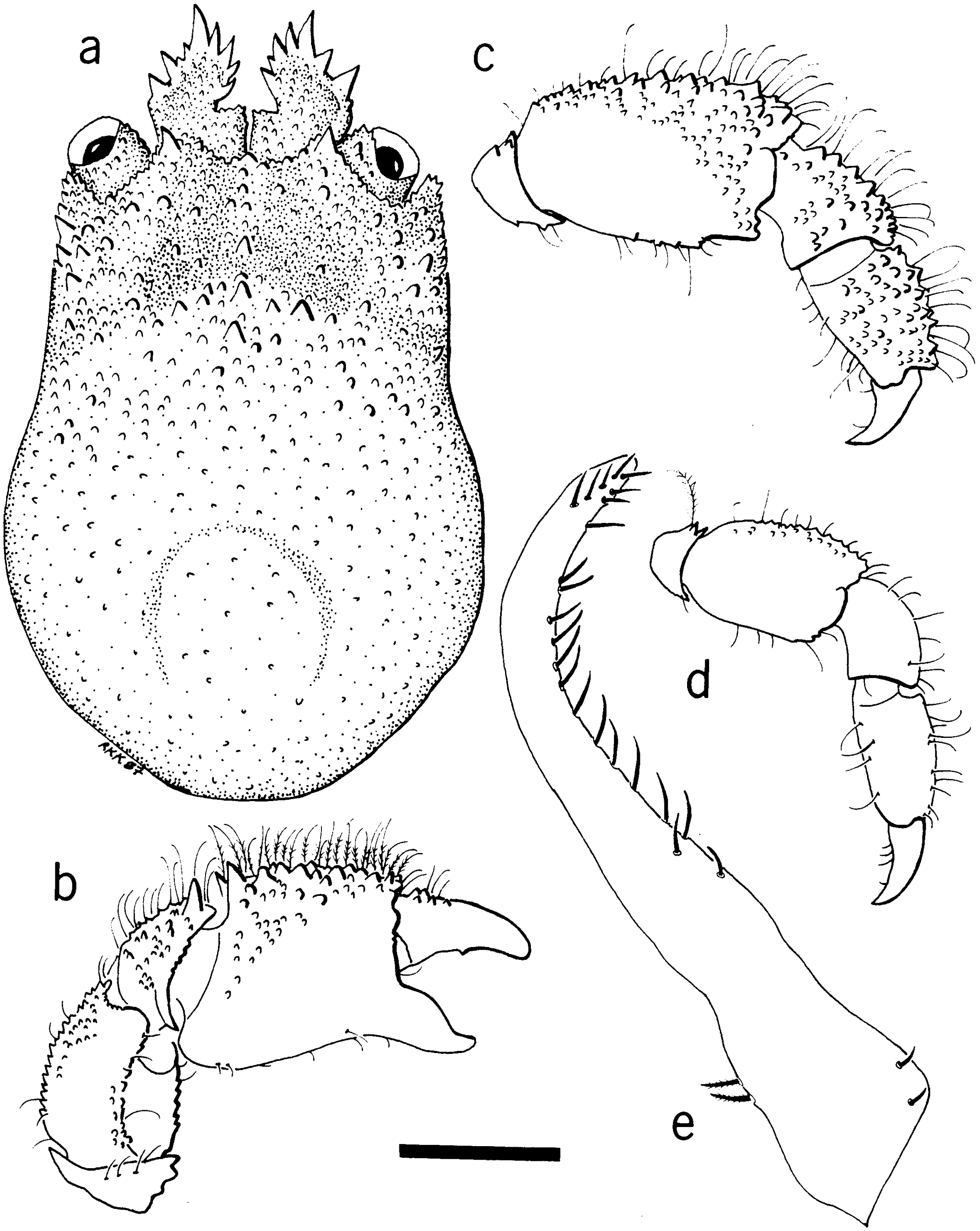
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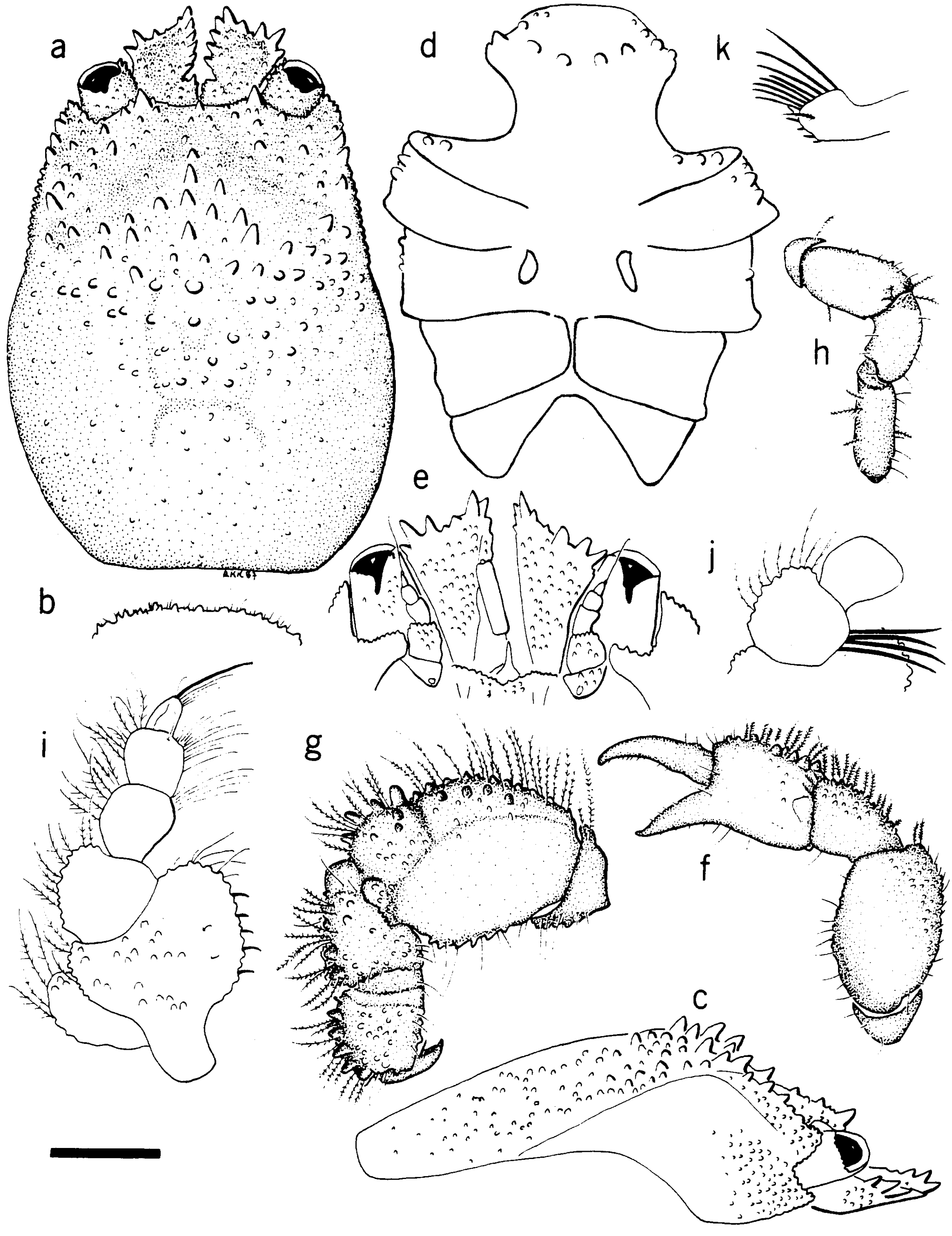
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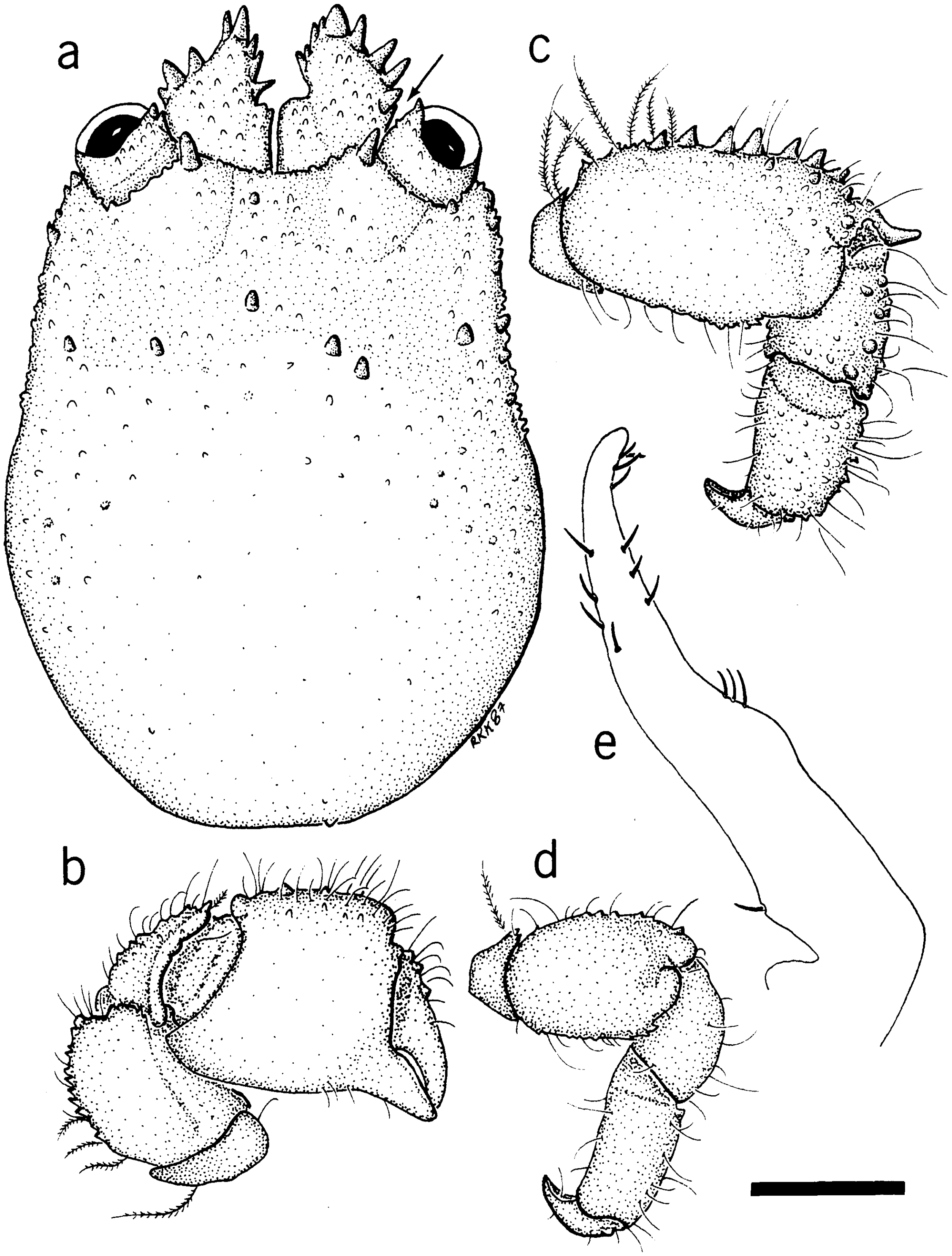
Fig. 29. *Opecarcinus peliops*, new species, o, Paratype. (Pohnpei: USNM 234273): a, carapace (dorsal view, arrow points to spine on IOA); b-d, right P-1, P-2, P-5; e, PLP-1 (outer view). Scale: a-d = 0.5 mm; e = 0.2 mm.

Fig. 30. *Opecarcinus pholeter*, new species, +, Holotype. (Guam: USNM 234275): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view); d, thoracic sternites; e, eyes, antennules (ventral view); f-h, right P-1, P-2, P-5; i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a-h = 1 mm; i = 0.5 mm; j-k = 0.2 mm.

Fig. 31. *Opecarcinus pholeter*, new species, o, Paratype (Guam: USNM 234276): a, carapace (dorsal view); b-d, right P-1, P-2, P-5; e, PLP-1 (outer view). Scale: a-d = 1 mm; e = 0.3 mm.

Fig. 32. *Opecarcinus sierra*, new species, +, Holotype. (Guam: USNM 234278): a, carapace (dorsal view); b, carapace (transverse section at midlength); c, carapace (lateral view); d, thoracic sternites; e, eyes, antennules (ventral view); f-h, right P-1, P-2, P-5; i, MXP-3 (outer view); j, MXP-3 (inner view of merus); k, MXL-1 (outer view). Scale: a, c, d, f-h = 0.5 mm; b = 0.8 mm; i-k = 0.2 mm.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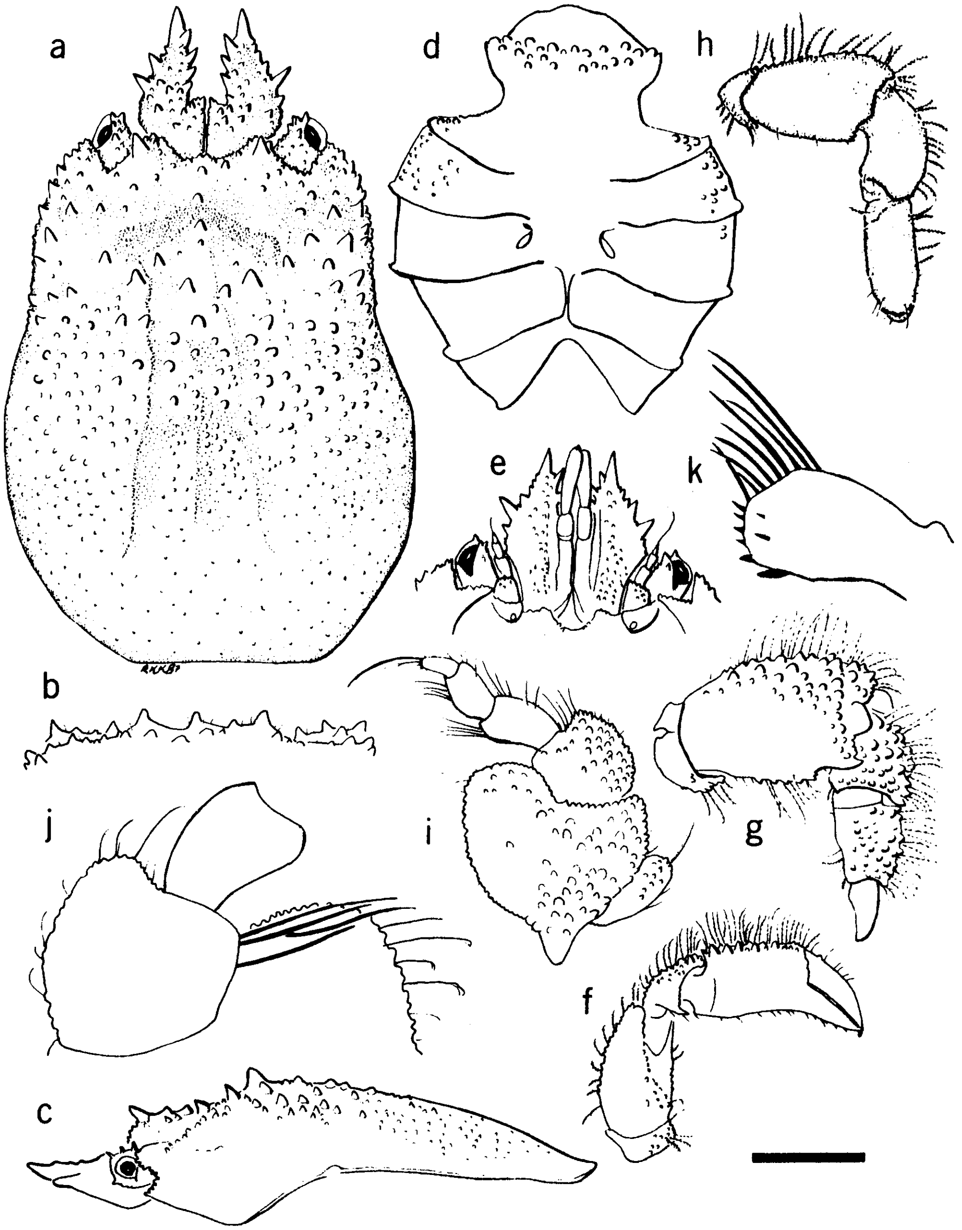
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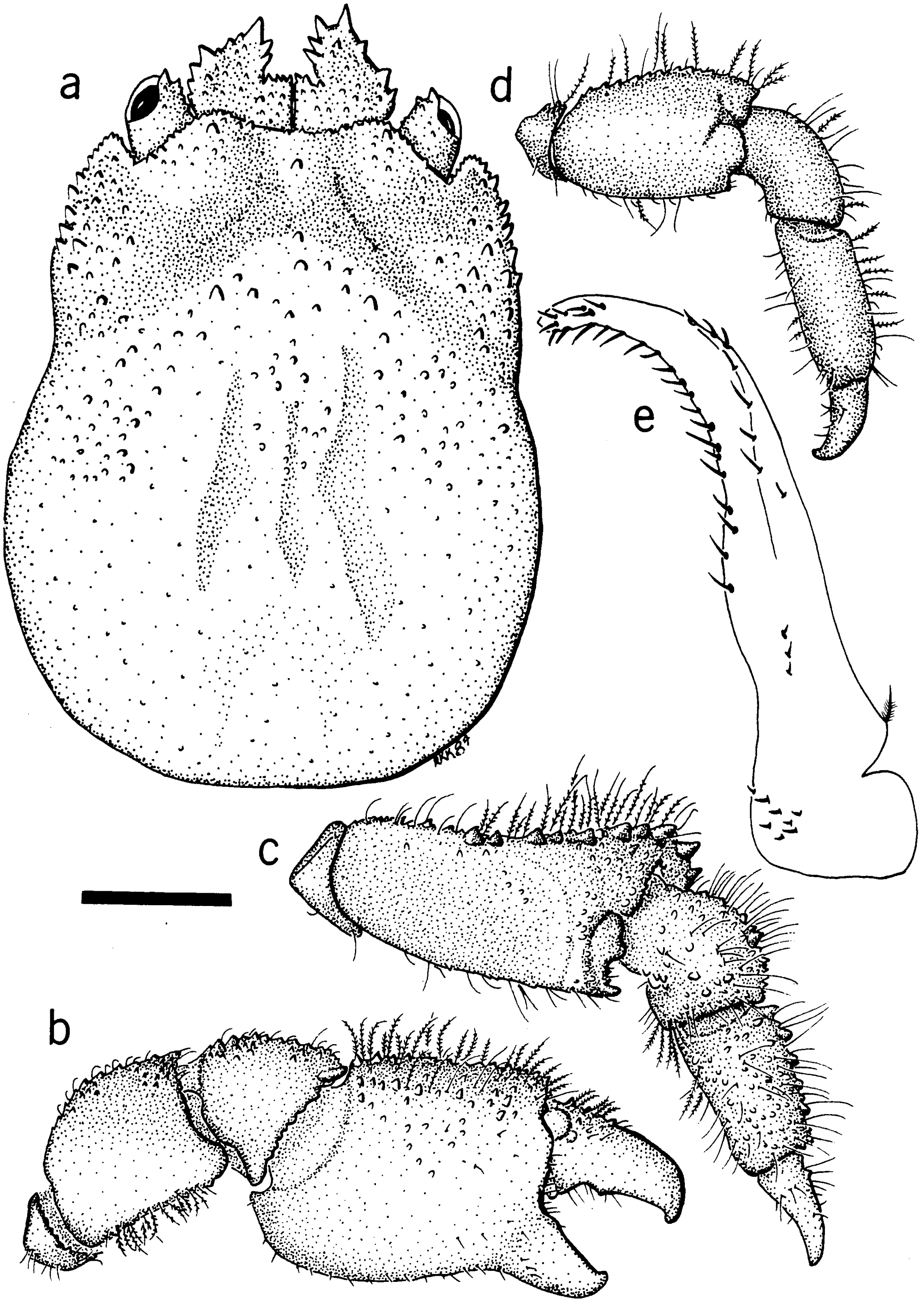
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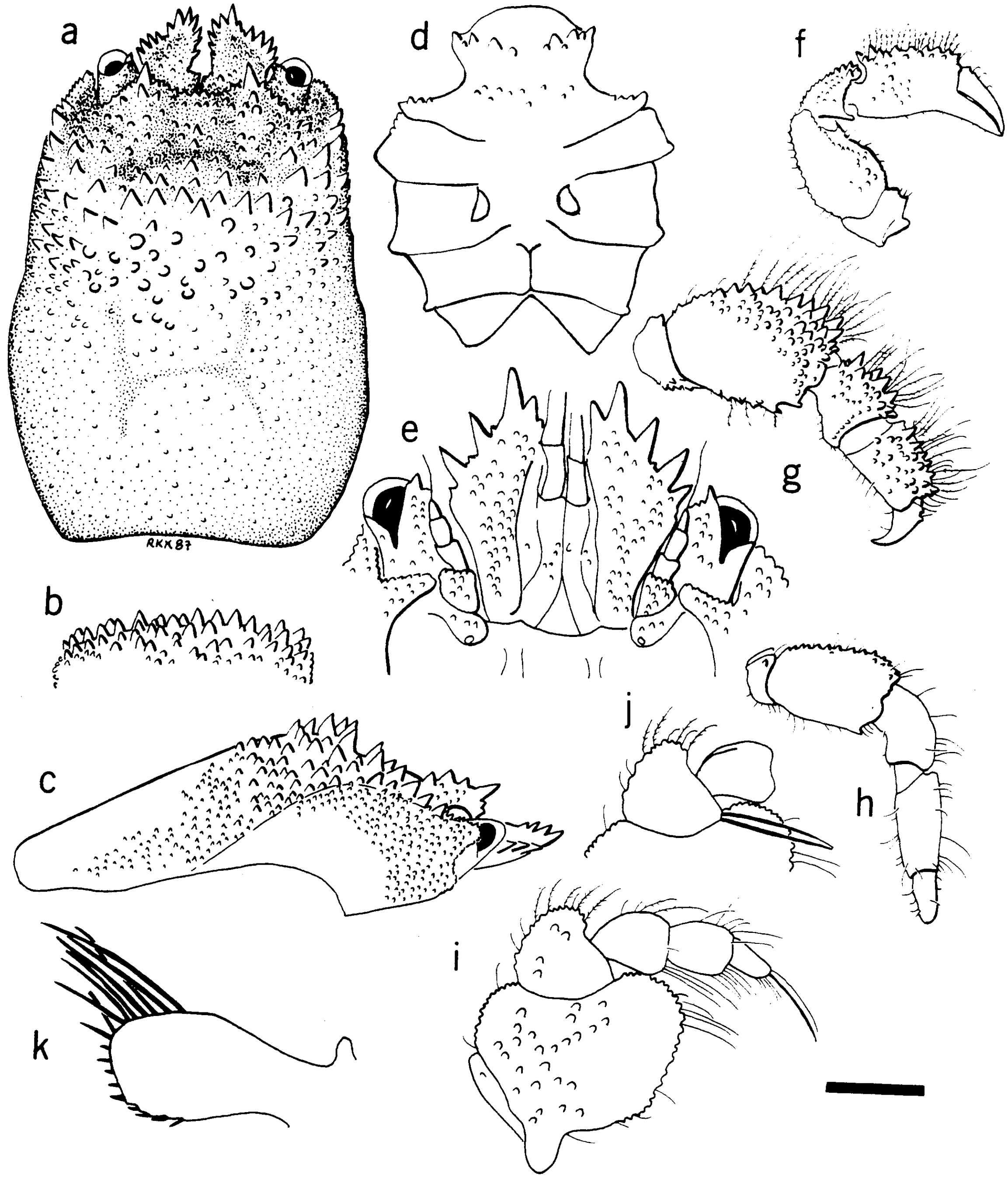
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Chapter 7

Fizesereneia Takeda and Tamura, 1980 (Crustacea, Decapoda): Proposed Designation of a Type Species.

This is a case of a genus with a misidentified type species and is referred to the Commission for a decision as prescribed by Article 70b of the International Code of Zoological Nomenclature.

2. As a part of a series of reports on the gall crab fauna of Japanese waters, Takeda and Tamura, 1980 (Bull. Natn. Sci. Mus. Tokyo, vol. 6) established the genus *Fizesereneia* to include two species formerly placed in *Troglocarcinus* Verrill, 1908 (Trans. Conn. Arts Sci. vol. 13) and a new species. These are *T. heimi* Fize and Serène, 1955 (Bull. Soc. Zool. France, vol. 80, no. 5-6), *T. stimpsoni* Fize and Serène, 1955, and *F. ishikawai* Takeda and Tamura, 1980, respectively. Takeda and Tamura designated *T. heimi* as the type species of *Fizesereneia*.

3. Examination of the figure and description of the type of *F. heimi* as published by Fize and Serène, 1957 (Arch. Mus. Nat. Hist. Nat., Paris, ser. 7, vol. 5) indicated that the figure and description of the species as published by Takeda and Tamura did not correspond to *F. heimi*, but to an undescribed species of *Fizesereneia*.

4. Thus, the genus *Fizesereneia* Takeda and Tamura, 1980, is based on a misidentified type species, and the Commission should now select the legal type species of that

genus. The options available to the Commission are: (1) to accept *Troglocarcinus heimi* Fize and Serène, 1955 as the type species of *Fizesereneia*; or (2) to select one of the other species included in the genus, *T. stimpsoni* Fize and Serène, 1955, *F. ishikawai* Takeda and Tamura, 1980, or the undescribed species as the type species.

5. In my opinion the first option is preferable as it will cause the least disturbance.

6. The following are the proposals I submit to the Commission, asking that it:

(1) use its plenary powers to set aside all designations of type species previously made for the nominal genus *Fizesereneia* Takeda and Tamura, 1980 and designate *Troglocarcinus heimi* Fize and Serène, 1955, as the type species of that genus;

(2) place *Fizesereneia* Takeda and Tamura, 1980 (gender: feminine), type species, by designation under the plenary powers in (1) above, *Troglocarcinus heimi* Fize and Serène, 1955, on the Official List of Generic Names in Zoology;

(3) place *heimi* Fize and Serène, 1955, as published in the binomen *Troglocarcinus heimi* (specific name of the type species of *Fizesereneia* Takeda and Tamura, 1980), on the Official List of Specific Names in Zoology.

Chapter 8

Revision of the Genera of Gall Crabs Occurring in the Pacific (Crustacea: Cryptochiridae)

Abstract

The coral gall crabs, Family Cryptochiridae, occurring in the Pacific Ocean are reviewed. Fifeteen genera, including four described herein, are recognised: *Cryptochirus* Heller; *Dacryomaia*, new genus; *Fizesereneia* Takeda and Tamura; *Fungicola* Serène; *Hapalocarcinus* Stimpson; *Hiroia* Takeda and Tamura; *Lithoscaptus* Milne Edwards; *Neotroglocarcinus* Takeda and Tamura; *Opecarcinus* Kropp and Manning; *Pelycomaia*, new genus; *Pseudocryptochirus* Hiro; *Pseudohapalocarcinus* Fize and Serène; *Sphenomaia*, new genus; *Utinomia* Takeda and Tamura; and *Xynomaia*, new genus. Host, depth, and distribution records are given for each genus. A key to all gall crab genera, including Atlantic taxa, is provided.

Introduction

The coral gall crabs, Family Cryptochiridae, are obligate associates of living scleractinian corals. Not only do they reside in galls, tunnels, or pits in the coral skeleton, they also feed on the host coral mucus and tissues (Kropp, 1986). Though the family has been known for 130 years, its taxonomy has been marred by many errors. These errors have resulted from (a) failures to consider type material or available literature, (b) use of inappropriate characters to define genera, or (c) failure to follow proper taxonomic procedure.

Two problems related to (a) above have been resolved by the reestablishment of *Lithoscaptus* Milne Edwards and *Cryptochirus hongkongensis* Shen, the latter as the type species of *Neotroglocarcinus* Fize and Serène (Kropp, 1988a; b).

Two characters inappropriate for use in the definition of genera were the nature (uniramous or biramous) of the second pleopod of the female and the host coral taxon on which crab species occurred. The form of the second pleopod has been shown to be variable within a species. McCain and Coles (1979) found the second pleopod to be uniramous on one side of the abdomen, biramous on the other, and variable among individuals of *Utinomia dimorpha* (Henderson, 1906). I have made similar observations for this species and others among my collections from Micronesia. Cryptochirids show some degree of host specificity, and some authors thought that this specificity could be used to define genera (Fize and Serène, 1957; McCain and Coles, 1979). Both features subsequently were shown to be unreliable (Kropp and Manning, 1987).

In a monograph of the gall crabs from Vietnam, Fize and Serène (1957) created a new genus, *Neotroglocarcinus* and initiated the use of subgenera in the genus *Troglocarcinus* Verrill. The subgenera they established were based on the family of corals on which the crabs were found. However, they did not follow proper taxonomic procedure by creating the subgenus *Mussicola* and including within it *T. corallicola* Verrill, the type species of *Troglocarcinus* and by not naming type species for any of their newly created genus-group taxa. Thus, those new names were unavailable.

Serène (1966) validated two genera when he designated *Cryptochirus rugosus* Edmondson as the type species of *Favicola* and *Troglocarcinus utinomi* Fize and Serène as the type species of *Fungicola*. His actions also helped to establish the host taxon as a generic character.

By the beginning of the 1980s the taxonomic situation of the family was far from serene, but the work of Takeda and Tamura in Japan had begun to unravel some of the remaining confusion. Their primary contribution was to remove *Pseudocryptochirus* as a "catch all" taxon by creating two new genera, *Hiroia* and *Utinomia* (Takeda and Tamura, 1981b), for species previously assigned to *Pseudocryptochirus*. However, *Utinomia* Takeda and Tamura, 1981 is a junior homonym of *Utinomia* Tomlinson, 1963, a genus of acrothoracican barnacle (Tomlinson, 1963; 1969). The gall crab genus name needs to be replaced. Takeda and Tamura (1980b) also erected a new genus, *Fizesereneia*, to accomodate species in the erroneously created *Mussicola* Fize and Serène, 1957. They did not realize that *Mussicola* could be used as an available name by designating one of the species inluded in it as its type. Kropp and Manning (1987) rectified this by naming *T. corallicola* as the type of *Mussicola*, rendering *Mussicola* a junior synonym of *Troglocarcinus*. Takeda and Tamura (1980b) further erred in misidentifying the type species of their new genus *Fizesereneia*, a situation that must be solved by the International Commission on Zoological Nomenclature.

By the mid 1980's many morphological inconsistencies within the generic structure of the family still remained.

Here I use morphology to reorganize the species of gall crabs occurring in the Pacific, removing totally the concept of host affinity as a generic character. I also provide a key to the females of all known cryptochirid genera. The species of gall crabs occurring in the Atlantic were reviewed by Kropp and Manning (1987).

Materials and Methods

I collected much of the material used in this revision in Micronesia in 1984 and 1986. Specimens from these collections have been deposited in the Allan Hancock Foundation (AHF), Los Angeles, California; the B. P. Bishop Museum (BPBM), Honolulu, Hawaii; the British Museum of Natural History (BMNH), London, England; the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D. C.; and the Muséum National d'Histoire Naturelle (MNHN), Paris, France. Supplementary material was borrowed from each of the above museums and the Naturhistorisches Museum (NMW), Vienna, Austria and the

National Science Museum (NSMT), Tokyo, Japan. I examined the types of many species; these are marked by an * in the lists of species.

Most of the figures are based on material from Micronesia and were prepared with the use of a camera lucida on a Wild M-5 dissection microscope or were traced from Scanning Electron Microscope (SEM) micrographs. The type species of each genus is figured. Setae on the surface of the carapace and pereopods are not shown. Specimens for SEM study were prepared as described in Kropp (1986).

I have restricted the synonymies to the first useage of a particular name for a taxon, including erroneous spellings. Abbreviations used in the text are: MXP, maxilliped; P, pereopod; PLP, pleopod; and TL, type locality.

I have listed only those host, depth, and distribution records that I am reasonably certain are accurate. The abbreviation "RKK" indicates unpublished data from my collections in Micronesia and Hawaii.

Key to the Genera of Gall Crabs, Cryptochiridae

(Based on females)

1\. Thoracic sternites flat 2

\- Thoracic sternites concave mesially 13

2\. Epistome with lateral ridges 3

\- Epistome lacking lateral ridges 10

3. Gonopore semicircular 4

- Gonopore elliptical 8

4. Orbit V-shaped 5

- Orbit broadly U-shaped 7

5. P-1 sternite with large tubercles 6

- P-1 sternite without tubercles ....*Troglocarcinus*

6. P-4 sternite with median suture ....*Opecarcinus*

- P-4 sternite lacking median suture ....*Neotroglocarcinus*

7. Carapace longer than wide, vase-shaped ....*Pseudocryptochirus*

- Carapace as long as wide, quadrate ....*Pseudohapalocarcinus*

8. Carapace with 2 large concavities anteriorly, deflected anteriorly 9

- Carapace lacking large concavities anteriorly, not deflected anteriorly ....*Fungicola*

9. Distal margin of antennal segment 2-3 with lateral spine ....*Fizesereneia*

- Distal margin of antennal segment 2-3 lacking lateral spine ....*Pelycomaia*

10. PLP-3 biramous 11

- PLP-3 uniramous 12

11. Pterygostomial region fused to carapace; MXP-3 lacking exopod ....*Detocarcinus*

- Pterygostomial region not fused to carapace; MXP-3 with exopod ....*Cecidocarcinus*

12. Carapace longer than wide; MXP-3 lacking exopod...... ....*Utinomia*

\- Carapace as long as wide; MXP-3 with exopod ....*Hapalocarcinus*

13. Anterior carapace deflected 14

\- Anterior carapace not deflected 17

14. P-4 coxal lobe well-developed 15

\- P-4 coxal lobe reduced 16

15. Posterior regions of carapace divided by series of grooves ....*Cryptochirus*

\- Posterior regions of carapace not divided by series of grooves ....*Dacryomaia*

16. Mesogastric region of carapace inflated ....*Lithoscaptus*

\- Mesogastric region of carapace not inflated ..*Sphenomaia*

17. Pterygostomial region fused to carapace; distal margin of antennal segment 2-3 lacking lateral spine ..*Hiroia*

\- Pterygostomial region not fused to carapace; distal margin of antennal segment 2-3 with lateral spine .. ..*Xynomaia*

Systematic Account

CRYPTOCHIRIDAE Paulson 1875

Lithoscaptes Milne Edwards, 1862:F10. [Vernacular name; type genus *Lithoscaptus* Milne Edwards, 1862].

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, 1900:49.

Hapalogarcinidae.--Coêlho and Ramos, 1972:205 [erroneus spelling].

Cryptochirus Heller, 1861

Fig. 33

Cryptochirus Heller, 1861:19 [type species: *Cryptochirus coralliodytes* Heller (1861:19), by monotypy; gender masculine].

Cryptochyrus.--Nobili, 1906:325 [erroneous spelling].

Favicola Fize and Serène, 1957:84 [name unavailable].

Favicola Serène, 1966:396 [type species: *Cryptochirus rugosus* Edmondson (1933:6), by original designation; gender masculine (see Kropp, 1988b)].

Diagnosis.--Carapace longer than broad, widest at midlength, convex in lateral view, not deflected anteriorly, mesogastric region inflated. Posterior region of carapace isolated by system of grooves, cardio-intestinal region outlined. Pterygostomial region fused to carapace. Epistome with parallel lateral ridges, anterior margin sinuous with shallow, wide median indentation. Lateral lobe of antennule elliptical, extending beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distal to midlength; distal margin convex. Ventral thorax longer than wide, concave mesially. Anterior extension of sternite of P-1 with granules. Sternite of P-4 with suture. Female gonopore oval, with anterior hood. P-1 cutting edges entire. P-2 merus lacking distomesial projection; propodus slender. P-3 coxa with reduced, P-4 coxa with well developed anterior lobe. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 3.3 times width, segments subequal in width, lateral margins parallel; PLP-1 curved laterally, apex pointed, lateral margin with simple setae, mesial margin with few pappose setae proximally.

Included species: Two:

Cryptochirus coralliodytes Heller, 1861

Cryptochirus coralliodytes Heller, 1861:19 [TL: Red Sea; lectotype* NMW].

Cryptochirus rugosus Edmondson, 1933:6. [TL: Washington Is.; holotype* BPBM S3668].

Troglocarcinus (*Favicola*) *rugosus*.--Fize and Serène, 1957:85.

Favicola rugosus.--Serène, 1966:396.

Favicola rugosum.--Lundoer, 1974:10.

Favicola rugosa.--Takeda and Tamura, 1981a:43.

Cryptochirus planus (Takeda and Tamura, 1983), new combination

Favicola plana Takeda and Tamura, 1983:4 [TL: Koza, Japan; holotype* NSMT-Cr. 8556].

Remarks: Fize and Serène (1957) failed to designate a type species for *Troglocarcinus* (*Favicola*), thus rendering *Favicola* Fize and Serène unavailable for use as a genus-group name [International Code of Zoological Nomenclature Art. 13 (b)]. Serène (1966) designated *Cryptochirus rugosus* Edmondson as the type species of *Favicola*.

Hosts: Faviidae--*Cyphastrea*, *Barabattoia*, *Favia*, *Favites*, *Goniastrea*, *Leptoria*, *Montastrea*, *Platygyra* (Fize and Serène, 1957; RKK): Oculinidae--*Cyathelia* (Takeda and Tamura, 1983).

Depth: < 1 m to 30 m (Takeda and Tamura, 1983; RKK).

Distribution: Indo-West Pacific--Red Sea (Heller, 1861); Vietnam (Fize and Serène, 1957); Japan (Takeda and Tamura, 1983); Micronesia: Belau, Guam, Pohnpei (RKK).

Dacryomaia, new genus

Fig. 34

Dacryomaia, new genus [type species *Cryptochirus edmonsoni* Fize and Serène (1955b:379), by original designation; gender feminine].

Diagnosis.--Carapace longer than broad, widest anterior to midlength, convex in lateral view, deflected anteriorly, with deep inverted V-shaped groove flanking mesogastric, latter inflated. Cardiointestinal outlined by depression. Pterygostomial region fused to carapace. Epistome with parallel lateral ridges, anterior margin straight with slight median indentation. Lateral lobe of antennule oval, extending to or just beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest at midlength; distal margin evenly convex. Ventral thorax longer than broad, flat. Anterior extension of sternite of P-1 with transverse band of granules. Sternite of P-4 with suture. Female gonopore elliptical, with anterior hood. P-1 dactylus with low tooth proximally on cutting edge. P-2 merus lacking distomesial projection; propodus thick. P-3, P-4 coxae with well-developed anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 2.6 times width, segment 3 widest, lateral margins subparallel; PLP-1 slightly curved laterally, apex pointed, lateral margin with several simple setae, with few pappose setae proximally, mesial margin with few simple setae proximally.

Etymology.--From the Greek, *dakryon*, meaning droplet, in combination with *maia*, a kind of crab, in reference to the shape of the tubercles on the anterior part of the carapace.

Included species: Two:

Dacryomaia edmonsoni (Fize and Serène, 1955),
new combination

Cryptochirus edmonsoni Fize and Serène, 1955b:379 [TL: Nhatrang, Vietnam; location of type unknown].

Dacryomaia japonica (Takeda and Tamura, 1981a),
new combination

Favicola japonica Takeda and Tamura, 1981a:47 [TL: Kuroshima, Ryukyu, Japan; holotype[*] NSMT-Cr 7422].

Hosts: Thamnasteriidae--*Psammocora* (Fize and Serène, 1957); Siderastreidae--*Coscinaraea* (RKK); Faviidae--*Cyphastrea*, *Goniastrea*, *Leptastrea* (Takeda and Tamura, 1981a; RKK). Fize and Serène (1957) listed *Pavona* (Agariciidae) as a host for *D. edmonsoni*. However, the host was figured and the crescentic pit pictured is more typical of *Opecarcinus* species than it is of *D. edmonsoni*. Therefore, I think that the record is probably an error.

Depth: < 1 m to 8 m (RKK).

Distribution: Pacific Ocean--Vietnam (Fize and Serène, 1957); Japan: Izu Is., Ogasawara Is., Ryukyu Is. (Takeda and Tamura, 1980d; 1981a; 1983); Micronesia: Belau, Guam (RKK).

Fizesereneia Takeda and Tamura, 1980

Fig. 35

Fizesereneia Takeda and Tamura, 1980b:137 [type species: *Troglocarcinus heimi* Fize and Serène (1955:378), by plenary powers of International Commission on Zoological Nomenclature; gender feminine].

Fizeserenia.--Kropp and Manning, 1987:2 [erroneous spelling].

Diagnosis.--Carapace longer than broad, widest anterior to midlength, convex in lateral view, deflected anteriorly, formed into 2 bowl-shaped concavities, mesogastric region inflated. Cardio-intestinal flanked by 2 depressions. Pterygostomial region not fused to carapace. Epistome with parallel lateral ridges, anterior margin sinuous with shallow, wide median indentation. Lateral lobe of antennule oval, extending just beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin with lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distal to midlength; distal margin convex. Ventral thorax longer than wide, flat. Anterior extension of sternite of P-1 smooth. Sternite of P-4 with suture. Female gonopore elliptical, with anterior hood. P-1 cutting edges entire. P-2 merus lacking distomesial projection; propodus slender. P-3, P-4 coxae with moderate anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 2.3 times width, segment 4 widest, lateral margins convex; PLP-1 curved laterally, apex pointed, lateral margin with many simple setae, mesial margin with few simple setae proximally.

Included species: Three:

Fizesereneia heimi (Fize and Serène, 1955)

Troglocarcinus heimi Fize and Serène, 1955a:378 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Mussicola*) *heimi*.--Fize and Serène, 1957:111.

Fizesereneia heimi.--Takeda and Tamura, 1980a:137.

Fizesereneia ishikawai Takeda and Tamura, 1980

Fizesereneia ishikawai Takeda and Tamura, 1980b:144 [TL: Ishigakijima Is., Ryukyu Is., Japan; holotype * NSMT-Cr 6340].

Fizesereneia stimpsoni (Fize and Serène, 1955)

Troglocarcinus stimpsoni Fize and Serène, 1955b:380 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Mussicola*) *stimpsoni*.--Fize and Serène, 1957:116.

Fizesereneia stimpsoni.--Takeda and Tamura, 1980b:146.

Remarks: Takeda and Tamura (1980b) designated *T. heimi* as the type species of *Fizesereneia*, a genus named in honor of two Gaul crab specialists. However, the species they described and figured was not *T. heimi*, but an undescribed species. Their figured species differs from *T. heimi* by having the median ridge incompletely separating the concavities on the anterior carapace, by having a hexagonally shaped carapace, and by being a different color. The type of *T. heimi* (see Fize and Serène, 1957: fig. 29A) has the median ridge completely dividing the anterior concavities and has a rectangular carapace. The color of *T. heimi* that I collected in Guam is predominately gray, matching that figured by Fize and Serène (1957: pl. 18B) and differing from the predominant green color of the undescribed species, also figured by Fize and Serène (1957: pl. 18A). Because the genus was based on a misidentified type species, I have petitioned the International Commission on Zoological Nomenclature to designate a type species (Kropp, ms 2). *Fizesereneia stimpsoni* differs markedly from the other two described species of *Fizesereneia* and is probably not congeneric with them (Kropp, unpublished). However, until the Commission selects a type species for the genus, the three cannot be separated.

Hosts: Mussidae--*Lobophyllia*, *Symphyllia*, *Acanthastrea* (Fize and Serène, 1957; Takeda and Tamura, 1980b).

Depth: 1 m to 15 m (Takeda and Tamura, 1980b; RKK).

Distribution: Indo West Pacific--Vietnam (Fize and Serène, 1957); Indonesia (Serène et al, 1974); Japan: Izu Is., Ryukyu Is. (Takeda and Tamura (1980b); Australia (McNeill, 1968); Micronesia: Belau, Guam, Pohnpei (RKK).

Fungicola Serène, 1966

Fig. 36

Fungicola Fize and Serène, 1957:122 [name unavailable].

Fungicola Serène, 1966:396 [type species: *Troglocarcinus utinomi* Fize and Serène (1955:377), by original designation (Serène, 1966:396); gender masculine (see Remarks)].

Fungicora.--Takeda and Tamura, 1986:64 [erroneous spelling].

Diagnosis.--Carapace longer than broad, widest anterior to midlength, flat in lateral view, not deflected anteriorly, with broad inverted U-shaped depression, mesogastric region slightly inflated. Cardiointestinal region outlined. Pterygostomial region fused to carapace. Epistome with parallel lateral ridges, anterior margin sinuous with shallow, wide median indentation. Lateral lobe of antennule oval, extending just beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distal to midlength; distal margin convex. Ventral thorax longer than broad, flat. Anterior extension of sternite of P-1 with few granules. Sternite of P-4 with suture. Female gonopore oval, with anterior hood. P-1 cutting edges entire. P-2 merus without distomesial projection; propodus thick. P-3, P-4 coxae with well developed anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with slender P-1; abdomen length 1.2 times width, segment 3 widest, lateral margins markedly convex; PLP-1 slightly curved laterally, apex pointed; lateral margin with simple setae distally, pappose setae proximally, mesial margin with pappose and simple setae.

Included species: Two:

Fungicola utinomi (Fize and Serène, 1955)

Troglocarcinus utinomi Fize and Serène, 1955a:377 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Fungicola*) *utinomi*.--Fize and Serène, 1957:124.

Fungicola utinomii.--Serène, 1966:396 [unjustified emendation].

Pseudocryptochirus ishigakiensis Takeda and Tamura, 1979:188 * [TL: Ishigaki-jima Is., Ryukyu, Japan; holotype NSMT-Cr 5898].

Hiroia ishigakiensis.--Takeda and Tamura, 1981b:20.

Fungicola fagei (Fize and Serène, 1955)

Troglocarcinus fagei Fize and Serène, 1955a:378 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Fungicola*) *fagei*.--Fize and Serène, 1957:131.

Fungicola fagei.--Serène, 1966:397.

Remarks.--Because Fize and Serène (1957) did not designate a type species for *Troglocarcinus* (*Fungicola*), the name *Fungicola* was unavailable [International Code of Zoological Nomenclature Art. 13 (b)] until Serène (1966) designated *T. utinomi* as the type species.

The International Code of Zoological Nomenclature (1985) specifies that a genus-group name ending in a noun of variable gender should be treated as masculine unless its author specifies that that it is feminine or treats it as feminine by the use of feminine species-group names [Art. 30 (a) (i)]. Serène (1966) was the first to use *Fungicola* as an available generic name and did so with masculine species-group names. Therefore, the gender of *Fungicola* is masculine.

Serène (1966) and later Takeda and Tamura (1979) emended the specific name *utinomi* to *utinomii*. These actions were improper as the Code [Art. 31 (a) (ii)] specifies that the stem of a species-group name is determined by the action of the original author. Fize and Serène (1955a) originally used *utinomi*, thus making the stem "utinom."

I have examined the holotype, a male, of *Pseudocryptochirus ishigakiensis* and determined that it differs from other males of *F. utinomi* only by having a less convex abdominal outline. However, this condition occurs in other material of *F. utinomi* that I have examined thereby making it of dubious value for distinguishing the two species, much less placing them in separate genera.

Hosts: Fungiidae--*Fungia*, *Podobacia*, *Sandalolitha* (as *Parahalomitra*) (Fize and Serène, 1957; Monod and Serène, 1976).

Depth: 1 m to 15 m (RKK).

Distribution: West Pacific--Vietnam (Fize and Serène, 1957); Indonesia (Serène et al., 1974); Japan: Ryukyu Is. (Takeda and Tamura, 1979); Micronesia: Belau, Guam (RKK).

Hapalocarcinus Stimpson, 1859

Fig. 37

Hapalocarcinus Stimpson, 1859:412 [type species: *Hapalocarcinus marsupialis* Stimpson (1859:412), by monotypy; gender masculine].

Diagnosis.--Carapace as long as wide, widest at midlength, slightly convex in lateral view, not deflected anteriorly, lacking depressions, mesogastric region not inflated. Cardiointestinal region not outlined by depression. Pterygostomial region fused to carapace. Epistome without lateral ridges, anterior margin sinuous with deep median indentation. Antennule not produced past midlength of eyestalk, apex pointed or rounded. Antennal segment 2-3 longer than broad, margin lacking lateral spine. MXP-3 with exopod; merus without distolateral projection, mesial margin lacking setae. Second segment of MXP-2 endopod with setae at distal margin of inner surface. MXP-1 endopod quadangular. Ventral thorax wider than long, flat. Sternite of P-1 smooth. Sternite of P-4 without suture.

Female gonopore circular, without hood. P-1 dactylus with or without proximal tooth on cutting edge. P-2 merus lacking distomesial projection, propodus thin. P-3, P-4 coxae lacking anterior lobes. P-5 dactylus not rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 1.7 times width, segment 4 widest, lateral margins convex; PLP-1 curved laterally, apex pointed, lateral margin lacking setae, mesial margin with few pappose setae.

Included species: One:

Hapalocarcinus marsupialis Stimpson

Hapalocarcinus marsupialis Stimpson, 1859:412 [TL: Hilo, Hawaii; location of type unknown].

Cryptochirus marsupialis.--Taylor, 1971:100.

Hosts: Pocilloporidae--*Pocillopora*, *Stylophora*, *Seriatopora* (Fize and Serène, 1957).

Depth: < 1 m to 27 m (RKK).

Distribution: Indo-West Pacific--South Africa and Red Sea to Columbia (see references in Takeda and Tamura, 1986).

Hiroia Takeda and Tamura, 1981

Fig. 38

Hiroia Takeda and Tamura, 1981b:20 [type species: *Troglocarcinus krempfi* Fize and Serène (1955:378), by original designation; gender feminine].

Diagnosis.--Carapace longer than broad, widest at midlength, flat in lateral view, not deflected anteriorly, with broad, shallow W-shaped depression, mesogastric region slightly inflated. Cardiointestinal region outlined by depression. Pterygostomial region fused to carapace. Epistome with subparallel lateral ridges, converging slightly anteriorly, anterior margin sinuous with slight median indentation. Lateral lobe of antennule oval, extending beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distal to midlength; distal margin convex. Ventral thorax longer than wide, concave mesially. Anterior extension of sternite of P-1 with few granules. Sternite of P-4 with suture. Female gonopore oval, with anterior hood. P-1 cutting edges entire. P-2 merus lacking distomesial projection; propodus thick. P-3 coxa lacking, P-4 coxa with reduced, anterior lobe. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 1.9 times width, segment 4 widest, lateral margins convex; PLP-1 slightly curved laterally, apex pointed, lateral margin with several pappose, few simple setae, mesial margin with several simple setae proximally.

Included species: One:

Hiroia krempfi (Fize and Serène, 1955)

Troglocarcinus krempfi Fize and Serène, 1955a:378 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Troglocarcinus*) *krempfi*.--Fize and Serène, 1957:79.

Pseudocryptochirus krempfi.--Serène, 1966:396.

Hiroia krempfi.--Takeda and Tamura, 1981b:20.

Hosts: Faviidae--*Cyphastrea*, *Hydnophora*, (Fize and Serène, 1957; RKK); Merulinidae--*Merulina* (Fize and Serène, 1957).

Depth: 1 m to 19 m (RKK).

Distribution: West Pacific--Vietnam (Fize and Serène, 1957); Japan: Izu Is., Ryukyu Is. (Takeda and Tamura, 1981b; 1985); Micronesia: Belau, Guam (RKK).

Lithoscaptus Milne Edwards, 1862

Fig. 39

Lithoscaptus Milne Edwards, 1862:F10 [type species: *Lithoscaptus paradoxus* Milne Edwards (1862:F10), by monotypy; gender masculine].

Diagnosis.--Carapace longer than broad, widest near midlength, sharply convex in lateral view, deflected anteriorly, with broad W-shaped depression, mesogastric region inflated. Cardiointestinal region outlined by inverted U-shaped depression. Pterygostomial region fused to carapace. Epistome with parallel lateral ridges, anterior margin straight with slight median indentation. Lateral lobe of antennule oval, extending beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distal to midlength; distal margin convex. Ventral thorax longer than wide, concave mesially. Anterior extension of sternite of P-1 smooth. Sternite of P-4 with suture. Female gonopore oval, with anterior hood. P-1 dactylus cutting edge with tooth proximally. P-2 merus lacking distomesial projection; propodus slender. P-3, P-4 coxae with reduced anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 3.8 times width, segment subequal in width, lateral margins parallel; PLP-1 curved laterally, apex pointed; lateral margin with simple setae, mesial margin with shorter simple setae proximally.

Included species: Six:

Lithoscaptus paradoxus Milne Edwards, 1862

Lithoscaptus paradoxus Milne Edwards, 1862:F10 [TL: Reunion Is.; lectotype * MNHN].

Cryptochirus coralliodytes var. *rubrolineatus* Fize and Serène, 1957:40. [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus coralliodytes var. *fusca* Fize and Serène, 1957:40. [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus coralliodytes var. *parvulus* Fize and Serène, 1957:40. [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus bani Fize and Serène, 1957:44 [TL: Nhatrang, Vietnam; location of type unknown].

? *Lithoscaptus pacificus* (Edmondson, 1933), new combination

Cryptochirus pacificus Edmondson, 1933:8 [TL: Palmyra Is.; holotype* BPBM S3669].

Lithoscaptus tri (Fize and Serène, 1955), new combination

Cryptochirus tri Fize and Serène, 1955:379 [TL: Nhatrang, Vietnam; location of type unknown].

Cryptochirus trii.--Takeda and Tamura, 1980d:51 [unjustified emendation].

Lithoscaptus helleri (Fize and Serène, 1957), new combination

Troglocarcinus (*Favicola*) *helleri* Fize and Serène, 1957:93 [TL: Nhatrang, Vietnam; type unknown].

Favicola helleri.--Serène, 1966:397.

Lithoscaptus nami (Fize and Serène, 1957), new combination

Cryptochirus nami Fize and Serène, 1957:46 [TL: Nhatrang, Vietnam; location of type unknown].

Lithoscaptus grandis (Takeda and Tamura, 1983), new combination

Cryptochirus grandis Takeda and Tamura, 1983:2 [TL: Kushimoto, Japan; holotype * NSMT-Cr. 8551].

Remarks: The emendation of the specific name *tri* to *trii* by Takeda and Tamura (1980d) is not justified as the root of the name is "tr" (see analogous argument for *Fungicola utinomi* in "Remarks" section under the genus *Fungicola*.

The type of *Cryptochirus pacificus* Edmondson is not in good condition, therefore the placement of that species in *Lithoscaptus* is tentative.

Hosts: Faviidae--*Cyphastrea*, *Echinopora*, *Favia*, *Favites*, *Hydnophora*, *Goniastrea*, *Leptastrea*, *Platygyra*, *Plesiatrea*, (Fize and Serène, 1957, RKK); Merulinidae--*Merulina*, (Fize and Serène, 1957).

Depth: < 1 m to 12 m (RKK).

Distribution: Indo-Pacific--Reunion (Milne Edwards, 1862); Vietnam (Fize and Serène, 1957); Sumatra (Serène, 1966); Japan: Izu Is., Kushimoto, Ogasawara Is., Ryukyu Is. (Takeda and Tamura, 1980d; 1981a; 1983; 1985); Micronesia:

Belau, Guam; Pohnpei (RKK); Palmyra (Edmondson, 1933); Teraina (Edmondson, 1933).

Neotroglocarcinus Takeda and Tamura, 1980

Fig. 40

Neotroglocarcinus Fize and Serène, 1957:135 [name unavailable].

Neotroglocarcinus Takeda and Tamura, 1980c:147 [type species: *Troglocarcinus monodi* Fize and Serène (1955a:375), a subjective junior synonym of *Cryptochirus hongkongensis* Shen, 1936 (see Kropp, 1988a), by original designation; gender masculine].

Diagnosis.--Carapace longer than broad, widest posterior to midlength, flat in lateral view, deflected anteriorly, with irregular depression flanking mesogastric, latter slighlty inflated. Cardiointestinal outlined by depression. Pterygostomial region not fused to carapace. Epistome with parallel lateral ridges, anterior margin straight with deep, narrow median indentation. Lateral lobe of antennule triangular, extending beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus without distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod lacking setae at distal margin. MXP-1 endopod triangular, widest near distal margin; latter concave. Ventral thorax about as long as broad, flat. Anterior extension of sternite of P-1 with tubercles. Sternite of P-4 lacking suture. Female gonopore semicircular, with anterior hood. P-1 cutting edges entire. P-2 merus with distomesial projection; propodus thick. P-3, P-4 coxae with well developed anterior lobes. P-5 dactylus not rotated anteriorly. PLP-3 of female biramous. Male with slender P-1; abdomen length 1.7 times width, segment 3 widest, lateral margins convex; PLP-1 angularly curved laterally, apex blunt, lateral and mesial margins with long pappose setae at midlength.

Included species: Two:

Neotroglocarcinus hongkongensis (Shen, 1936)

Cryptochirus hongkongensis Shen, 1936:23 [TL: Hong Kong; location of type unknown].

Pseudocryptochirus hongkongensis.--Takeda and Tamura, 1981b:15.

Troglocarcinus monodi Fize and Serène, 1955a:375 [TL: Nhatrang, Vietnam; location of type unknown].

Neotroglocarcinus monodi.--Fize and Serène, 1957:137.

Neotroglocarcinus hongkongensis.--Kropp, 1988a.

Neotroglocarcinus dawydoffi (Fize and Serène, 1955)

Troglocarcinus dawydoffi Fize and Serène, 1955a:376 [TL: Nhatrang, Vietnam; location of type unknown].

Neotroglocarcinus dawydoffi.--Fize and Serène, 1957:144.

Remarks: Fize and Serène (1957) did not designate a type species for *Neotroglocarcinus* rendering that name unavailable [International Code of Zoological Nomenclature

Art. 13 (b)]. Takeda and Tamura (1980c) made *Neotroglocarcinus* available by designating *Troglocarcinus monodi* as the type species of the genus. Kropp (1988a) determined that *T. monodi* is a subjective junior synonym of *Cryptochirus hongkongensis* Shen.

Hosts: Dendrophylliidae--*Turbinaria* (Fize and Serène, 1957).

Depth: < 1 m to 13 m (RKK).

Distribution: Indo-West Pacific--Vietnam (Fize and Serène, 1957); Japan: Izu Is., Ryukyu Is. (Takeda and Tamura, 1980c; 1985); Micronesia: Belau, Guam, Pohnpei (RKK), Enewetak (Garth et al., 1987).

Opecarcinus Kropp and Manning, 1987

Fig. 41

Opecarcinus Kropp and Manning, 1987:9 [type species: *Pseudocryptochirus hypostegus* Shaw and Hopkins (1977:179), by original designation; gender masculine].

Diagnosis.--Carapace longer than broad, widest posterior to midlength, convex in lateral view, deflected anteriorly, with transverse depression on protogastric, mesogastric slightly inflated. Cardiointestinal outlined by depression. Pterygostomial region fused to carapace. Epistome with parallel lateral ridges, anterior margin sinuous with deep, wide median indentation. Lateral lobe of antennule triangular, extending beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod lacking setae at distal margin. MXP-1 endopod triangular, widest near midlength; distal margin convex. Ventral thorax longer than wide, flat. Anterior extension of sternite of P-1 with tubercles. Sternite of P-4 with suture. Female gonopore oval, lacking or with anterior hood. P-1 cutting edges entire. P-2 merus with distomesial projection; propodus thick. P-3, P-4 coxae with well developed anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 1.8 times width, segment 3 widest, lateral margins convex; PLP-1 curved laterally, apex blunt, lateral margin with several, mesial margin with few, stout simple setae.

Included species: Eight:

Opecarcinus crescentus (Edmondson, 1925)

Cryptochirus crescentus Edmondson, 1925:33 [TL: Johnston Is.; holotype* BPBM S1805].

Pseudocryptochirus crescentus.--Utinomi, 1944:697.

Troglocarcinus (*Troglocarcinus*) *crescentus*.--Fize and Serène, 1957:62.

Opecarcinus crescentus.--Kropp and Manning, 1987:9.

Opecarcinus granulatus (Shen, 1936)

Cryptochirus granulatus Shen, 1936:23. [TL: Hong Kong; holotype* BM(NH) 1911.8.15.2].

Opecarcinus granulatus.--Kropp, ms 1.

Opecarcinus hypostegus (Shaw and Hopkins, 1977)

Pseudocryptochirus hypostegus Shaw and Hopkins, 1977:179 [TL: Florida Middle Ground, Florida; holotype* USNM 168533].

Opecarcinus hypostegus.--Kropp and Manning, 1987:10.

Opecarcinus aurantius Kropp

Opecarcinus aurantius Kropp, ms 1 [TL: Cetti Bay, Guam; holotype* USNM 234266].

Opecarcinus lobifrons Kropp

Troglocarcinus (*Troglocarcinus*) *crescentus*.--Garth, 1965:8 [not *Cryptochirus crescentus* Edmondson].

Pseudocryptochirus crescentus.--Garth and Hopkins, 1968:41 [in part; not *Cryptochirus crescentus* Edmondson].

Opecarcinus lobifrons Kropp, ms 1 [TL: Tanguisson Pt., Guam; holotype* USNM 234269].

Opecarcinus peliops Kropp

Opecarcinus peliops Kropp, ms 1 [TL: Pakin Atoll, Pohnpei; holotype* USNM 234272].

Opecarcinus pholeter Kropp

Opecarcinus pholeter Kropp, ms 1 [TL: Cetti Bay, Guam; holotype* USNM 234275].

Opecarcinus sierra Kropp

Opecarcinus sierra Kropp, ms 1 [TL: Agat Bay, Guam; holotype * USNM 234278].

Hosts: Agariciidae--*Agaricia*, *Gardineroseris*, *Leptoseris*, *Pavona*, (Fize and Serène, 1957; Scott, 1985; RKK); Siderasteriidae--*Siderastrea*, *Coscinaraea* [recorded as ?*Coscinastrea* of Agariciidae] (Takeda and Tamura, 1983; Scott, 1985).

Depth: < 1 m to 82 m (Shen, 1936; RKK).

Distribution: West, Central Atlantic--(see Kropp and Manning, 1987). Indo-Pacific--Christmas Is. (Indian Ocean; Shen, 1936); Vietnam and Japan to Mexico (see Kropp, ms 1).

Pelycomaia, new genus

Fig. 42

Pelycomaia, new genus [type species *Troglocarcinus minutus* Edmondson (1933:12), by original designation, gender feminine].

Diagnosis.--Carapace longer than broad, widest anterior to midlength, convex in lateral view, deflected anteriorly, with two isolated bowl-shaped concavities, mesogastric region slightly inflated. Pterygostomial region fused to carapace. Epistome with lateral ridges, anterior margin straight with slight median indentation. Lateral lobe of antennule oval, extending just beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distal to midlength; distal margin convex. Ventral thorax longer than broad, concave mesially. Anterior extension of sternite of P-1 smooth. Sternite of P-4 with suture. Female gonopore elliptical, with anterior hood. P-1 dactylus with low tooth proximally on cutting surface. P-2 merus lacking distomesial projection; propodus thick. P-3 coxa with reduced, P-4 coxae with well-developed anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 3.0 times width, segment 5 widest; PLP-1 not available for study.

Etymology.--From the Greek, *pelykos*, bowl, in combination with *maia*, a kind of crab, in reference to the bowl-shaped concavities on the anterior carapace.

Included species: One:

Pelycomaia minuta (Edmondson, 1933), new combination

Cryptochirus minutus Edmondson, 1933:12 [TL: Oahu, Hawaii, holotype* BPBM S3671].

Troglocarcinus (*Favicola*) *minutus*.--Fize and Serène, 1957:106.

Favicola minutus.--Serène, 1966:397.

Favicola minutum.--Serène et al., 1976:20.

Favicola minuta.--Takeda and Tamura, 1981b:43.

Hosts: Faviidae.--*Cyphastrea*, *Leptastrea* (Fize and Serène, 1957).

Depth: < 2 m (RKK).

Distribution: Pacific Ocean--Vietnam (Fize and Serène, 1957); Micronesia: Guam (RKK); Hawaii (Edmondson, 1933; RKK).

Pseudocryptochirus Hiro, 1938

Fig. 43

Pseudocryptochirus Hiro, 1938:149 [type species: *Pseudocryptochirus viridis* Hiro (1938:149), by monotypy; gender masculine].

Diagnosis.--Carapace longer than broad, widest posterior to midlength, slightly convex in lateral view, not deflected anteriorly, lacking depression, mesogastric very slightly inflated. Cardiointestinal regions not outlined by depression. Pterygostomial region not fused to carapace. Epistome with parallel lateral ridges, anterior margin sinuous with shallow, narrow median indentation. Lateral lobe of antennule quadrangular, extending beyond eyestalk. Antennal segment 2-3 shorter than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus without distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod lacking setae at distal margin. MXP-1 endopod triangular, widest near distal margin; latter concave. Ventral thorax about as long as wide, flat. Anterior extension of sternite of P-1 with few granules. Sternite of P-4 with partial suture. Female gonopore oval, with anterior hood. P-1 cutting edges entire. P-2 merus with distomesial projection; propodus thick. P-3, P-4 coxae with well developed anterior lobes. P-5 dactylus not rotated anteriorly. PLP-3 of female uniramous. Male with slender P-1; abdomen length 1.4 times width, segment 3 widest, lateral margins concave; PLP-1 slightly curved laterally, apex sharply pointed, lateral and mesial margins with long pappose setae at midlength.

Included species: One:

Pseudocryptochirus viridis Hiro, 1938

Pseudocryptochirus viridis Hiro, 1938:150 [TL: Tanabe Bay, Japan; location of type unknown].

Hosts: Dendrophylliidae--*Turbinaria* (Fize and Serène, 1957).

Depth: 1 m to 6 m (RKK).

Distribution: West Pacific--Vietnam (Fize and Serène, 1957); Indonesia (Serène, et al., 1974); Japan: Izu Is. (Takeda and Tamura, 1981b; 1985); Micronesia: Belau, Guam, Pohnpei (RKK). The record from Enewetak (Garth and Hopkins, 1968) are apparently erroneous (Garth et al., 1987).

Pseudohapalocarcinus Fize and Serène, 1955

Fig. 44

Pseudohapalocarcinus Fize and Serène, 1955a:378 [type species: *Pseudohapalocarcinus ransoni* Fize and Serène (1955a:378), by monotypy; gender masculine].

Diagnosis.--Carapace as long as wide, widest posterior to midlength, evenly convex in lateral view, not deflected anteriorly, lacking depression, mesogastric region not inflated. Cardiointestinal not outlined by depression. Pterygostomial region fused to carapace. Epistome with parallel lateral ridges, anterior margin sinuous, with deep, wide median indentation. Lateral lobe of antennule quadrangular, not extending beyond eyestalk. Antennal segment 2-3 shorter than broad, distal margin lacking lateral spine. MXP-3 with exopod; merus lacking distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod lacking setae at distal margin. MXP-1 endopod triangular, widest near midlength; distal margin convex. Ventral thorax wider than long. Anterior extension of sternite of P-1 smooth. Sternite of P-4 without suture. Female gonopore semicircular, lacking anterior hood. P-1 cutting edges entire. P-2 merus lacking distomesial projection; propodus slender. P-3, P-4 coxae with well developed anterior lobes. P-5 dactylus not rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 1.4 times width, segment 4 widest, lateral margin convex; PLP-1 slightly curved distally, apex blunt; lateral and mesial margins with few simple setae.

Included species: One:

Pseudohapalocarcinus ransoni Fize and Serène, 1955

Pseudohapalocarcinus ransoni Fize and Serène, 1955a:378 [TL: Nhatrang, Vietnam; location of type unknown].

Hosts: Agariciidae--*Pavona* (Fize and Serène, 1957)

Depth: < 1 m to 21 m (RKK).

Distribution: West Pacific--Vietnam (Fize and Serène, 1957); Japan: Ryukyu Is. (Takeda and Tamura, 1980a); Micronesia: Belau, Guam, Pohnpei (RKK).

Sphenomaia, new genus

Fig. 45

Sphenomaia, new genus [type species: *Cryptochirus pyriformis* Edmondson (1933:10); by original designation and monotypy; gender feminine].

Diagnosis.--Carapace longer than broad, widest at midlength, strongly convex in lateral view, not deflected anteriorly, with broad depression over entire anterior, mesogastric not inflated. Cardiointestinal region outlined by inverted U-shaped depression. Pterygostomial region fused to carapace. Epistome with lateral ridges, anterior margin sinuous with broad, shallow median indentation. Lateral lobe of antennule extending to or just beyond eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking spine. MXP-3 with exopod; merus lacking distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest distally;

distal margin slightly convex. Ventral thorax longer than broad, concave mesially. Anterior extension of sternite of P-1 with granules. Sternite of P-4 with suture. Female gonopore elliptical, with anterior hood. P-1 dactylus entire. P-2 merus lacking distomesial projection; propodus slender. P-3, P-4 coxae anterior lobes. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male not available for study.

Etymology.--From the Greek, *sphenos*, wedge, in combination with *maia*, a kind of crab, in reference to the appearance of the carapace in lateral view.

Included species: One:

Sphenomaia pyriforma (Edmondson, 1933),
new combination

Cryptochirus pyriformis Edmondson, 1933:10 [TL: Washington Island, holotype * BPBM S3670].

Troglocarcinus (*Favicola*) *pyriformis*.--Fize and Serène, 1957:84.

Favicola pyriformis.--Serène, 1966:397.

Hosts: Faviidae--*Favites*, *Hydnophora*, and *Platygyra* (Edmondson, 1933).

Depth: Not recorded.

Distribution: Known from Teraina (= Washington Island) in the central Pacific (Edmondson, 1933).

Utinomia Takeda and Tamura, 1981

Fig. 46

Utinomia Takeda and Tamura, 1981b:23 [type species: *Cryptochirus dimorphus* Henderson (1906:214), by original designation and monotypy; gender feminine].

Diagnosis.--Carapace longer than broad, widest posterior to midlength, flat in lateral view, not deflected anteriorly, with broad, shallow depression, mesogastric slightly inflated. Cardiointestinal region outlined by depression. Pterygostomial region fused to carapace. Epistome lacking lateral ridges, anterior margin sinuous with shallow, wide median indentation. Lateral lobe of antennule rectangular, extending to tip of eyestalk. Antennal segment 2-3 longer than broad, distal margin lacking lateral spine. MXP-3 lacking exopod; merus lacking distolateral projection, mesial margin lacking setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest near distal margin; latter convex. Ventral thorax longer than broad, flat. Anterior extension of sternite of P-1 smooth. Sternite of P-4 with partial suture. Female gonopore semicircular, lacking anterior hood. P-1 cutting edges entire. P-2 merus without distomesial projection; propodus slender. P-3 coxa with reduced, P-4 coxa with well developed anterior lobe. P-5 dactylus not rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 1.7 times width, segment 3 widest, lateral margin convex; PLP-1 slightly curved distally, apex blunt, lateral and mesial margins with few long pappose setae distally.

Remarks.--Tomlinson (1963:264) used the name *Utinomia* for a genus of acrothoracican barnacle; though it was later synonymized with *Weltneria* Berndt, 1907 (Tomlinson, 1969). *Utinomia* is therefore unavailable for use as a gall crab genus and needs to be replaced. In accordance with the recommendation of the International Code of Zoological Nomenclature (Appendix A, 3), I have contacted Dr. Takeda regarding this homonomy.

Included species: One:

Utinomia dimorpha (Henderson, 1906)

Cryptochirus dimorphus Henderson, 1906:214 [TL: Andaman Is.; location of type unknown].

Pseudocryptochirus kahe McCain and Coles, 1979:81 [TL: Kahe Pt., Oahu, Hawaii; holotype * BPBM S8512].

Pseudocryptochirus dimorphus.--Takeda and Tamura, 1980d:47.

Utinomia dimorpha.--Takeda and Tamura, 1981b:23.

Hosts: Pocilloporidae--*Pocillopora*, *Stylophora* (Takeda and Tamura, 1981b; RKK).

Depth: 1 m to 29 m (RKK).

Distribution: Indo-West Pacific--Andaman Is. (Henderson, 1906); Japan: Ryukyu Is. (Takeda and Tamura, 1981b); Micronesia: Belau, Guam, Pohnpei (RKK); Hawaii (McCain and Coles, 1979).

Xynomaia, new genus

Fig. 47

Xynomaia, new genus [type species: *Troglocarcinus sheni* Fize and Serène (1955b:380), by original designation; gender feminine].

Diagnosis.--Carapace longer than broad, widest at midlength, convex in lateral view, not deflected anteriorly, with broadly W-shaped depression, mesogastric region slightly inflated. Cardiointestinal outlined by depression. Pterygostomial region not fused to carapace. Epistome with parallel lateral ridges, anterior margin straight with slight median indentation. Lateral lobe of antennule oval, extending to tip of eyestalk. Antennal segment 2-3 longer than broad, distal margin with lateral spine. MXP-3 with exopod; merus with distolateral projection, mesial margin with setae. Inner surface of second segment of MXP-2 endopod with setae at distal margin. MXP-1 endopod triangular, widest proximal to midlength; distal margin evenly convex. Ventral thorax longer than broad, concave mesially. Anterior extension of sternite of P-1 smooth or with fine granules. Sternite of P-4 with suture. Female gonopore elliptical, with anterior hood. P-1 dactylus with low tooth on cutting edge. P-2 merus lacking distomesial projection; propodus slender. P-3 coxa with poorly-developed anterior lobe, P-4 coxa with well-developed anterior lobe. P-5 dactylus rotated anteriorly. PLP-3 of female uniramous. Male with robust P-1; abdomen length 2.8 times width, segment 4 widest, lateral margins subparallel; PLP-1 slightly curved laterally, apex pointed, lateral margin with many proximally pappose setae, few simple setae, mesial margin with several short simple setae.

Etymology.--From the Greek *xynon*, companion, in combination with *maia*, a kind of crab, in reference to the symbiotic lifestyle of the crab.

Included species: Three:

Xynomaia sheni (Fize and Serène, 1955),
new combination

Troglocarcinus sheni Fize and Serène, 1955b:380 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Troglocarcinus*) *sheni*.--Fize and Serène, 1957:74.

Pseudocryptochirus sheni.--Serène, 1966:396.

Hiroia sheni.--Takeda and Tamura, 1981b:20.

Xynomaia boissoni (Fize and Serène, 1955a),
new combination

Troglocarcinus boissoni Fize and Serène, 1955a:376 [TL: Nhatrang, Vietnam; location of type unknown].

Troglocarcinus (*Troglocarcinus*) *boissoni*.--Fize and Serène, 1957:69.

Pseudocryptochirus boissoni.--Serène, 1966:396.

Hiroia boissoni.--Takeda and Tamura, 1981b:20.

Xynomaia verrilli (Fize and Serène, 1957),
new combination

Troglocarcinus (*Favicola*) *verrilli* Fize and Serène, 1957:101 [TL: Nhatrang, Vietnam; location of holotype unknown, paratype MNHN].

Favicola verrilli.--Serène, 1966:397.

Hosts: Faviidae--*Favia*, *Goniastrea*, *Montastrea*, *Oulophyllia*, *Platygyra* (Fize and Serène, 1957; RKK); Merulinidae--*Merulina* (Fize and Serène, 1957). Pectiniidae--*Pectinia* (RKK).

Depth: 1 m to 15 m (RKK).

Distribution: West Pacific--Vietnam (Fize and Serène, 1957); Sumatra (Serène, 1966); Japan: Izu Is., Kushimoto (Takeda and Tamura, 1983; 1985); Micronesia: Belau, Guam (RKK).

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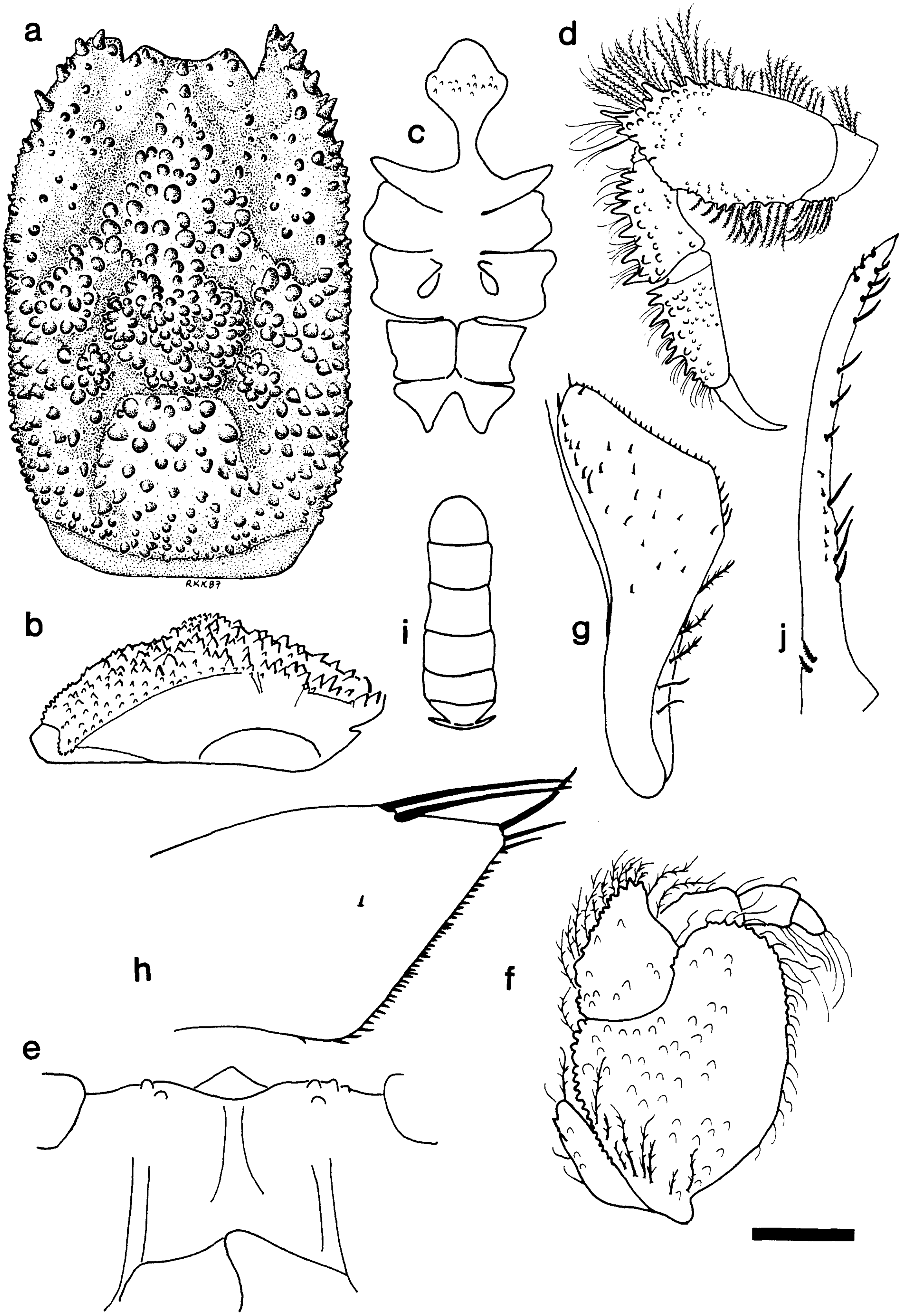
Fig. 33. *Cryptochirus coralliodytes* Heller. Female lectotype (Red Sea): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: b = 2.1 mm; c = 1 mm; a = 0.8 mm; d, i = 0.7 mm; f = 0.4 mm; e = 0.3 mm; g = 0.2 mm; h = 0.1 mm.

Fig. 34. *Dacryomaia edmonsoni* (Fize and Serène). Female (Guam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: a-c, i = 1 mm; d = 0.5 mm; e = 0.2 mm; f, g = 0.1 mm.

Fig. 35. *Fizesereneia heimi* (Fize and Serène). Female (Guam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male Guam: i, abdomen; j, gonopod. Scale: a, b, d, i = 1 mm; c = 0.9 mm; e = 0.3 mm; g, h = 0.1 mm.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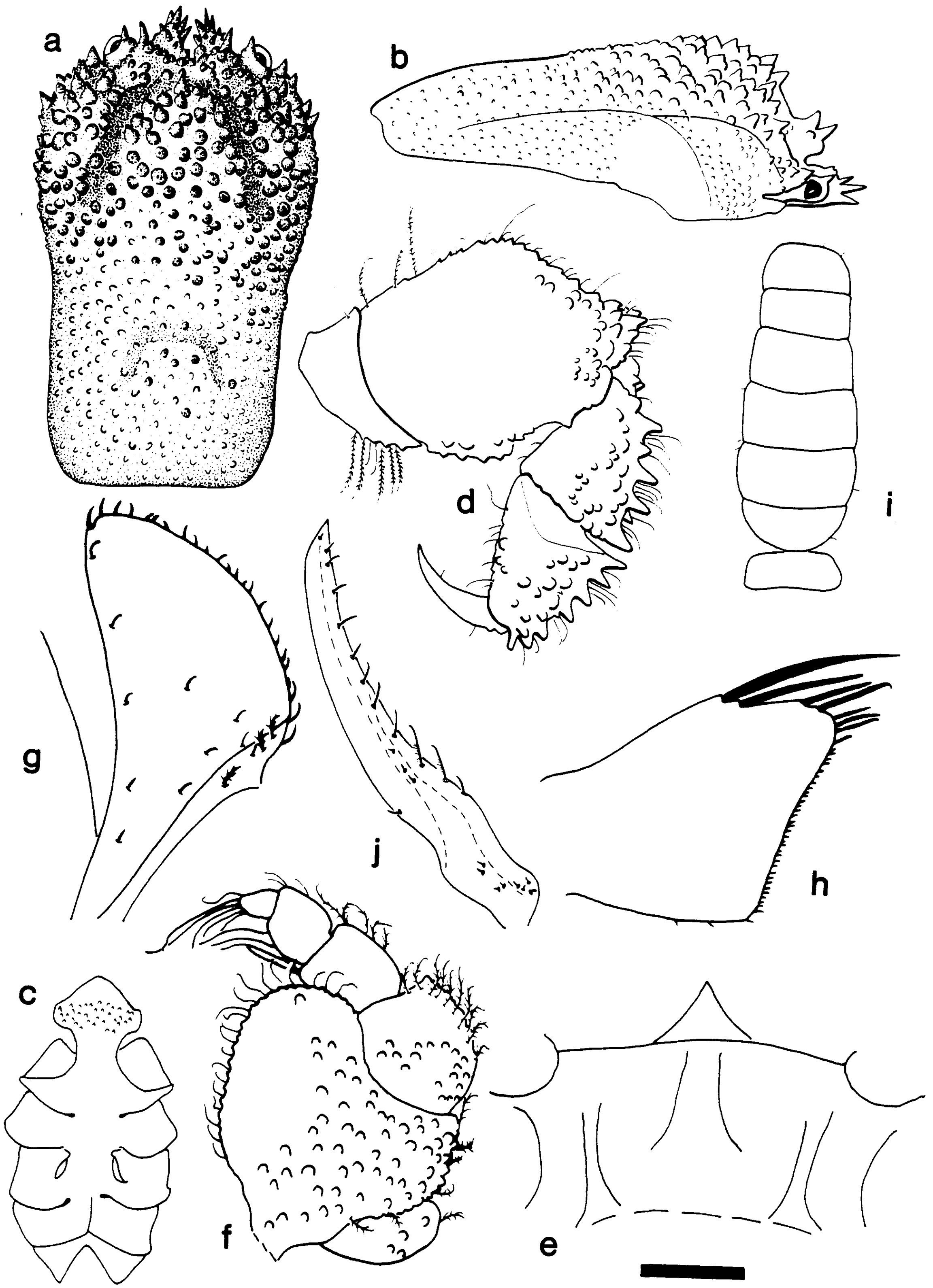
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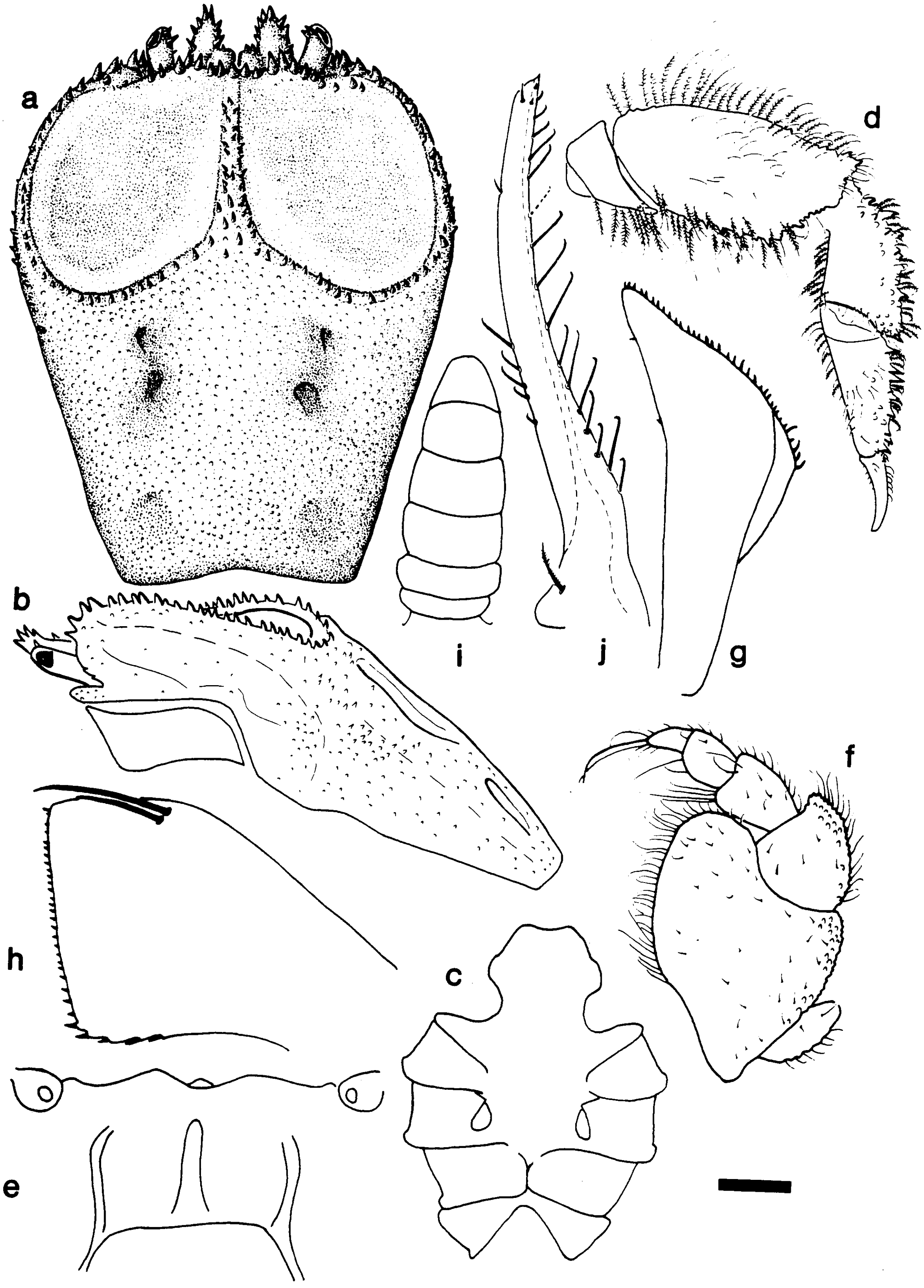
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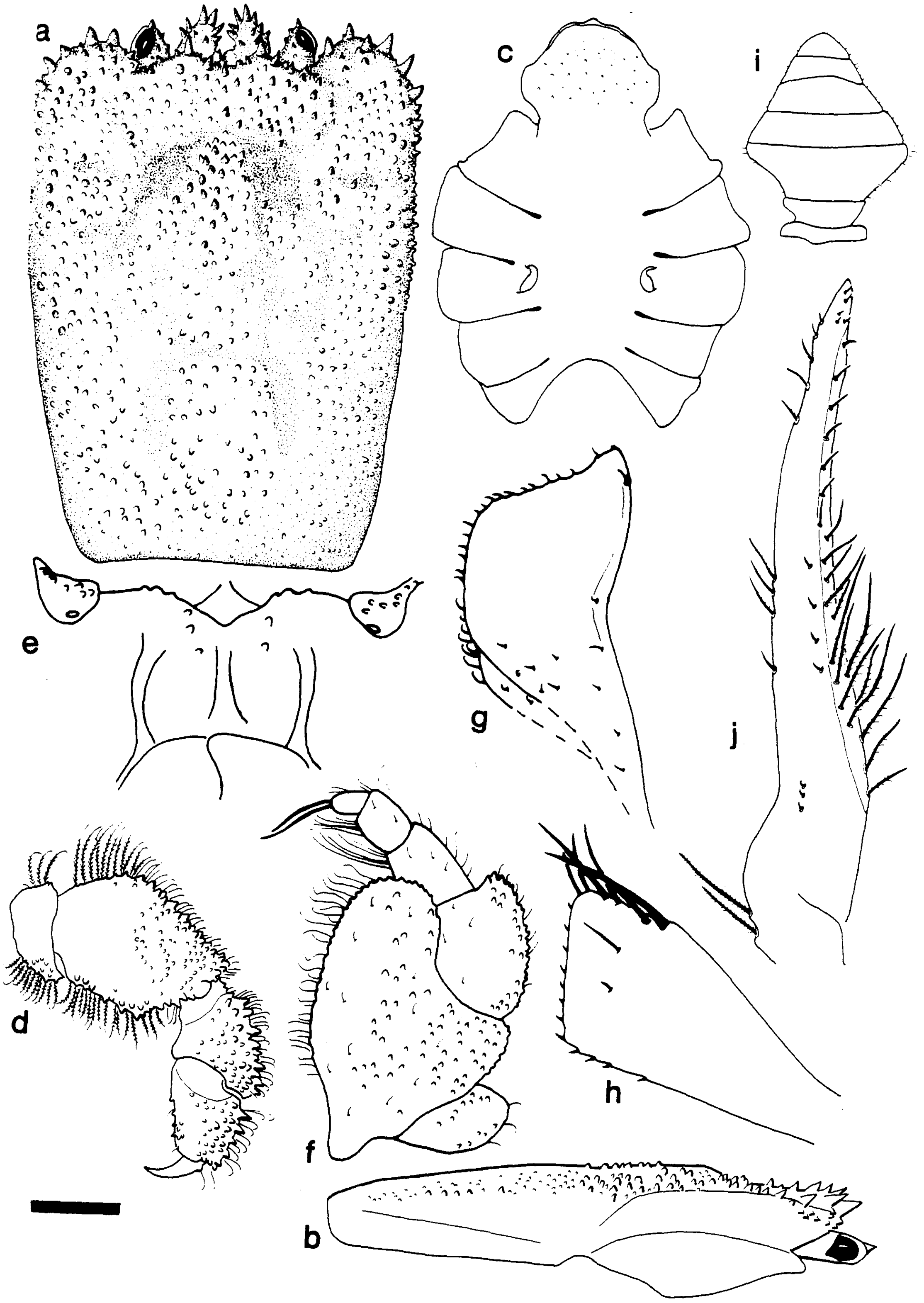
Fig. 36. *Fungicola utinomi* (Fize and Serène). Female (Belau): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Palau): i, abdomen; j, gonopod. Scale: a, b = 1 mm; c, d, i = 0.9 mm; e, f = 0.3 mm; g = 0.2 mm; h = 0.1 mm.

Fig. 37. *Hapalocarcinus marsupialis* Stimpson. Female (Guam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Papua New Guinea): i, abdomen; j, gonopod (from MacNamee, 1961). Scale: a-c = 2.1 mm; d = 1 mm; i = 0.4 mm; f = 0.3 mm; e, g = 0.2 mm; h = 0.1 mm.

Fig. 38. *Hiroia krempfi* (Fize and Serène). Female (Belau): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Pohnpei): i, abdomen; j, gonopod. Scale: a-c = 1 mm; d, i = 0.5 mm; f = 0.3 mm; e = 0.2 mm; g, h = 0.1 mm.

Fig. 39. *Lithoscaptus paradoxus* Milne Edwards. Female (Guam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: b = 2.1 mm; a = 0.8 mm; c = 1 mm; d = 0.7 mm; f = 0.5 mm; e = 0.3 mm; g = 0.2 mm.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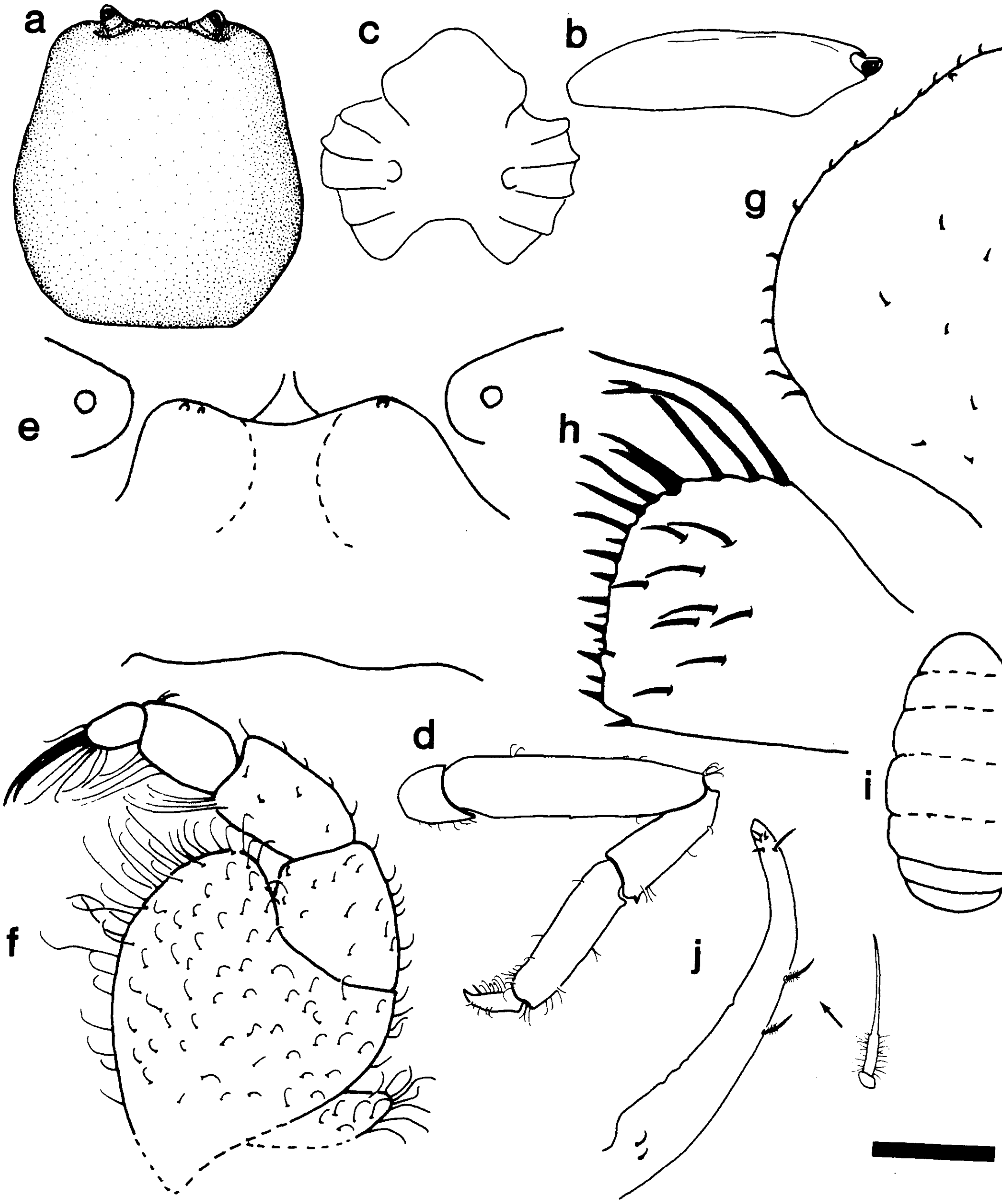
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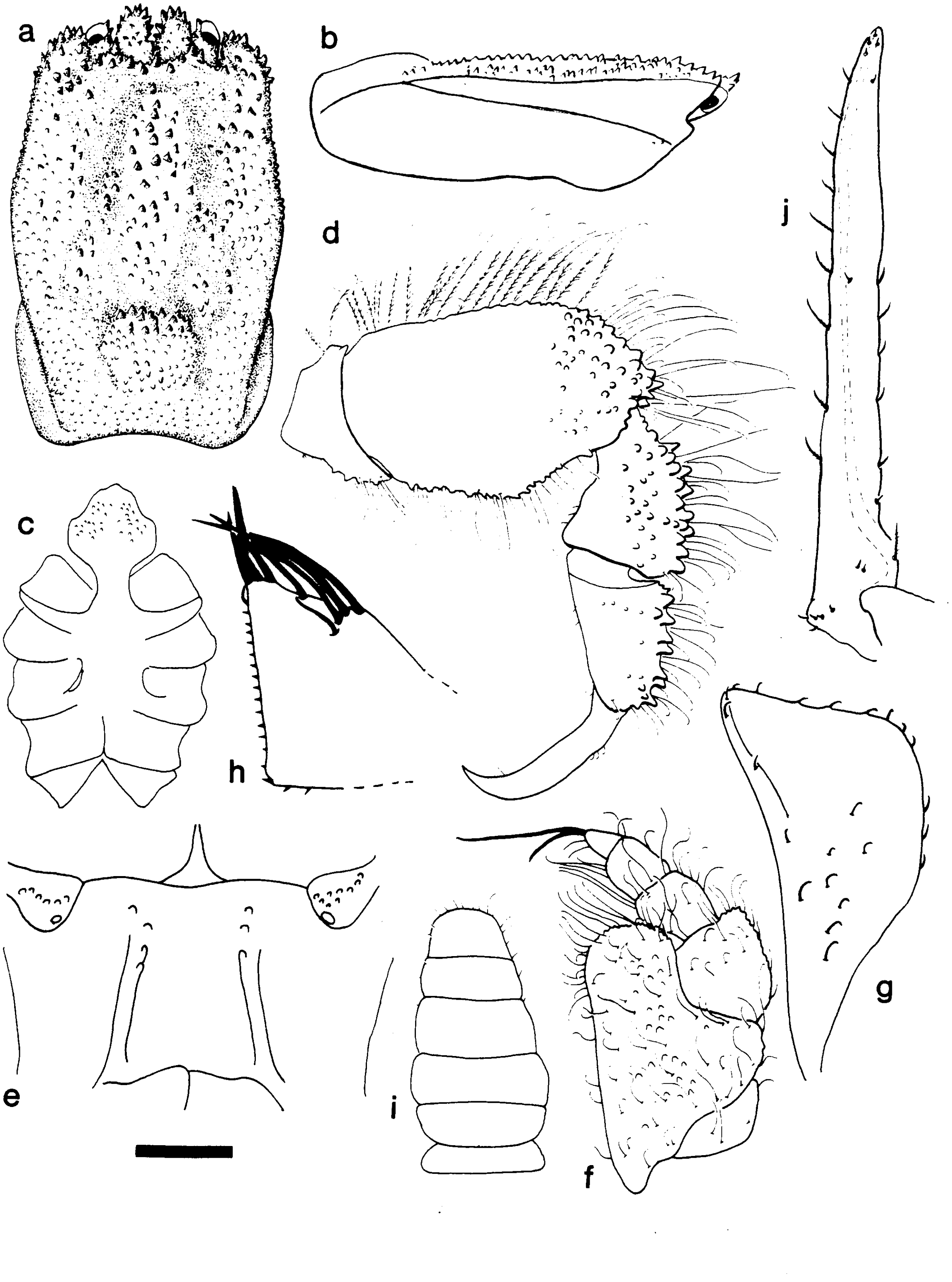
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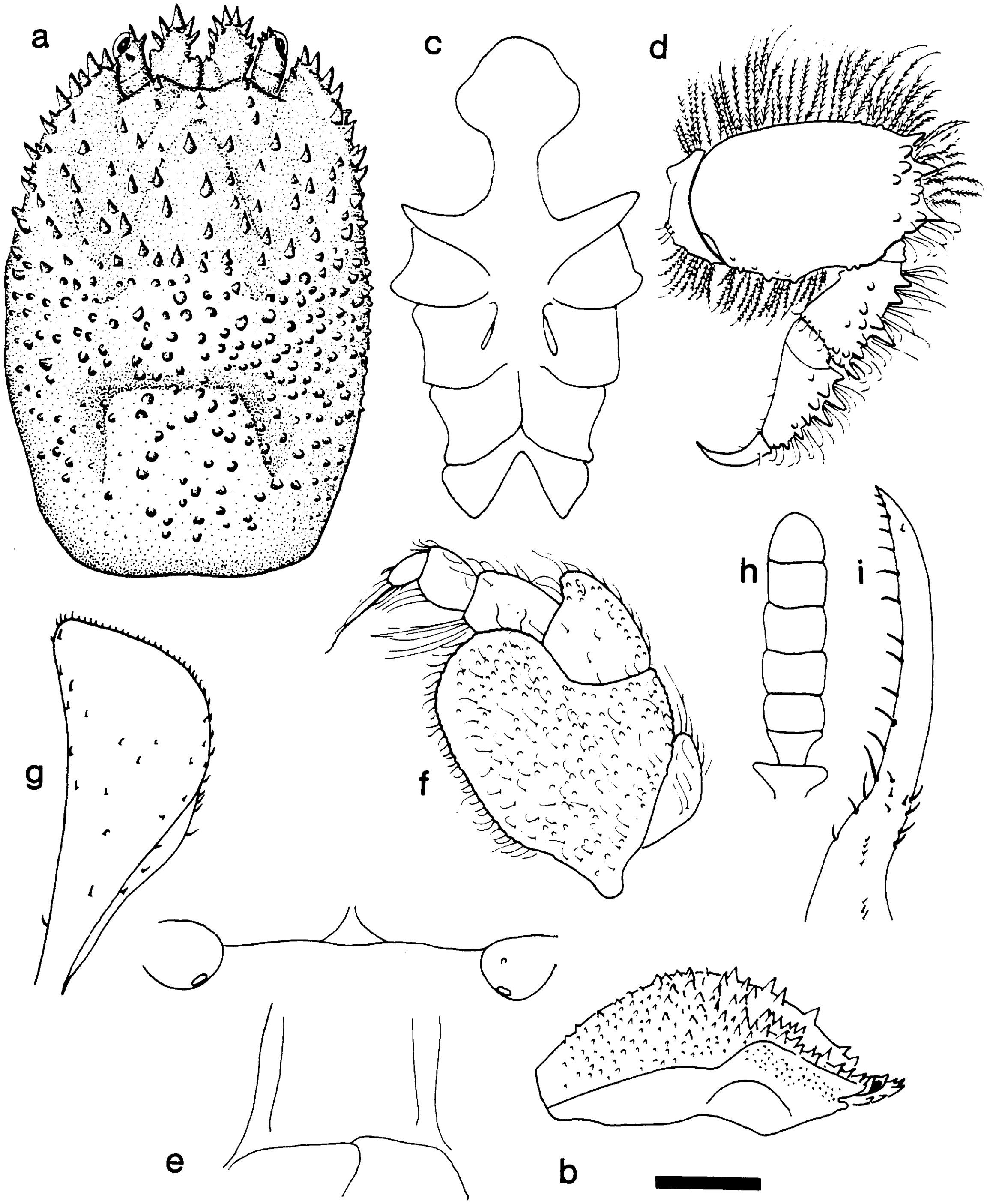
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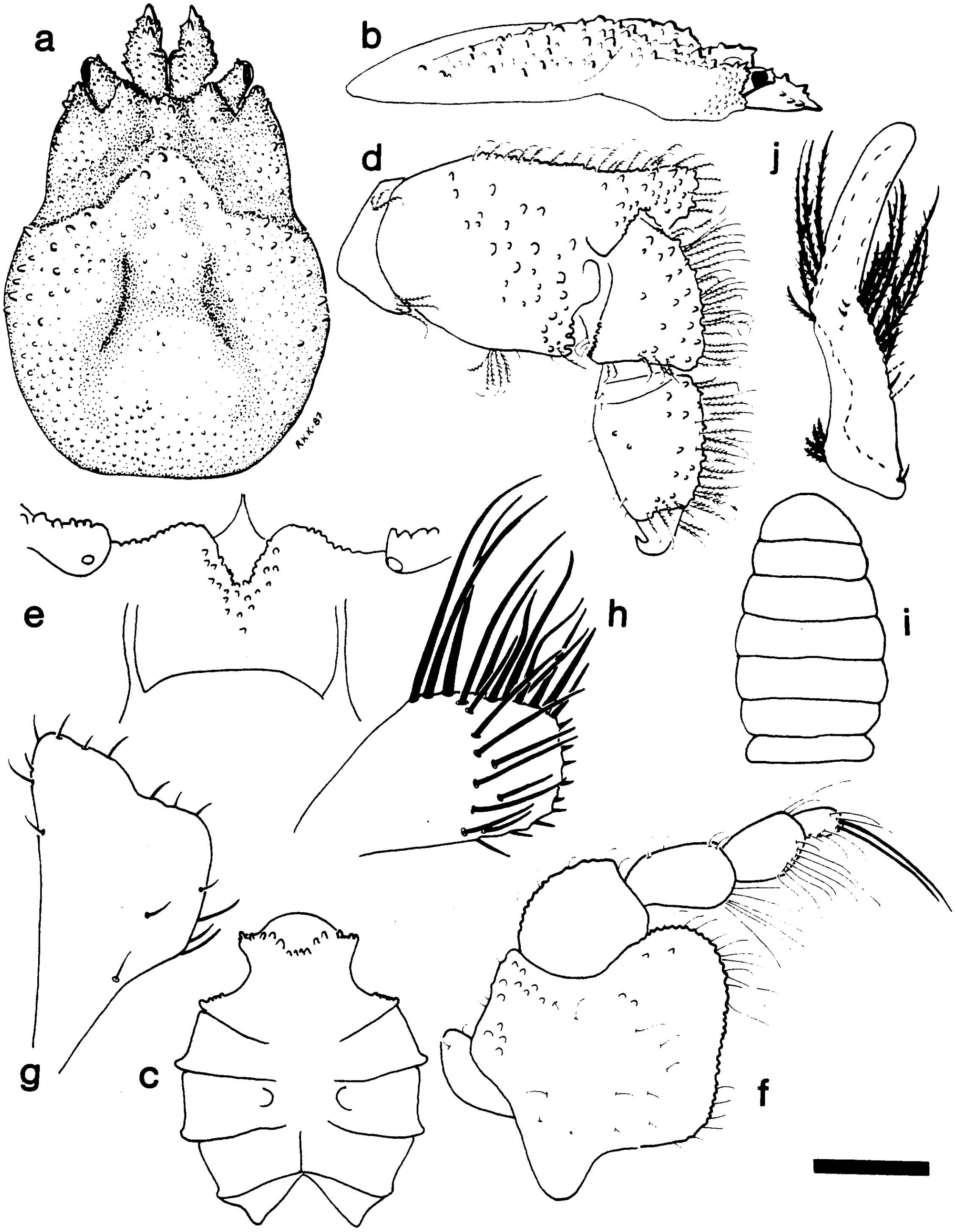
Fig. 40. *Neotroglocarcinus hongkongensis* (Shen). Female (Vietnam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: a-c = 2.1 mm; d = 1 mm; e = 0.5 mm;

Fig. 41. *Opecarcinus hypostegus* (Shaw and Hopkins). Female holotype (Florida): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male paratype (Florida): i, abdomen; j, gonopod. Scale: c = 1.2 mm; b, d = 1 mm; a = 0.7 mm; f, i = 0.5 mm; e = 0.3 mm; h, j = 0.2 mm; g = 0.1 mm.

Fig. 42. *Pelycomaia minuta* (Edmondson). Female (Hawaii): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Hawaii, from Edmondson, 1933): h, abdomen. Scale: c = 0.8 mm; a, b, d = 0.5 mm; f = 0.2 mm; e, g, h = 0.1 mm.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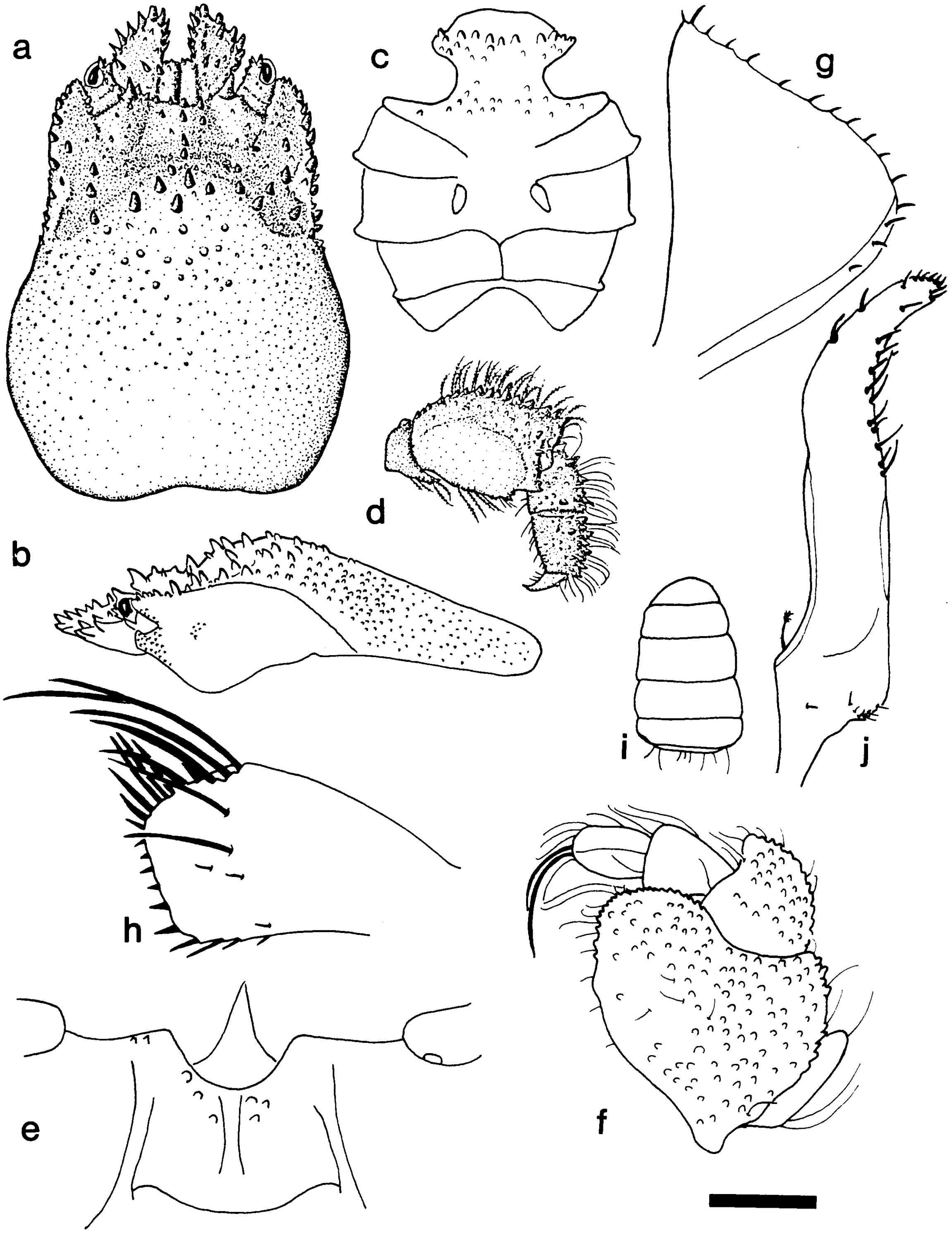
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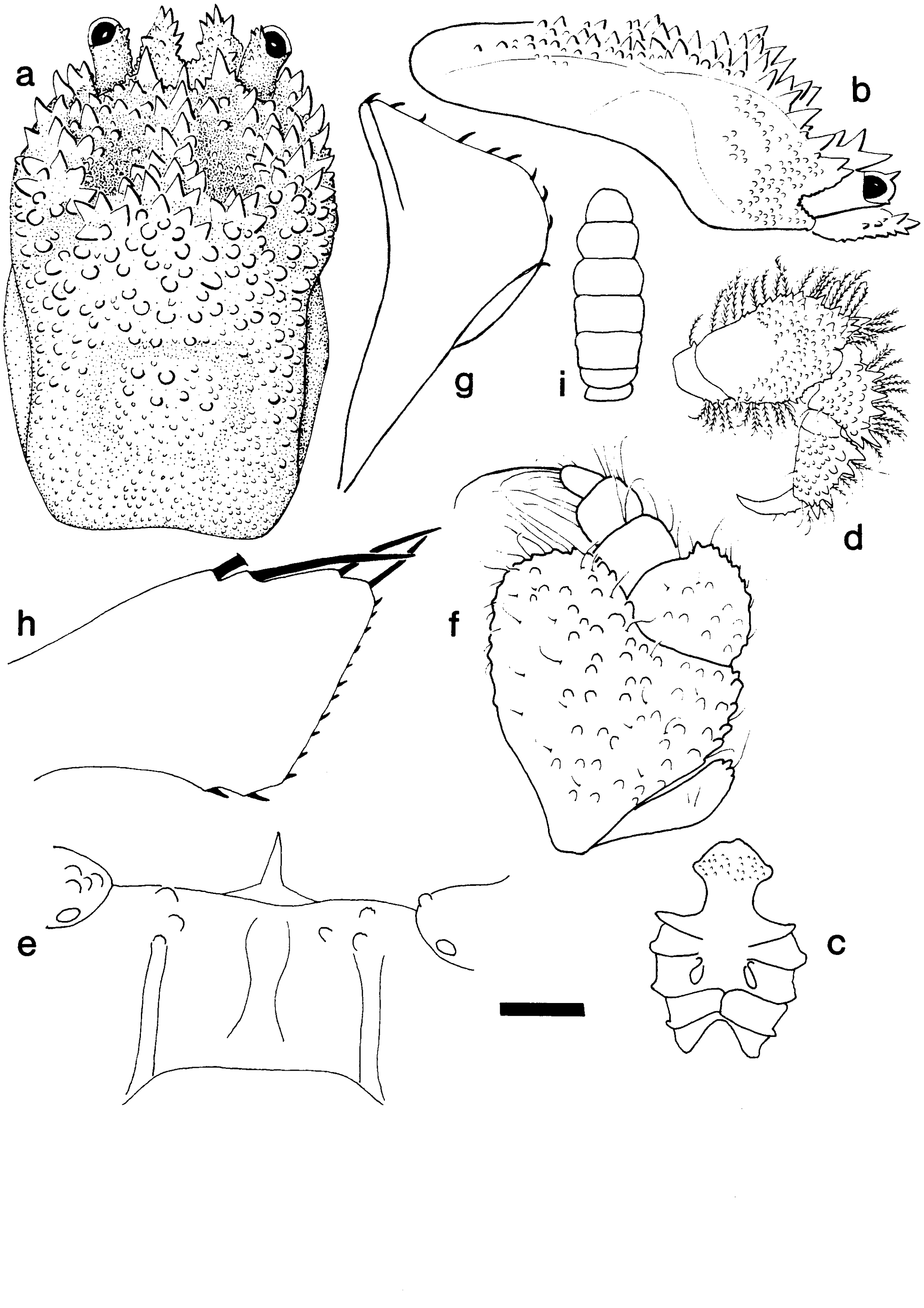
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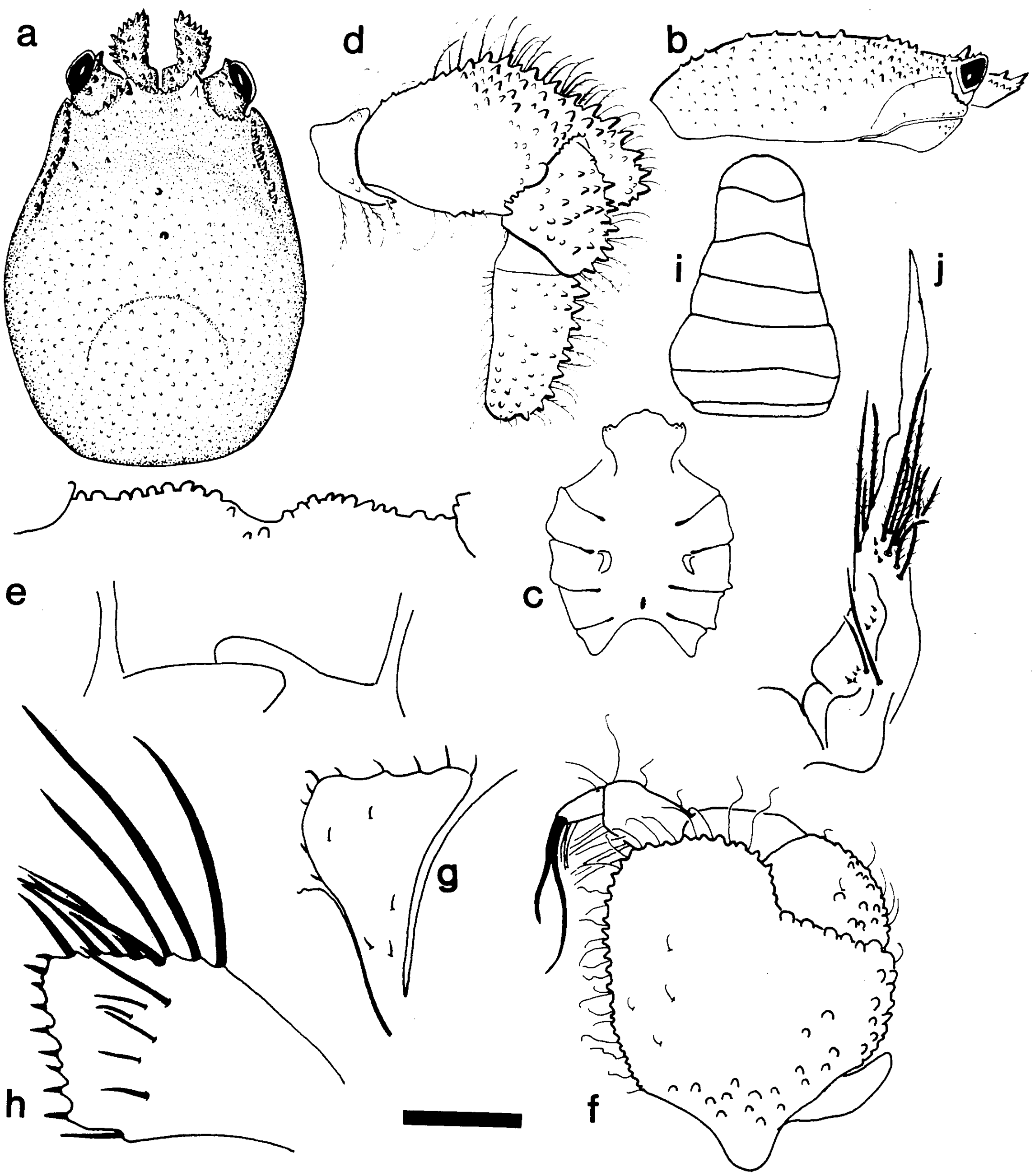
Fig. 43. *Pseudocryptochirus viridis* (Hiro). Female (Belau): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Belau): i, abdomen; j, gonopod. Scale: a = 1.2 mm; b, c = 1 mm; d = 0.5 mm; e, f = 0.2 mm; g, h = 0.1 mm.

Fig. 44. *Pseudohapalocarcinus ransoni* Fize and Serène. Female (Guam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Belau): i, abdomen; j, gonopod. Scale: a, b = 1 mm; c, i = 0.5 mm; e, f = 0.3 mm; g, h = 0.1 mm.

Fig. 45. *Sphenomaia pyriforma* (Edmondson). Female (Teraina): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1. Scale: a-d = 1 mm; e = 0.5 mm;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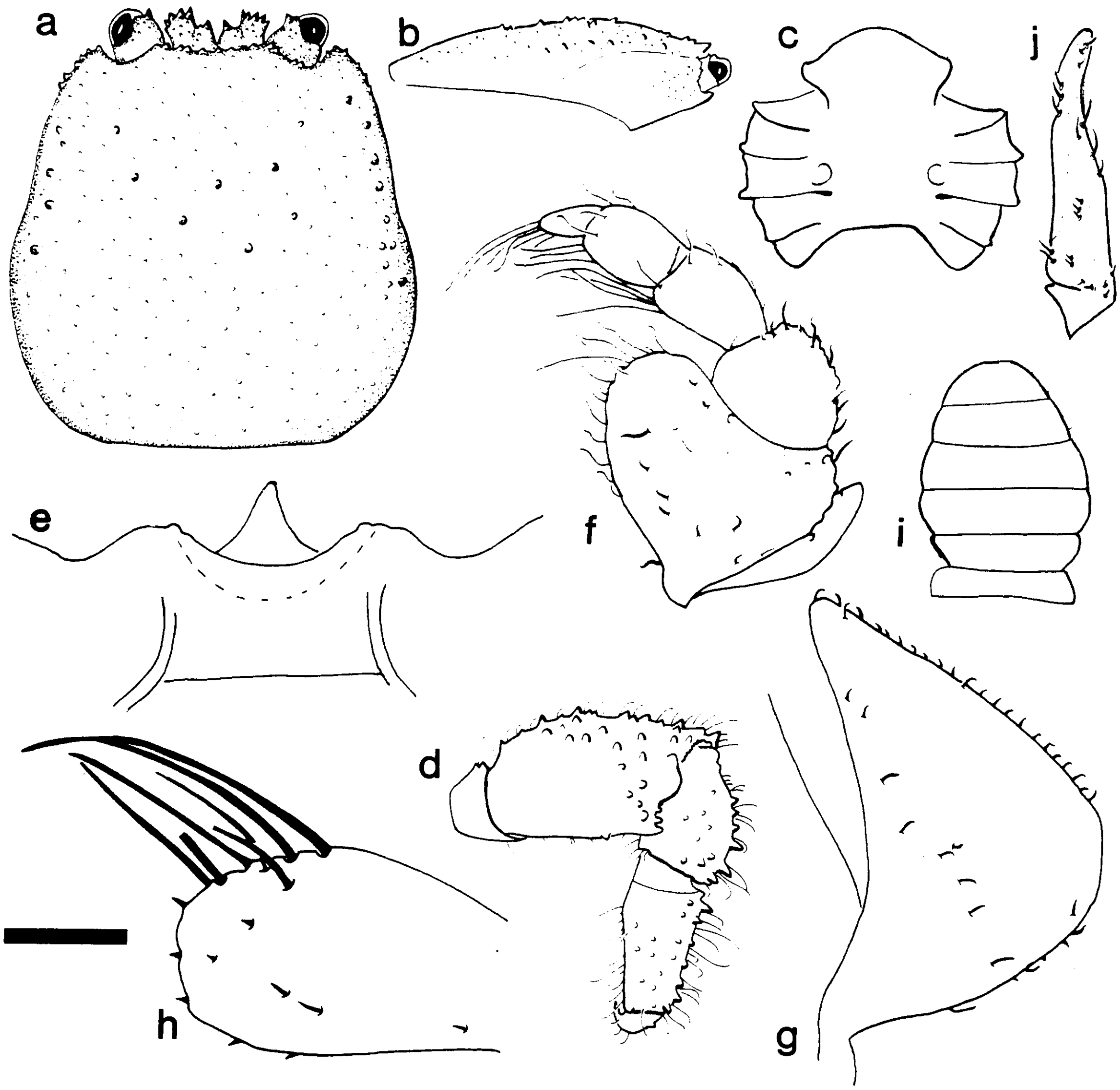
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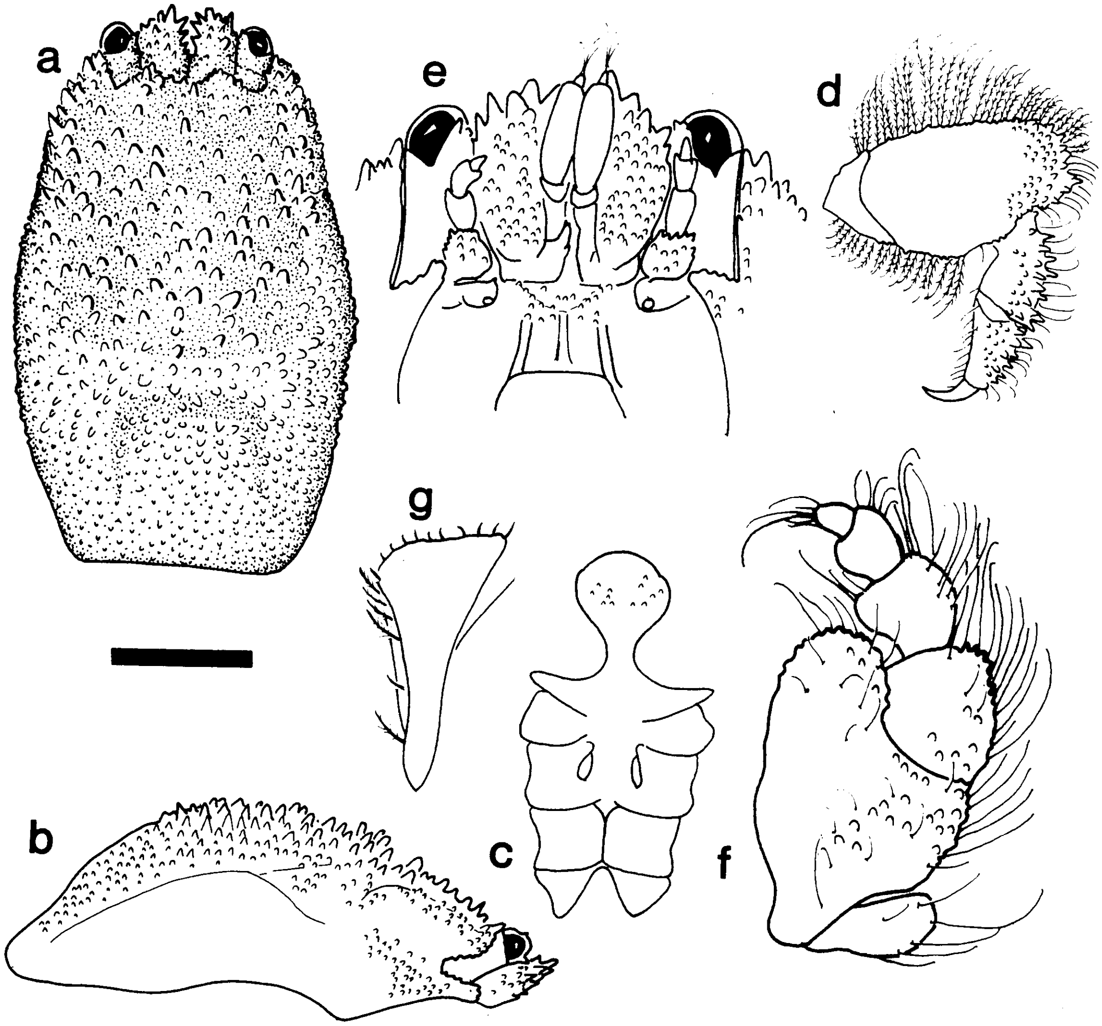
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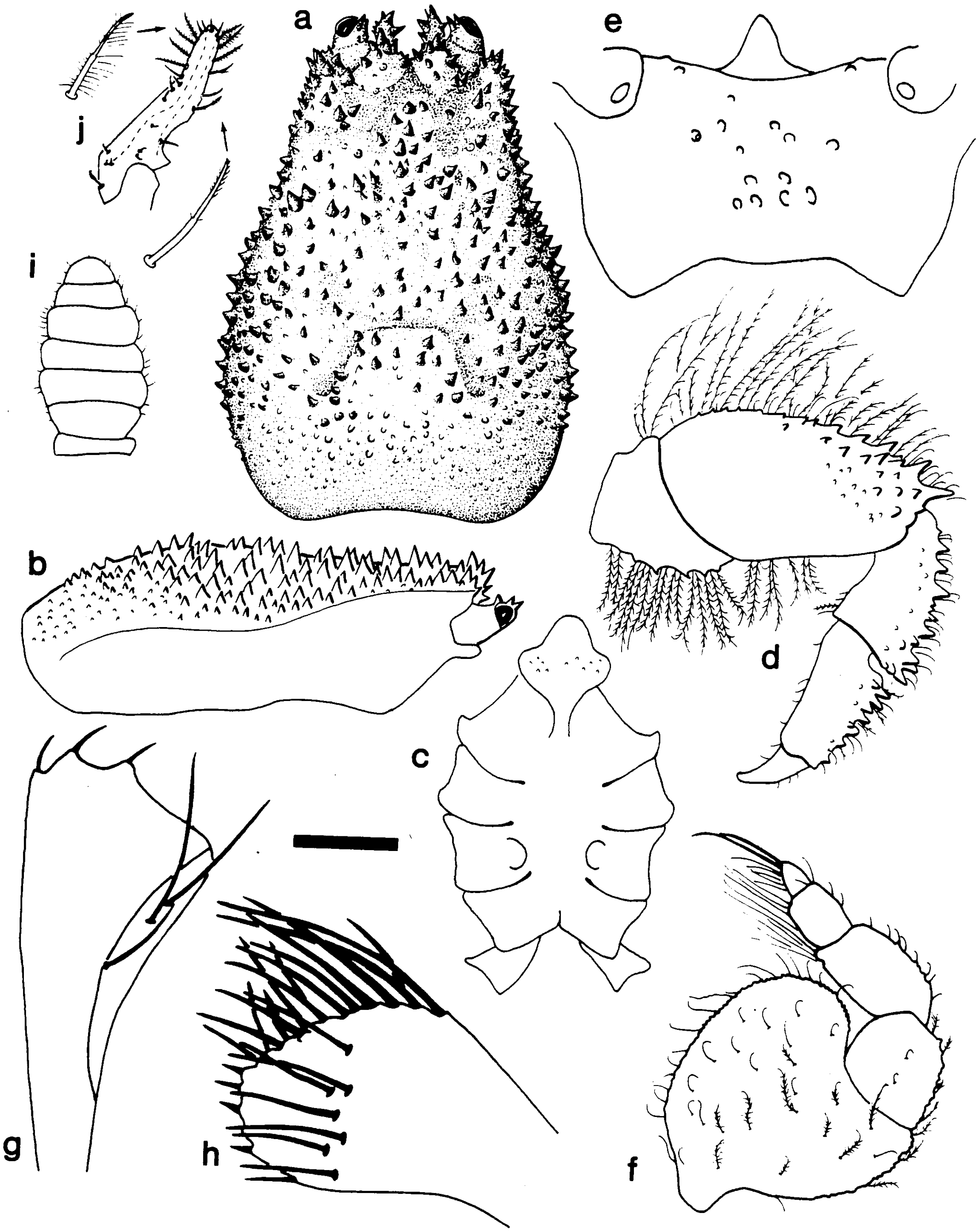
Fig. 46. *Utinomia dimorpha* (Henderson). Female (Belau): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: a-c, i = 1 mm; d = 0.5 mm; f = 0.3 mm; e = 0.2 mm; g, h = 0.1 mm.

Fig. 47. *Xynomaia sheni* (Fize and Serène). Female (Guam): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: a-c, i = 1 mm; e = 0.5 mm; d, f = 0.3 mm; g, h = 0.1 mm.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Chapter 9

Phylogeny and Host Specificty of the Coral-Dwelling Gall Crabs

(Crustacea: Cryptochiridae)

Abstract

Cladistic analyses were used to estimate the relationships among the genera of coral-dwelling gall crabs. These relationships were then compared to patterns of host specificity exhibited by the crabs. The results showed that the general trend has been for crabs to inhabit increasingly aggressive corals as demonstrated by the presence of the most ancestral crabs on relatively benign corals and the most derived crabs on very aggressive corals. A second trend was the radiation of one clade into dendrophylliine corals which may also offer protection, though they are not aggressive. Host specificity patterns show highly predator-resistant corals being occupied by more gall crab taxa than less resistant corals; and crabs in the Pacific were more host specific than those in the Atlantic. Gall crab dwellings have evolved from complex closed galls to simple cylindrical pits.

Introduction

Cryptochirid crabs are small brachyurans that live as obligate symbionts on scleractinian corals. They reside in peculiar modifications of the host coral skeleton, ranging from simple cylindrical pits to completely enclosed galls.

Once thought to feed on nanoplankton (Potts, 1915), they have recently been shown to feed on coral mucus and occasionally coral tissue (Kropp, 1986).

The obligatory, from the crab point of view, nature of the symbiosis and the dependence of the crabs on the host coral for food as well as shelter make this relationship one that would be of interest to test hypotheses about how symbionts are distributed on their host taxa.

One hypothesis used to explain distributions of symbionts on hosts is the idea of cospeciation (Mitter and Brooks, 1983). This idea has been in the literature for some time, explained as Farenholz's Rule (see Mitter and Brooks, 1983), but has received renewed interest because of the use of numerical taxonomic methods to determine relationships among organisms. Studies using this approach include studies of vertebrates and their flatworm parasites (Brooks, 1979; Brooks et al., 1981), pinworms and their primate hosts (Brooks and Glen, 1982), and fungal rusts parasitic on grasses (Baum and Savile, 1985). Some examples of recent studies involving marine taxa are those of copepods parasitic on scombrid fishes (Cressey et al. 1982; Collette et al., 1985). Some recent studies have taken a similar approach, differing in that numerical taxonomic methods have not been used (Ho, 1983; Timm, 1983). Ho (1983) used the relationships of the copepod parasites to test ideas about the host fish (Embiotocidae) relationships.

An alternative approach suggests that ecological factors involving host shifts can explain the distribution of symbionts on hosts. This hypothesis, called "Resource Tracking" by Timm (1983), implies that symbionts follow a particular feature of the host that is independant of the host phylogeny. For example, the distribution of mites parasitic on certain birds was found to be best explained by quill size (Kethley and Johnston, 1975).

Here I use cladistic techniques to reconstruct the phylogeny of the coral gall crabs and attempt to explain the distribution of the crabs on their coral hosts by the competing hypotheses of cospeciation and resource tracking.

Materials and Methods

Taxonomic studies on cryptochirids have been plagued by many errors which have only recently been corrected in a series of papers by Takeda and Tamura (references in Kropp, ms 3) and my own work (Kropp and Manning, 1985; 1987; Kropp, 1988a; 1988b; ms 1; ms 2; ms 3). Therefore, it now appears that the group is an appropriate one on which to perform cladistic analyses.

The specimens on which this study was based were those used in my previous work on cryptochirids. I collected much of that material in Micronesia in 1984 and 1986. Other material was borrowed from several museums as listed in previous publications (Kropp and Manning, 1987; Kropp, ms 1; ms 2).

Crabs were examined by a combination of light and scanning electron microscopy (SEM). Specimens were prepared for SEM and observed as described in Kropp (1986).

I examined representatives of several brachyuran families for use as possible outgroup taxa. These specimens were obtained from the National Museum of Natural History, Smithsoniam Institution, Washington, D. C. or from my own collections. Families examined included: Atelecyclidae; Cancridae; Hymenosomatidae; Leucosiidae; Ocypodidae; Palicidae; Pinnotheridae; Retroplumidae; and Xanthidae.

Gall crab phylogeny was estimated by using D. L. Swofford's (1985) Phylogenetic Analysis Using Parsimony (PAUP) computer program. The Global Branch-swapping (GLOBAL) and Multiple Parsimony (MULPARS) options were used to estimate the shortest tree. As advocated by Platnick (1987), prior to invoking branch-swapping, I varied the Hold and Add Sequence options which determine the number of trees retained at each step and the sequence in which taxa are added, respectively, in the initial estimate of the tree. For each of the Add Sequence options, CLOSEST, SIMPLE, ROOTLESS, and ASIS, I used initial Holds of 10, 15, 20, and 25 trees. I haphazardly varied the user-selected tree on which the branch-swapping option was run. Cladograms were rooted by the outgroup method.

Multistate characters were originally considered unordered. They were subsequently ordered to fit a preliminary estimate of the cladogram. This reordering was repeated until the resulting tree stabilized (Michevich, 1982). All characters were weighted equally. Character and character state definitions are presented in Table 2 and the character matrix in Table 3.

After the final trees were derived, I optimized the suborders (after Wells, 1956) of the coral hosts on the trees using Farris optimization (Michevich, 1982). Where more than one most parsimonious ancestral host was possible, the one assigned was the one not requiring a change from the previous ancestor.

Outgroup Selection

Largely because of the unusual morphology of cryptochirids, the exact relationship of gall crabs to the remaining Brachyura has been uncertain (e. g. Warner, 1977). Traditionally the group has been placed as the only member of the superfamily, Cryptochiroidea (see Kropp and Manning, 1985). Stevcic (1971) regarded the group as showing regressive evolution because of its commensal lifestyle, yet the family usually has been placed among the "higher" Brachyura (Bowman and Abele, 1982). Recent studies of the larvae of some gall crabs, though limited, have led to hypotheses that the closest relatives of gall crabs are the Hymenosomatidae, Leucosiidae, or Pinnotheridae (Scotto and Gore, 1981; Gore et al., 1983). These three families were considered as possible outgroups. Cursory examinations of the other crab families listed above indicated that two other families, Palicidae and Retroplumidae, might be outgroup candidates. After further examination, I eliminated the Hymenosomatidae and Leucosiidae from consideration. Most taxonomic schemes do not place leucosids and cryptochirids as close relatives (Bowman and Abele, 1982) and hymenosomatids were not found to be morphologically comparable to gall crabs.

A preliminary analysis was run, using all three outgroup taxa (Palicidae, Pinnotheridae, and Retroplumidae) and the cryptochirid genera, with the resulting cladogram showing the outgroups clustered together outside the cryptochirids. Separate runs were performed using each outgroup alone with the ingroup gall crabs. For the Palicidae and Retroplumidae each run resulted in more than 100 most parsimonious trees. For the Pinnotheridae only two trees were found in the preliminary analysis, each several steps shorter than the trees for the other two outgroups. Because of the large number of trees associated with the first two outgroup taxa and the greater homoplasy shown in those trees which could be traced to the outgroups, I completed the analyses using only the Pinnotheridae as the outgroup taxon.

Monophyly of the Cryptochiridae

The gastric mill provides the strongest evidence for the monophyly of the Cryptochiridae. The mill of cryptochirids differs in general from typical brachyurans by being much less calcified (Mocquard, 1883; Patwardhan, 1935;

Coen, 1987). Additionally, the lateral and median teeth of the mill differ from those found in any other brachyuran crab family. Typically the lateral tooth found in brachyurans has relatively large molariform cusps anteriorly with a series of transverse rows posteriorly or is entirely molariform (Fig. 48; see Coen, 1987). Coen (1987) also mentions that the cuticular surfaces of the teeth are dark brown-black in color; I have noticed this color only in those gall crabs having cusp-like structures. In cryptochirids, the lateral tooth does not have large cusps anteriorly, although some taxa do have cusp-like structures anteromesially (discussed below; Fig. 48). The posterior portion of the tooth is comprised entirely of papillae which are not organized into discrete rows (Fig. 48). In some gall crabs papillae on the mesial margin of the tooth may be thickened.

A typical brachyuran median tooth is a robust molariform structure which in some families may be complexly divided (Coen, 1987). The tooth is characterized by paired, ventrally-projecting brushes (Coen, 1987). In contrast, all gall crabs have a median tooth that is not robust and that has many, long anteriorly directed papillae (Fig. 48). These papillae may be homologous to the paired brushes found in other brachyurans.

The use of the gastric mill in phylogenetic reconstruction has been questioned because of apparent diet related differences in mill morphology (Kunze and

Anderson, 1979; Skilleter and Anderson, 1986). Others have proposed that the mill morphology reflects common ancestry (Felgenhauer and Abele, 1983; 1985). I support the latter view. Though gall crabs all probably have very similar diets consisting of coral mucus and tissue (Kropp, 1986), which may explain the reduced state of the mill, the variation of the teeth within the family is not easily explained by dietary differences. *Trapezia* (Xanthidae) also feeds on coral mucus (Knudsen, 1967) and yet has a mill anatomy close to that of other xanthids (Kropp, 1986). *Pinnotheres* is also likely to have a soft food diet and has a robust gastric mill (Fig. 48).

The peculiar expansion of the lateral lobe of the antennule (Fig. 49) provides additional evidence for cryptochirid monophyly. In most gall crabs the lateral lobe extends to or beyond the distal part of the eyestalk. In *Hapalocarcinus* and *Pseudohapalocarcinus* the antennule reaches to half or less the length of the eyestalk, but still is more expanded than is usual in the Brachyura.

All gall crabs except *Hapalocarcinus* have unusual anteriorly directed extension on the coxae of the fourth and fifth pereopods (Fig. 50). I have not seen these "lobes" in any othe crab family.

The gall crabs are unique among brachyurans in lacking a mandibular palp, although caution should be used in using a missing feature as evidence for monophyly. Typically, brachyurans have a two- or three-segmented palp (Patwardan, 1935).

The unusual lifestyle of cryptochirids, living within modifications of scleractinian corals, does not provide evidence for monophyly of the group. Several other decapod crustaceans, including the palaemonid shrimp, *Paratypton*, and the xanthid crabs, *Cymo*, *Maldivia*, and *Domecia* are obligate symbionts of stony corals and also live within modifications of the host skeleton (Bruce, 1969; Eldredge and Kropp, 1982; Coles, 1982).

I have found no characters that contradict the monophyly of the Cryptochiridae.

Morphology of the Cryptochiridae

Head

Antennules (Fig. 49).--The expansion of the lateral lobe of the antennule (character 1) is often spectacular, extending to or beyond the distal part of the eyestalk in most genera. However, in *Pseudohapalocarcinus* the lateral lobe only extends to about half the length of the eyestalk. In *Hapalocarcinus* the maximum extent of the antennule is about half the length of the eyestalk, but this condition occurs in young specimens. The antennule is often more reduced in adults.

Antenna.--The fused segment 2-3 of the antenna (character 2) varies from being wider than long in

Hapalocarcinus, *Pseudohapalocarcinus*, *Pseudocryptochirus*, and *Neotroglocarcinus* to being longer than wide or subequal in the other genera. Segment 2-3 has a spine present laterally on the anterior margin (character 3) in *Fizesereneia* and *Xynomaia* whereas none is present in the other genera. The length of segment 4 varies relative to that of segment 5 (character 4), being longer in most genera, but shorter in *Fungicola*, *Hiroia*, and *Xynomaia*.

Maxilla 1 (Fig. 52 a-c).--Four morphological types of the first maxilla were recognized. One type, found in *Detocarcinus* and *Utinomia*, has a convex mesial margin having few stout simple setae. The other three are characterized by a straight mesial margin, but differ in other respects. In *Fizesereneia* and *Xynomaia* the mesial margin is perpendicular to the midline of the body and has many (> 14) stout setae. In *Hapalocarcinus* and four other genera (Table 3) the mesial margin is straight and perpendicular to the midline of the body, but has few stout setae. The remaining genera, for which the morphology of the appendage is known, have the mesial margin straight, with many stout setae, but oriented oblique to the midline of the body (Table 3, state 2).

Epistome (Fig. 51).--The epistome provided three characters. A longitudinal ridge (character 6) is present laterally in all genera except *Hapalocarcinus*, *Utinomia*, *Cecidocarcinus*, and *Detocarcinus*. A median ridge (character 7) is present in some of the genera. The anterior margin of the epistome (character 8) is relatively straight in *Hiroia*, *Lithoscaptes*, *Dacryomaia*, and *Pelycomaia*. The margin is sinuous in the other genera, markedly so in *Neotroglocarcinus*.

Thorax

Carapace (Fig. 49 a-c).--Three basic carapace shapes (character 9) were found: square in *Hapalocarcinus* and *Pseudohapalocarcinus*; rectangular, widest posteriorly (vase-like), in *Cecidocarcinus*, *Detocarcinus*, *Neotroglocarcinus*, *Opecarcinus*, *Pseudocryptochirus*, *Troglocarcinus*, and *Utinomia*; and rectangular, widest anteriorly, in the remaining genera. Typically the orbit (character 12) of cryptochirids is V-shaped, however it is broadly U-shaped in *Hapalocarcinus* and *Pseudohapalocarcinus*. The pterygostomial region (character 11) is fused to the carapace in all genera except *Cecidocarcinus*, *Pseudocryptochirus*, *Troglocarcinus*, *Fizesereneia*, and *Xynomaia*.

Sternal plastron (Fig. 49 d-f).--The sternal plastron (character 12) is as long as wide in *Hapalocarcinus* and *Pseudohapalocarcinus*, but longer than wide in the other genera. The surface topography of the plastron (character 13) is flat in 13 genera, but distinctly concave mesially in *Cryptochirus*, *Hiroia*, *Lithoscaptes*, *Sphenomaia*, and *Dacryomaia*. In cryptochirids, the first thoracic sternite extends anteriorly toward the buccal cavity. At about the midlength of the sternite, in the vicinity of the basis of the cheliped, the sternite becomes constricted. This constriction (character 14) is either slight or marked, the latter condition occurring only in *Cryptochirus*, *Lithoscaptes*, *Sphenomaia*, and *Utinomia*. The fourth thoracic sternite (character 15) has a median suture in all genera except *Hapalocarcinus*, *Pseudohapalocarcinus*, *Neotroglocarcinus*, and *Detocarcinus*.

Female gonopore (Fig. 49 d-f).--Two basic shapes of the gonopore (character 16) were found. The gonopore is oval and transverse in eight genera, as compared to the elliptical, longitudinal condition found in the other ten. Gonopore shape did not appear to be related to carapace or sternal plastron features. The gonopore is frequently characterized by the presence of an anteromesial projection ("hood", character 17) that is not correlated with gonopore shape. *Opecarcinus* shows both conditions, with one species having and the other species lacking the projection, and was coded as "missing" data.

Maxillipeds .--*Detocarcinus* and *Utinomia* are unusual in lacking the exopod of the third maxilliped (character 18). In the other genera, the exopod is present although considerably reduced and lacking a flagellum typical of most other brachyurans. The inner surface of the merus of the third maxilliped (character 19) has mesially directed pappose setae in all genera except the two inhabiting pocilloporid corals, *Hapalocarcinus* and *Utinomia*. Four genera, *Neotroglocarcinus*, *Opecarcinus*, *Pseudocryptochirus*, and *Pseudohapalocarcinus*, lack setae distally on the inner surface of the third segment of the second maxilliped endopod (character 20). Such setae are otherwise present. The endopod of the first maxilliped (Fig. 52 d-f; character 21) was useful, though difficult to characterize. Four types were recognized. It is subquadrate in *Hapalocarcinus* and triangular in the rest. The latter form can be subdivided further: being roundly triangular, having the widest dimension proximal to the midlength as found in *Pseudohapalocarcinus* and *Opecarcinus*; roundly triangular, but widest proximal to the midlength as occurs in eight genera as listed in Table 3; and angularly triangular in the remaining seven genera.

Cheliped (pereopod 1).--Sexual dimorphism of the chelipeds (character 22) is expressed in most gall crab genera by a relatively more robust cheliped in males than that of females. Chelipeds are not dimorphic in *Fungicola*, *Neotroglocarcinus*, *Pseudocryptochirus*, or *Pelycomaia*. Female chelae provided two characters which are unrelated; chela thickness (character 23) and dactylus length (character 24). For nine genera the chela height is about equal to the length of the dorsal margin of the palm (stout); in nine the dorsal margin of the palm is markedly greater than the height (slender). In *Utinomia* this elongation of the palm is exaggerated much more than any other genus. Usually the length of the dactylus exceeds that of the dorsal margin of the palm. However, the opposite condition occurs in *Fungicola*, *Hapalocarcinus*, *Neotroglocarcinus*, *Opecarcinus*, *Pseudohapalocarcinus*, and *Utinomia*.

Pereopod 2 .--The merus of the second pereopod (character 25) for all genera having a vase-like carapace shape, except *Utinomia*, is expanded distomesially. In *Utinomia* and all other genera there is not such an expansion. The dactylus of the second pereopod (Fig. 50 a, b; character 26) of *Hapalocarcinus*, *Opecarcinus*, *Troglocarcinus*, and all genera having a rectangular carapace shape has a subterminal pore. No pore is present in any of the remaining genera for which such determination could be made. The presence or absence of a pore is undetermined for *Cecidocarcinus* and *Sphenomaia* because the pore is visible only by SEM which could not be performed on those two genera.

Pereopod 5.--The dactylus of the pereopod 5 (character 28) of many cryptochirids is unusual because it is rotated anteriorly with respect to the dorsoventral axis of the other leg segments. This rotation occurs in all but *Hapalocarcinus*, *Cecidocarcinus*, *Detocarcinus*, and *Utinomia*.

Most genera except *Hapalocarcinus* have peculiar modifications of the coxae of pereopods 3 to 5 (Fig. 50 c, d). A flap-like projection extends anteriorly into the space between a pereopod and the coxa of the leg immediately anterior. On pereopod 3 (character 29) the coxal flap is absent in *Cryptochirus*, *Hapalocarcinus*, *Hiroia*, and

Xynomaia. The coxal flap on pereopod 4 (character 30) is well-developed in eight genera, reduced in eight genera, and absent in *Cryptochirus* and *Hapalocarcinus*. The flap on the coxa of pereopod 5 (character 31) is well-developed in all genera, except *Hapalocarcinus*. I have not seen a comparable coxal extension in other brachyurans.

Abdomen

Female pleopod 3.--The third pleopod does not show the within species variability that has been reported for other pleopods (McCain and Coles, 1979; Kropp and Manning, 1987). Pleopod 3 (character 32) is biramous in *Cecidocarcinus*, *Detocarcinus*, and *Neotroglocarcinus* and uniramous in all other genera.

Male gonopod .--The male gonopod (character 32) varies considerably within the family and here I recognize eight states, five of which are autapomorphic (gonopods were figured by Kropp and Manning, 1987 and Kropp, ms 3). In *Cecidocarcinus* and *Detocarcinus* the gonopod is long, sharply (~90°) turned laterally and having many plumose setae at the tip; in *Neotroglocarcinus* and *Pseudocryptochirus* the gonopod is long, slightly to moderately curved distally and has clumps of plumose setae on the lateral and mesial surfaces at midlength; the remaining genera share a gonopod type that is long, slightly curved, and is sparsely setose.

The autapomorphic conditions are as listed in Tables 2 and 3.

I analyzed the data with the autapomorphic conditions coded as unknown and again with those states coded included. The only effect of the autapomorphic states was to increase the overall consistency index of the tree from 0.48 to 0.50.

Male abdomen .--The male abdomen (character 33) could be described as having sides subparallel (*Cryptochirus* and *Lithoscaptus*), concave (*Pseudocryptochirus*), or convex (the other genera). The abdomen is very convex in *Fungicola*.

Gastric Mill

Lateral tooth (Fig. 48 b-d).--Three basic types of lateral tooth structure (character 35) were recognized. All have papillate occlusal surfaces and lack robust, molariform cusps. *Fungicola*, *Hapalocarcinus*, *Opecarcinus*, *Pseudohapalocarcinus*, and *Troglocarcinus* all have more stout papillae mesially. The five genera most closely related to *Cecidocarcinus* have enlarged cusp-like structures anteromesially. The remaining genera have teeth entirely comprised of subequal papillae.

Median tooth (Fig. 48 f-g).--The median tooth (character 36) was superficially similar in all cryptochirid taxa, consisting of parallel brushes of pappillae laterally. The length of the lateral papillae varies from short in *Hapalocarcinus*, *Neotroglocarcinus*, *Pseudocryptochirus*, *Pseudohapalocarcinus*, and *Utinomia* to long in the remaining taxa.

Relationships of the Cryptochiridae

Results of the final analyses using the Pinnotheridae as the outgroup yielded five most parsimonious trees (Figs. 53, 54), each 100 steps in length. The consistency index associated with each tree was 0.48. Varying the Hold option and the selection of the tree used as the initial estimate for the branch-swapping option did not change the final results. However, the sequence of taxon addition did have an effect. The Add Sequence options SIMPLE, ROOTLESS, and ASIS each yielded four trees, but the trees derived from the latter two options were the same as the four from the SIMPLE option. The Add Sequence option, CLOSEST resulted in one tree of a topology differing from those resulting from the other options.

The number of steps added to the tree by the distribution of coral host ancestors was 12 for one of the trees resulting from the Add Sequence = SIMPLE analyses (Tree 1) and the tree resulting from the Add Sequence = CLOSEST option (Tree 2). This distribution of hosts on Tree 1 is shown in Fig. 55. Placing coral hosts on the remaining three trees added 13 steps. In any case, the number of steps added was greater than expected by the number of possible "states" as Wells (1956) lists five coral suborders. The increase resulted from the combined effect of homoplasy and the presence of a crab taxon on more than one host suborder (Table 4). A likely cladogram of coral suborders was derived from Wells (1956) and is shown in Fig. 56 A.

Tree 1

To simplify presentation of the main features of Tree 1, I recognize four major groups: genus *Hapalocarcinus*, genus *Pseudohapalocarcinus*, the clade "detocarcini" (comprised of *Cecidocarcinus*, *Detocarcinus*, *Utinomia*, *Neotroglocarcinus*, and *Pseudocryptochirus*), and "cryptochirini" (comprised of the remaining genera). Detocarcini and cryptochirini are, for now, not meant to be given formal taxonomic status.

Several clades were supported by one or more synapomorphies in addition to conditions occurring elsewhere in the tree. The detocarcini and cryptochirini were linked by synapomorphies expressed by the length of the lateral lobe of the antennule being greater than 1/2 the length of the eyestalk, by having a broadly U-shaped orbit, a rectangular carapace, and the sternal plastron length exceeding its width.

A single synapomorphy, the cusp-like development of the lateral tooth of the gastric mill, supports the detocarcini. This clade occurs primarily on dendrophylliine corals with radiations into astrocoeniine (by *Utinomia*) and faviine or caryophylliine (both by *Detocarcinus*) corals.

Within the detocarcini the *Neotroglocarcinus*-*Pseudocryptochirus* pair was linked by the development of of an anteromesial projection on the female gonopore, by not showing sexual dimorphism in the male cheliped, and by having the width of the fused antennal segments 2-3 exceeding its length. This crab pair occurred in all of the analyses performed, except Tree 2. The troika of *Utinomia*, *Cecidocarcinus*, and *Detocarcinus* was supported in the tree figured by the presence of setae distally on the inner surface of the carpus of the second maxilliped endopod, but the taxa were not linked in other trees.

Cecidocarcinus and *Detocarcinus* paired together, except in Tree 2, linked most convincingly by the strongly curved tip of the male gonopod, but also by the long lateral pappillae of the median tooth of the gastric mill, by the stout female manus, and a biramous female pleopod 3.

The cryptochirini was supported by the development of a subterminal pore on the dactylus of the second pereopod of the female, a feature otherwise found only in *Hapalocarcinus*. Cryptochirins also developed a median ridge on the epistome although this ridge was lost twice, in *Hiroia* and *Lithoscaptus*.

The cryptochirini exclusive of *Opecarcinus* was supported by the presence of the setae on the inner surface of the carpus of the second maxilliped and the long pappillae laterally on the median tooth of the gastric mill. Both, however, occurred elsewhere on the tree.

A major clade of the cryptochirini, one found exclusively in the Pacific Basin, was strongly supported by having a rectangluar carapace that is widest anteriorly, an elliptical female gonopod on which an anteromesial projection is found, by a reduction of the anterior lobe on the coxae of the third and fourth pereopods, and by not having a distomesially expanded merus of the second pereopod.

The *Fizesereneia*-*Xynomaia* pair was well defended by two synapomorphies, the presence of a lateral spine on the distal margin of the anterior margin of the antennal segment 2/3 and by having a common first maxilla.

Cryptochirus and *Lithoscaptus* always clustered together despite being linked only by having the sides of the male abdomen subparallel, a feature also known in *Cecidocarcinus*.

It is of interest to compare characters that were entirely consistent with Tree 1 and those that were quite a bit less so. Among the major consistent features were general features of the carapace or body; carapace shape, orbit shape, and sternal plastron length-width relationship; the first maxilla; and the lateral tooth of the gastric mill. Characters showing reduction or loss were quite homoplasious. For example, the reduction of the coxal lobe of pereopods 3 and 4, the loss of the setae from the inner distal margin of the second maxilliped endopod, and the loss of the exopod of the female pleopod 3 had consistency indices of 0.40 or less.

Tree 2

Tree 2 had several features in common with Tree 1. These were the placement of *Hapalocarcinus* and *Pseudocryptochirus* as the most ancestral taxa and the placement of *Troglocarcinus* and all more derived taxa as the most removed from the root.

Major differences appeared in the relationships of *Opecarcinus*, *Neotroglocarcinus*, *Pseudocryptochirus*, *Cecidocarcinus*, *Detocarcinus*, and *Utinomia*. *Opecarcinus* was removed from the cryptochirini and placed next to *Pseudohapalocarcinus*. The clade *Neotroglocarcinus*-*Pseudocryptochirus* was dissolved and each joined the tree in sequence after *Opecarcinus*. Though the troika *Cecidocarcinus*-*Detocarcinus*-*Utinomia* remained, the relationships within it differed. The usual pairing of the first two members was replaced by a pairing of the latter two.

It appeared that the evidence supporting the groups as presented in Tree 1 was stronger than that supporting the groups in Tree 2. The three major groups in Tree 1 were each defended by a synapomorphy found nowhere else in the tree. The *Cecidocarcinus*-*Detocarcinus* pair was supported by a long, strongly curved male gonopod that bears plumose setae at the tip, a feature unique to this pair. The group was also united by long pappillae on the median tooth, a biramous female pleopod 3, and a stout female cheliped having fingers longer than the dorsal margin of the palm, though these features all occurred elsewhere in the tree. The male pleopod also provides the strongest evidence linking *Neotroglocarcinus* and *Pseudocryptochirus*. Only in this pair is the gonopod long, slightly curved, and has many plumose setae at midlength on the lateral and mesial margins. Minor support came from the lack of cheliped dimorphism, the absence of a hood on the female gonopore, and having the second segment of the antenna wider than long. The five-taxon detocarcini was strongly united by the cusp-like structure of the lateral tooth of the gastric mill, a condition found only in this clade. The only feature on Tree 2 grouping any of the taxa in question that was not found elsewhere in the tree was the absence of the third maxilliped palp uniting *Detocarcinus*-*Utinomia*.

Discussion

The results of the cladistic analyses of the Cryptochiridae were contradictory to the predictions of the cospeciation hypothesis to explain the distribution of the crabs on the coral hosts. The host phylogeny proposed by Wells (1956) predicts that the crabs found on the Dendrophylliina would be highly derived and constitute a sister taxon to those found on the Faviina. Instead the detocarcini diverges relatively early from those taxa inhabiting corals of the Fungiina. A coral phylogeny derived from the gall crab phylogeny is compared to a coral phylogeny derived from Wells (1956) in Fig. 56.

The fossil record provides additional evidence for falsification of the cospeciation hypothesis. Wells (1956) provided an estimate of divergence times for the major coral taxa (including families). In his Figure 259 and accompanying text he estimated the split of the Fungiina and Faviina to have occurred in the mid- to late Triassic; the Faviina-Caryophylliina divergence about the early Jurassic; and the Caryophylliina-Dendrophylliina separation about the middle Cretaceous. The Astrocoeniina-Fungiina split had occurred at least by the early Triassic although Wells raised the possibility that the two had independent origins and that the Scleractinia is therefore polyphyletic.

The crustacean fossil record is much less clear, but from what is known the radiation of the Brachyura occurred after the origin of the major coral clades. There is no known fossil record of the Cryptochiridae (Glaessner, 1969; Warner, 1977). The Brachyura is known from as early as the late Jurassic (Warner, 1977; Schram, 1982), but the major radiation did not begin until the Cretaceous. The primary divergence of the more derived Brachyura, among which the cryptochirids are included, began in the Eocene (Warner, 1977; Schram, 1982). Therefore, all of the coral suborders and most of the families had evolved before the earliest probable origin of the cryptochirids.

It seems likely that the evolution of the gall crabs has involved a host shift following some particular property of the host. One such property might be host availability in which case the occurrence of crabs on corals might be related to chance encounters with hosts. Such an explanation has been used to explain host specialization of pierid butterflies on their host plants (Capparales) (Courtney and Chew, 1987). This is not the case here. Three of the most abundant coral genera in terms of areal coverage and species number are *Acropora*, *Montipora* (both Acroporidae), and *Porites* (Poritidae) (e. g. Randall, 1982; Colgan, 1987), yet none houses a gall crab. Additionally, within certain coral families known to host gall crabs, some common genera may not be inhabited by the crabs. For example, the Faviidae and Oculinidae host several gall crab genera, yet *Diploastrea*, a large, often locally common faviid (Kropp, personal observation), and *Galaxea*, an abundant oculinid (Colgan, 1987), do not house cryptochirids (Kropp, unpublished).

Another resource that gall crabs may be tracking is the relative degree of safety provided by the host. Predator-resistant hosts are more likely to be selected by symbionts over those less resistent, especially in regions of intense predation (Vermeij, 1983; 1987). It is likely that the occurrence of crabs on corals has been an evolutionary response to predation; corals being a safer place to live than the surrounding reef habitats. Predation by fishes on gall crabs appears to be rare, as only two studies have recorded instances of gall crabs being eaten by fishes (Kropp and Manning, 1987; Parrish, unpublished). However, corals provide varying degrees of safety as reflected by variation in competitive ability and susceptibility to predation. Many different animals are known to feed selectively on corals, including fishes (Glynn et al., 1972), molluscs (Moyer et al, 1982; Glynn, 1985), crustaceans (Gilchrist, 1985), and echinoderms (Birkeland, ms). Members of the first three categories may be important locally or have important effects on a few coral species, but an echinoderm, *Acanthaster planci*, can dramatically affect entire reef systems (Glynn, 1976; Moran, 1986).

Interactions among corals depend in part on relative level of aggression. Coral aggression has been measured in several ways, including extracoelenteric digestion (Lang, 1973; Cope, 1982), the development of sweeper tentacles (Richardson, et al., 1979; Wellington, 1980), interactive distance (Sheppard, 1982), and features of the coral nematocyst complement (the "cnidom" of Thomason and Brown, 1986). Though the patterns of aggression are not always clearcut, some competitive hierarchies have been established (Lang, 1973; Cope, 1982; Logan, 1984). The above references also allow some generalizations about coral aggression to be made. Smaller polyped corals are less aggressive than those having larger polyps. Aggression is also related to the number of nematocysts per polyp and aggressive corals tend to be located farther from neighboring corals than do less aggressive corals.

Though competitive interactions among corals, mediated in part by aggressive capability, may be important in structuring coral reefs (Sheppard, 1982; but see Bradbury and Young, 1982), the effectiveness of aggressive capability as an anti-predator feature has not been determined. In the literature concerning predation on corals, there are no records of aggressive corals being preferred as prey. Fish that graze on colonies, browse polyps, or destroy portions of colonies to create algal gardens all select relatively nonaggressive corals such as *Pocillopora*, *Acropora*, or *Pavona* (Glynn et al., 1972; Reese, 1977; Harmelin-Vivien and Bouchon-Navaro, 1982; Wellington, 1982). Molluscs and crustaceans show similar preferences (Moyer et al, 1982; Gilchrist, 1985). *Acanthaster*, the major predator on corals, also prefers less aggressive corals such as *Acropora*, *Montipora*, or *Porites* (Moran, 1986; Colgan, 1987) and avoids aggressive corals such as *Diploastrea* and *Galaxea* (Birkeland, ms). *Acanthaster* also avoids a benign coral, *Pocillopora*, which is host to a suite of coral-guarding crustaceans (Glynn, 1983). During catastrophic outbreaks of *Acanthaster*, previously avoided corals may be eaten by the sea stars (Done, 1985; Moran, 1986). In spite of the lack of confirmation by appropriate experiments, it seems that aggressive corals may provide places for symbionts to live that are relatively free from predation.

Consider Tree 1; gall crabs have taken two paths toward increasingly safe places to live. The first path was toward living on progressively more aggressive corals. The tree shows that crabs first colonized relatively benign corals and have progressively invaded more noxious corals though this has not occurred in a one-to-one stepwise fashion and multiple host invasions have taken place. The most ancestral gall crabs, *Hapalocarcinus* and *Pseudohapalocarcinus*, inhabit the relatively nonaggressive Pocilloporidae and Agariciidae respectively. From there the crabs (clade detocarcini) radiated into the Dendrophylliina (discussed below). The clade cryptochirini is marked by radiations into more aggressive fungiine and faviine corals culminating with the presence of the most derived taxa on highly aggressive faviine corals. This is exemplified by the occurrence of *Fizesereneia* on mussid corals, which include the most aggressive corals known (Thomason and Brown, 1986).

The second path toward safe places has been followed by the detocarcini, which has radiated primarily into dendrophylliine corals. Within this clade, *Utinomia* has independently colonized the Astrocoeniina and *Detocarcinus* has exhibited additional invasions into the Faviina and Caryophylliina. Dendrophylliines are small-polyped (Randall and Myers, 1983) and, with the exception of *Turbinaria*, are not prominent members of shallow-water reef communities. Wellington and Trench (1985) compared levels of aggression between a dendrophylliine coral, *Dendrophyllia* (= *Tubastrea*) *micranthus*, and selected astrocoeniine (*Pocillopora*, *Stylophora*, *Acropora*, *Montipora*) and fungiine (*Porites*) corals. They found that *Dendrophyllia* was less aggressive than the acroporids but more aggressive than the poritids but was able to compete with other reef corals because of its relatively high growth rate. That *Dendrophyllia* ranks below relatively nonaggressive corals (Sheppard, 1982) is further evidence that dendrophylliins are not very aggressive. Wellington and Trench also found that *Acanthaster* avoided *Dendrophyllia*. Birkeland (ms) mentioned that another dendrophylliine, *Turbinaria*, is also avoided by *Acanthaster*. I could find no information concerning predation on dendrophylliines by other organisms. Therefore, it is possible that dendrophylliines also offer a relatively safe place in which to live.

The general trend of crabs inhabiting increasingly noxious corals held for the other trees derived from the cladistic analyses. However, the apparent parallel development of two paths, one toward dendrophylliines and one toward aggressive corals, was lost. The scenario resulting from the other trees showed crabs radiating from non aggressive corals into the dendrophylliines, then into the more aggressive fungiine and faviine corals.

Another interesting point that arose from the cladistic analyses was the placement of dwelling type on the tree. Gall crabs have three basic types of dwellings; the well-known gall in which the crab lives enclosed in a chamber formed by the host coral skeleton (Hiro, 1937), shallow crypts or tunnels capped by an outgrowth of the coral skeleton (Shaw and Hopkins, 1977), or cylindrical pits (Hiro, 1937). It is a bit surprising that the seemingly most complex dwelling, the gall, occurs in the two most ancestral taxa, *Hapalocarcinus* and *Pseudohapalocarcinus*. Another fairly complex dwelling, the roofed tunnel occurs primarily in *Opecarcinus*, a relatively ancestral taxon. Crypts and pits are generally inhabited by the most derived taxa of the crab family, crypts in the detocarcini except *Utinomia*, which lives in shallow pits (Kropp, 1986), and pits in the cryptochirini except *Opecarcinus*. Thus, the trend has been to relatively simple types of dwellings. It is tempting to contrast this progression to simpler dwellings to situations such that occuring in spiders where, in general, web complexity has increased evolutionarily (Foelix, 1982). However, it is probable that the crab dwelling type is constrained by the growth form of the particular host coral colony. Hence, galls occur only in branching corals and crypts and tunnels only in foliaceous corals. Pits occur in any of the colony types, but are the only dwelling type found in massive corals.

Vermeij (1983) intimated that in regions of high predation symbiotic associations would tend to be more specific and that hosts providing greater safety would be more susceptible to colonization by symbionts. My study supports both predictions. In the Pacific, an area of high predation (Vermeij, 1978), gall crabs are host specific at the level of coral suborder (Table 3); most crabs occur on corals of one suborder. Corals belonging to relatively safe suborders (Faviina, Fungiina) are hosts to more crab taxa both at the generic and the specific levels than are the other orders (Table 4). The major radiation of gall crabs in the Pacific has been into corals providing safer habitats. Cryptochirids in the Atlantic include the two least host specific genera, *Detocarcinus* and *Troglocarcinus*, which live on corals belonging to three and four suborders respectively (Table 4).

It is useful to compare the results presented here with other known coral reef symbioses. The trend shown by pyrgomatin barnacles (Ross and Newman, 1973; Newman et al., 1976) is generally similar to that for the gall crabs; more symbionts occur on safe corals than other corals. However, the coral-dwelling copepods of the family Xarifiidae differ in that relatively safe corals are hosts to fewer copepod taxa than are corals of limited safety (Humes, 1985). It is possible that the copepods are of relatively recent origin (post Pliocene, Humes, 1985) and the major radiation into safe corals has yet to occur.

An intriguing question remains. Though the analyses here indicate that adult gall crabs probably have evolved to inhabit progressively more noxious corals, the adult stage is not the one that must seek out and colonize the host. Little is known of the morphology of gall crab larvae (Scotto and Gore, 1981; Gore et al., 1983), so no estimate can be made of whether or not larval morphology supports phylogenetic hypotheses based on adult morphology. Such a comparison is of interest because it is the larval stage that must be able to overcome coral defenses in order to make colonization possible. It is not known if larval morphology would indicate the features necessary to do so.

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Table 2. Character and state summary. Character number is given to the left, followed by the character, character states, and character consistencies on Tree 2 [in brackets]. States are listed in order of undirected transformation series.

Head

1 Antennule length: $\leq$ 1/2 eyestalk length (0); $\geq$ eyestalk length (1); [1.00].

2 Antenna fused segment 2/3: length < width (0); length > width (1); [0.50].

3 Antenna segment 2/3 distal margin: lacking spine laterally (0); with spine laterally (1); [1.00].

4 Antenna segment 4 vs. 5: 4 < 5 (0); 4 > 5 (0); [0.50].

5 Maxilla 1 endopod: mesial margin convex, with few stout setae (0); mesial margin straight, perpendicular to midline of body, with few stout setae (1); mesial margin straight, oblique to midline of body, with many stout setae (2); mesial margin straight, perpendicular to midline of body, with many stout setae (3); [1.00].

6 Epistome lateral ridge: absent (0); present (1); [0.50].

7 Epistome anterior margin: sinuous (0); straight (1); [0.50].

8 Epistome median ridge: absent (0); present (1); [0.33].

Thorax

9 Carapace shape: square (0); rectangular, posterior widest (1); rectangular, anterior widest (2); [1.00].

10 Orbit: widely U-shaped (0); deeply V-shaped (1); [1.00].

11 Pterygostomial region: fused to carapace (0); not fused to carapace (1); [0.25].

12 Sternal plastron: Length $\leq$ width (0); length > width (1); [1.00].

13 Sternal plastron surface: flat (0); concave mesially (1); [0.50].

14 Pereopod 1 sternite: not sharply constricted at midlength (0); sharply constricted at midlength (1); [0.33].

15 Pereopod 4 sternite: lacking median suture (0); having median suture (1); [0.33].

16 Female gonopore: oval (0); elliptical (1); [0.50].

17 Female gonopore anterior hood: absent (0); present (1); [0.33].

18 Maxilliped 3 palp: present (0); absent (1); [0.50].

19 Maxilliped 3 merus inner surface: having mesially projecting pappose setae (0); lacking setae (1); [0.50].

20 Maxilliped 2 endopod carpus: inner surface having setae distally (0); inner surface lacking setae (1); [0.33].

21 Maxilliped 1 endopod: subquadrate (0); roundly triangluar, widest proximal to midlength (1); angularly triangular, widest near distal margin (2); roundly triangular, widest distal to midlength (3); [0.60].

22 Cheliped (pereopod 1): sexually dimorphic (0); not sexually dimorphic (1); [0.50].

23 Female cheliped manus: stout (0); slender (1); [0.17].

24 Female cheliped dactylus: longer than dorsal margin of manus (0); shorter than dorsal margin of manus (1); [0.25].

25 Female pereopod 2 merus: not expanded distomesially (0); expanded distomesially (1); [0.33].

26 Female pereopod 2 propodus: stout (0); slender (1); [0.25].

27 Female pereopod 2 dactylus: having subterminal pore (0); lacking subterminal pore (1); [0.50].

28 Female pereopod 5 dactylus: not rotated anteriorly (0); rotated anteriorly (1); [0.50].

29 Female pereopod 3 coxa: lacking anterior projection (0); having well-developed anterior projection (1); having reduced anterior projection (2); [0.22]. 0-1-2-0

30 Female pereopod 4 coxa: lacking anterior projection (0); having well-developed anterior projection (1); having reduced anterior projection (2); [0.50].

31 Female pereopod 5 coxa: lacking anterior projection (0); having well-developed anterior projection (1); [1.00].

ABDOMEN

32 Female pleopod 3: biramous (0); uniramous (1); [0.33].

33 Male gonopod: long, slightly curved, many plumose setae at midlength (0); long, slightly curved, many simple setae (1); long, sharply curved (˜90°), many plumose setae at tip (2); short, slightly curved, sparsely setose (3); short, slightly curved, many plumose setae on tip (4); moderate length, moderately curved (˜60°), few simple setae (5); long, slightly curved, many plumose setae at tip (6); long, moderately curved (˜60°), many simple setae (7); [1.00]*.

34 Male abdomen: sides convex (0); sides concave (1); sides subparallel (2); [0.67].

GASTRIC MILL

35 Lateral tooth occlusal surface: having stout pappillae mesially (0); having cusp-like structures anteromesially (1); entirely composed of subequal pappillae (2); [1.00].

36 Median tooth pappillae: short (0); long (1); [0.50].

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[*] --Character 33, states 3-7 are autapomaorphic, included here and in Table 3 for morphological completeness; inclusion of these states in the analysis increased the overall consistency index of the tree from 0.48 to 0.50. The transformation series for all states is:

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5-3-7-0-1-6
        |
        2
        |
        4
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Table 3. Character state matrix for Cryptochiridae. See Table 2 for list of characters and state codes. Ce = *Cecidocarcinus*; Cr = *Cryptochirus*; Da = *Dacryomaia*; De = *Detocarcinus*; Fi = *Fizesereneia*; Fu = *Fungicola*; Ha = *Hapalocarcinus*; Hi = *Hiroia*; Li = *Lithoscaptus*; Ne = *Neotroglocarcinus*; Op = *Opecarcinus*; Pc = *Pseudocryptochirus*; Pe = *Pelycomaia*; Ph = *Pseudohapalocarcinus*; Sp = *Sphenomaia*; Tr = *Troglocarcinus*; Ut = *Utinomia*; Xy = *Xynomaia*; Pi = *Pinnotheres* (outgroup); ? = unknown condition.

Char. #-	Ce	Cr	Da	De	Fi	Fu	Ha	Hi	Li	Ne	Op	Pc	Pe	Ph	Sp	Tr	Ut	Xy	Pi
1-	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0
2-	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	0
3-	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
4-	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
5-	?	2	2	0	3	2	1	2	2	1	1	1	2	1	?	2	0	3	?
6-	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0
7-	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	?
8-	0	1	1	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1	0
9-	1	2	2	1	2	2	0	2	2	1	1	1	2	0	2	1	1	2	0
10-	1	1	1	1	1	1	0	1	1	1	1	?	1	0	1	1	1	1	0
11-	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0
12-	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0
13-	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0
14-	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0

#-	Ce	Cr	Da	De	Fi	Fu	Ha	Hi	Li	Ne	Op	Pc	Pe	Ph	Sp	Tr	Ut	Xy	Pi
15-	1	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0
16-	1	1	1	0	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0
17-	1	1	1	0	1	1	0	1	1	1	?	1	1	0	1	0	0	1	0
18-	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
19-	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	?
20-	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	?
21-	2	3	3	2	3	3	0	3	3	2	1	2	3	1	2	2	2	3	?
22-	0	0	0	0	?	1	0	0	0	1	0	1	1	0	?	0	0	0	?
23-	0	1	0	0	1	1	0	0	1	1	1	0	0	1	0	0	1	1	?
24-	1	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	?
25-	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0
26-	0	0	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0
27-	?	1	1	0	1	1	1	1	1	0	1	0	1	0	?	1	0	1	0
28-	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0
29-	2	0	1	2	1	1	0	0	1	2	2	2	1	2	1	2	1	0	0
30-	2	1	2	2	1	1	0	1	1	2	2	2	1	2	1	2	1	1	0
31-	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0
32-	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0
33-	2	1	1	2	1	1	5	1	1	0	7	0	?	3	?	6	4	1	?
34-	2	2	1	1	1	1	1	1	2	1	1	0	?	1	?	1	1	1	1
35-	1	3	3	1	3	2	2	3	3	1	2	1	?	2	?	2	1	3	0
36-	1	1	1	1	1	1	0	1	1	0	0	0	1	0	?	1	0	1	?

Table 4. Hosts and distribution of coral gall crabs. AST = Astrocoeniina; FUN = Fungiina; FAV = Faviina; CAR = Caryophylliina; DEN = Dendrophylliina. EA = East Atlantic; WA = West, Central Atlantic; AA = amphi-Atlantic; WP = West, Central Pacific; IWP = Indian Ocean to West Pacific; IP = Indian Ocean to East Pacific. (Compiled from Kropp and Manning, 1987 and Kropp, ms 3).

Crab Genus # of (species)	Ocean Basin	Coral Suborder	Coral Family
Cecidocarcinus (1)	EA	DEN	Dendrophylliidae
Cryptochirus (2)	WP	FAV	Faviidae, Oculinidae
Dacromaia (2)	WP	FUN	Thamnasteriidae*
		FAV	Faviidae
Detocarcinus (1)	EA	DEN	Dendrophylliidae?
		CAR	Caryophylliidae
		FAV	Rhizangiidae, Oculinidae
Fizesereneia (3)	WP	FAV	Mussidae
Fungicola (2)	WP	FUN	Fungiidae
Hapalocarcinus (1)	IP	AST	Pocilloporidae
Hiroia (1)	WP	FAV	Faviidae, Merulinidae
Lithoscaptus (6)	IWP	FAV	Faviidae, Merulinidae
Neotroglocarcinus (2)	WP	DEN	Dendrophylliidae

Opecarcinus (8)	WA/IP	FUN	Agariciidae, Siderastreidae
Pseudocryptochirus (1)	WP	DEN	Dendrophylliidae
Pelycomaia (1)	WP	FAV	Faviidae
Pseudohapalocarcinus (1)	WP	FUN	Agariciidae
Sphenomaia (1)	WP	FAV	Faviidae
Troglocarcinus (1)	AA	CAR	Caryophylliidae
		FAV	Faviidae, Oculinidae, Meandrinidae, Mussidae
		FUN	Siderastreidae
		AST	Astrocoeniidae
Utinomia (1)	WP	AST	Pocilloporidae
Xynomaia (3)	WP	FAV	Faviidae, Merulinidae, Pectiniidae

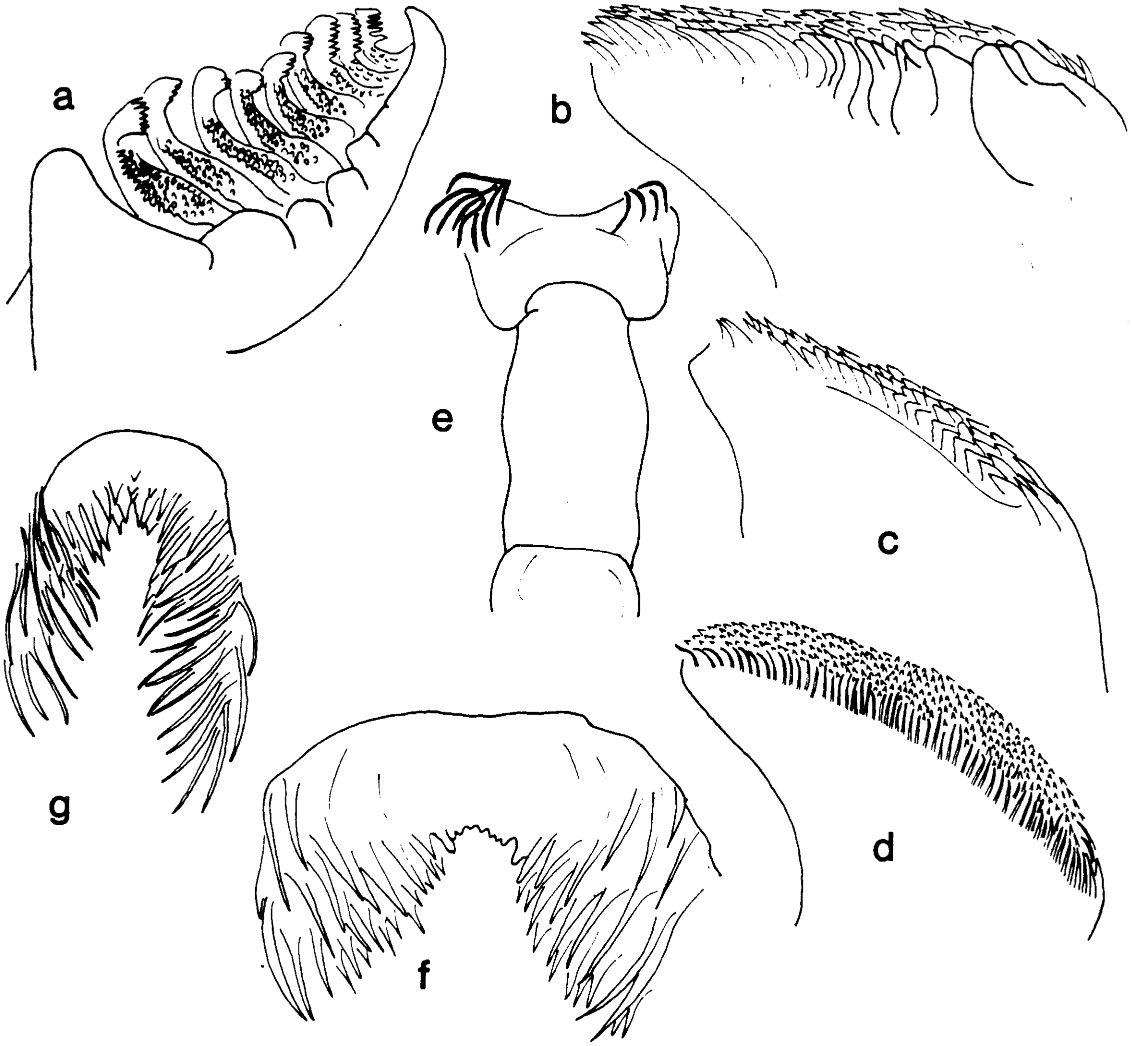
?--Record uncertain, see Kropp and Manning, 1987.

*--Traditionally, the family Thamnasteriidae has been included in the Astrocoeniina (Wells, 1956; Veron and Pichon, 1976), but has recently been placed in the Fungiina (Beauvais, 1984).

Fig. 48. Selected gastric mill teeth. a-d, lateral teeth of: a, *Pinnotheres clavipedatum* Glassell; b, *Pseudocryptochirus viridis* Hiro; c, *Opecarcinus sierra* Kropp; d, *Cryptochirus coralliodytes* Heller. e-g, median teeth of: e, *Pinnotheres clavipedatum*; f, *Utinomia dimorpha* (Henderson); g, *Cryptochirus coralliodytes*. Not to same scale.

Fig. 49. Carapace and sternal plastron features. a-c, dorsal view of carapace of: a, *Utinomia dimorpha*; b, *Hapalocarcinus marsupialis* Stimpson; c, *Cryptochirus coralliodytes*. d-f, sternal plastron of: d, *Pseudohapalocarcinus ransoni* Fize and Serène; e, *Lithoscaptus paradoxus* Milne Edwards; f, *Opecarcinus hypostegus* (Shaw and Hopkins). an = antennule, g = gonopore. Not to same scale.

Fig. 50. Pereopod features. a, b, dactylus of second pereopod of: a, *Detocarcinus balssi* (Monod); b, *Dacryomaia edmonsoni* (Fize and Serène), arrow indicates subterminal pore. c, d, Coxae of pereopods 2-5 of *Opecarcinus pholeter* Kropp, arrows indicate anterior extensions: c, pereopods 2-3; d, pereopods 4-5.


a
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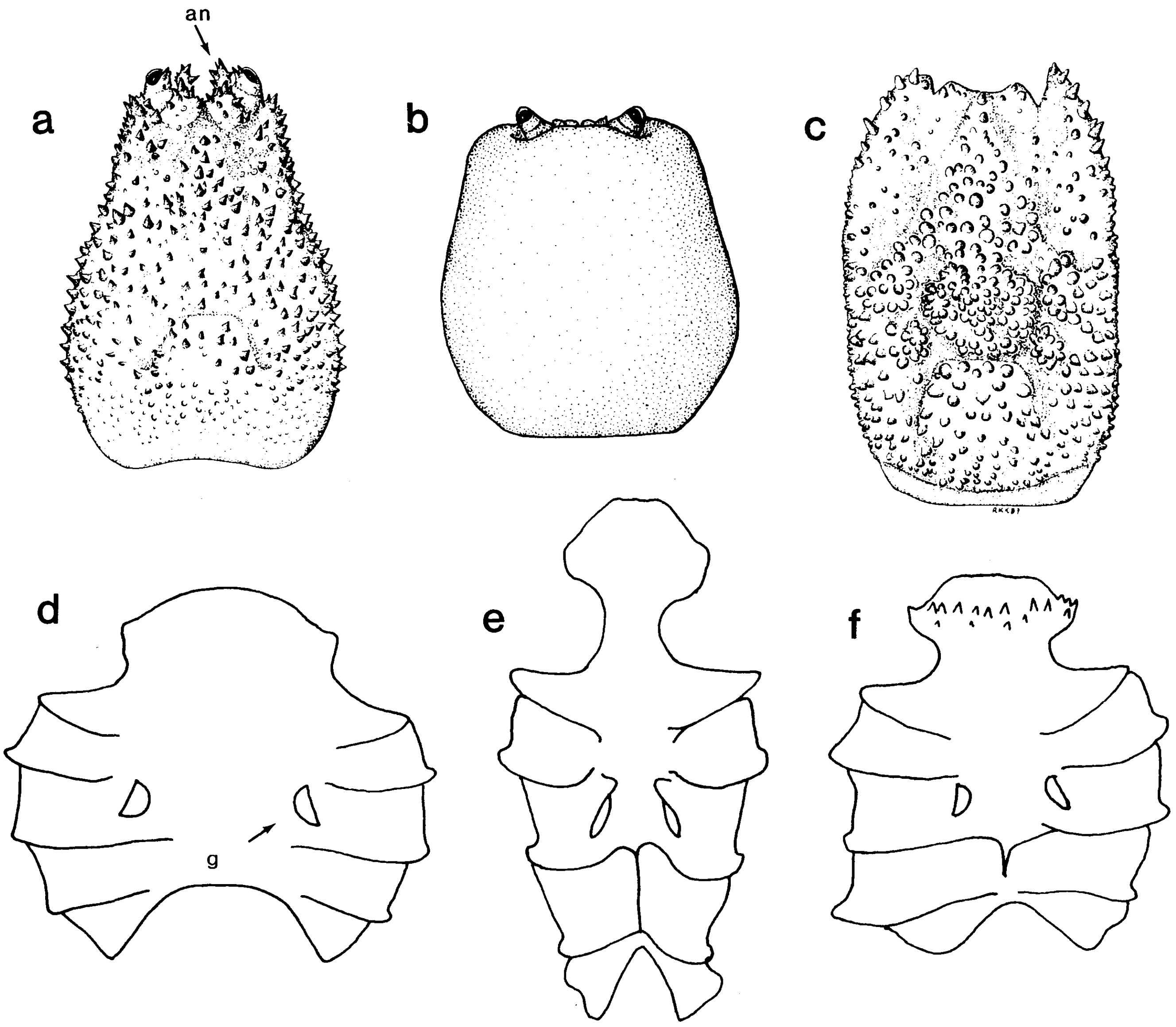
an
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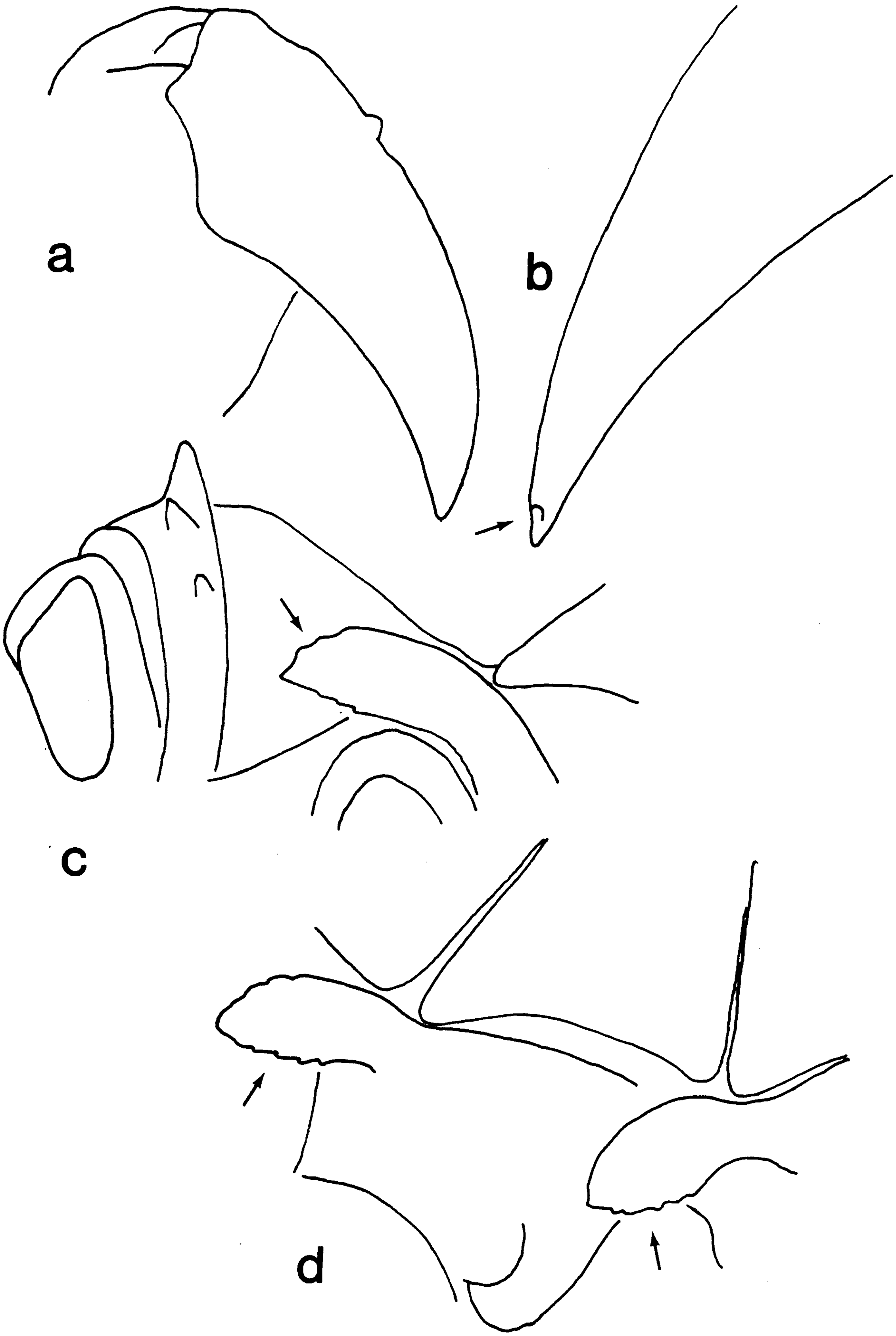
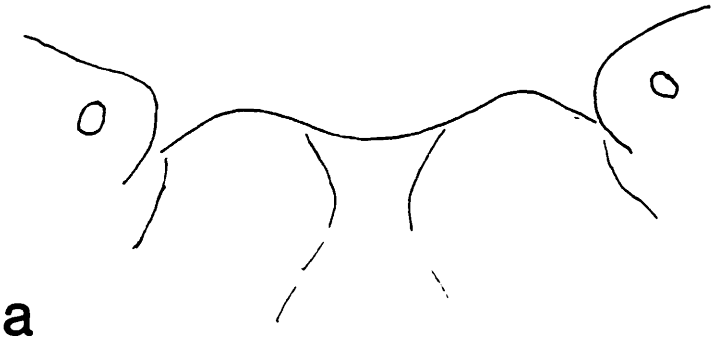

a
b
c
d

Fig. 51. Epistome features. a, *Hapalocarcinus marsupialis*; b, *Cryptochirus coralliodytes*; c, *Lithoscaptus paradoxus*. Not to same scale.

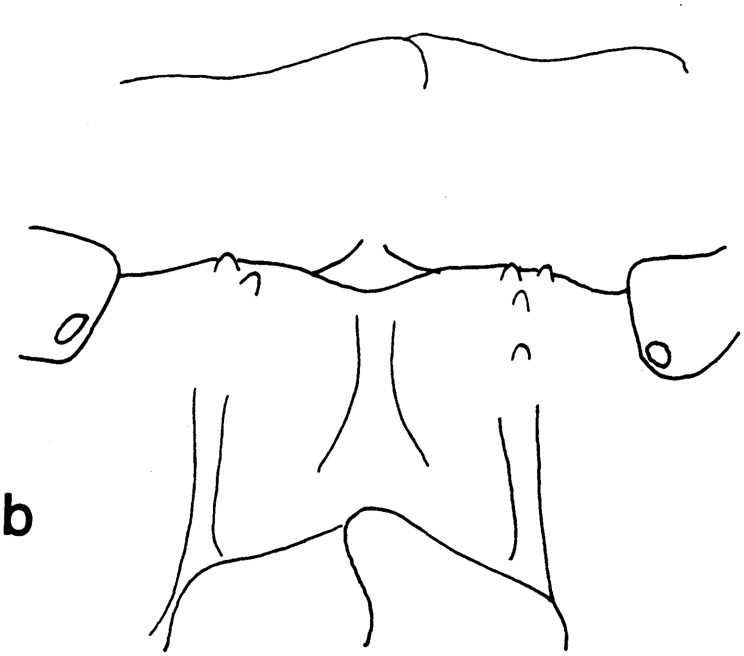
Fig. 52. Selected mouthparts. a-c, first maxilla of: a, *Opecarcinus hypostegus*; b, *Fizesereneia heimi* (Fize and Serène); c, *Cryptochirus coralliodytes*. d-f, first maxilliped of: d, *Pseudohapalocarcinus ransoni*; e, *Neotroglocarcinus hongkongensis* (Shen); f, *Lithoscaptus paradoxus*. Not to same scale.

Fig. 53. Tree 1. One of the most parsimonious trees derived from the data set; character state changes included.

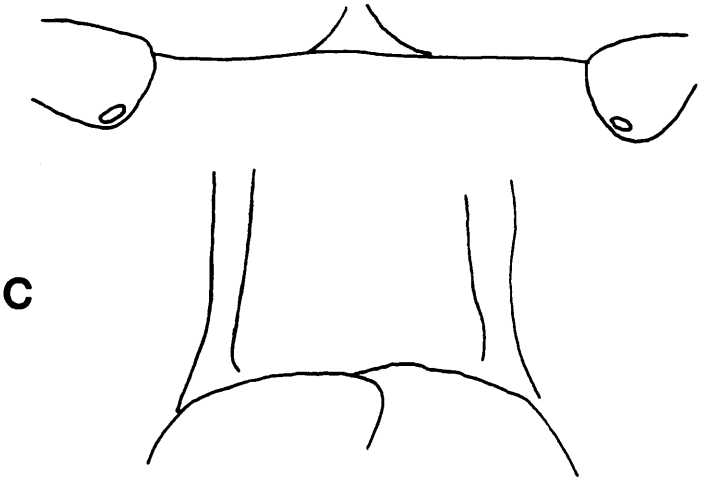
Fig. 54. Trees 2-5. Remaining trees derived from the data set showing those relationships varying among the trees. Arrow indicates position of the clade including *Troglocarcinus* and all more derived taxa. Stem arises from ancestor shared with *Pseudohapalocarcinus*. CECI = *Cecidocarcinus*; DETO = *Detocarcinus*; UTIN = *Utinomia*; PCRY = *Pseudocryptochirus*; NEOT = *Neotroglocarcinus*; OPEC = *Opecarcinus*.



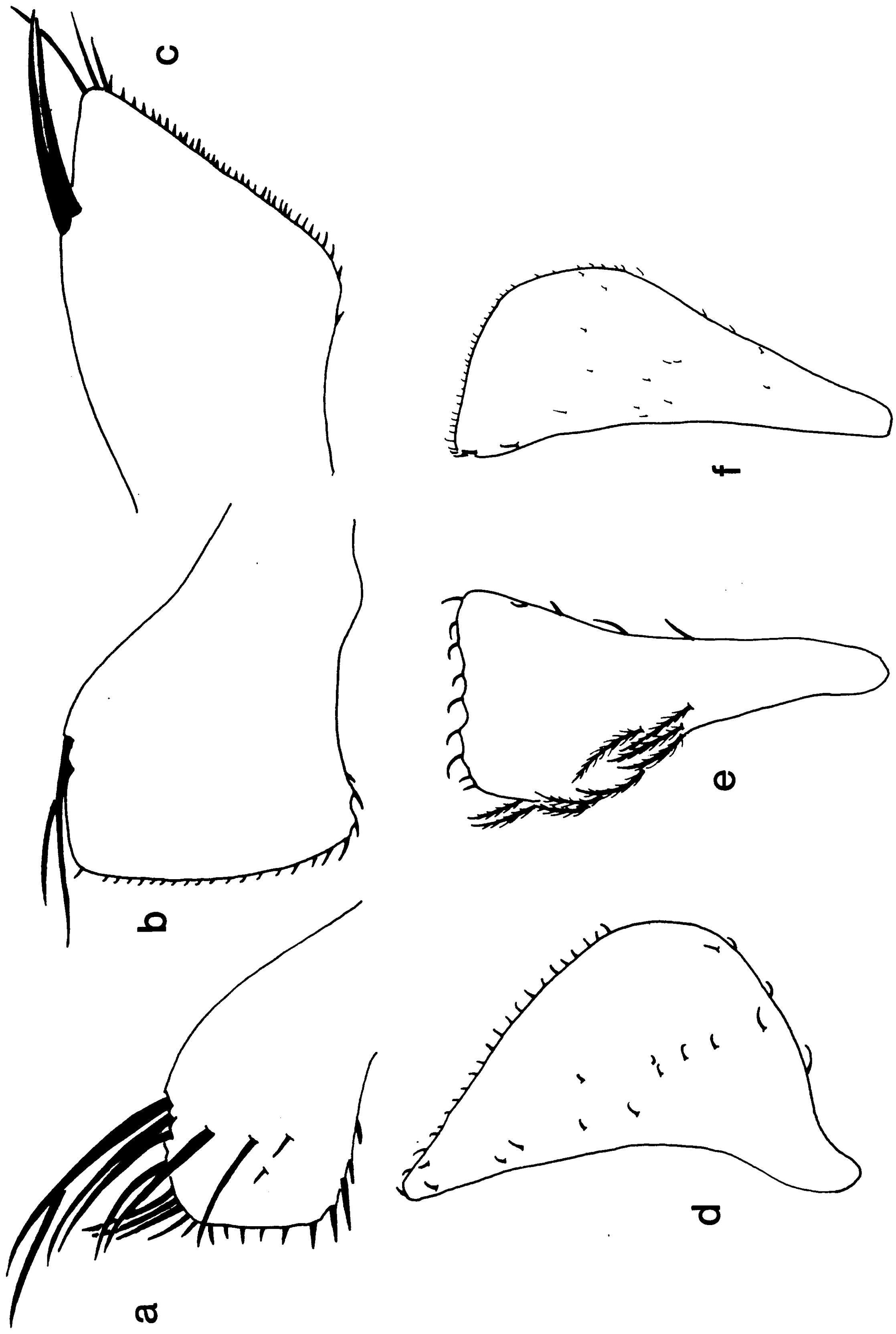
a



b



c


a
b
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d
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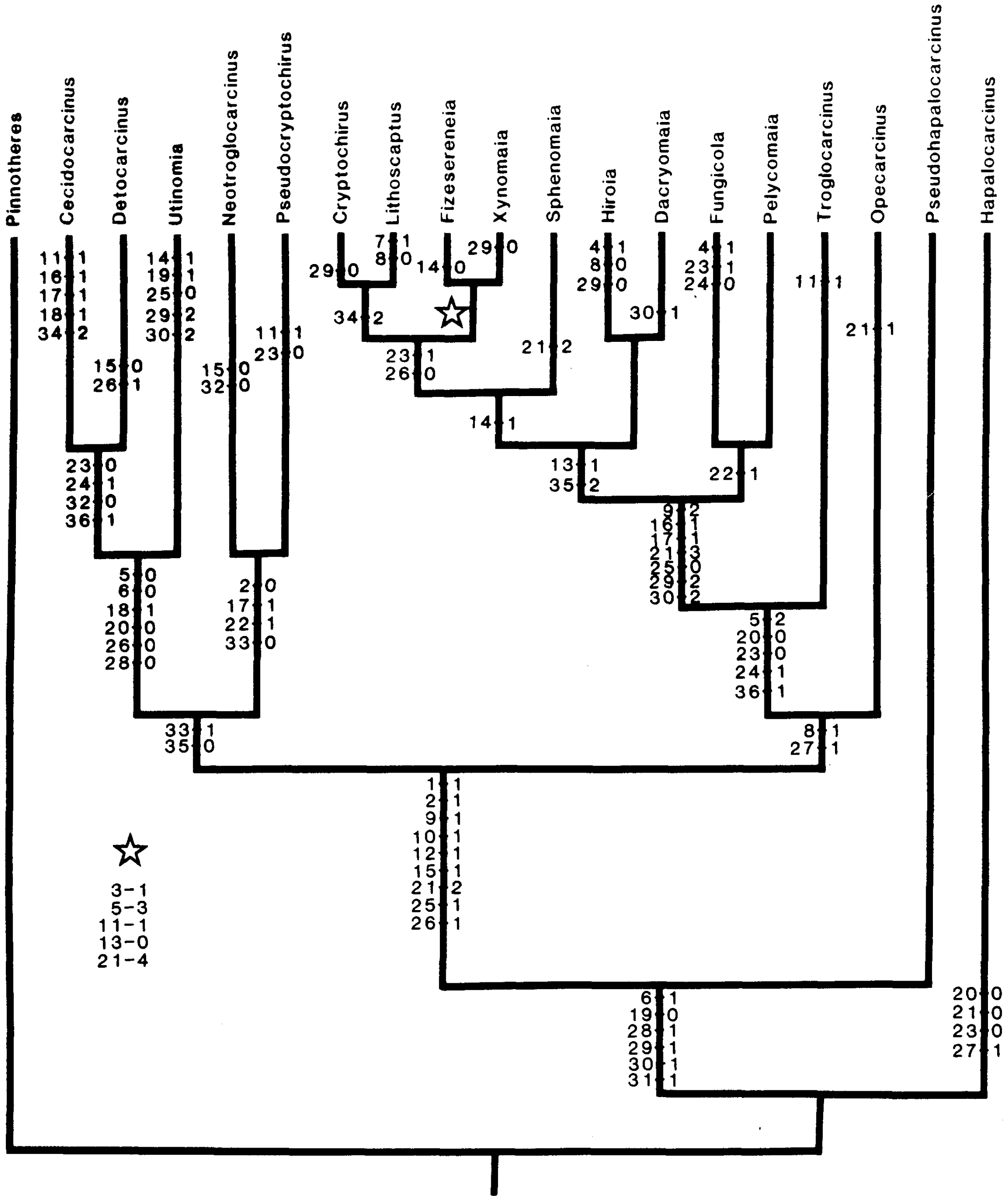
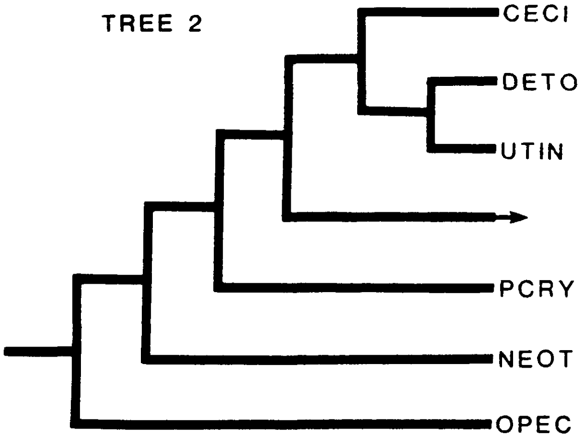
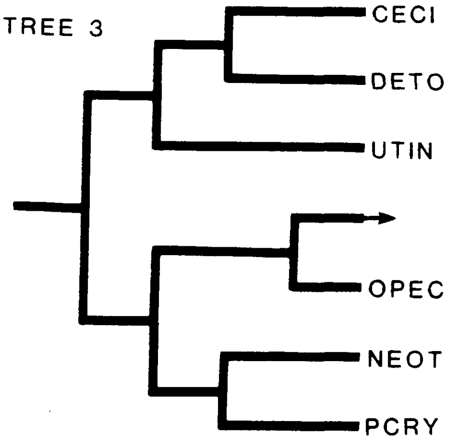
f


Pinnotheres
Cecidocarcinus
Detocarcinus
Utinomia
Neotroglocarcinus
Pseudocryptochirus
Cryptochirus
Lithoscaptus
Fizesereneia
Xynomaia
Sphenomaia
Hiroia
Dacryomaia
Fungicola
Pelycomaia
Troglocarcinus
Opecarcinus
Pseudohapalocarcinus
Hapalocarcinus
3-1
5-3
11-1
13-0
21-4

TREE 2



TREE 3



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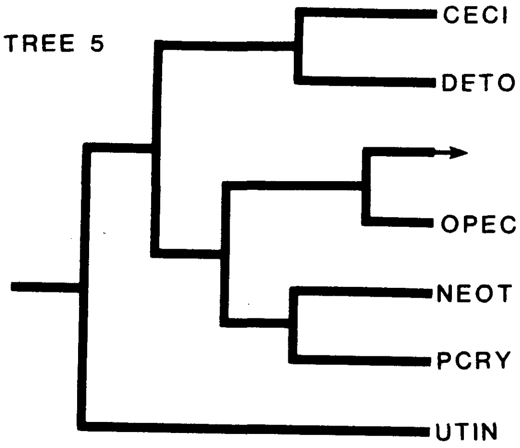


TREE 4

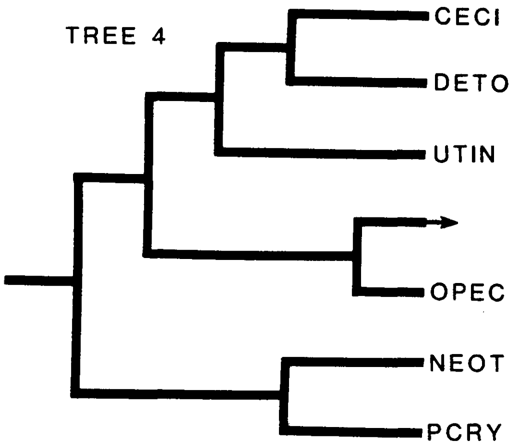
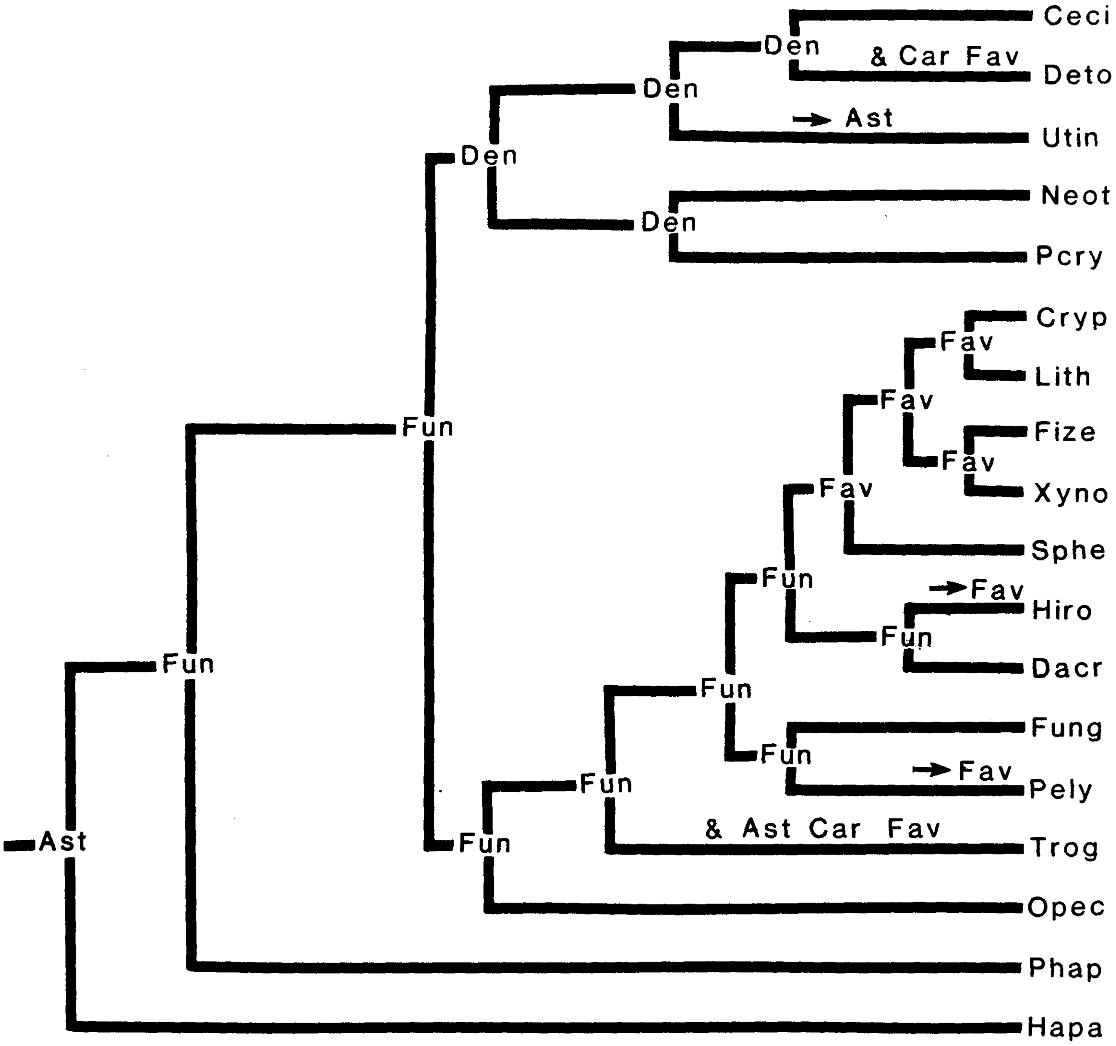


Fig. 55. Distribution of host coral suborders on Tree 1. Possible hosts of gall crab ancestors optimized on Tree 1 using Farris optimization. Arrow indicates a switch from host of ancestor to host shown on line; & indicates crab taxon occurs on host of ancestor as well as those indicated on line; all other crab taxa occur on same host as nearest ancestor. Ast = Astrocoeniina; Car = Caryophylliina; Den = Dendrophylliina; Fav = Faviina; Fun = Fungiina. Crab taxa are indicated by first four letters of generic names as in Fig. 53.

Fig. 56. Coral suborder relationships. A, as derived form Wells (1956); B, as predicted by the relationships of gall crabs.


Ceci
Den
& Car Fav
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→ Ast
Utin
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Neot
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Pcry
Cryp
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Lith
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Fize
Fav
Xyno
Fav
Sphe
Fun
→ Fav
Hiro
Fun
Fun
Dacr
Fun
Fung
Fun
→ Fav
Pely
Fun
Ast
& Ast Car Fav
Trog
Fun
Opec
Phap
Hapa

CURRICULUM VITAE

Name: Roy Karl Kropp.

Permanent address: P. O. Box 82/Rosecroft Rd., St. Mary's
City, Maryland 20686.

Degree and date to be conferred: Ph.D., 1988.

Date of birth: 8 September 1946.

Place of Birth: Detroit, Michigan.

Secondary education: Oceanside High School
Oceanside, California, 1964.

Collegiate institutions attended	Dates	Degree	Date of Degree
San Diego State University	9/67-5/78	B.S.	1978
University of Guam	8/78-7/81	M.S.	1981
University of Maryland	8/81-2/88	Ph.D.	1988

Major: Zoology

Professional publications:

1979 Marine environmental survey of Okat, Kosrae. University of Guam Marine Lab Technical Report 63:1-101. (with L.G. Eldredge, B.R. Best, M.I. Chernin, R.F. Myers, and T.L. Smalley)

1981 Ammonia excretion by the freshwater prawn, *Macrobrachium lar* (Crustacea, Palaemonidae), in relation to diet. University of Guam Marine Lab Technical Report 67:1-12. (with S.G. Nelson)

1981 Preliminary list of anomuran crustaceans from Guam. In: A working list of marine organisms from Guam. Pp. 39-41. University of Guam Marine Lab Technical Report 70. (with D.S. Wooster, L.G. Eldredge)

1981 Preliminary checklist of shelled gastropods from Guam. In: A working list of marine organisms from Guam. Pp. 42-45. University of Guam Marine Lab Technical Report 70. (with L.G. Eldredge, B.D. Smith)

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1982 Crustacean-induced skeletal modification in *Acropora*. Proceedings of the Fourth International Coral Reef Symposium, Manila 2:115-119. (with L.G. Eldredge)

1982 Comparison of crustacean associates of *Pocillopora* from high islands and atolls. Proceedings of the Fourth International Coral Reef Symposium, Manila 2:627-632. (with C. Birkeland)

1982 Responses of five holothurian species to attacks by a predatory gastropod, *Tonna perdix*. Pacific Science 36:445-452.

1983 Three new species of Porcellanidae (Crustacea, Anomura) from the Mariana Islands and a discussion of Borradaile's *Petrolisthes lamarckii* complex. Micronesica 19:91-106.

1984 *Tanaocheles stenochilus*, a new genus and species of crab from Guam, Mariana Islands (Brachyura, Xanthidae). Proceedings of the Biological Society of Washington 97:744-747.

1985 Ammonia excretion and nitrogen assimilation by the tropical freshwater prawn *Macrobrachium lar* (Crustacea, Palaemonidae). Comparative Biochemistry and Physiology 81A:699-704. (with S.G. Nelson)

1985 Cryptochiridae, the correct name for the family containing the gall crabs (Crustacea, Decapoda, Brachyura). Proceedings of the Biological Society of Washington 98:954-955. (with R.B. Manning)

1985 Volcanic ashfall effects on intertidal and shallow-water coral reef zones at Pagan, Mariana Islands. Proceedings of the Fifth Coral Reef Congress, Tahiti 4:189-194. (with L.G. Eldredge)

1986 Feeding biology and mouthpart morphology of three species of coral gall crabs (Decapoda: Cryptochiridae). Journal of Crustacean Biology, 6(3):377-384.

1986 A neotype designation for *Petrolisthes tomentosus* (Dana), and the description of a new species of *Petrolisthes* from the Mariana Islands (Anomura, Porcellanidae). Proceedings of the Biological Society of Washington, 99(3):452-463.

1987 The Atlantic gall crabs, family Cryptochiridae. Smithsonian Contributions to Zoology, 462:1-21. (with R.B. Manning)

1987 Descriptions of some endolithic habitats for snapping shrimp (Alpheidae) in Micronesia. Bulletin of Marine Science, 41(2):204-213.

1988 The status of *Cryptochirus hongkongensis* Shen, 1936 (Brachyura: Cryptochiridae). Proceedings of the Biological Society of Washington, in press.

1988 The status of *Cryptochirus coralliodytes* Heller and *Lithoscaptus paradoxus* Milne Edwards (Brachyura: Cryptochiridae). Proceedings of the Biological Society of Washington, in press.

1988 *Petrolisthes eldredgei*, a new porcellanid crab from the Indo-West Pacific, with redescription of two related species. Micronesica, 20 (1-2):in press. (with J. Haig)

ms A revision of the Pacific species of the gall crab genus *Opecarcinus* (Crustacea: Cryptochiridae). Bulletin of Marine Science, in press.

ms *Fizesereneia* Takeda and Tamura, 1980 (Crustacea, Decapoda): Proposed designation of a type species. Bulletin of Zoological Nomenclature, Case 2636, in press.

Professional positions held:

1978-1981 Graduate Research Assistant, Marine Laboratory, University of Guam.

1981-1985, 1987	Graduate Teaching Assistant, Department of Zoology, University of Maryland, animal diversity.
1981-1986	Graduate Research Assistant, Department of Zoology, University of Maryland.
1983	NOAA Hydrolab Aquanaut, Salt River Canyon, St. Croix.
1984	Instructor, High School Marine Science, Koror, Republic of Palau.