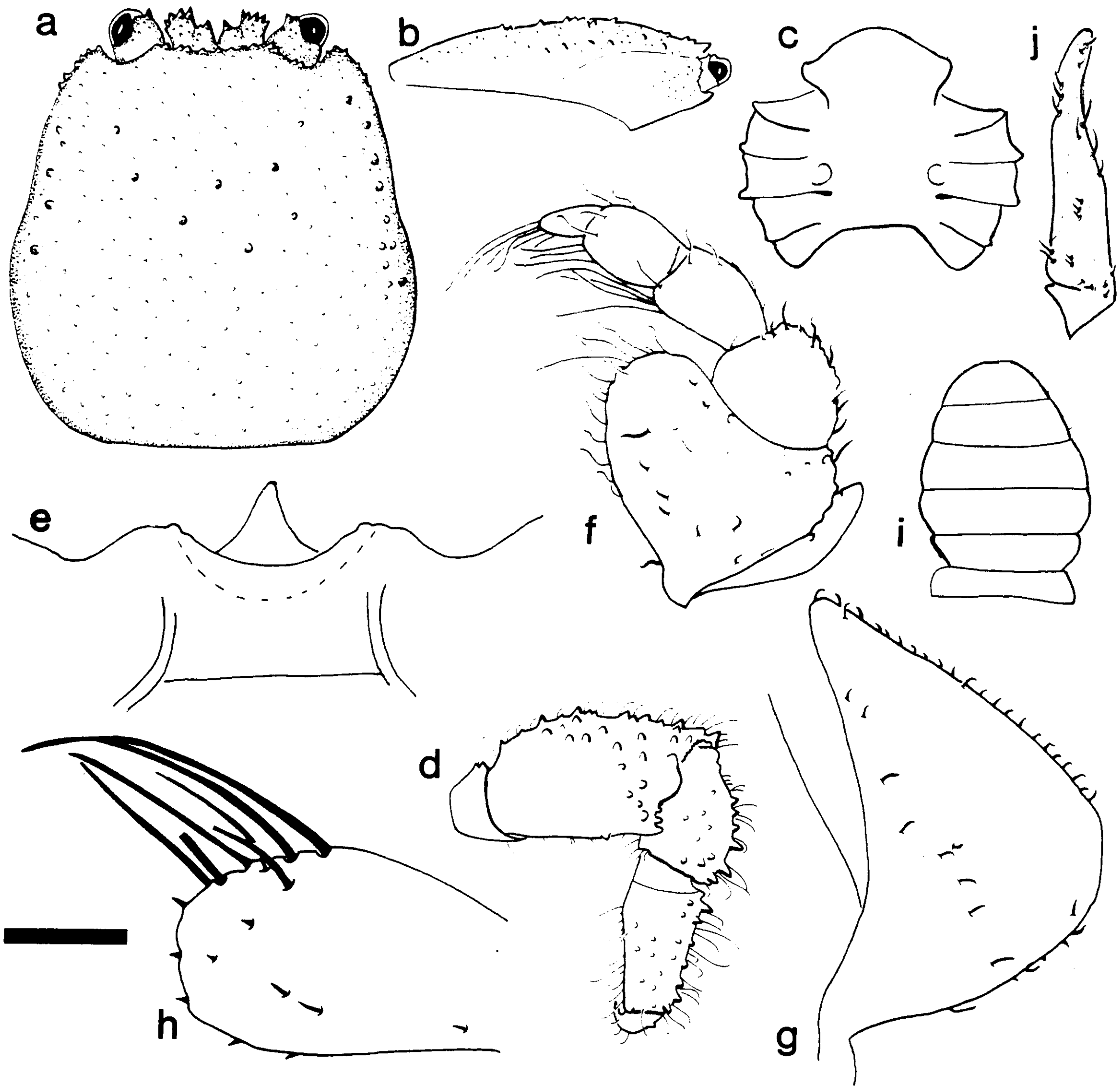
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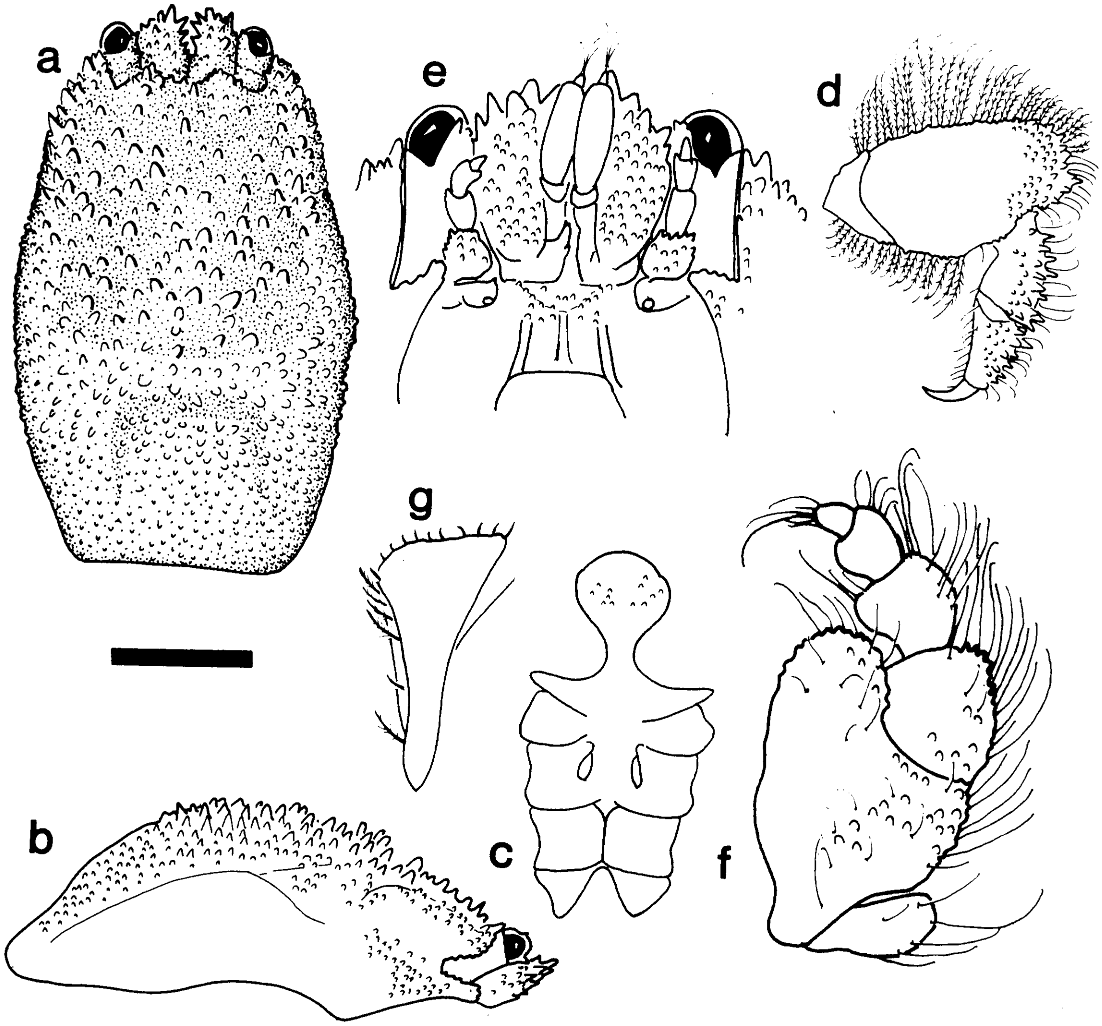
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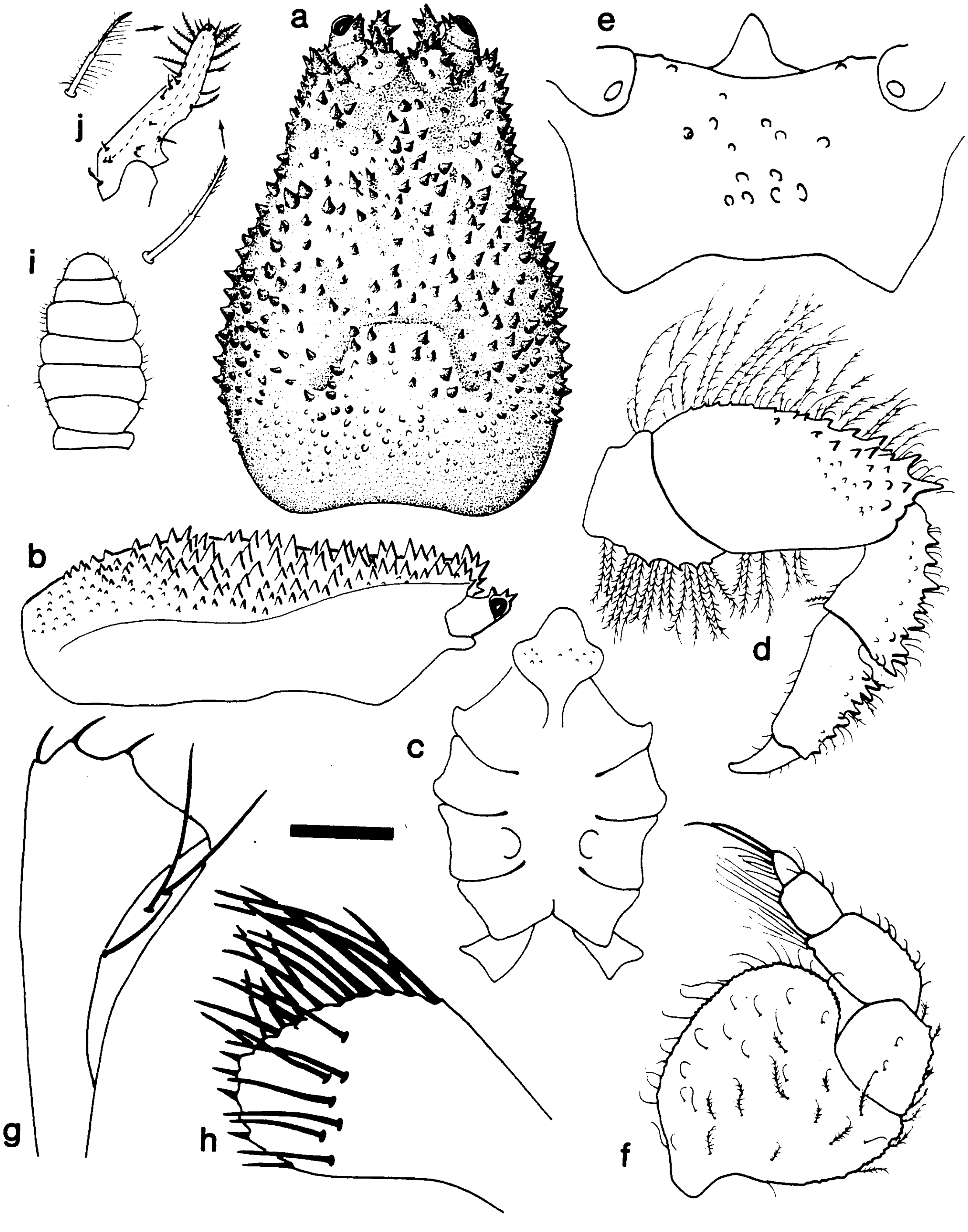
Fig. 46. *Utinomia dimorpha* (Henderson). Female (Belau): a, dorsal view of carapace; b, lateral view; c, thoracic sternites; d, Pereopod 2; e, epistome; f, MXP-3; g, endopod of MXP-1; h, MXL-1; male (Guam): i, abdomen; j, gonopod. Scale: a-c, i = 1 mm; d = 0.5 mm; f = 0.3 mm; e = 0.2 mm; g, h = 0.1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

---

* --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:

```
5-3-7-0-1-6
        |
        2
        |
        4
```

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

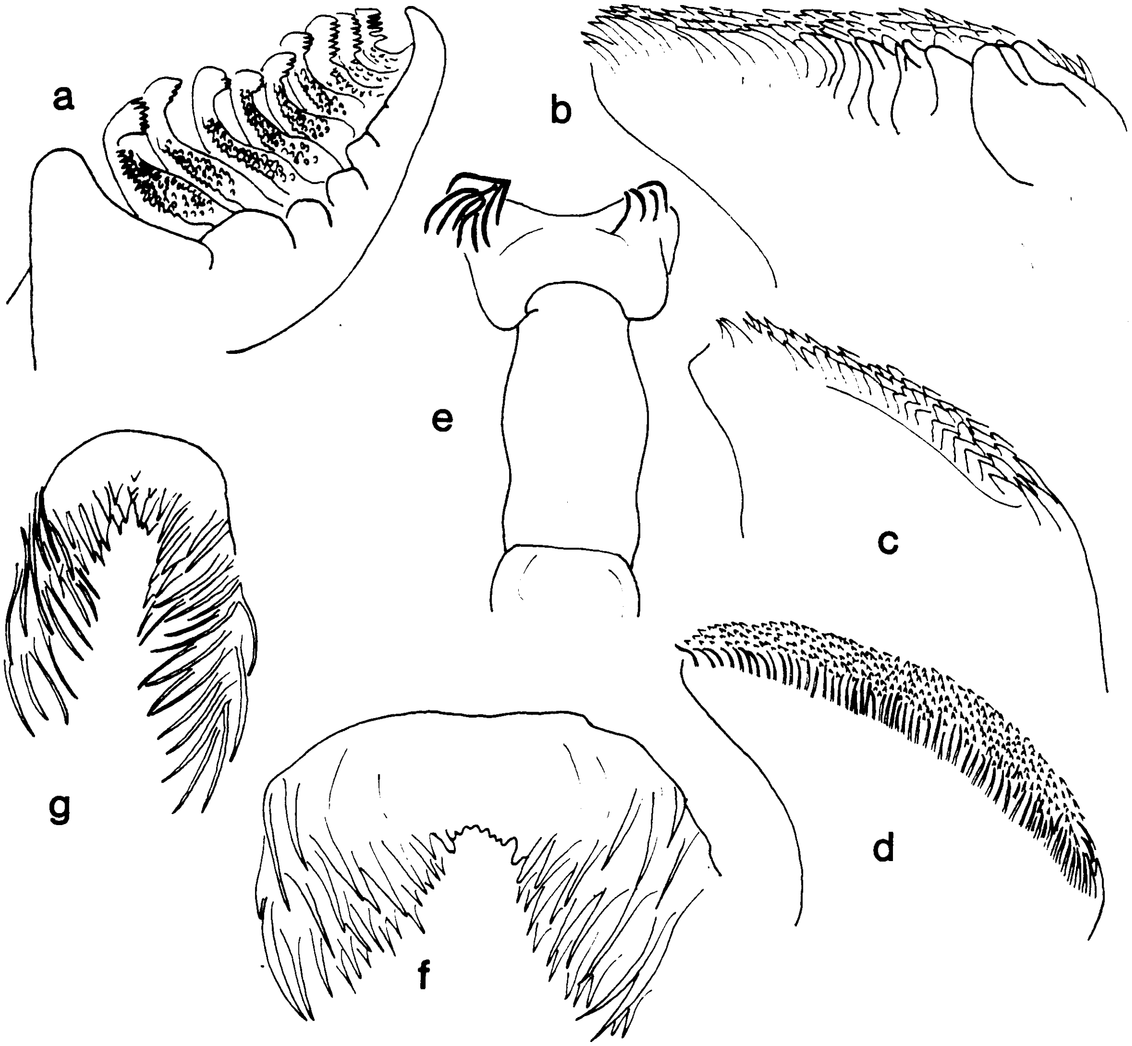
?--Record uncertain, see Kropp and Manning, 1987.

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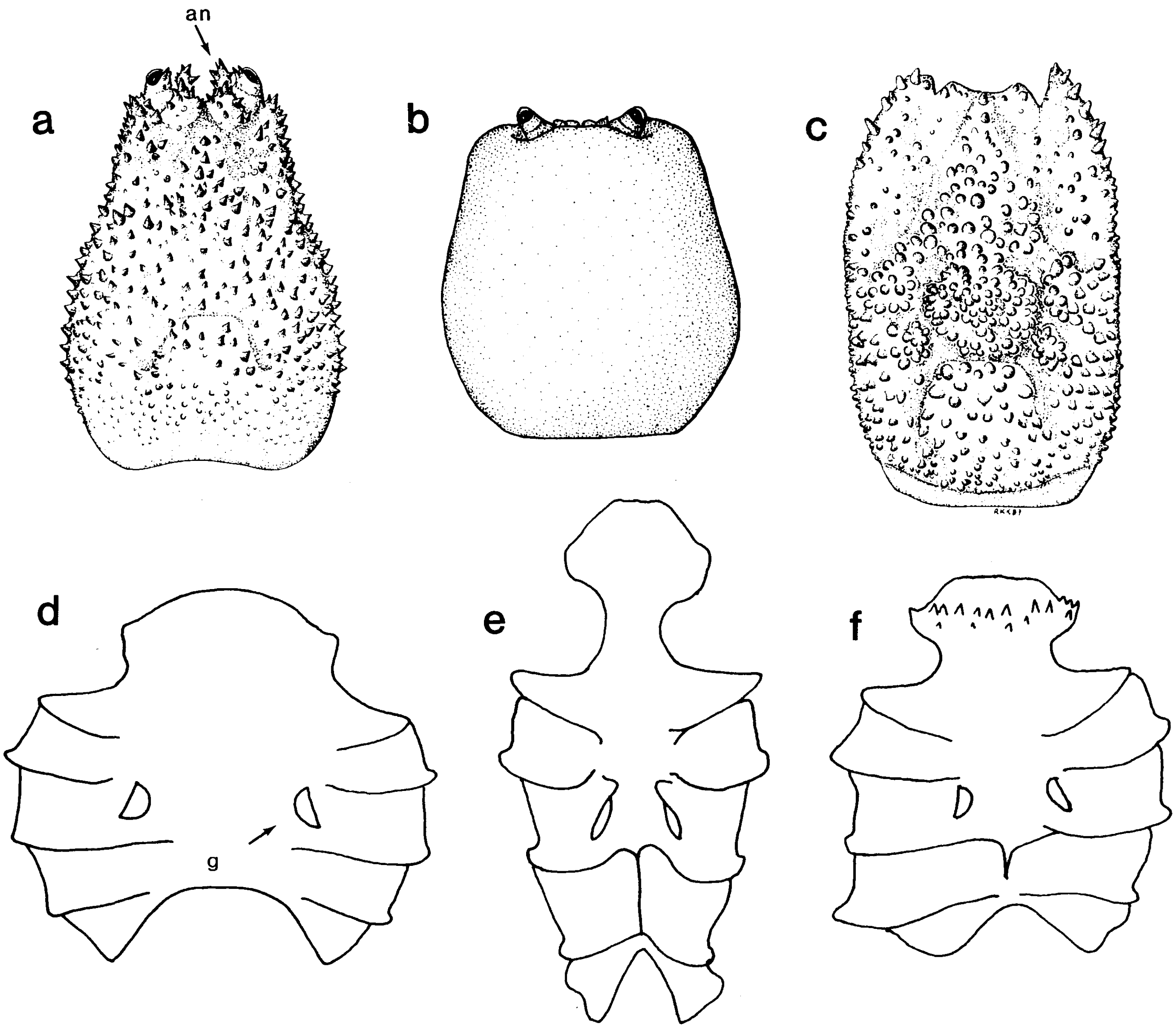
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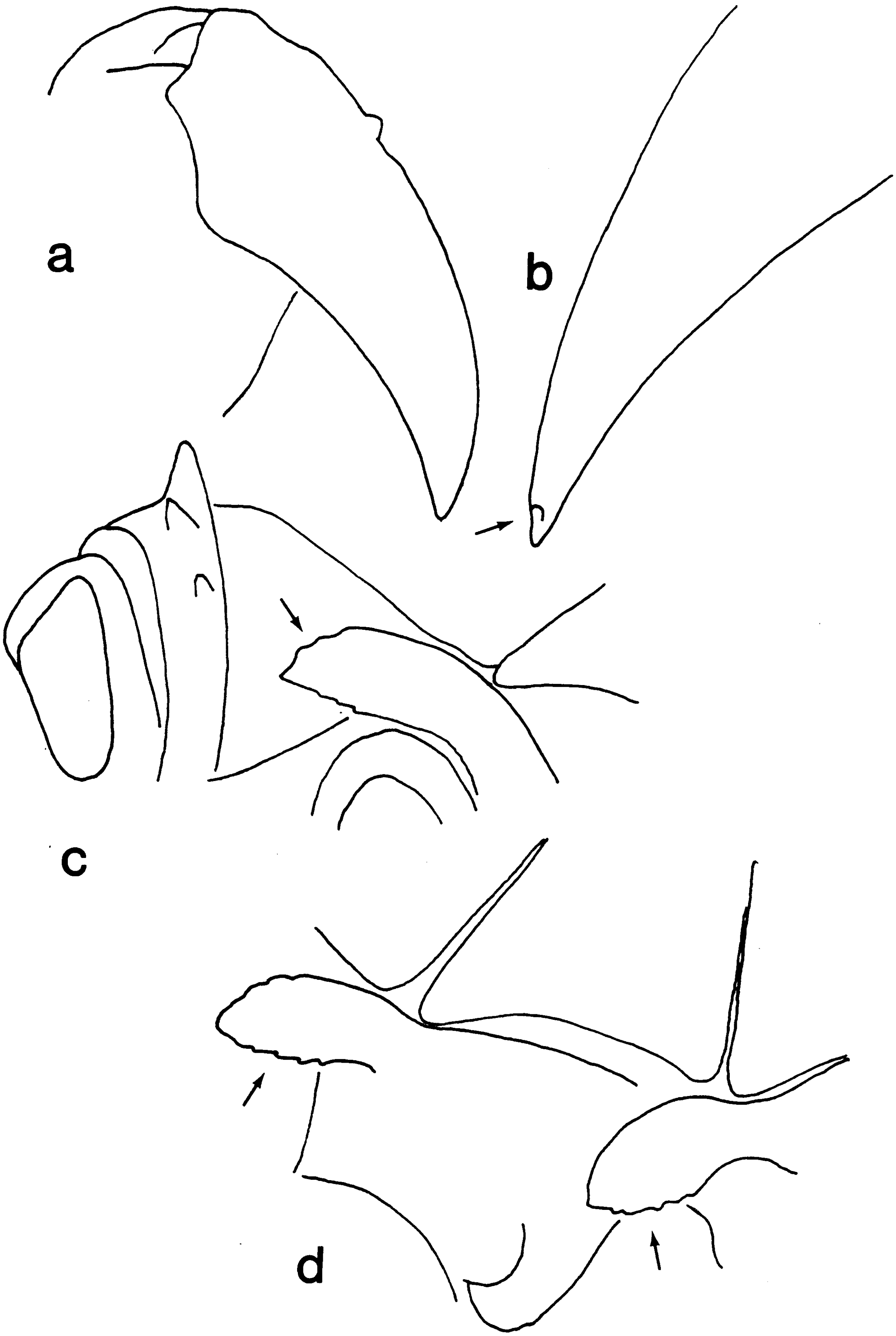
a
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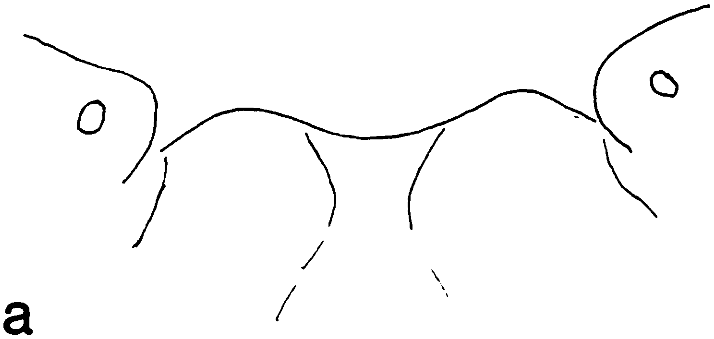
Fig. 51. Epistome features. a, *Hapalocarcinus marsupialis*; b, *Cryptochirus coralliodytes*; c, *Lithoscaptus paradoxus*. Not to same scale.

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*.



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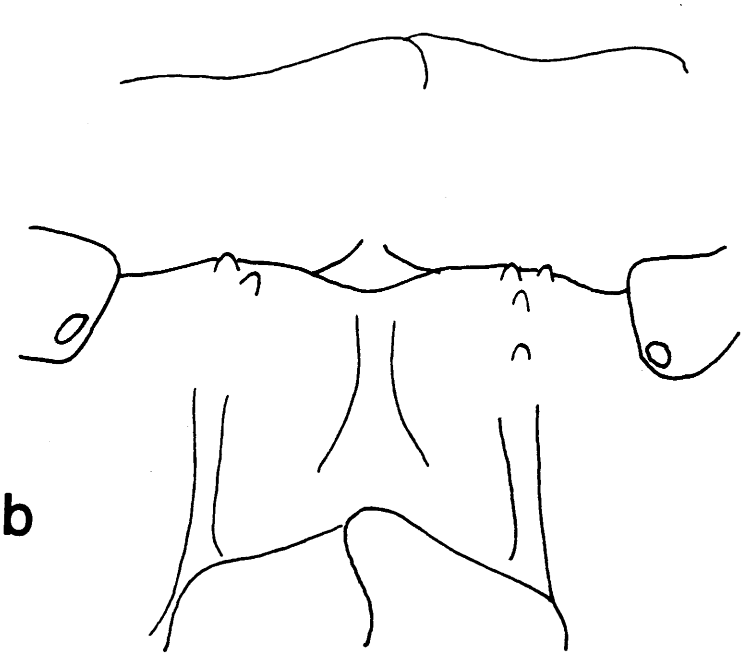

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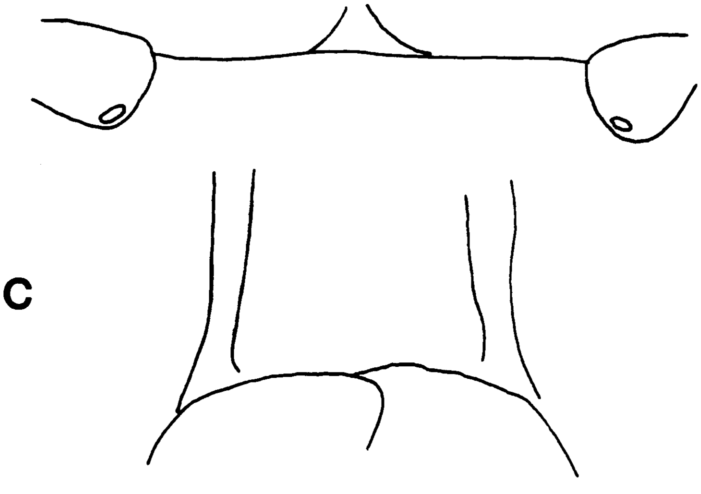

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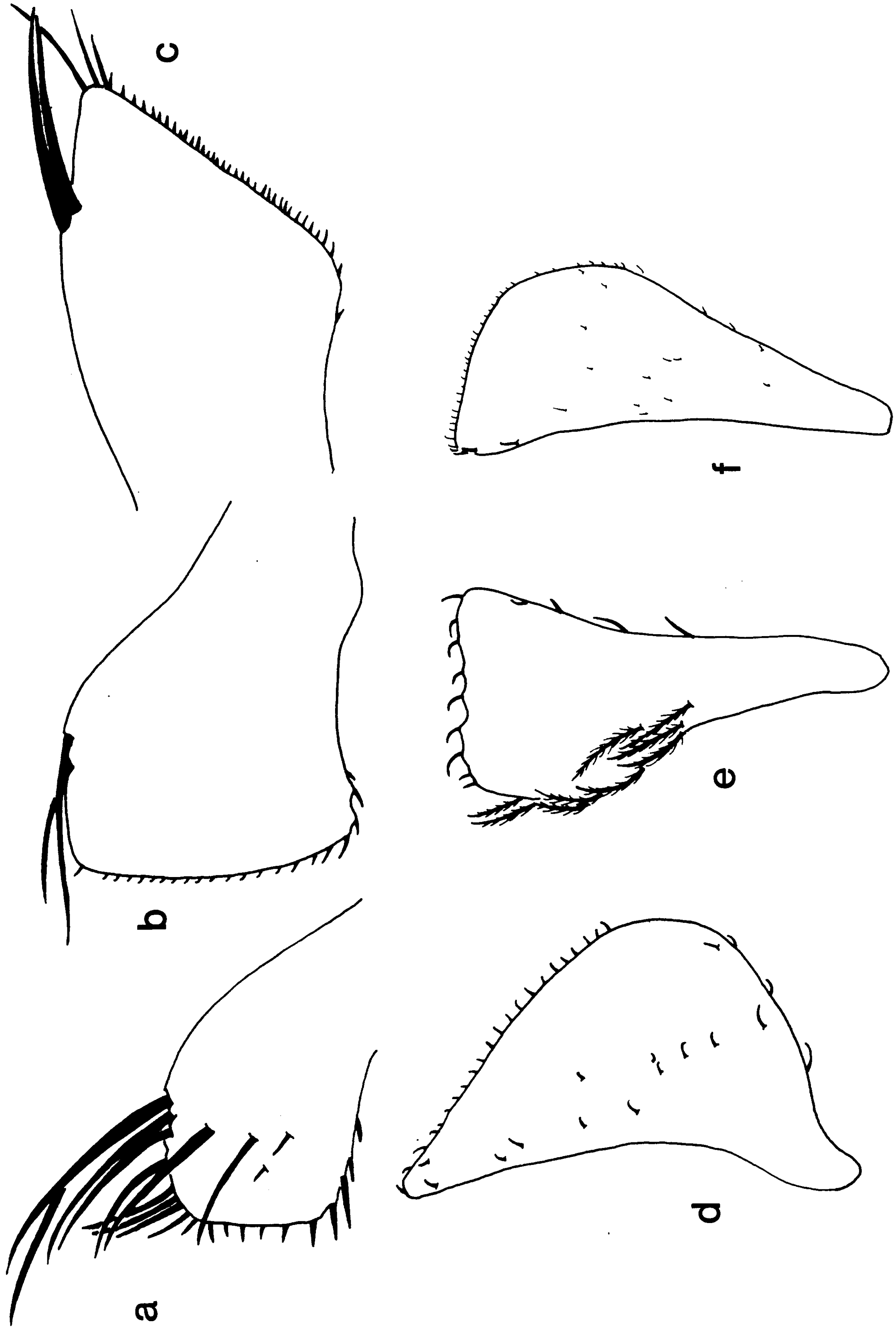
a
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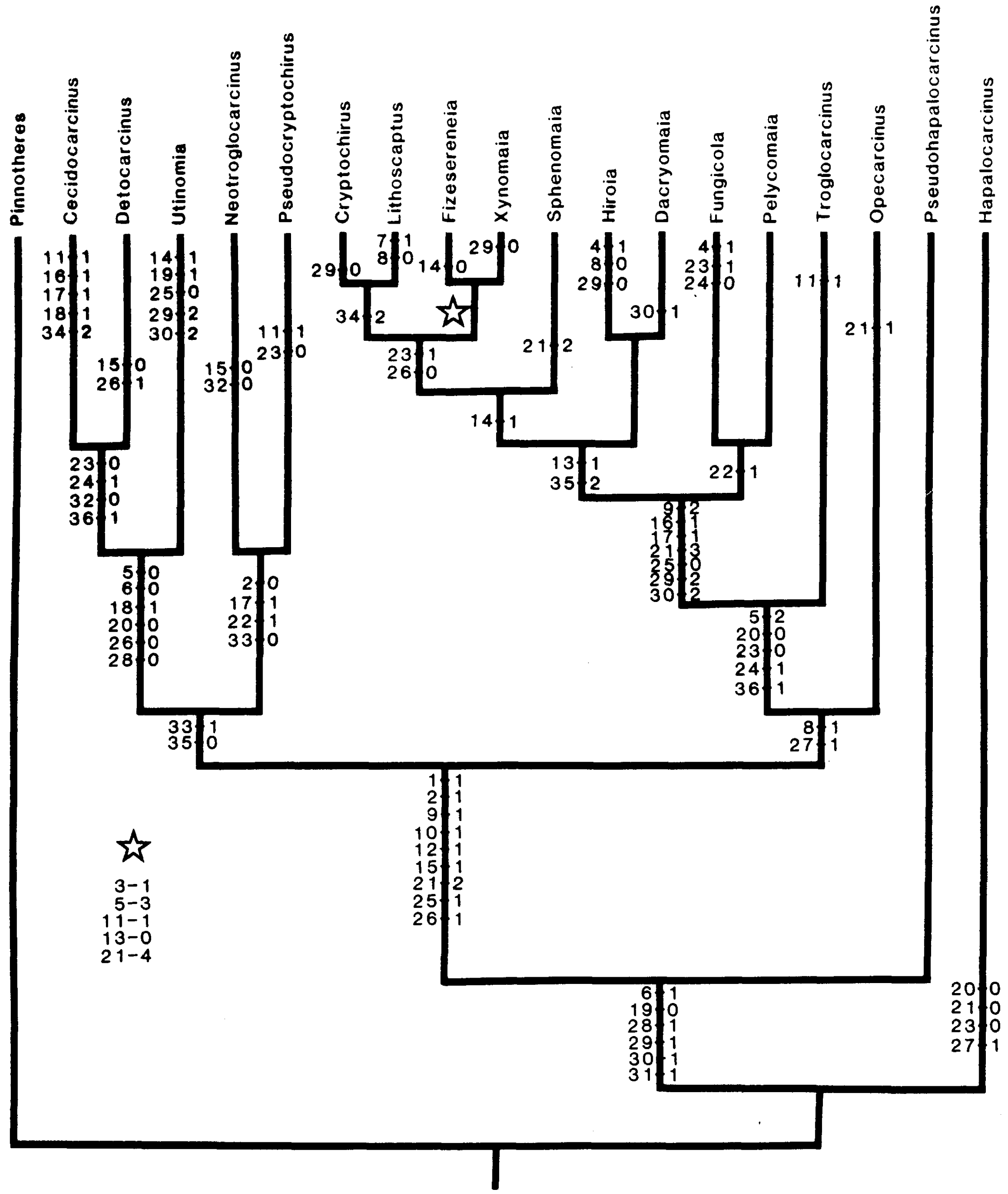
Pinnotheres
Cecidocarcinus
Detocarcinus
Utinomia
Neotroglocarcinus
Pseudocryptochirus
Cryptochirus
Lithoscaptus
Fizesereneia
Xynomaia
Sphenomaia
Hiroia
Dacryomaia
Fungicola
Pelycomaia
Troglocarcinus
Opecarcinus
Pseudohapalocarcinus
Hapalocarcinus
11 1
16 1
17 1
18 1
34 2
15 0
26 1
23 0
24 1
32 0
36 1
14 1
19 1
25 0
29 2
30 2
5 0
6 0
18 1
20 0
26 0
28 0
15 0
32 0
11 1
23 0
2 0
17 1
22 1
33 0
33 1
35 0
29 0
7 1
8 0
34 2
14 0
29 0
23 1
26 0
21 2
14 1
4 1
8 0
29 0
30 1
13 1
35 2
4 1
23 1
24 0
22 1
9 2
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21 3
25 0
29 2
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11 1
5 2
20 0
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6 1
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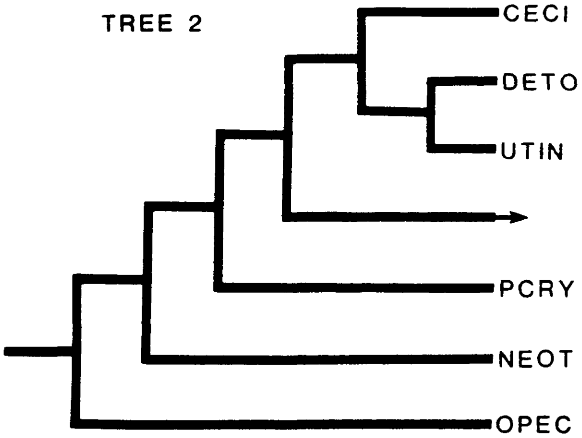
21-4

TREE 2



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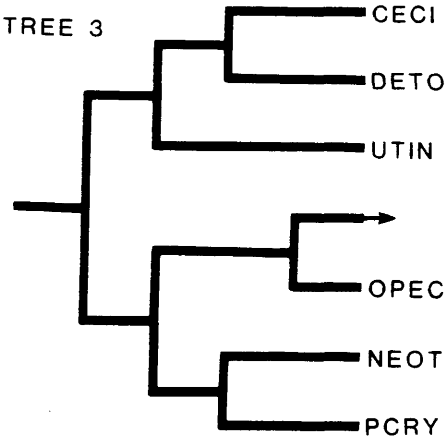

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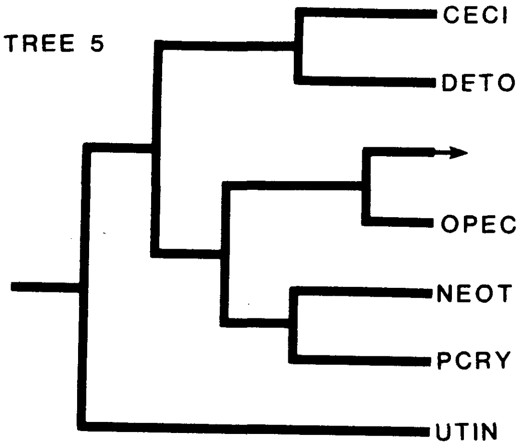

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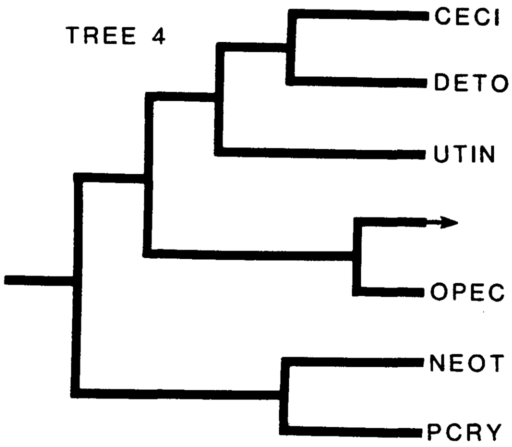
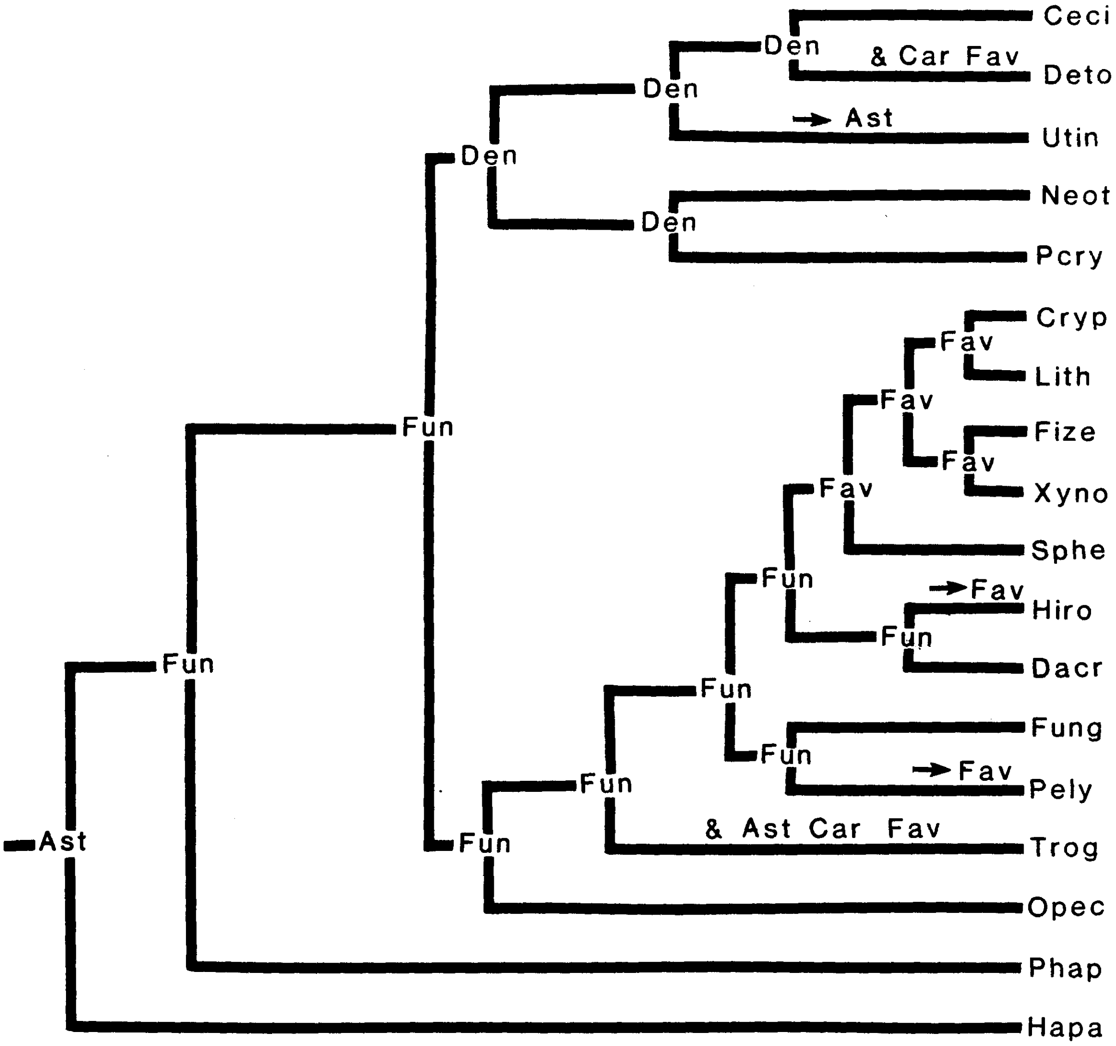


Fig. 55. Distribution of host coral suborders on Tree 1. Possible hosts of gall crab ancestors optimized on Tree 1 using Farris optimization. Arrow indicates a switch from host of ancestor to host shown on line; & indicates crab taxon occurs on host of ancestor as well as those indicated on line; all 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
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& Car Fav
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Fun
→ Fav
Hiro
Fun
Dacr
Fun
Fun
Fung
Fun
→ Fav
Pely
Fun
Ast
& Ast Car Fav
Trog
Fun
Opec
Phap
Hapa

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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)

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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.
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1984	Instructor, High School Marine Science, Koror, Republic of Palau.