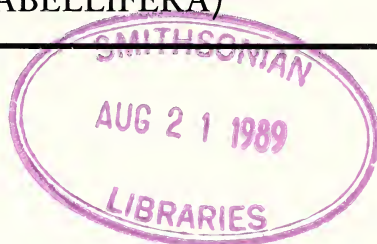


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# PHYLOGENY AND BIOGEOGRAPHY OF THE MARINE ISOPOD FAMILY CORALLANIDAE (CRUSTACEA, ISOPODA, FLABELLIFERA)

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**ABSTRACT.** Isopod crustaceans of the marine family Corallanidae (Flabellifera) were examined using light and electron microscopy. Type-species, type-specimens, and non-type material for each of the six corallanid genera were used to prepare new (revised) generic diagnoses and additional descriptions. The genus *Austroargathona* was synonymized with *Tachaea*.

A matrix of external morphological characters was developed for the corallanid genera and the outgroups Tridentellidae and Cirolanidae. This character matrix was analyzed with the cladistic computer program PAUP (Swofford, 1985) and the program package PHYLIP (Felsenstein, 1984); PHYLIP programs used included WAGNER, PENNY, DOLLOP, MIX (Camin-Sokal option), and CLIQUE. Fifty trees derived from these programs were compared for topology and tree length. Homoplasy statistics, if provided by the program, were also compared. A single PAUP tree produced using "unordered" characters was determined to be the most parsimonious tree; it was the shortest tree, with the lowest homoplasy, and with the topology most corroborated by trees from other programs. This tree was considered the best estimate of cladistic relationships (genealogy) among the corallanid genera.

Limited congruence between a proposed cladogram of tropical ocean areas and a taxon-area cladogram derived from cladistic analysis supports the hypothesis that divergence of the Corallanidae from the Tridentellidae was related to the opening of the Atlantic and Indian Oceans. The Corallanidae are hypothesized to have evolved from ancestors present in a circumtropical warm-water Tethyan-track fauna, with modern genera existing prior to the Pliocene.

**RESUMEN.** Los crustáceos isópodos marinos de la familia Corallanidae (Flabellifera) fueron examinados usando microscopía de luz y electrónica. Se examinaron especies tipo, especímenes tipo, y material no tipo de cada uno de los seis géneros coralánidos para preparar nuevas diagnosis genéricas (revisadas) y descripciones adicionales. El género *Austroargathona* fue sinonimizado con *Tachaea*.

Se desarrolló una matriz de caracteres morfológicos externos para los géneros coralánidos y los grupos externos Tridentellidae y Cirolanidae. Esta matriz de caracteres fue analizada con el programa de computación cladístico PAUP (Análisis Filogenético usando Parsimonia) (Swofford, 1985) y la colección de programas PHYLIP (Felsenstein, 1984); los programas PHYLIP usados incluyen WAGNER, PENNY, DOLLOP, MIX (opción Camin-Sokal), y CLIQUE. Se compararon topología y longitud de cincuenta cladogramas derivados de estos programas. Se determinó que un solo cladograma PAUP producido usando caracteres "desordenados" era el más corto, con la homolasia más baja y con la topología más corroborada por cladogramas de otros programas. Se considera que este cladograma es la mejor estimación de las relaciones cladísticas (genealogía) entre los géneros coralánidos.

La hipótesis de que la divergencia de Corallanidae y Tridentellidae estuvo relacionada con la apertura de los Océanos Atlántico e Índico es sostenida por la congruencia limitada existente entre un cladograma de áreas oceánicas tropicales propuesto y un cladograma taxon-área derivado de análisis cladístico. Se hipotetiza que los Corallanidae han evolucionado desde ancestros presentes en una fauna del Mar de Tethys, característica de aguas cálidas circumtropicales, con géneros modernos que existen desde antes del Plioceno.

## INTRODUCTION

The Isopoda is one of nine orders of peracarid Crustacea. There are nine suborders of Isopoda, including the Flabellifera. Within the Flabellifera there are 13 families, including a group of five families that superficially resemble one another and are presumably closely related; these are the Cirolanidae, Tridentellidae, Corallanidae, Aegidae, and Cymothoidae. These families are thought to make up an "ecological and phylogenetic lineage" trending from a free-living, scavenging-predatory lifestyle in

the Cirolanidae to a parasitic and specialized existence in the Cymothoidae (Menzies et al., 1955; Brusca, 1981). The Corallanidae have been collected as both free-living and "parasitic," and show many morphological adaptations toward an increasingly parasitic lifestyle. The Corallanidae are thought to occupy a position between the Tridentellidae and Aegidae in the evolutionary lineage above (Brusca, 1981; Delaney, 1984).

This study concerns the Corallanidae and consists of three sections: 1) the systematics of the family and its six component genera; 2) a genus-

level cladistic analysis, using two related families from the evolutionary lineage (above) as out-groups; and 3) a phylogenetic and historical biogeographic analysis of the family.

**SYSTEMATICS**

**MATERIALS AND METHODS**

Specimens were obtained via field collections and bulk loans from various museums around the world. A complete list of museums from which specimens were borrowed during this study, with the abbreviations for them used herein, follows:

- AHF—Allan Hancock Foundation, University of Southern California, Los Angeles, California
- AM—Australian Museum, Sydney
- BMNH—British Museum (Natural History), London
- CAS—California Academy of Sciences, San Francisco, California
- LACM—Los Angeles County Museum of Natural History, Los Angeles, California
- NTM—Northern Territory Museum, Darwin, Australia
- SAfM—South African Museum, Cape Town
- USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.
- ZMHUB—Museum für Naturkunde der Humboldt-Universität zu Berlin
- ZML—Zoological Museum, Leiden, Netherlands (Rijksmuseum van Natuurlijke Historie)
- ZMUC—Zoologiske Museum, University of Copenhagen, Denmark

Other abbreviations used in the Materials Examined sections include: coll. (collected by), fe. (female), ma. (male), and spec. (specimens).

Gross morphology of specimens was studied via dissection and examination using a Wild M-5 stereomicroscope and a Zeiss phase-contrast microscope. Drawings were made with the assistance of a camera lucida. Types of slide mounts made for study included temporary mounts in glycerol as well as permanent mounts stained with one of the following methods: fast green with lactic acid, chlorazol black, lignin pink in polyvinyl acetate, methylene blue with lactic acid, or silver nitrate and Dektol.

Ultrastructural morphology was studied using three types of scanning electron microscopes: ISI SuperMini, Cambridge S-100 Stereoscan, and Cambridge S4-10. Specimens were prepared for electron microscopy using standard techniques (Felgenhauer, 1987).

Terminology used in this study is consistent with that of current literature on the Corallanidae (e.g. Delaney and Brusca, 1985; Bruce et al., 1982).

**HISTORICAL REVIEW OF CORALLANID TAXONOMY**

The history of the Corallanidae is a tangled one, with considerable taxonomic and nomenclatural

activity having taken place. The family was proposed by Hansen in 1890, along with the family Alcironidae. The latter family was placed in synonymy with Corallanidae (by Stebbing, 1904b), as was the family Argathonidae (by Hale, 1925). Various genera have been removed from the Corallanidae and used to erect new families: *Barybrotetes* was used to establish the Barybrotidae by Hansen (1890), but was later placed in synonymy with the Aegidae of Dana, 1853, by Pillai (1967); *Tridentella* was removed to the family Tridentellidae by Bruce (1984); *Excorallana* was removed to the Excorallanidae by Stebbing (1904a), but was returned to the Corallanidae by Bruce et al. (1982). Bruce et al. (1982) discussed the status of the Corallanidae and considered it to contain eight valid genera. As mentioned above, one of these (*Tridentella* Richardson, 1905) was subsequently removed to a new family; another, *Austroargathona* Riek, 1953, is herein placed in junior synonymy with the genus *Tachaea*. Delaney and Brusca (1985) discussed the status of the Tridentellidae and provided a key to the genera of the Corallanidae and Tridentellidae. Because the Corallanidae resembles four other flabelliferan families, a key to these five very similar families is provided below.

**KEY TO THE FLABELLIFERAN FAMILIES  
CYMOTHOIDAE, AEGIDAE,  
CIROLANIDAE, TRIDENTELLIDAE,  
AND CORALLANIDAE**

- 1) Pereopods 4-7 prehensile (dactyli longer than propodi and markedly curved); antenna reduced, without clear distinction between peduncle and flagellum; maxillipedal palp 2-articulate . . . . . Cymothoidae
- Pereopods 4-7 ambulatory (dactyli shorter than propodi and not markedly curved); antenna not as above, with clear distinction between peduncle and flagellum; maxillipedal palp 2-5-articulate . . . . . 2
- 2) Maxilliped and maxilla with stout, recurved apical spines; maxillule lateral lobe forms a slender stylet; maxillule medial lobe small, without stout circumplumose spines; mandible sometimes with molar process, usually without lacinia mobilis . . . . . Aegidae
- Maxilliped and maxilla without stout, recurved apical spines; maxillule lateral lobe does not form a slender stylet; maxillule medial lobe with or without stout circumplumose spines; mandible with or without lacinia mobilis and molar process . . . . . 3
- 3) Mandible with well-developed lacinia mobilis and large, spinose, bladelike molar process; maxilliped with endite; maxillule lateral lobe with 11-14 apical spines; maxillule medial lobe large, with 3-4 stout, circumplumose spines; maxilla biramous . . . . . Cirolanidae

- Mandible with lacinia mobilis absent, or weakly developed if present; molar process sparsely spined and small or moderately sized, or absent; maxilliped with or without endite; maxillule lateral lobe with 1-5 stout apical spines; maxillule medial lobe small, without 3-4 stout circumplumose spines; maxilla uniramous . . . . . 4
- 4) Mandible without lacinia mobilis; mandible with nonspinose, moderately sized molar process; maxilliped with endite, palp always 5-articulate; maxillule lateral lobe styliform, slightly curved, tapering to apex with 3-5 stout, hooklike spines and smaller subapical spines; maxilla stout, 2-articulate, conical apical article often with tridentate scalelike spines . . . . . Tridentellidae
- Mandible with lacinia mobilis absent, or with lacinia mobilis represented by small, feeble spine row; mandible molar process nonspinose, small or absent; maxilliped without endite, palp 3-5-articulate; maxillule lateral lobe falcate with 1-3 large hooklike apical spines and 0-3 smaller subapical spines; maxilla small, represented by 1-4-articulate lobe, apex either a simple rounded lobe, a bifid or trifid lobe, or a sublinear and elongate article; maxilla apex without tridentate, scalelike spines . . . . . Corallanidae

The following synonymy lists only those references that are directly pertinent to the taxonomic and nomenclatural history of the family.

### Corallanidae Hansen, 1890

- Corallanidae Hansen, 1890:280, 311, 376; Stebbing, 1893:345, 1904a:13, 1904b:703, 1907:39; Richardson, 1905:156; Thielemann, 1910:19; Hale, 1925:160; Kussakin, 1979:222; Bruce et al., 1982:464; Delaney, 1984:1; Bruce, 1984:447; Delaney and Brusca, 1985:728.
- Alcironidae Hansen, 1890:312, 390; Stebbing, 1893:346, 1900:637; Richardson, 1901:519; Moore, 1902:170.
- Argathonidae Stebbing, 1905:17, 1911:179; Richardson, 1910:9.
- Excorallanidae Stebbing, 1904b:704; Thielemann, 1910:19; Menzies and Glynn, 1968:41; Delaney, 1982:273.
- Exocorallanidae Richardson, 1905:138 (*lapsus calami*).
- Corallaninae Nierstrasz, 1917:102, 1931:163; Hale, 1940:293; Menzies, 1962a:115.
- Non Corallanidae: *Tridentella* Richardson, 1905 (now in Tridentellidae Bruce, 1984); and *Barybrotos* Schioedte and Meinert, 1879 (now in Aegidae Dana, 1853).
- Incertae cedis*: *Corilana erythraea* Kossman, 1880. This poorly defined genus and species was regarded as *genus et species inquirenda* by Monod (1933) and regarded as closest to *Lanocira* by Bruce et al. (1982).

**DIAGNOSIS.** Flabellifera with eyes well developed; dorsum often ornamented with setae, spines, tubercles, or carinae; sexual dimorphism in ornamentation common. Antennule peduncle 2- or 3-articulate, basal article sometimes expanded. Antenna peduncle 5-articulate, articles 4-5 elongate. Frontal lamina always flat. Mandible with incisor variously modified; lacinia mobilis and molar process reduced or absent. Maxillule lateral lobe with 1-2 large falcate apical spines, with 0-3 smaller subapical (accessory) spines in some genera; medial lobe with simple apex, devoid of spines, sparsely setose. Maxilla uniramous, reduced, 1-4-articulate; apex morphology various, devoid of spines, sparsely setose. Maxilliped without endite; palp slender, 3-5-articulate, without apical spines; various maxilliped articles elongate in different genera.

**ADDITIONAL DESCRIPTION.** Dorsum moderately arched. Pereonites II-VII with distinct coxae. Pleon of 5 free segments plus pleotelson. Antennule and antenna flagella distinct, multiarticulate. Frontal lamina sessile, narrow, sometimes minute or absent in *Corallana* species. Clypeus generally short, wide, may or may not encompass labrum. Labrum usually small, narrower than clypeus, covering distal part of mandible incisor in some genera. Mandible with narrow 1-3 dentate incisor; molar process absent or reduced to small fleshy lobe; palp 3-articulate, either the middle or proximal article may be longest. Maxilla various: 1- or 2-articulate, short, round lobe; or simple lobe with bi- or trilobed apex; or 3- or 4-articulate, with apical article sublinear and elongate. Pereopods I-III subprehensile or "grasping" (dactylus as long as or longer than propodus), occasionally ambulatory (dactylus shorter than propodus), spinose. Pereopods IV-VII longer, always ambulatory, spinose. Pleopods biramous, lamellar; coupling spines and plumose setae present on medial margin of pleopod peduncles 1-4; peduncle lateral margin with simple spine. Pleopod exopods broader and more setose than endopods. Endopod of pleopod 5 without plumose marginal setae; endopod of pleopods 2-4 without plumose marginal setae in some species of *Tachaea* and *Corallana*. Male pleopod 2 with rodlike appendix masculina arising from proximal medial margin of endopod. Uropods inserted at base of pleotelson, both rami unfused.

**TYPE GENUS.** *Corallana* Dana, 1853.

**REMARKS.** The Corallanidae is a relatively small flabelliferan family. Museum specimens of the group are somewhat uncommon, with a few notable exceptions such as the collections of the USNM, BMNH, and ZMUC. The current study, though not an exhaustive treatment of the family at the species level, attempts to clarify the limits of the genera and provide a cladistic/biogeographic hypothesis about the evolution of the family.

The Corallanidae superficially resembles four other flabelliferan families (Cymothoidae, Aegidae, Tridentellidae, and Cirolanidae). Useful field characters that help in distinguishing corallanids from

the very similar cirolanids include the generally larger eyes of the former, the distinctly visible coxae (in dorsal view), and the often present heavy setosity or dorsal tuberculation. However, for accurate determinations the appendages (particularly those of the head) must be examined.

## CHARACTERS OF DIAGNOSTIC UTILITY

Most of the diagnostic characters used to distinguish genera within the Corallanidae are those of mouthpart morphology, along with others such as features of the pereopods, antennae, pleotelson, frontal lamina, and eyes. A discussion of these characters in relation to the closely related families Tridentellidae and Cirolanidae (both used as outgroups in the cladistic analysis) follows.

There is a trend towards reduction of the lateral (outer) lobe of the maxillule among these three families. The Cirolanidae have the lateral lobe of the maxillule with 10–14 apical spines, whereas in the Tridentellidae and Corallanidae the spines are reduced in number but increased in size. This trend culminates in a large single-spined (falcate) maxillule in the corallanid genera *Corallana*, *Excorallana*, *Lanocira*, and *Tachaea*.

The medial (inner) lobe of the maxillule likewise shows reduction, from the circumplumose spination in cirolanids to a simpler, nonsetose or sparsely setose lobe with simple apex in tridentellids and corallanids. In the corallanid genera *Alcirona* and *Argathona*, the medial lobe of the maxillule is sometimes distally expanded, with a truncate apex.

The maxillae of cirolanids usually have both medial and lateral lobes; tridentellids and corallanids have reduced, uniramous maxillae with several different types of apex morphology, the most derived being the small, 2–3-articulate rounded lobe seen in *Alcirona*, *Argathona*, *Tachaea*, and *Corallana*. In *Lanocira* the maxilla is 3–4-articulate, with a sublinear, elongate apical article. In *Excorallana* the maxilla is a simple lobe, 1–2-articulate, with a bi- or trilobed apex. Tridentellid maxillae are stout, with rounded/conical apices and often with dentate, scalelike apical spines.

Mandible morphology trends from the short, broad, generally tricuspid-incisored cirolanid mandible to a mandible with a more slender trunk and long, falcate incisor seen in *Excorallana* and some species of *Corallana* (whose species show both conditions of long- and short-incisored mandibles). The mandibular molar process is reduced from the more robust, saw-toothed blade of cirolanids to a smaller, spineless, more slender, blade-shaped or lobelike molar process in corallanids. The robustly spined lacinia mobilis of the Cirolanidae is reduced to a small, sparsely spined lobe in some corallanid genera or lost in others and in the Tridentellidae. The mandibles of *Lanocira* have a unique character of dentate processes or teeth behind the incisor region.

The maxillipeds of corallanids show various degrees of palp fusion, as in many other isopod fam-

ilies (see generic Remarks sections for detailed discussion of palp article fusion in *Argathona* and *Tachaea*). Cirolanids and tridentellids generally possess a 5-articulate palp, but *Argathona* and *Tachaea* exhibit palps that vary from 3- to 4- to 5-articulate. The most derived corallanid genera, *Tachaea*, *Excorallana*, and *Corallana*, have unique characters of maxilliped article size; elongate middle palp articles in *Excorallana*, and elongate maxilliped bases in *Tachaea* and *Corallana*. The large endite evident on cirolanid maxillipeds and retained in the Tridentellidae is lost in the Corallanidae.

The 3-articulate antennule peduncle of cirolanids and tridentellids shows varying degrees of reduction in the Corallanidae. In *Alcirona*, *Argathona*, *Lanocira*, and *Tachaea* it is 2-articulate but varies from 2- to 3-articulate in *Excorallana* and *Corallana*. The antennule peduncle is expanded in size in the most derived corallanid genera, *Tachaea*, *Excorallana*, and *Corallana*, compared to the antennule peduncles of cirolanids and tridentellids.

In contrast to the Cirolanidae, where many genera have frontal laminae that project antero- or posteroventrally, the frontal laminae of tridentellids and corallanids are always flat and “sessile.” The most derived genus, *Corallana*, has some species with the frontal lamina either greatly reduced or absent altogether.

The pereopods of tridentellids and corallanids are usually quite spinose; some corallanid genera have unique pereopod characters, such as the medially produced carpi on the first pereopods of *Tachaea* species, and the serrate dactyli typical of many species of *Alcirona* and several of *Argathona* and *Lanocira*.

Two unique characters present in certain corallanids are the lateral pleotelson incisions found only in some *Excorallana* species and the unpigmented, transverse band bisecting the eyes of several *Argathona* species.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The Corallanidae contains six genera, with 67 species as of this writing (Table 1). The family is confined mainly to tropical and subtropical shallow-water marine habitats, although *Tachaea* has been collected primarily from freshwater habitats, and *Corallana* has many species recorded from brackish water. Corallanids have been reported from depths of 287 m to the intertidal zone, as well as from freshwater lakes 362 m above sea-level (*Tachaea*). Every genus contains species recorded from coral reefs, thus the family name is appropriate. A variety of substrate and habitat types has been reported for corallanids, including coral reefs, limestone conglomerate reefs, sandy beaches, basalt boulder reefs, mangroves, wood burrows, brackish areas, and freshwater. Corallanid species frequent cryptic habitats, and they are often found living on or in corals, calcareous sponges, ascidians, bryozoans, gorgonians, coralline algae, tubeworms, scypho-

**Table 1. Species list for the Corallanidae Hansen, 1890 (Flabellifera).**

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Genus *Alcirona* Hansen, 1890

- Alcirona indica* Nierstrasz, 1931
- Alcirona krebsii* Hansen, 1890 (type-species)
- Alcirona multidigita* (Dana, 1853)
- Alcirona niponia* Richardson, 1909
- Alcirona papuana* Nobili, 1905

Genus *Argathona* Stebbing, 1905

- Argathona confine* Hale, 1925
- Argathona crenulata* Bruce, 1982
- Argathona japonica* Shiino, 1961
- Argathona macronema* (Bleeker, 1857)
- Argathona muraeneae* Bal and Joshi, 1959 (*genus inquirenda*)
- Argathona normani* Stebbing, 1905 (type-species)
- Argathona parca* Hale, 1940
- Argathona rhinoceros* (Bleeker, 1857)
- Argathona rostrata* Bruce, 1982
- Argathona setosa* Richardson, 1910
- Argathona stebbingi* Nierstrasz, 1931 (*genus inquirenda*)
- Argathona sulcata* Richardson, 1910

Genus *Corallana* Dana, 1853

- Corallana africana* Barnard, 1914
- Corallana basalis* (Heller, 1868)
- Corallana bidentata* Jones, Icely, and Cragg, 1983
- Corallana brevipes* Schioedte and Meinert, 1879
- Corallana collaris* Schioedte and Meinert, 1879
- Corallana estuaria* Jones, Icely, and Cragg, 1983
- Corallana furcilla* Barnard, 1955
- Corallana glabra* Nierstrasz, 1931
- Corallana hirsuta* Schioedte and Meinert, 1879
- Corallana hirticauda* Dana, 1853
- Corallana kulai* Bruce, 1982
- Corallana leopoldi* (Nierstrasz, 1930)
- Corallana nodosa* Schioedte and Meinert, 1879
- Corallana sculpta* (Milne-Edwards, 1840)
- Corallana* sp. Bruce, 1982 (female only)
- Corallana tridentata* Jones, Icely, and Cragg, 1983

Genus *Excorallana* Stebbing, 1904

- Excorallana acuticauda* (Miers, 1881)
- Excorallana angusta* Lemos de Castro, 1960
- Excorallana berbicensis* Boone, 1919
- Excorallana bruscai* Delaney, 1984
- Excorallana costata* Lemos de Castro, 1960
- Excorallana fissicauda* (Hansen, 1890)
- Excorallana houstoni* Delaney, 1984
- Excorallana longicornis* Lemos de Castro, 1960
- Excorallana meridionalis* Carvacho and Yanez, 1971
- Excorallana mexicana* Richardson, 1905
- Excorallana oculata* (Hansen, 1890)
- Excorallana quadricornis* (Hansen, 1890)
- Excorallana richardsonae* Lemos de Castro, 1960
- Excorallana sexticornis* (Richardson, 1901)
- Excorallana stebbingi* Lemos de Castro and Lima, 1976
- Excorallana subtilis* (Hansen, 1890)
- Excorallana tricornis occidentalis* Richardson, 1905

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**Table 1. Continued.**

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- Excorallana tricornis tricornis* (Hansen, 1890) (type-species)
- Excorallana truncata* (Richardson, 1899)
- Excorallana warmingii* (Hansen, 1890)

Genus *Lanocira* Hansen, 1890

- Lanocira anasicula* Jones, 1982
- Lanocira gardineri* Stebbing, 1904
- Lanocira glabra* Jones, 1982
- Lanocira kroyeri* Hansen, 1890 (type-species)
- Lanocira latifrons* Stebbing, 1909
- Lanocira rapax* (Moore, 1902)
- Lanocira rotundicauda* Stebbing, 1904
- Lanocira zeylanica* Stebbing, 1905

Genus *Tachaea* Schioedte and Meinert, 1879

- Tachaea caridophaga* Riek, 1953
- Tachaea chinensis* Thielemann, 1910
- Tachaea crassipes* Schioedte and Meinert, 1879 (type-species)
- Tachaea lacustris* Weber, 1892
- Tachaea picta* Riek, 1967
- Tachaea spongillicola* Stebbing, 1907

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zoans, and tube-building snails. Corallanids emerge from these cryptic habitats and “commensal” associations to temporarily parasitize or prey on fish, rays, shrimp, and turtles, as well as to prey on microcrustaceans such as mysids (Guzman et al., 1988).

Various species in different genera have been reported from more than one habitat and/or host. The number of species within a genus that have been reported as temporary parasites of either fish, rays, turtles, or shrimps varies greatly as follows: *Tachaea*—84%, *Argathona*—50%, *Alcirona*—40%, *Excorallana*—25%, *Corallana*—20%, and *Lanocira*—13%.

Three of the genera, *Argathona*, *Corallana*, and *Tachaea*, are restricted to the Indo-West Pacific. *Excorallana* is generally restricted to tropical and subtropical regions of the New World (Delaney, 1984), with only one species found outside that range: *Excorallana oculata*, a Caribbean species, which has also been reported off West Africa. The two remaining genera, *Alcirona* and *Lanocira*, are circumtropical, both being most diverse in the Indo-West Pacific, with only two to three species in each genus occurring in the New World.

The predilection for temporary parasitism noted above may partly account for the presence of *Alcirona* in both the Old and New World tropics, as individuals may have dispersed via temporary association with fish (or other) “hosts.” However, both *Argathona* and *Tachaea* have a high percentage of species recorded as temporary parasites (50% and 84%, respectively) and yet are restricted to the Indo-West Pacific region. *Tachaea* has the highest percentage of temporary parasitism in the family and is known almost exclusively from fresh-

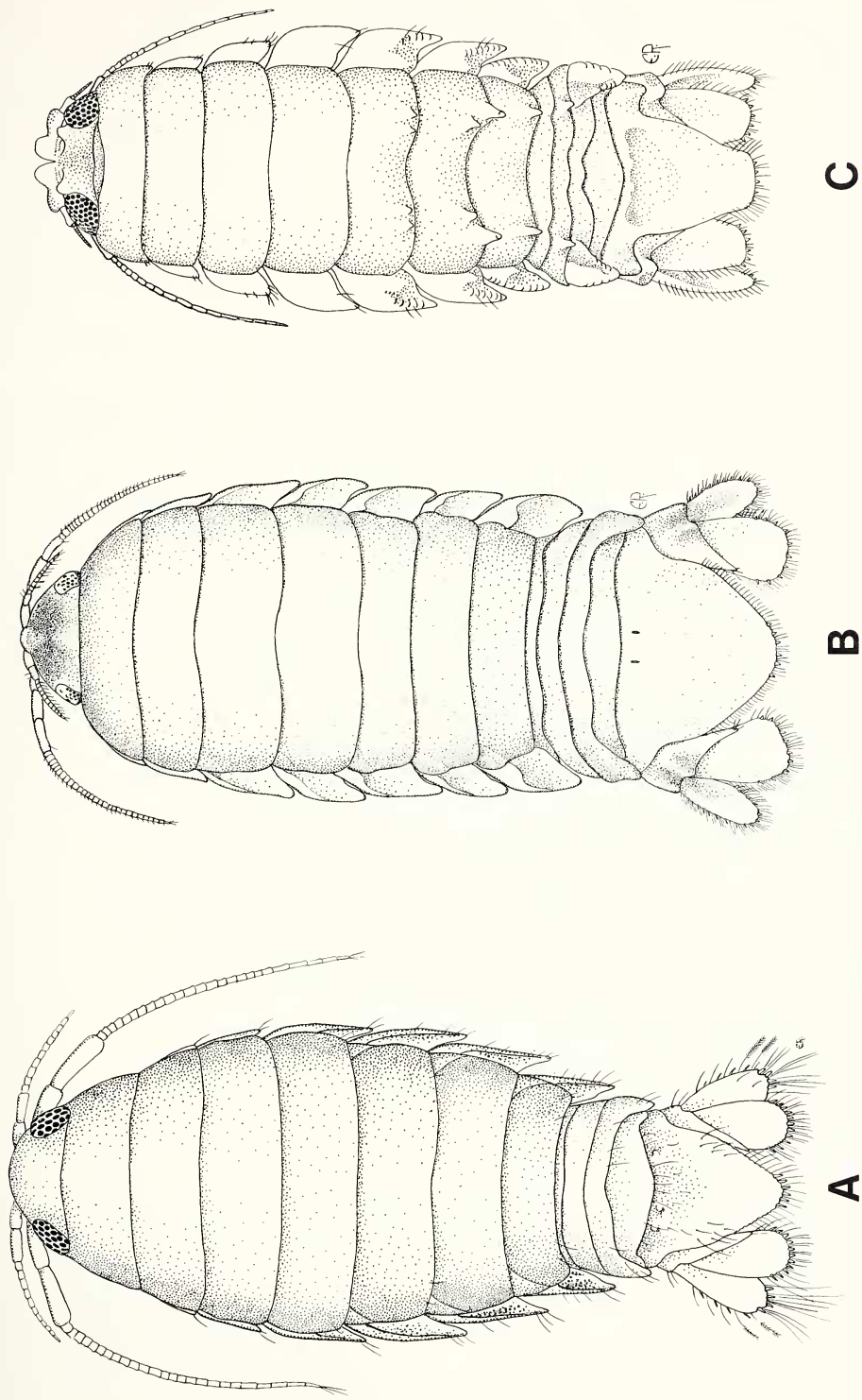


Figure 1A-C. Dorsal views: A, *Alcirona krebssii*, AHF male, length = 10 mm; B, *Argathona rhinoceros*, CAS 018845, male, length = 18.4 mm; C, *Corallana estuaria*, BMNH 1921.5.23: 80-82, male, length = 10 mm.

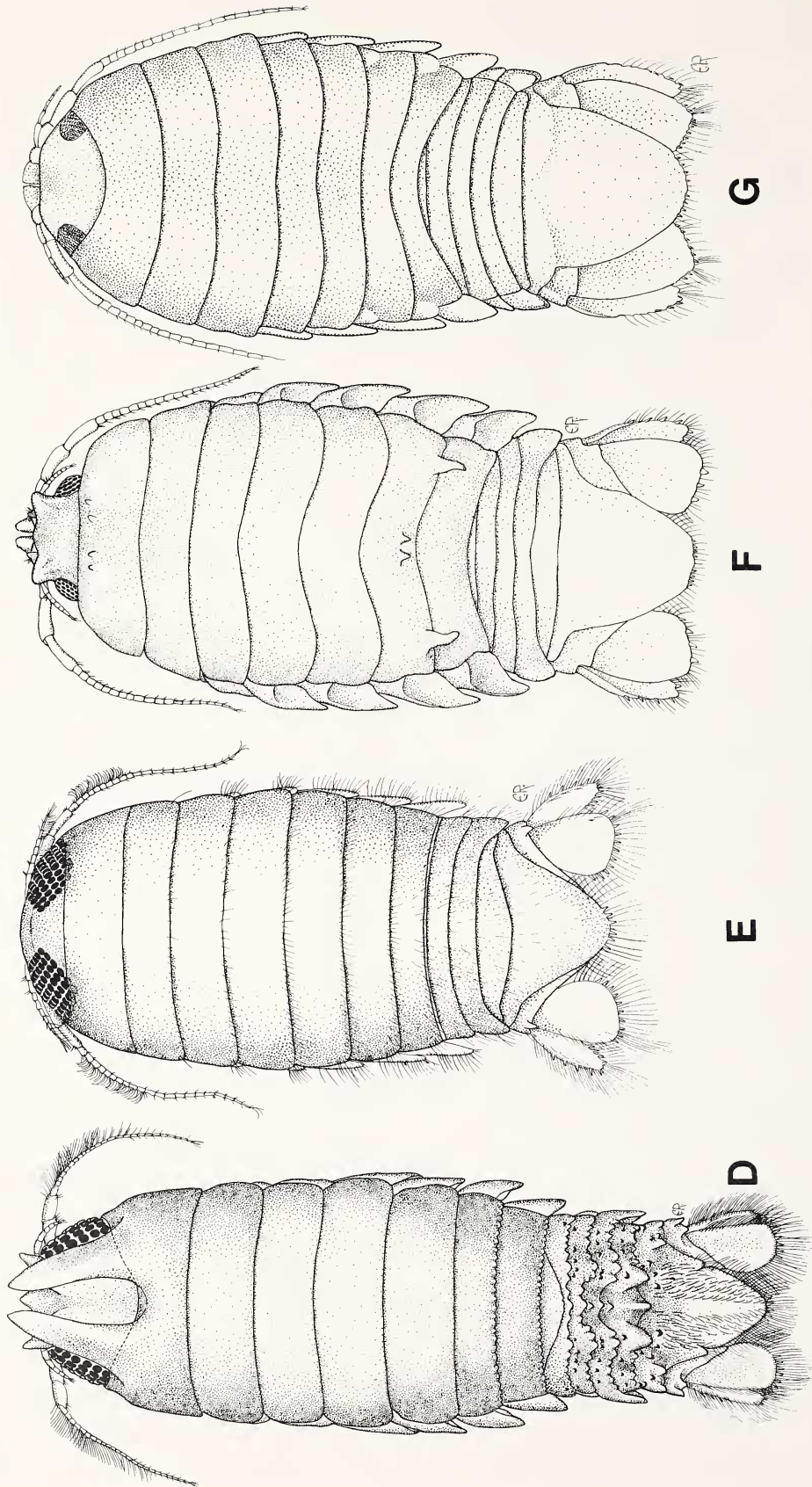


Figure 1D-G. Dorsal views: D, *Excorallana bruscai*, AHF 6611, male holotype, length = 7.88 mm; E, *Lanocira zeylanica*, AHF, male, length = 7.5 mm; F, *Tachaea lacustris*, ZML



water shrimp hosts; only one species is marine, collected from a coral reef. *Corallana* is also an Indo-West Pacific endemic, yet has only 20% of its species reported as temporary parasites. However, 40% of *Corallana* species are reported from wood burrows, in estuarine or brackish-water habitats, indicating a slightly different ecological orientation.

There is only one record (this study) of a species of *Lanocira* being collected as a temporary parasite of a fish (*Variola louti*, family Serranidae). The genus has never been reported from rays, turtles, or shrimp. Besides the usual cryptic habitats of corals, sponges, ascidians, and tubeworms, *Lanocira* has also been collected from the umbrella of the scyphozoan *Cassiopea andromeda*. Dispersal via such "hosts" may be partly responsible for the presence of *Lanocira* in both the Old and New World tropics.

Only three genera are found in the New World: *Excorallana*, *Lanocira*, and *Alcirona*. *Excorallana* is the largest genus in the family and its species exploit a wide variety of hosts and habitats—temporary parasitism of fish and rays, and "commensal" associations with sponges, ascidians, gorgonians, bryozoans, tube-molluscs, corals, and mangroves. Many *Excorallana* species have been collected with night-lights, and one species (*E. tricomis occidentalis*) exhibits definite nocturnal mass-migrating behavior into the water column, perhaps preying on other microcrustaceans (Guzman et al., 1988). Menzies and Kruczynski (1983) presented evidence suggesting that some species of *Excorallana*, *Alcirona*, and *Lanocira* may partition their habitat by depth range. *Excorallana* is restricted almost exclusively to the New World (save one species, see above). *Lanocira* and *Alcirona* are represented by only two to three species in the New World. The relative paucity of species of other corallanid genera in the New World may have allowed *Excorallana* to radiate in a greater variety of ecological niches in this region.

**CLASSIFICATION OF THE GENERA**

The following are recognized as valid genera in the Corallanidae:

Family Corallanidae Hansen, 1890

- Genus *Alcirona* Hansen, 1890
- Genus *Argathona* Stebbing, 1905
- Genus *Corallana* Dana, 1853
- Genus *Excorallana* Stebbing, 1904
- Genus *Lanocira* Hansen, 1890
- Genus *Tachaea* Schioedte and Meinert, 1879

A key to the genera of the Corallanidae follows; this key updates that of Delaney and Brusca (1985).

**KEY TO THE GENERA OF THE CORALLANIDAE**

- 1) Maxilliped palp middle article elongate; maxilla apex bi- or trilobed; mandible with elongate, falcate incisor ..... *Excorallana*

- Maxilliped palp middle article not elongate; maxilla apex not as above; mandible not as above ..... 2
- 2) Maxillule lateral lobe a single large falcate spine; maxilla 3- or 4-articulate, apical article sublinear, elongate; mandible with slender trunk and row of small spines behind incisor, mandible incisor not elongate ..... *Lanocira*
- Maxillule lateral lobe not a single large falcate spine; maxilla a short, rounded lobe; mandible not as above ..... 3
- 3) Maxillule lateral lobe with 1 large falcate spine and 1-4 small hooklike accessory spines; mandible trunk and apex wide, incisor well developed but not elongate or falcate; maxilliped palp 4- or 5-articulate ..... *Argathona*
- Maxillule lateral lobe not as above; mandible trunk and apex narrow, incisor not elongate; maxilliped palp 3-, 4-, or 5-articulate ..... 4
- 4) Maxillule lateral lobe with 2 large falcate spines and 0-3 small accessory spines between the large ones; maxilliped palp always 5-articulate; maxilliped basis not elongate ..... *Alcirona*
- Maxillule lateral lobe with 1 large falcate spine and without small accessory spines; maxilliped palp 3-, 4-, or 5-articulate; maxilliped basis elongate ..... 5
- 5) Maxilliped palp 3-, 4-, or 5-articulate; maxilliped basis length 1.5-2.0 times width; mandible with small, moncuspid incisor; inner angle of pereopod I carpus strongly produced; frontal lamina elongate, length 2.0-3.0 times width, quadrangular, rounded anteriorly, narrowing posteriorly ..... *Tachaea*
- Maxilliped very narrow, palp always 5-articulate; maxilliped basis length 2.0-4.0 times width; mandible with bi- or tricuspid incisor; inner angle of pereopod I carpus not produced; frontal lamina not elongate, shape various, occasionally reduced or absent ..... *Corallana*

**Genus *Alcirona* Hansen, 1890**

*Alcirona* Hansen, 1890:391; Stebbing, 1893:315, 1900:637, 1904b:708; Richardson, 1900a:217, 1901:519, 1902:277, 1905:156, 1909:78, 1910:8, 1914:361; Moore, 1902:170; Nobili, 1905:502; Nierstrasz, 1917:97, 1918:106, 1931:166; Hale, 1925:161; Monod, 1926:97; Nordenstam, 1946:10; Menzies and Glynn, 1968:43; Birkeland et al., 1976:159; Monod, 1975:1003, 1976:853; Bruce, 1982a:13; Bruce et al., 1982:464; Menzies and Kruczynski, 1983:67; Delaney and Brusca, 1985:728; Delaney, 1986:734.

**MATERIAL EXAMINED**

*Alcirona krebsii*: 1) West Indies, ZMUC syntype, "coll. from *Pseudoscarus coeruleus*," 1 fe., 16.4

mm; 2) West Indies, ZMUC syntype, "coll. from *Pseudoscarus psittacus*," 1 fe., 6.4 mm; 3) West Indies, ZMUC syntype, "coll. from *Scarus* sp.," 1 spec. (pleon missing), 8.8 mm; 4) West Indies, ZMUC syntype, "coll. from *Pseudoscarus superbus*," 1 fe., 8.4 mm; 5) West Indies, ZMUC syntype, "from *Priacanthus macrophthalmus*," 1 fe., 14 mm; 6) West Indies, St. Thomas, 1 ma., 9.1 mm; 7) Florida, west coast, Pepperfish Key, USNM 44262, Sta. 7161, depth 14 m, 1 ma.; 8) no locality, USNM 20475, *Albatross*, Sta. 2365, 2 fe. and 1 ma.; 9) Panama, Panama Bay, USNM 66055, Smithsonian Biological Survey Sta. 139/465, 1 ma.; 10) Florida, Tortugas, USNM 39855, "from *M. venenosa*," 1 fe.; 11) Florida, Hillsborough County, about 29 km west of Egmont Key, USNM 170828, R/V *Hernan Cortez* Sta. 67-328, 27°37'N, 83°07'W, depth 18 m, 26 spec.; 12) Costa Rica, Playas Blancas, USNM Acc. No. 131571, "from 2 lumps *Pavonia* coral, south shore of bay," 1 fe. and 1 ma.; 13) West Indies, USNM Acc. No. 208263, Sta. 106-56, 1 fe. (gravid); 14) Mexico, Baja California Sur, off Cabo San Lucas, USNM 39364, R/V *Albatross*, Sta. 2829, depth 56 m, 1 spec.; 15) Costa Rica, Cocos Island, Roca Sucia, "from grunge under rocks and coral," 1 fe.; 16) Indian Ocean, USNM IIOE Program, SOSC Acc. No. 23, *Anton Bruun* Cruise 4B, Sta. 269c, 7 fe. and 5 ma.; 17) (as *Alcirona insularis* holotype) Samoa, Mus Godeffroy, ZMUC, 1 fe., 4.1 mm; 18) Haiti, east coast, USNM 90445, coll. Johnson-Smithsonian Deep-Sea Expedition, Sta. 52/289, 19°10'5"N, 69°21'25"W, depth 25-40 m, 1 fe.; 19) Bahamas, USNM 119496, coll. Böhlke, Sta. 516, 1 ma.; 20) South Pacific Ocean, Tuvalu, Ellice Islands, Funafuti, USNM 46431, coll. 1899-1900 U.S. Fish Commission Expedition, Steamer *Albatross*, 1 spec.; 21) Panama, Panama City, San Francisco reef, USNM Acc. No. 144344, "Taken from eel *Echidna nocturna*"; 22) Panama, Miraflores Locks, coll. P.W. Glynn, 1 adult and 1 manca. *Alcirona niponia*: 1) Japan, Korea Strait, east channel off Oki Shima, USNM 039498 (type), coll. Bureau of Fisheries, Sta. 4879, depth 106 m, 1 ma. *Alcirona* spp.: 1) Colombia, Gorgona Island, AHF 412-35, coll. R/V *Velero*, "off coconut beach," 1 ma.; 2) Mexico, Sonora, Puerto Penasco, Gulf of California, University of Arizona No. 75-40, "Station beach reef poison station, water temp. 23-26 C.," 1 fe. (gravid); 3) Marquesas Islands, Fatu Hiva, west coast, USNM Acc. No. 291828, coll. Marquesas Expedition, Sta. FHI, Haul 2, "with broken shell, rubble and flat live coral," depth 67-72 m, 2 ma. and 4 fe.; 4) Panama, Farfan Point, 8°56'N, 79°34'W, "in sand/mud/rocks at low tide with an ichthyocide, depth 0-1.3 m," 6 spec.; 5) Colombia, Ensenada de Utria, Choco, "between dead coral," 2 fe., 9.5 and 11.4 mm, and 1 ma., 8.5 mm; 6) Panama, Isla Perlas, "from interstices of *Pocillopora*," coll. P.W. Glynn, 4 spec.

## DIAGNOSIS

Antennule peduncle 2-articulate; basal article of peduncle narrow, not expanded. Frontal lamina

narrow, pentagonal; clypeus large, crescent-shaped or subtriangular; labrum small, width twice length. Mandible with short incisor, molar process and lacinia small or absent. Maxillule lateral lobe apex with 2 large falcate spines, and 0-3 smaller spines between the large ones; medial lobe apex simple, blunt. Maxilla 2-articulate, rounded lobe. Maxilliped without endite; maxilliped basis not elongate; palp always 5-articulate, middle article not elongate. Anterior pereopods often with serrate dactyli and propodi; carpi not greatly produced on posteromedial margins as in *Tachaea*.

## ADDITIONAL DESCRIPTION

Corallanidae with eyes small, round, placed at posterolateral angles of cephalon. Body often with dorsal setae or tubercles (Fig. 1A). Postlateral angles of clypeus produced almost to articulation of mandibular palps (Fig. 2D). Mandible trunk and apex narrow, incisor short; molar process usually absent, but small molar process present in some species (Figs. 2A, B); lacinia mobilis absent (Figs. 2A-C, 3E, F). Palp inserted near mandible base, 3-articulate, middle article longest, middle and distal articles with simple and comb setae (Figs. 2A, C). Maxillule lateral (outer) lobe slender, tapering apically (Figs. 2G, 3C, D) and often with comblike cuticular structures on medial margin (Figs. 4B-D). Maxilla simple, with small setae on rounded apical article (Figs. 2F, 3B). Maxilliped palp apical article with plumose setae, groups of 1-3 setae on margins of other articles (Figs. 2E, 3A, 4A). Pereopods I-III prehensile, with simple setae and robust spines on posteromedial margins; dactyli and propodi of some species with digitiform processes (Fig. 5A). Pereopods IV-VII longer than I-III, ambulatory, with stout spines and simple setae on posteromedial margins (Figs. 5B, C). Pleopod peduncles broader than long, with 3-5 coupling spines and group of proximal plumose setae on medial margins, lateral margins with 1 simple spine (Figs. 5D-H). Exopod of pleopods broader, longer, and with more plumose marginal setae than endopod. Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 5H). Male pleopod 2 with rodlike appendix masculina, with simple apex, arising from proximal medial margin of endopod (Fig. 5E).

## TYPE SPECIES

*Alcirona krebsii* Hansen, 1890:391, plate VIII, figures 1a-q, by designation (Menzies and Kruczynski, 1983).

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

- 1) *Alcirona multidigita* (Dana, 1853):768, figures 3a-f, plate 51. *Alcirona multidigitata* Stebbing, 1900:637; Nierstrasz, 1917:102, 1931:168; Monod, 1926:99 (*lapsus calami*). *Aega multidigita* Dana, 1853:768.

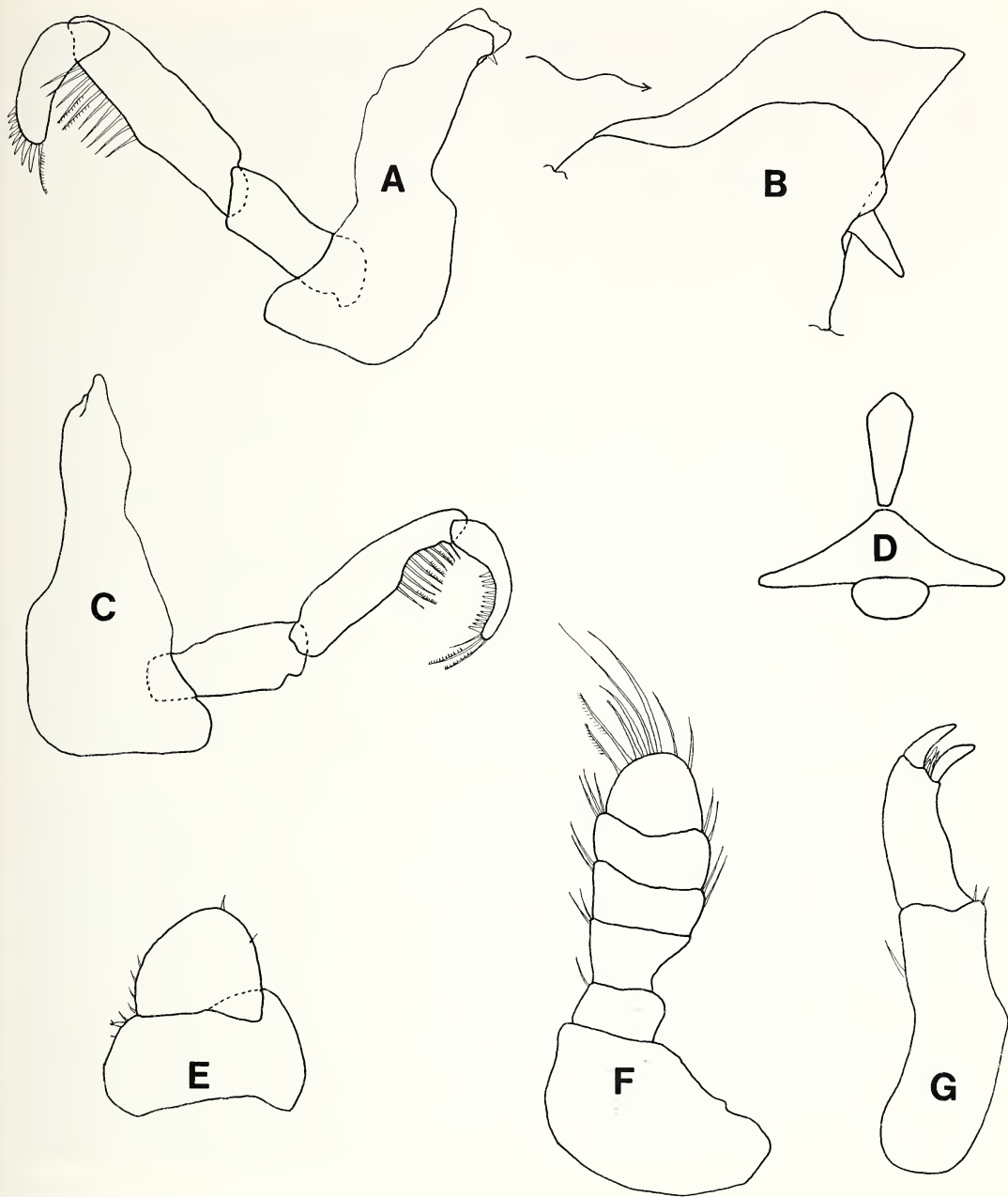


Figure 2. *Alcirona* sp., LACM specimen: A, left mandible; B, apex of left mandible; C, right mandible; D, frontal lamina, clypeus, and labrum; E, maxilliped; F, maxilla; and G, maxillule.

*Cirolana multidigitata* Miers, 1878:511, 1884:301 (*lapsus calami*).

**DISTRIBUTION.** North Borneo; West Australia; and Zebu, Philippines.

- 2) *Alcirona krebsii* Hansen, 1890:391, figures 1a–q, table VIII. For synonymy see Menzies and Kruczynski, 1983:69.

**DISTRIBUTION.** Apparently a circumtropical species from collection records, but possibly a complex of sibling species. Localities for the

synonyms listed above include Maldive Islands, Ellice Islands, Fiji Islands, Gulf of Mexico, Caribbean Sea, Bermudas, Marquesas Islands, Senegal, Samoa, New Britain, Papua New Guinea, Pacific Panama, Pacific Costa Rica, Baja California, Puerto Rico, and Bahamas.

- 3) *Alcirona papuana* Nobili, 1905:502, figures 5a–h, plate XIII. Nierstrasz, 1917:102, 1931:169; Nordenstam, 1946:10.

**DISTRIBUTION.** Dutch New Guinea.

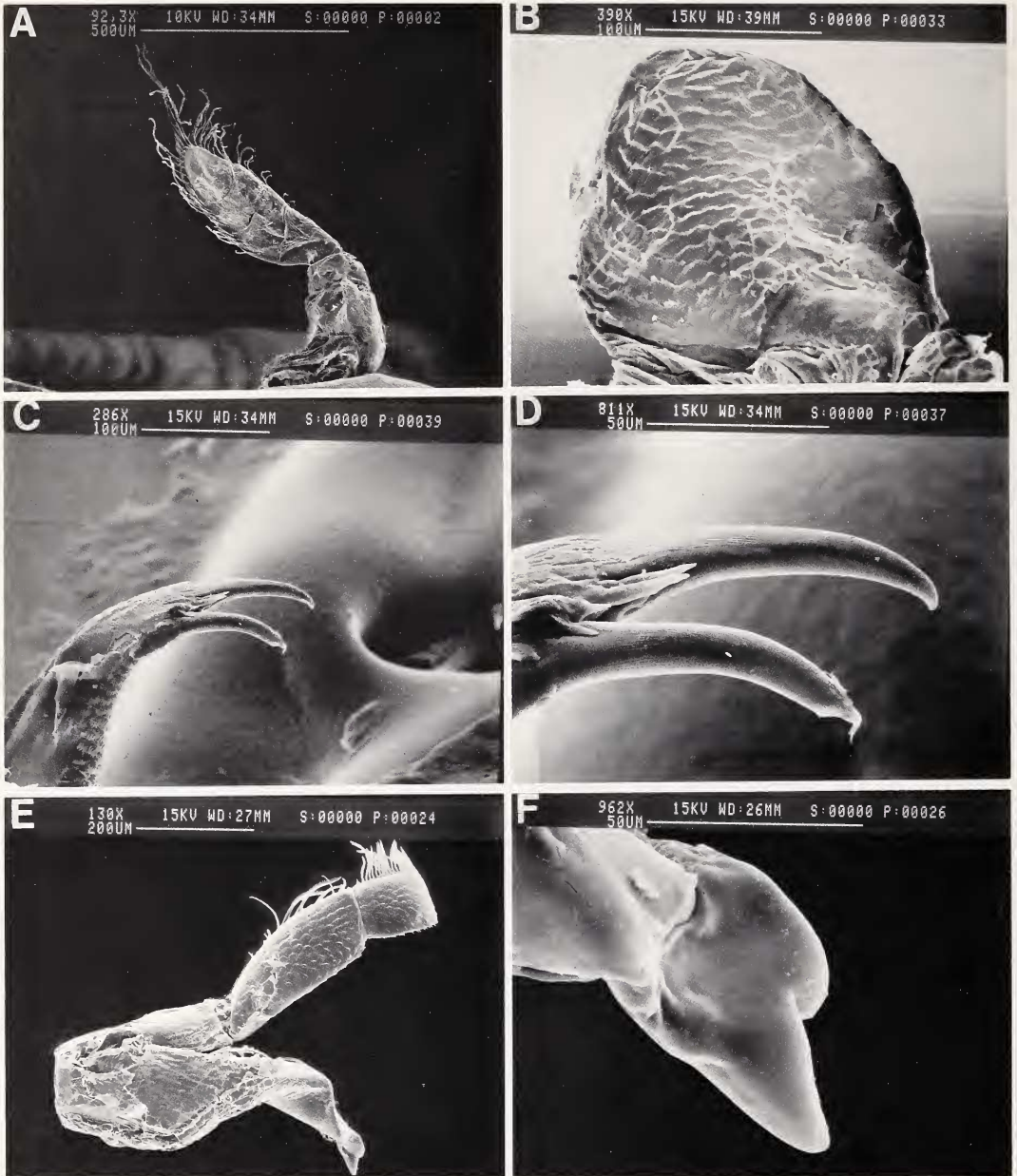


Figure 3. Scanning electron micrographs of *Alcirona krebsii*: A, maxilliped; B, maxilla; C, maxillule; D, maxillule apex; E, mandible; and F, mandible incisor.

- 4) *Alcirona niponia* Richardson, 1909:78, figure 6; Nierstrasz, 1917:102, 1931:167; Monod, 1926:99.

**DISTRIBUTION.** Korea Strait, near Oki Shima.

- 5) *Alcirona indica* Nierstrasz, 1931:166, figures 38-45.

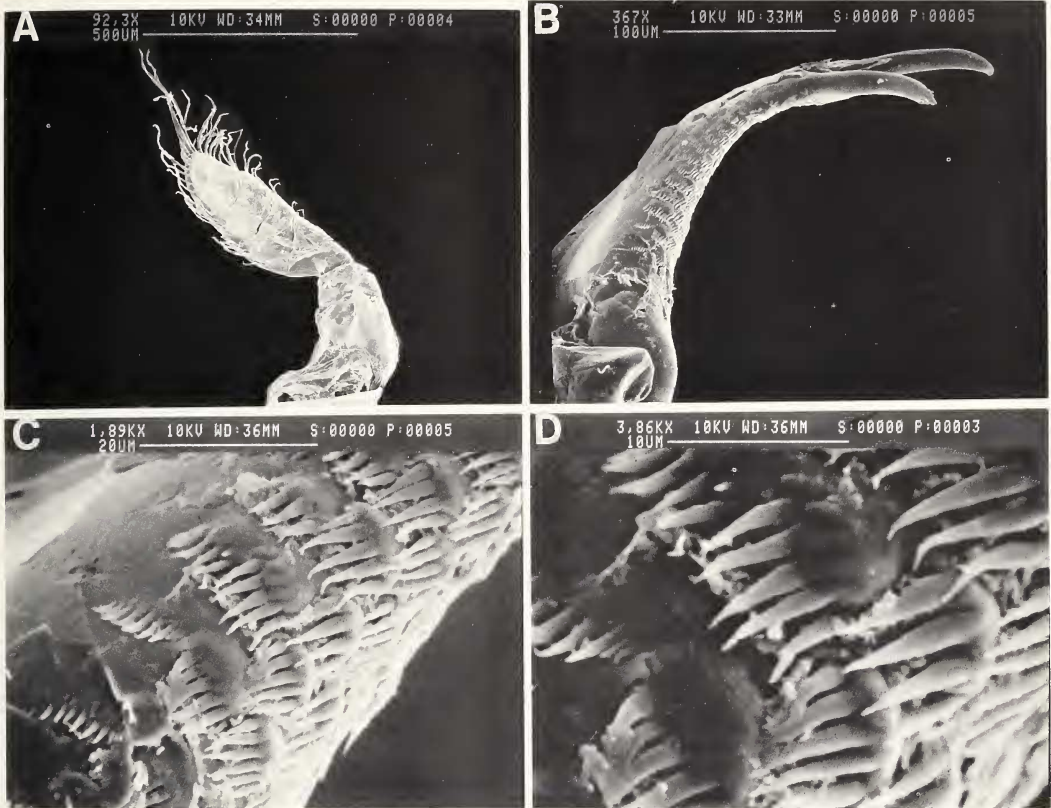
**DISTRIBUTION.** Dutch East Indies.

**Non-*Alcirona*:** *Alcirona pearsoni* Monod, 1926 (now *Argathona rhinoceros*); *Alcirona mac-*

*ronema* (Bleeker, 1857) (now *Argathona macronema*); and *Alcirona tuberculata* Richardson, 1910 (now *Cirolana tuberculata*).

#### REMARKS

In 1890 H.J. Hansen proposed a new family, Alcironidae, for his new genera *Alcirona* Hansen, 1890; *Lanocira* Hansen, 1890; and *Tachaea* Schioedte and Meinert, 1879. The validity of Alcironidae was upheld by subsequent workers (Stebbing, 1893; Richardson, 1901; Moore, 1902) until Stebbing



**Figure 4.** Scanning electron micrographs of *Alcirona krebsii*: **A**, maxilliped; **B**, medial margin of maxillule; **C**, cuticular structures on maxillule (detail of **B**); and **D**, detail of cuticular structures.

(1904b) concluded that the alcironid genera (*Alcirona*, *Lanocira*, and *Tachaea*), as well as *Corallana* Dana, 1853, should be placed in the Corallanidae.

With five species, *Alcirona* is the smallest genus in the Corallanidae. Menzies and Kruczynski (1983) recently synonymized *Alcirona insularis*, *A. hirsuta*, and *A. maldivensis* with *A. krebsii*. Some sexual variation is evident in the pleonal tuberculation, pereonal and pleonal setation, and dactyli serration of pereopods I-II in *Alcirona krebsii*; usually females have tuberculation, setation, and serration either reduced or absent (see Stebbing, 1900: 638; Nordenstam, 1946:12; Menzies and Glynn, 1968:43). According to Nordenstam (1946:12) and Menzies and Kruczynski (1983:69) variation in setosity and dactyli serration is also known to occur in males, and this led the latter authors, following Nordenstam's suggestion, to synonymize *A. hirsuta*, *A. insularis*, and *A. maldivensis* with *A. krebsii*. The five species of *Alcirona* are very similar to one another; given the sexual dimorphism in dactyli and propodi serration, and the amount of variation in the characters of setosity, tuberculation, and pleotelson shape within *A. krebsii*, females should be identified with care.

*Alcirona* is morphologically similar to *Argathona*, the major differences being the shape of the

mandibles, the two large falcate spines on the apex of the lateral lobe of the maxillule, and the serrate dactyli of the anterior pereopods in *Alcirona* (the latter feature also has been reported in *Lanocira zeylanica* by Monod, 1933:184). Several species originally placed in *Alcirona* have been removed to *Argathona* (*Argathona macronema* and *Argathona rhinoceros*) by various authors. Bruce (1982a) suggested that *Argathona stebbingi* Nierstrasz, 1931, and *Argathona muraeneae* Bal and Joshi, 1959, may belong to the genus *Alcirona*, based on the figures of the maxillules and pereopods published for those species. The types of *A. stebbingi* and *A. muraeneae* have yet to be reexamined. Delaney (1986) removed *Alcirona tuberculata* Richardson, 1910, to the genus *Cirolana* based on features of mouth appendages.

#### BIOGEOGRAPHIC AND ECOLOGICAL NOTES

All described *Alcirona* species except *A. krebsii* are found only in tropical/subtropical marine habitats in the Indo-West Pacific (Fig. 6). *Alcirona krebsii* is apparently a circumtropical species, occurring in the Pacific, Indian, and Atlantic Oceans.

Two *Alcirona* species have been collected as

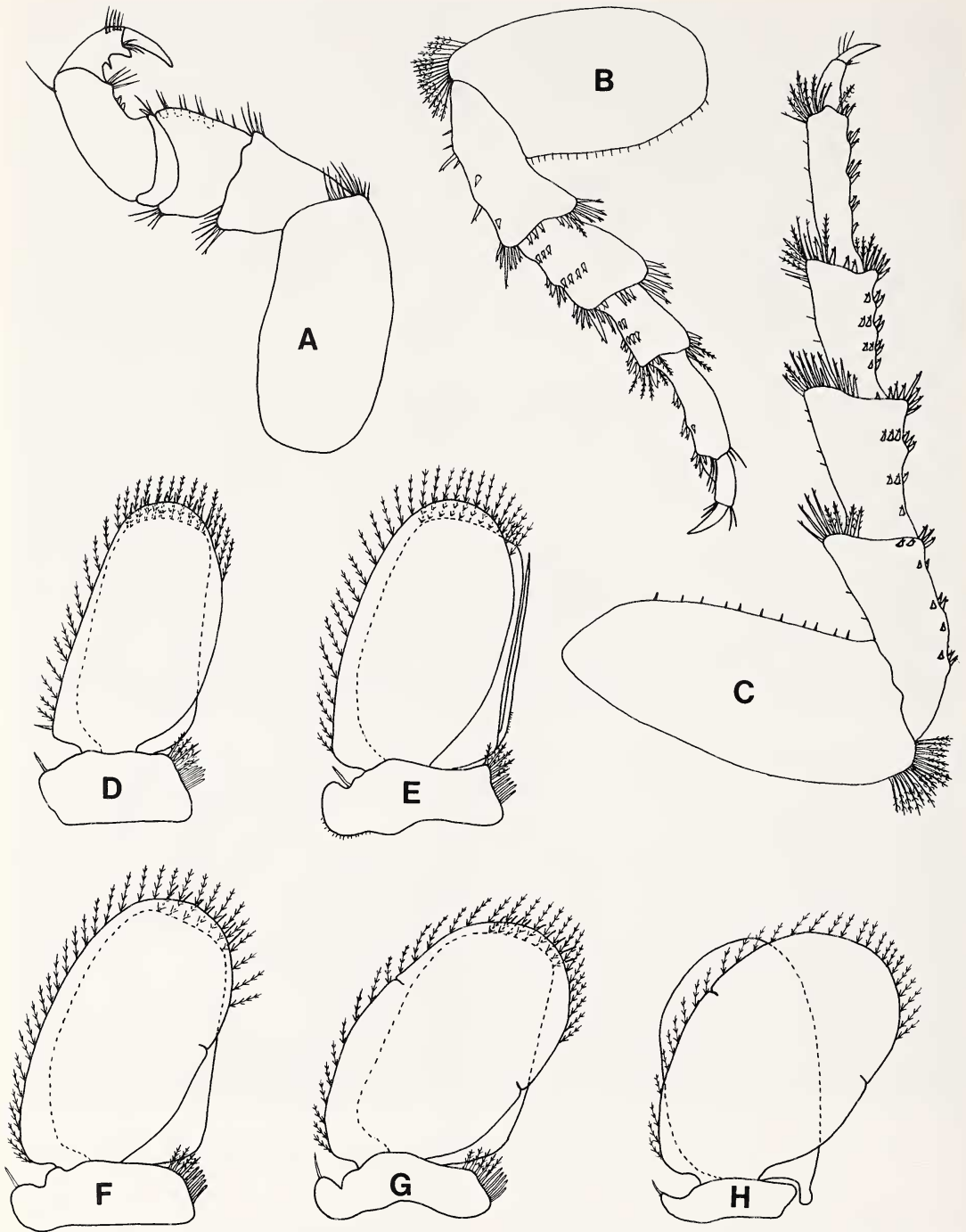


Figure 5. *Alcirona* sp., LACM specimen (Colombia): A, pereopod I; B, pereopod IV; C, pereopod VII; D, pleopod 1; E, pleopod 2; F, pleopod 3; G, pleopod 4; and H, pleopod 5.

“parasites”: *A. krebsii* (from “fins of Hamlet Grouper,” from fish “*M. venenosa*,” *Pseudoscarus coeruleus*, *Pseudoscarus psittacus*, *Pseudoscarus superbis*, *Priacanthus macrophthalmus*, *Scarus* sp., and the eel *Echidna nocturna*) and *A. indica* (from *Amphacanthus (Teuthis) hexagonalus*). Other *Alcirona* species have been collected from a variety

of substrates, including andesite rock, “*Pavonia* coral,” coral reef rock, and fine gray sand/broken shell. *Alcirona krebsii* has been reported as a “commensal” from “living bathing sponges” (Hansen, 1890), and *A. multidigita* has been reported as a “commensal” from *Euplectella* or *Meyerina claviformis* (by Miers, 1878). *Alcirona* species have been

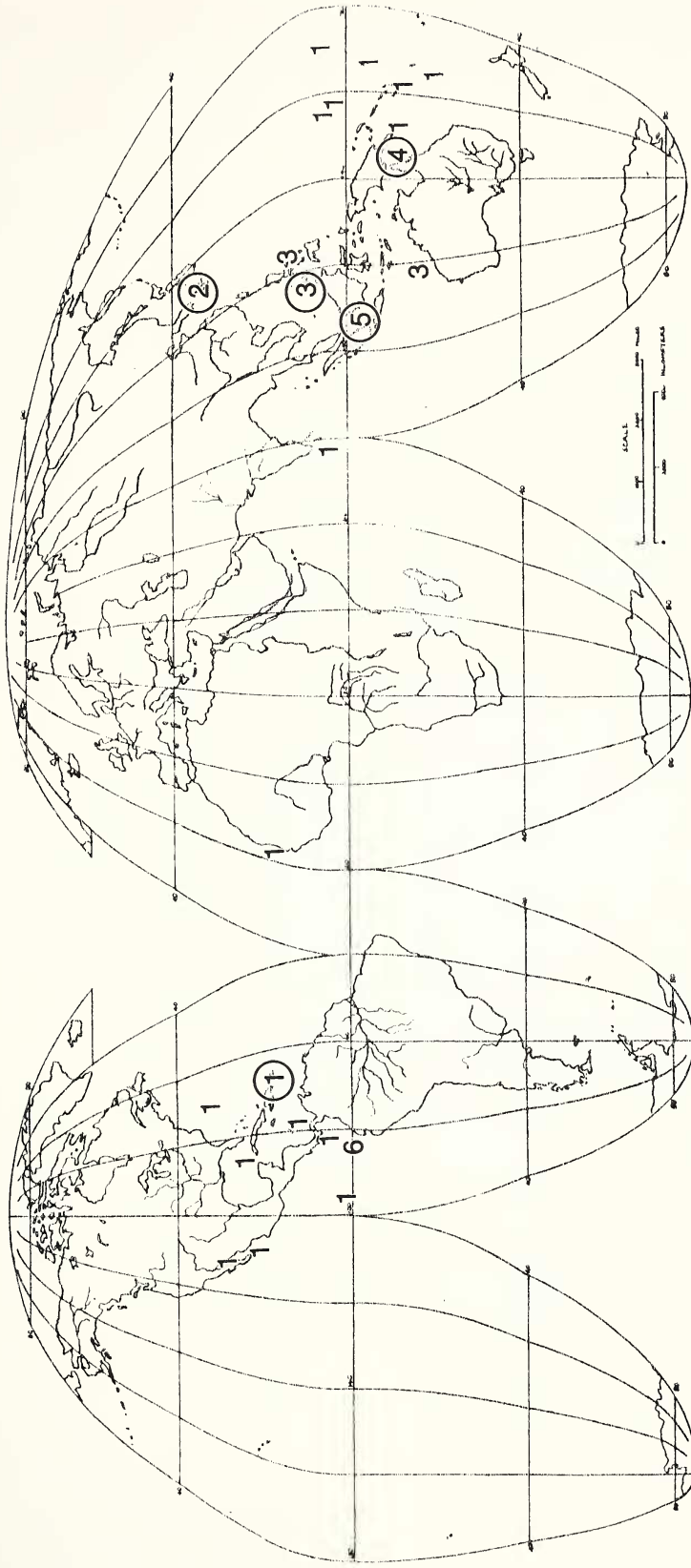


Figure 6. Distribution of *Alcionna* species; type localities are circled. Species numbers are: 1, *A. krebsii*; 2, *A. niponia*; 3, *A. multidigita*; 4, *A. papuana*; 5, *A. indica*; and 6, *A. sp.*

collected at depths ranging from the intertidal zone to 106 m. Menzies and Kruczynski (1983), conducting trawling operations in the Gulf of Mexico over a three year period, found *Alcirona krebsii* predominately at 18 m depth.

### Genus *Argathona* Stebbing, 1905

*Argathona* Stebbing, 1905:17, 1910:100, 1911:179; Richardson, 1910:9; Nierstrasz, 1917:102, 1931:172; Hale, 1925:161, 1929:251, 1940:293; Monod, 1933:162, 161, 1929:251, 1940:293; Monod, 1933:162, 1975:999, 1976:853; Barnard, 1936:154, 1940:500; Nordenstam, 1946:1; Bal and Joshi, 1959:563; Shiino, 1961:93; Pillai, 1967:272; Trilles and Paperna, 1980:445; Bruce, 1982a:12; Bruce, Brusca, and Delaney, 1982:464; Delaney and Brusca, 1985:728.

*Brotherus* Budde-Lund, 1908:306; Stebbing, 1911:179; Nierstrasz, 1917:102; Hale, 1925:161; Monod, 1933:162, 1975:999.

*Gurida* Budde-Lund, 1908:305; Nierstrasz, 1917:102, 1931:176; Monod, 1933:162, 1975:999.

*Orcilana* Nierstrasz, 1931:170; Monod, 1933:162, 1975:999.

### MATERIAL EXAMINED

*Argathona normani*: 1) Indian Ocean, USNM IIOE Program, SOSC Ref. No. 23, Sta. 206A, coll. International Indian Ocean Expedition, R/V *Anton Bruun* Cruise 4B, 20°23'N, 70°00'E, depth 73 m, 2 fe.; 2) Persian Gulf, Jaraid Island, USNM 101915, from shallow reef with *Aega basalis*, 1 fe.; 3) Australia, USNM Acc. No. 275759, BPI 13, 1 spec. *Argathona macronema*: (as syntype of *Corallana macronema*) Malaysia, BMNH 1880:6, coll. Bleeker, 1 fe., 15.4 mm. *Argathona rostrata*: 1) Papua New Guinea, Bootless Bay, Motapore Island, AM No. P32349, 09°31'S, 147°17'E, from sponge, 1 ma., 7.4 mm. *Argathona setosa*: 1) Philippine Islands, off Linao Point, USNM No. 40911 (holotype), R/V *Albatross*, Sta. 5254, depth 38 m, 1 fe. (gravid), 10.2 mm. *Argathona sulcata*: 1) Philippine Islands, Luzon, east coast, USNM No. 41010 (holotype), depth 263 m, coll. R/V *Albatross*, Sta. 5453, 1 fe., 19.5 mm. *Argathona macronema*: 1) Australia, AM No. P28791, LI-61, 1 fe., 11.6 mm, and 4 ma., 4.8, 4.9, 10, and 10 mm; 2) Seychelle Islands, ZMHUB No. 15732, 1 fe., 12.4 mm; 3) Taiwan, Takao, ZMHUB No. 14782, 1 ma., 15 mm; 4) Indian Ocean, Amirantes Islands, African Islands, off north end of north island, USNM Acc. No. 276969, depth 8–10 m, International Indian Ocean Expedition, Sta. F-78, 1 fe.; 5) Philippine Islands, Batananan Island, USNM No. 101935, 1 fe. (gravid); 6) Ponape, USNM Acc. No. 339879, UGS 80-2, 05°51'N, 158°20'E, depth 2 m, "with rotenone," 1 fe.; 7) Saudi Arabia, Red Sea, Jidda, SAMS Pier, USNM Acc. No. 17832, U-48-121, 2 fe.; 8) Seychelle Islands, Faon Island, off south shore of island, USNM Acc. No. 276969, depth 11–15 m, International Indian Ocean Expedition, Sta. F-11,

1 fe.; 9) Philippine Islands, Luzon, near Palag Bay, USNM No. 101936, 1 fe.; 10) Australia, Northern Territory, Cobourg Peninsula, Caiman Ck., USNM, "in mangrove, from nares of *Lutjanus argentimaculata*," 3 juveniles; 11) Australia, Northern Territory, Cobourg Peninsula, Table Point, USNM, "from *Plectropoma maculata*," 2 fe. and 13 juveniles; 12) Australia, Northern Territory, Cobourg Peninsula, Coral Bay, USNM, SM CP/62, 2 fe.; 13) (as *Argathona similis*, holotype) Indian Ocean, Indonesia, Celebes, Limbe Strait, USNM No. 41015, 1 fe., 16.5 mm; 14) Red Sea, Ethiopia, Heart Island, Sheikh el Abu, off lighthouse just west of south end of island, USNM Acc. No. 284009, Sta. VGS 69-14, 16°08'N, 39°26.5'E, depth to 4 m, "rotenone and dip net," 1 fe.; 15) Australia, Queensland, Capricorn Group, One Tree Island, lagoon, AM No. P28795, low tide, FT 106, 1 fe., 5.3 mm, and 1 manca, 3.2 mm; 16) Australia, Queensland, Capricorn Group, One Tree Island, AM No. P28794, depth 20–23 m, "from nostrils of *Plectropoma leopardus*," FT 431, 1 fe., 14.7 mm, and 2 ma., 12.2 and 9.6 mm; 17) Israel, Gulf of Aqaba, north-west coast, about 1 mile north of Ras Burga, USNM Acc. No. 284009, Sta. VGS 69-6, depth to 8 m, "rotenone," 2 fe., 18 and 9 mm, and 1 ma., 8 mm; 18) Celebes, Limbe Strait, USNM, 1 fe., 15 mm. *Argathona rhinoceros*: 1) Thailand, Sattahip, Ko-I-Lao, CAS No. 018845, depth 1–3 m, Quad. #S-102720, 1 fe., 21 mm, 1 ma., 18.4 mm, and 3 mancas, 4.4, 4.8, and 5.2 mm; 2) Australia, Northern Territory, Cobourg Peninsula, Table Point, USNM, "from fish *Epinephelus malabaricus*," 5 fe.; 3) Persian Gulf, Jaraid Island, USNM 101916, 27°20'N, 49°49'E, near Sta. 8, "from nasal opening of *Epinephelus taurina*," 1 fe. and 3 ma.; 4) India, west of Cochin, USNM Acc. No. 280815, depth 90 m, "taken as parasite from nares of *Epinephelus chlorostigma*," 7 fe. and 5 ma.; 5) Australia, Northern Territory, Cobourg Peninsula, Coral Bay, USNM, 16 May 1983, CP/60, "from nares of *Epinephelus malabaricus*," 2 fe.; 6) Australia, Northern Territory, Cobourg Peninsula, Table Point, USNM, "from fish *Epinephelus malabaricus*," 4 fe., 5, 10, 10, and 13 mm; 7) Indian Ocean, USNM Acc. No. 27085, coll. W.L. Abbott, 2 fe., 23 and 27 mm, and 1 ma., 21 mm; 8) Indian Ocean, Mozambique Channel, USNM IIOE Program, SOSC, R/V *Anton Bruun* Cruise 8, Sta. 408-F, 16°21'S, 43°59'E, depth 27 m, poison station, 2 fe., 20 and 8.2 mm; 9) West Pacific Ocean, Eniwetok Atoll, Parry Island, USNM Acc. No. 228273, "from ventral apex of right gill cavity of serranid *Variola louti* with *Lanocira* sp. and juvenile cymothoid," 1 fe.; 10) Indian Ocean, between Mozambique and Madagascar, USNM IIOE Program, SOSC, R/V *Anton Bruun* Cruise 8, Sta. 407-k, 15°52'S, 44°23'E, depth 30 m, "shrimp trawl," 3 fe. and 1 ma.; Palau Islands, Ratakadokoru Island, USNM 99286–99288, Sta. 97, 07°17'N, 134°15'E, "from outer edge of outer reef, west of island, in gill cavities and nares of fish *Plectropomus leopardis*," 1 fe. and 2 ma. *Argathona con-*



*fine*: 1) Australia, Pt. Cairns, Alexander Reef, AM No. P31711, "from blue-spotted lagoon ray," 1 fe., 16 mm; 2) Australia, Northern Territory, Gulf of Carpentaria, reef at Yirrkala, northwest of Cape Arnhem, USNM 101918, coll. Arnhem Land Expedition, 7 spec.; 3) Australia, northwest of Cape Arnhem, from Ironstone Reef at Yirrkala, USNM 102146, "killed with 5% emulsified Rotenone," M48-21, 1 ma.; 4) Australia, northwest of Cape Arnhem, from coral reefs at Yirrkala, USNM 102147, M48-21, 16 spec. *Argathona* spp.: 1) Australia, Northern Territory, Cobourg Peninsula, USNM, CP/60/BCR, 1 fe., 16 mm, and 13 mancas; 2) Seychelle Islands, Anonyme Island, USNM Acc. No. 276969, International Indian Ocean Expedition, Sta. F-21, depth 0–2 m, "large sandy-bottom tidepool on east end of island," 1 manca; 3) Seychelle Islands, Anonyme Island, vicinity of Mahe, USNM Acc. No. 276969, IIOE, Sta. F-17, depth 0–3 m, 3 mancas; 4) Indian Ocean, Mozambique Channel, USNM, IIOE, Sta. 408-F, 16°21'S, 43°59'E, depth 27 m, coll. SOSC, R/V *Anton Bruun* Cruise 8, 1 fe., 9.5 mm; 5) Seychelle Islands, Beacon Island, off Port Victoria, USNM Acc. No. 276969, IIOE, Sta. F-26, depth 13–18 m, 1 ma.; 6) Indian Ocean, Admirantes Islands, D'Arros Island, off east side, USNM Acc. No. 276969, depth 18–30 m, 1 ma.

#### DIAGNOSIS

Antennule peduncle 2-articulate; basal article of peduncle not expanded. Frontal lamina flat, narrow, and pentagonal; clypeus large, crescent, or inverted V-shaped, encompassing small labrum. Mandible trunk and apex wide; incisor well developed but not long as in *Excorallana*, mono- or bicuspid; molar process small, lacinia mobilis absent. Maxillule lateral lobe apex with 1 large falcate spine, and 1–4 small hooklike accessory spines at base of large spine; medial lobe simple, with widened, truncate apex. Maxilla short, 2- or 3-articulate lobe with broadly rounded apex. Maxilliped without endite; maxilliped basis not elongate; with broad, 4- or 5-articulate palp, middle article not elongate. Anterior pereopods usually without serrate dactyli (but present in *A. muraeneae* and *A. stebbingi*); carpi not greatly produced on postero-medial margins as in *Tachaea*.

#### ADDITIONAL DESCRIPTION

Eyes well developed, at lateral margins of cephalon; in some species each eye bisected by transverse unpigmented band. Body occasionally with dorsal tubercles and setae; cephalon of some species with prominent, upwardly produced rostrum (Figs. 1B, 7I). Antennule basal article not expanded (Fig. 7H). Antenna peduncle articles 4–5 much longer than 1–3 (Fig. 7G). Frontal lamina, clypeus, and labrum visible anterior to mandibles; posterolateral angles of clypeus nearly reaching origin of mandibular palp (Fig. 7C). Mandible incisor short, well developed, mono- or bicuspid; palp inserted near mandible

base, 3-articulate, middle article longest and with plumose marginal setae; distal article with simple or plumose marginal setae and often with comblike cuticular structures (Figs. 7F, 8C, E, F). Maxillule lateral lobe with comblike cuticular structures on medial margin; medial (inner) lobe with 0–3 spines on medial margin (Figs. 7B, 8D). Maxilla with 1–2 apical simple setae (Figs. 7D, E, 8B). Maxilliped palp distal articles with simple or plumose marginal setae (Figs. 7A, 8A). Pereopods I–III short, subprehensile, with simple setae and robust spines on postero-medial margins (Figs. 9A, D). Pereopods IV–VIII longer, ambulatory, with simple setae and stout spines on posteromedial margins (Figs. 9B, C). Pleopod peduncles broader than long, with 3–5 coupling spines and group of proximal plumose setae on medial margins, often with small accessory lobe and simple spine on lateral margins (Figs. 9E–I). Pleopod exopods broader, longer, and with more plumose marginal setae than endopods. Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 9I). Appendix masculina rodlike, with simple apex, arising from proximal medial margin of pleopod 2 endopod (Fig. 9F).

#### TYPE SPECIES

*Argathona normani* Stebbing, 1905, by monotypy.

#### DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

- 1) *Argathona normani* Stebbing, 1905:17, plate 3A, 1910:100; Richardson, 1910:9; Nierstrasz, 1917:102, 1931:176; Hale, 1925:161; Monod, 1933:180, 1975:1003; Barnard, 1936:156; Bal and Joshi, 1959:565; Pillai, 1967:267; Bruce, 1982a:13.

**DISTRIBUTION.** Sri Lanka and Bay of Bengal.

- 2) *Argathona setosa* Richardson, 1910:9, figure 8; Nierstrasz, 1917:102, 1931:175; Hale, 1925:161; Monod, 1933:182; Bruce, 1982a:23.

**DISTRIBUTION.** Philippines.

- 3) *Argathona sulcata* Richardson, 1910:10, figure 9; Nierstrasz, 1917:102, 1931:176; Monod, 1933:181, 1975:1003; Bruce, 1982a:23.

**DISTRIBUTION.** Philippines.

- 4) *Argathona macronema* (Bleeker, 1857). For synonymy see Bruce, 1982a:13.

**DISTRIBUTION.** Throughout the Indo-West Pacific (Bruce, 1982a), including the Red Sea, Gulf of Aqaba, Gulf of Suez, Java, Celebes, Australia, New Guinea, Madagascar, Gilbert Islands, Fiji Islands, and Kenya.

- 5) *Argathona rhinoceros* (Bleeker, 1857). For synonymy see Bruce, 1982a:14.

**DISTRIBUTION.** Throughout the Indo-West Pacific, including Aldabra Island, Persian Gulf,

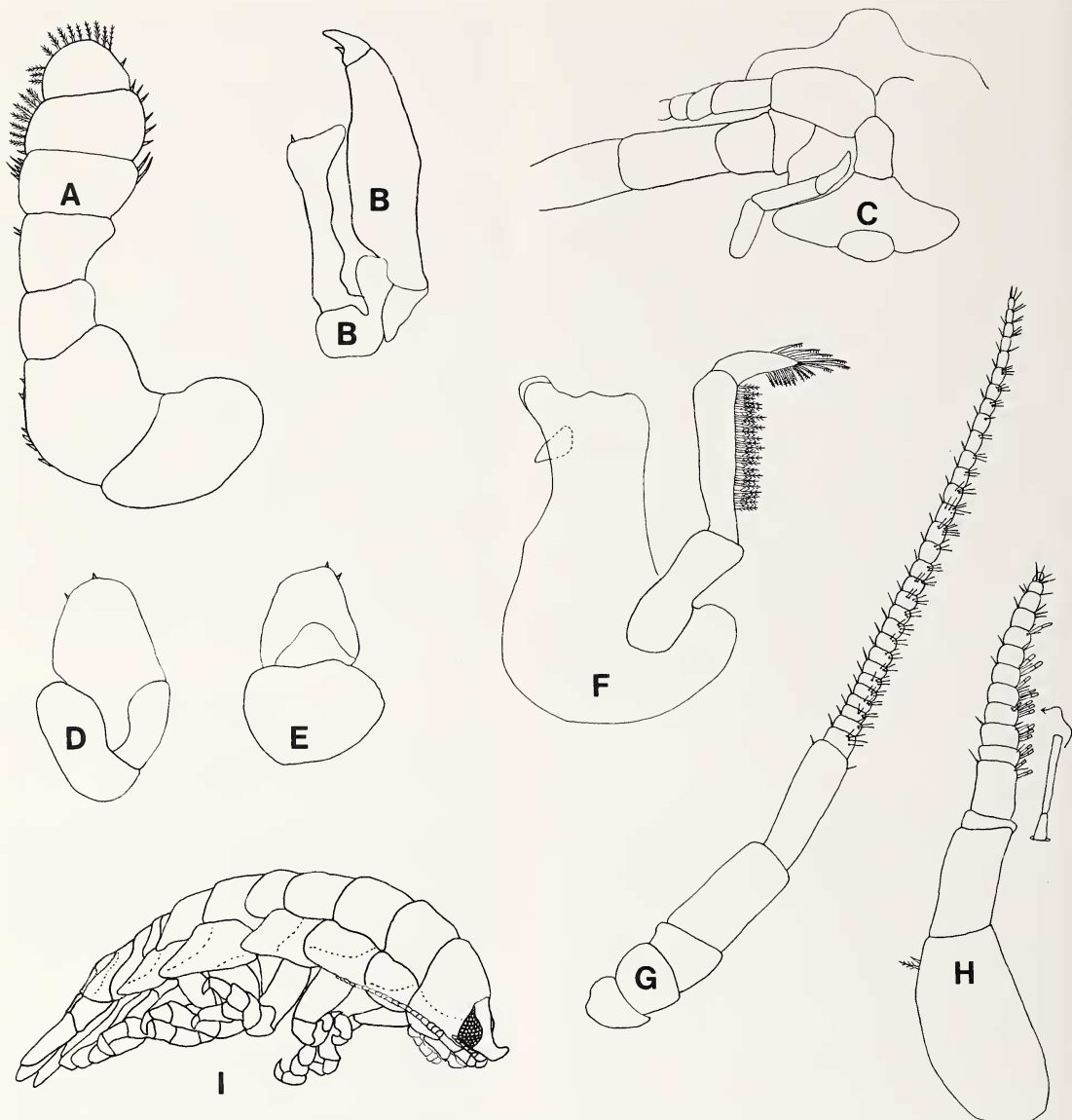


Figure 7. *Argathona rhinoceros*, USNM Acc. No. 27085: A, maxilliped; B, maxillule; C, frontal lamina, clypeus, and labrum; D, maxilla, dorsal view; E, maxilla, ventral view; F, mandible; G, antenna; H, antennule; and I, lateral view.

- Zanzibar, Sri Lanka, India, Java, Thailand, Australia, Palau Islands, and Eniwetok Atoll.
- 6) *Argathona confine* Hale, 1925:164, figure 17.  
*Argathona confinis* Nierstrasz, 1931:176; Monod, 1933:179, 1975:1003; Bruce, 1982a:23 (*lapsus calami*).  
**DISTRIBUTION.** Australia.
- 7) *Argathona parca* Hale, 1940:293, figures 3a-i; Bruce, 1982a:23.  
**DISTRIBUTION.** Australia.
- 8) *Argathona stebbingi* Nierstrasz, 1931:171, figures 58-68; Monod, 1933:182, 1975:1003; Bruce, 1982a:23 (*genus inquirenda*).  
**DISTRIBUTION.** Indonesia.
- 9) *Argathona muraeneae* Bal and Joshi, 1959:563, plate I, figures 1-10; Bruce, 1982a:23 (*genus inquirenda*).  
**DISTRIBUTION.** Bombay.
- 10) *Argathona japonica* Shiino, 1961:93, figures 1, 2; Bruce, 1982a:23.  
**DISTRIBUTION.** Japan.
- 11) *Argathona rostrata* Bruce, 1982a:16, figures 2-4.  
**DISTRIBUTION.** Australia.
- 12) *Argathona crenulata* Bruce, 1982a:20, figures 5, 6.  
**DISTRIBUTION.** Australia.

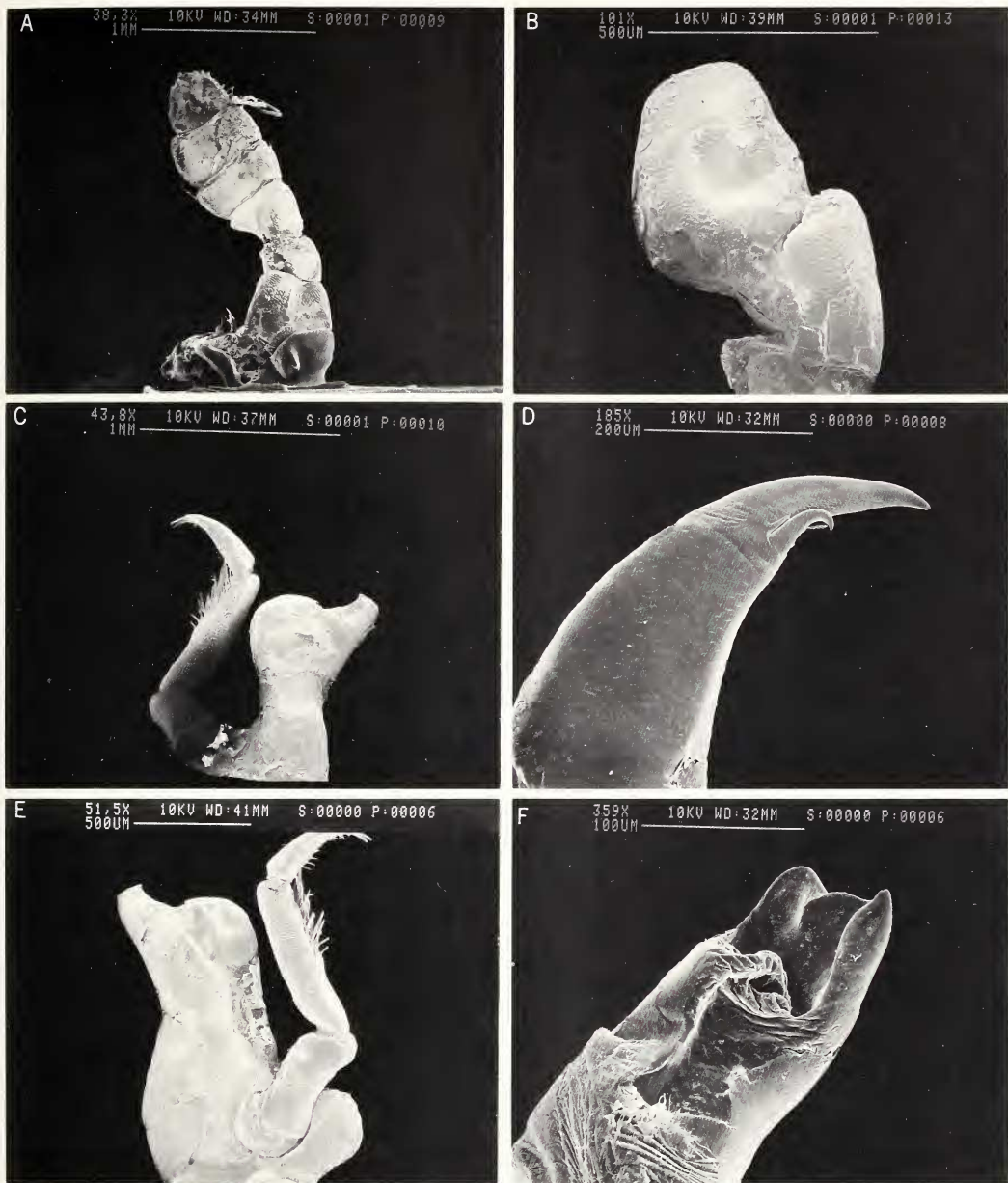


Figure 8. Scanning electron micrographs of *Argathona rhinoceros*: A, maxilliped; B, maxilla; C, dorsal view of mandible; D, apex of maxillule; E, ventral view of mandible; and F, apex of mandible.

#### REMARKS

The genus *Argathona* was erected by Stebbing (1905) for his new species *A. normani* and was placed in his new family Argathonidae. Hale (1925), Monod (1926, 1976), Barnard (1936), Bal and Joshi (1959), Shiino (1961), Bruce et al. (1982), and Delaney and Brusca (1985) placed *Argathona* in the family Corallanidae. Two species of *Arganotha* (*A. macronema* and *A. rhinoceros*) have been placed, at various times, in 8 different genera (*Aega*, *Alcirona*, *Brotherus*, *Corallana*, *Cymothoa*, *Gurida*, *Livoneca*, and *Orcilana*). In 1911 Stebbing synonymized

the genus *Brotherus* with *Argathona*. Monod (1933) synonymized *Orcilana* and *Gurida* with *Argathona*. The most comprehensive treatments of the genus have been those of Monod (1933, 1975) and Bruce (1982a).

The number of accessory spines at the base of the large apical spine on the maxillule varies among different species of *Argathona*. In *A. macronema*, *A. normani*, *A. rhinoceros*, and *A. stebbingi* there is usually 1 accessory spine; 2 such spines occur in *A. setosa*, 3 in *A. confine* and *A. sulcata*, and 4 in *A. japonica*.

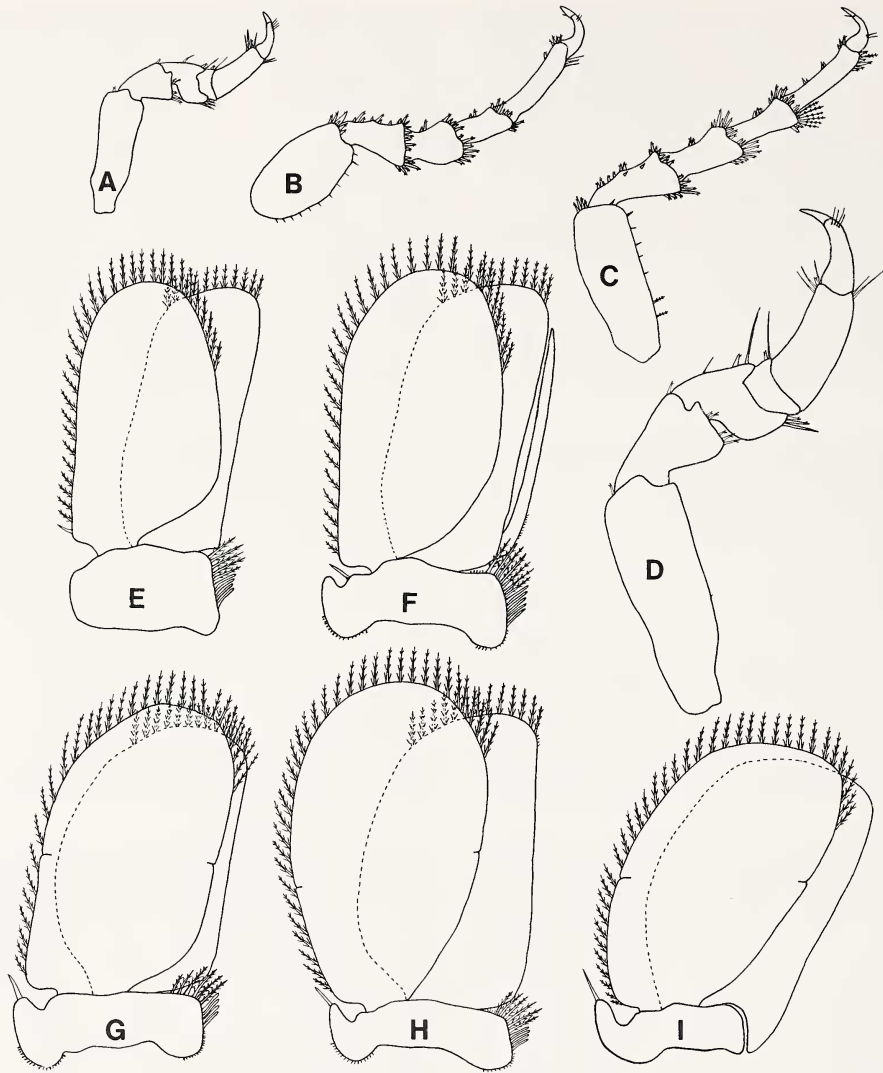


Figure 9. *Argathona confine*, USNM 102147: A, pereopod I; B, pereopod IV; C, pereopod VII; D, pereopod I, enlarged; E, pleopod 1; F, pleopod 2; G, pleopod 3; H, pleopod 4; and I, pleopod 5.

The number of maxilliped palp articles in *Argathona* species varies from 4 to 5, usually by complete or partial fusion of articles 2 and 3. In *A. macronema* articles 2 and 3 may be distinct (Monod, 1975:fig. 10) or partly fused (Hale, 1925:fig. 16g). In *A. parca* Hale (1940:fig. 3g), *A. rostrata* Bruce (1982a:figs. 2j, 4g), and *A. crenulata* Bruce (1982a:fig. 5l) the palp is distinctly 4-articulate, with no partial suture evident between articles 2 and 3. Loss or fusion of maxilliped palp articles in *Argathona* has also been reported by Stebbing (1905, 1911), Monod (1933), Barnard (1936), and Pillai (1967). Loss or fusion of maxilliped palp articles also occurs in the corallanid genus *Tachaea* Schioedte and Meinert, 1879, in which fusion of articles is known to differ between the right and left maxillipeds in the same specimen (Tattersall, 1921). Loss and/or fusion of maxilliped arti-

cles commonly occurs in many other families of isopods.

Two *Argathona* species, *A. stebbingi* Nierstrasz, 1931, and *A. muraeneae* Bal and Joshi, 1959, have been noted above as *genus inquirenda*. As noted by Bruce (1982a), both of these species may belong in *Alcirona*, as they are figured with pereopods, maxillules, and mandibles typical of *Alcirona*. The serrate processes on the dactyli of the anterior pereopods in *A. stebbingi* and *A. muraeneae* are unknown in other *Argathona* species but are figured for *Lanocira zeylanica* (in Monod, 1933:184). That feature and the two large falcate apical spines on the maxillule are features typical of many *Alcirona* species.

Weak sexual variation is evident in the dorsal ornamentation of some *Argathona* species. Females have less-developed rostral processes and ce-

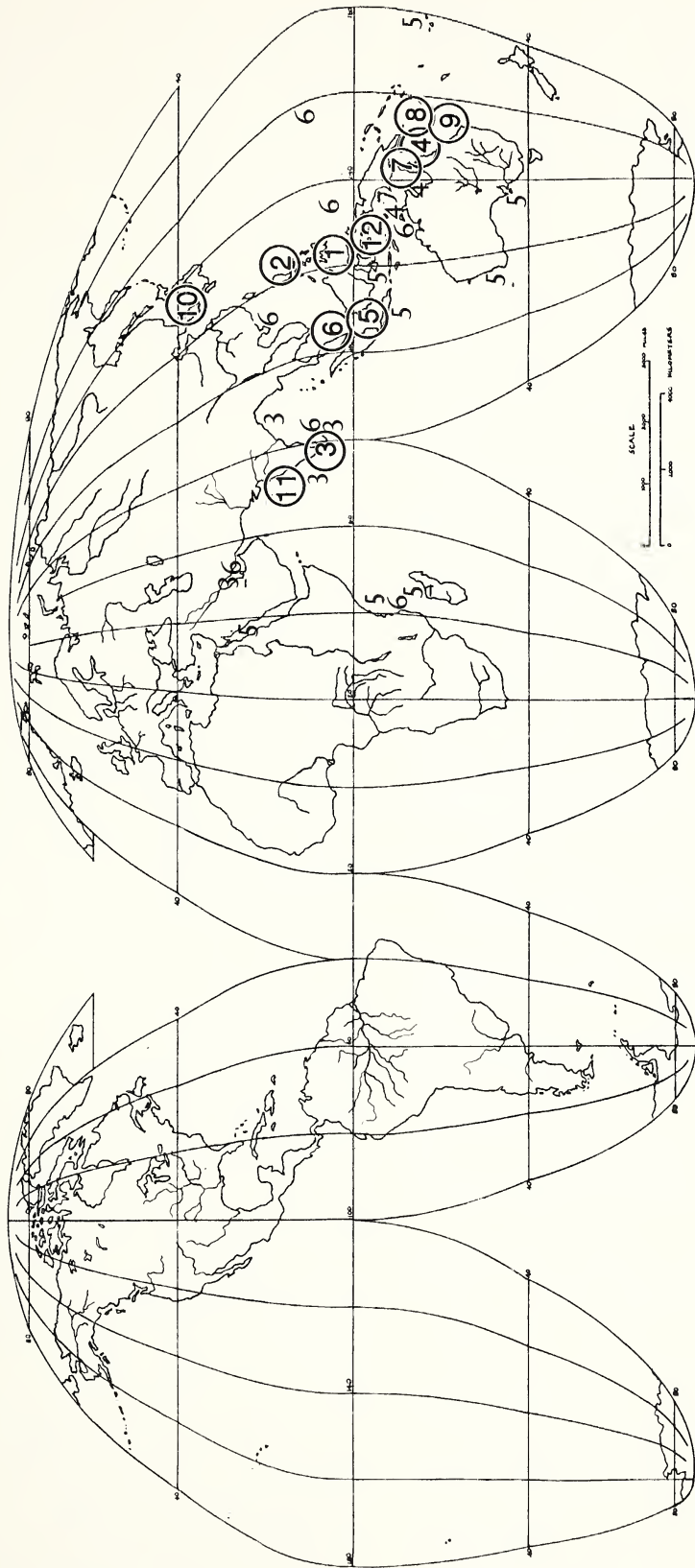


Figure 10. Distribution of *Argathona* species; type localities are circled. Species numbers are: 1, *A. setosa*; 2, *A. sulcata*; 3, *A. normani*; 4, *A. confinis*; 5, *A. macronema*; 6, *A. rhinoceros*; 7, *A. rostrata*; 8, *A. crenulata*; 9, *A. parca*; 10, *A. parca*; 11, *A. muraenae*; and 12, *A. stebbingi*.

phalic horns in *A. rostrata* and *A. rhinoceros*, respectively. The crenulation of the posterior margins of pereonal and pleonal segments in *A. crenulata* is somewhat less developed in females (Bruce, 1982a). Because of the sexual variation in dorsal ornamentation of some *Argathona* species noted above, females should be identified with care.

Bruce (1982a) notes that adult *A. rostrata* lack a molar process although it is present in juveniles.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The 12 species of *Argathona* are found in tropical/subtropical marine habitats throughout the Indo-West Pacific (Fig. 10) at depths ranging from 8 to 267 m. Five species have been collected as "temporary parasites" of fish: *A. macronema* (from *Epinephelus tauvina*, *Diagramma cinerascens*, *Pseudolabrus* sp., *Trachichthodes affinis*, *Cromileptes altivelis*, *Lutjanus argentimaculata*, *Plectropoma leopardus*, and *Plectropoma maculatum*); *A. rhinoceros* (from *Tetrodon leopardus*, *Epinephelus chlorostigma*, *Epinephelus malabaricus*, *Epinephelus taurina*, *Variola louti*, and *Plectropoma leopardus*); *A. parca* (from "eye of Queensland Grouper"); *A. muraeneae* (from *Muraena tessellata*); and *A. confine* (from "blue-spotted lagoon ray"). *Argathona macronema* has been reported from the eye of the sea turtle *Chelonia mydas* (by Monod, 1975). *Argathona macronema*, *A. setosa*, *A. rostrata*, and *A. crenulata* have been collected from among coral reef rock and from coral rubble and sand. *Argathona parca* and *A. rostrata* have been reported from sponges, and *A. confine* from *Comatula* sp.

## Genus *Corallana* Dana, 1853

*Corallana* Dana, 1853:773; Milne-Edwards, 1840:237; Heller, 1868:143; Schioedte and Meinert, 1879:286; Miers, 1881:78; Hansen, 1890:379; Stebbing, 1893:315, 1904a:13, 1904b:699; Richardson, 1900b:157; Moore, 1902:169; Barnard, 1914:358; Nierstrasz, 1917:101, 1930:1, 1931:163; Monod, 1934:1; Barnard, 1955:59; Pillai, 1954:6, 1961:49, 1967:272; Roman, 1970:167; Kensley, 1978:75; Bruce, 1982b:241; Bruce et al., 1982:464; Jones et al., 1983:837; Delaney and Brusca, 1985:728.

Non *Corallana*: Miers, 1881:78; Hansen, 1890:280; Richardson, 1900b:157; Moore, 1902:169 (= *Excorallana* Stebbing, 1904a).

## MATERIAL EXAMINED

*Corallana hirsuta*: 1) Laccadive Islands, Minikoi, BMNH 1928.12.: 1542-1551, 18 fe. and 14 ma. *Corallana africana*: 1) South Africa, Port Elizabeth, Zwartkops River, BMNH 1927.5.31: 71-75 (part) (syntypes), 4 ma., 4.4, 4.6, 5.2, and 5.2 mm. *Corallana nodosa*: 1) Sri Lanka, Lake Negombo, BMNH 1928.12.1: 1598-1600, 1 spec. (heavily dissected), 8.8 mm; 2) Siam, Koh Kut, USNM Acc.

No. 107725, "from jar H.M. Smith, Siam," 7 fe. and 3 ma.; 3) Siam, Koh Kut, USNM Acc. No. 107725, "from prawn," 1 fe. *Corallana furcilla*: 1) Siam, Koh Kut, USNM Acc. No. 107725, "from jar H.M. Smith, Siam," 11 fe.; 2) Philippine Islands, Aklan, New Washington, Tambuntingi Fishpond, USNM Acc. No. 271086, "isopods parasitic on *Chanos chanos*," 5 fe. *Corallana tridentata*: 1) Papua New Guinea, Port Moresby, BMNH 1982: 219:3 (part) (paratypes), 1 fe., 7.2 mm, and 1 ma., 7.2 mm. *Corallana bidentata*: 1) Papua New Guinea, Port Moresby, BMNH 1982: 221:3 (part) (paratypes), 1 fe., 12.4 mm, and 1 ma., 14 mm; 2) Australia, Queensland, Brisbane River, Kangaroo Point, AM No. P10691, "from submerged timber," 1981, 3 fe., 7.2, 8.2, 8.8, and 1 ma., 7.6 mm. *Corallana estuaria*: 1) Australia, Brisbane, BMNH 1921.3.23: 80-82, 2 fe., 8.0 and 12.0 mm, and 1 ma., 10.0 mm; 2) Papua New Guinea, Port Moresby, USNM Acc. No. 320977, "from wood," 1 fe. and 1 ma. *Corallana* spp.: 1) Siam, Bangkok, USNM Acc. No. 142233, "isopods parasitic on skin of *Puntius javanicus*," 2 fe., 3 ma., and 1 manca; 2) Eniwetok, Parry Island, USNM Acc. No. 197874, coll. H.S. Ladd, No. 1539, "from rounded block," 3 fe. and 2 ma.; 3) West Pacific, Japtan Island, USNM Acc. No. 197874, coll. H.S. Ladd, No. 1523, "seaward," 1 fe.; 4) Singapore, St. John's Island, CAS No. 025344, "bottom: rocks and mud," 3 fe., 7.6 ( gravid), 8.0, and 12.0 mm; 5) Australia, Hinchabrook Island, Nina Bay, "from rotting log in brackish creek," 2 fe. and 1 juvenile; 6) Australia, Queensland, Torres Strait, Prince of Wales Island, Off Bampfield Head, AM No. P28783, coll. CSIRO Coast Prawn Fisheries Project, "beam trawl over seagrass beds, time 1250 hrs.," 2 fe., 5.9 and 6.2 mm; 7) Australia, Queensland, near Lizard Island, 1 mile SW of Eagle Island, AM No. P28790, LI-61, depth 4-91 m, "sponge sample with some algae and coral rubble," 1 manca, 3.5 mm.

## DIAGNOSIS

Antennule peduncle 2- or 3-articulate; basal article of peduncle enlarged. Frontal lamina shape various, ovoid, triangular, pentagonal, or quadrangular, but not elongate; reduced or absent in some species. Clypeus short, small, not encompassing small labrum, or crescent-shaped and partly encompassing small labrum. Mandible with short incisor (long in *Corallana kulai* and *C. sp.* Bruce, 1982b); incisor bi- or tricuspid; molar process small, lacinia mobilis small or absent. Maxillule lateral lobe apex with 1 large falcate spine; medial lobe simple, blunt. Maxilla 2-articulate, rounded lobe. Maxilliped very narrow, without endite; basis very elongate, length 2.0-4.0 times width; palp always 5-articulate, middle palp article not elongate (except in *C. sp.* Bruce, 1982b). Anterior pereopods without serrate dactyli and propodi; carpi not produced on posteromedial margins ("inner angles") as in *Tachaea*.

## ADDITIONAL DESCRIPTION

Corallanidae with eyes well developed, at lateral margins of cephalon. Dorsum often with tubercles

and setae (Fig. 1C). Antennule peduncle basal article enlarged (Fig. 11F). Clypeus varies from short and small to inverted V- or semilunar shape, may or may not encompass small labrum (Figs. 12D, F). Mandible palp inserted near base, 3-articulate; middle article longest, all articles with comblike cuticular structures, middle and distal articles with ctenate marginal setae (Figs. 11A, 12E, G, H, 13B-F). Maxillule lateral (outer) lobe slender, tapering to form single, large falcate spine (Figs. 11C, 13A, 14E, F); some specimens of *Corallana* sp. (USNM 142233) have 1 minute, straight spine at base of large spine. Maxilla apex with 0–1 simple seta, occasionally with comblike cuticular structures (Figs. 11B, 14D). Maxilliped palp apical article and medial margins of other articles with short simple setae (Figs. 11D, E, 14A–C). Pereopods I–III subprehensile, with simple setae and robust spines on posteromedial margins (Fig. 12A). Pereopods IV–VII longer, ambulatory, with stout spines and setae on posteromedial margins (Figs. 12B, C). Pleopod peduncles broader than long, with 3–4 coupling spines and group of proximal setae on medial margins, and with simple spine on lateral margins (Figs. 15A–E). Exopods of pleopods broader, longer, with more plumose marginal setae than endopods. Endopods of pleopods 3–4 naked or with reduced setation in some species (Figs. 15C, D). Endopod of pleopod 5 naked, proximal medial margin produced, lobe-like (Fig. 15E). Male pleopod 2 with rodlike appendix masculina, with simple apex, arising from proximal medial margin of endopod (Fig. 15B). Pleotelson lateral margins often bisinuate, apex bluntly rounded or truncate. Uropodal exopods often elongate, narrow, with longitudinal keel (Fig. 1C).

#### TYPE SPECIES

*Corallana hirticauda* Dana, 1853:774, plate 51, figures 8a–c, by monotypy. Bruce (1982b:241, citing T.E. Bowman, personal communication) states that type specimens of the type-species have not been located and were probably lost when the sloop 'Peacock' sank off the mouth of the Columbia River in 1841.

#### DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

- 1) *Corallana hirticauda* Dana, 1853:774, plate 51, figures 8a–c; Schioedte and Meinert, 1879: 287; Hansen, 1890:388; Stebbing, 1893:315, 1904a:13, 1904b:705; Richardson, 1900b:157; Nierstrasz, 1917:101, 1931:163; Bruce, 1982b: 241; Jones et al., 1983:845.

**DISTRIBUTION.** Tongatabu, Philippines.

- 2) *Corallana hirsuta* Schioedte and Meinert, 1879: 287, table V, figure 11; Stebbing, 1904a:13, 1904b:704; Nierstrasz, 1931:163; Monod, 1934:1; Barnard, 1955:59; Bruce, 1982b:243; Jones et al., 1983:845.

**DISTRIBUTION.** Philippines, Maldives, and Indochina.

- 3) *Corallana collaris* Schioedte and Meinert, 1879: 287, table V, figures 1, 2; Nierstrasz, 1931: 165; Bruce, 1982b:248; Jones et al., 1983:845.

**DISTRIBUTION.** Philippines.

- 4) *Corallana brevipes* Schioedte and Meinert, 1879: 287, table V, figures 3, 4; Nierstrasz, 1931: 165; Bruce, 1982b:248; Jones et al. 1983:845.

**DISTRIBUTION.** Philippines.

- 5) *Corallana nodosa* Schioedte and Meinert, 1879: 287, table V, figure 7; Stebbing, 1904a:13; Nierstrasz, 1931:165; Barnard, 1955:59; Pillai, 1954:6, 1961:49, 1967:272; Bruce, 1982b:282; Jones et al., 1983:845.

**DISTRIBUTION.** Philippines, Sri Lanka, India, Australia, and Papua New Guinea.

- 6) *Corallana basalis* (Heller, 1868:143, table XII, figures 14, 14a); Schioedte and Meinert, 1879: 287; Nierstrasz, 1931:165; Bruce, 1982b:248. *Aega basalis* Heller, 1868.

**DISTRIBUTION.** Nicobar Islands, Indian Ocean.

- 7) *Corallana sculpta* (Milne-Edwards, 1840:237); Bruce, 1982b:248.

*Cirolana sculpta* Milne-Edwards, 1840.

**DISTRIBUTION.** Malabar, India.

- 8) *Corallana africana* Barnard, 1914:358, plate XXX, figure D; Nierstrasz, 1931:165; Roman, 1970:167; Kensley, 1978:75; Bruce, 1982b:242; Jones et al., 1983:845.

**DISTRIBUTION.** South Africa and Madagascar.

- 9) *Corallana leopoldi* (Nierstrasz, 1930:1); Bruce, 1982b:248.

*Tachaea leopoldi* Nierstrasz, 1930:1.

**DISTRIBUTION.** Aroe Islands, Moluccas.

- 10) *Corallana glabra* Nierstrasz, 1931:163, figures 30–37; Bruce, 1982b:248.

**DISTRIBUTION.** Kei Islands, Arafura Sea.

- 11) *Corallana furcilla* Barnard, 1955:59, figures 28c–e; Kensley, 1978:75; Bruce, 1982b:248; Jones et al., 1983:845.

**DISTRIBUTION.** Inhambane, Mozambique; Siam; and Philippines.

- 12) *Corallana kulai* Bruce, 1982b:243, figures 2, 3; Jones et al., 1983:845.

**DISTRIBUTION.** Western Australia.

- 13) *Corallana* sp. Bruce, 1982b:246, figures 4a–i.

**DISTRIBUTION.** New Guinea.

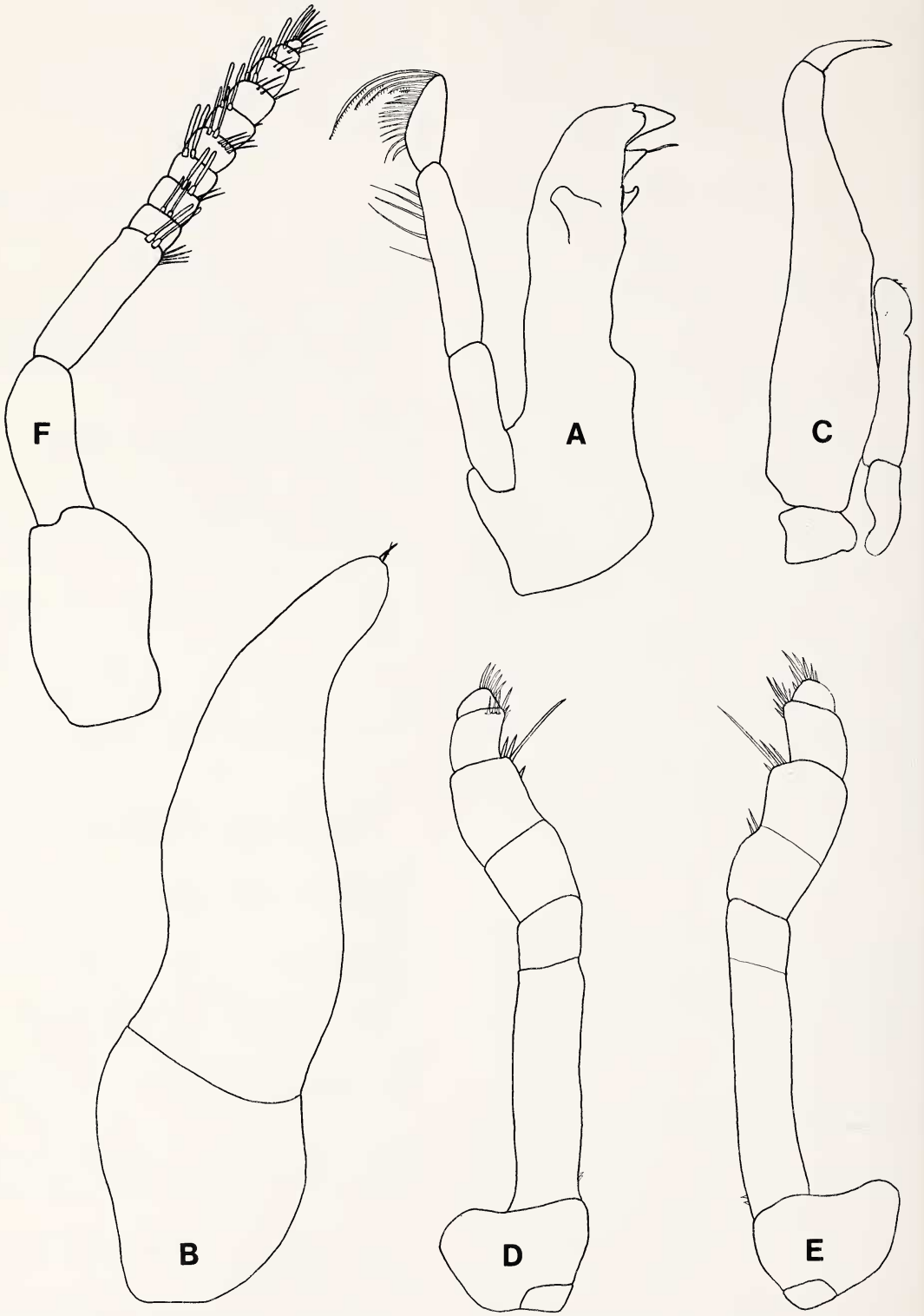


Figure 11. *Corallana* sp., USNM Acc. No. 142233: A, mandible; B, maxilla; C, maxillule; D, right maxilliped; E, left maxilliped; and F, antennule.



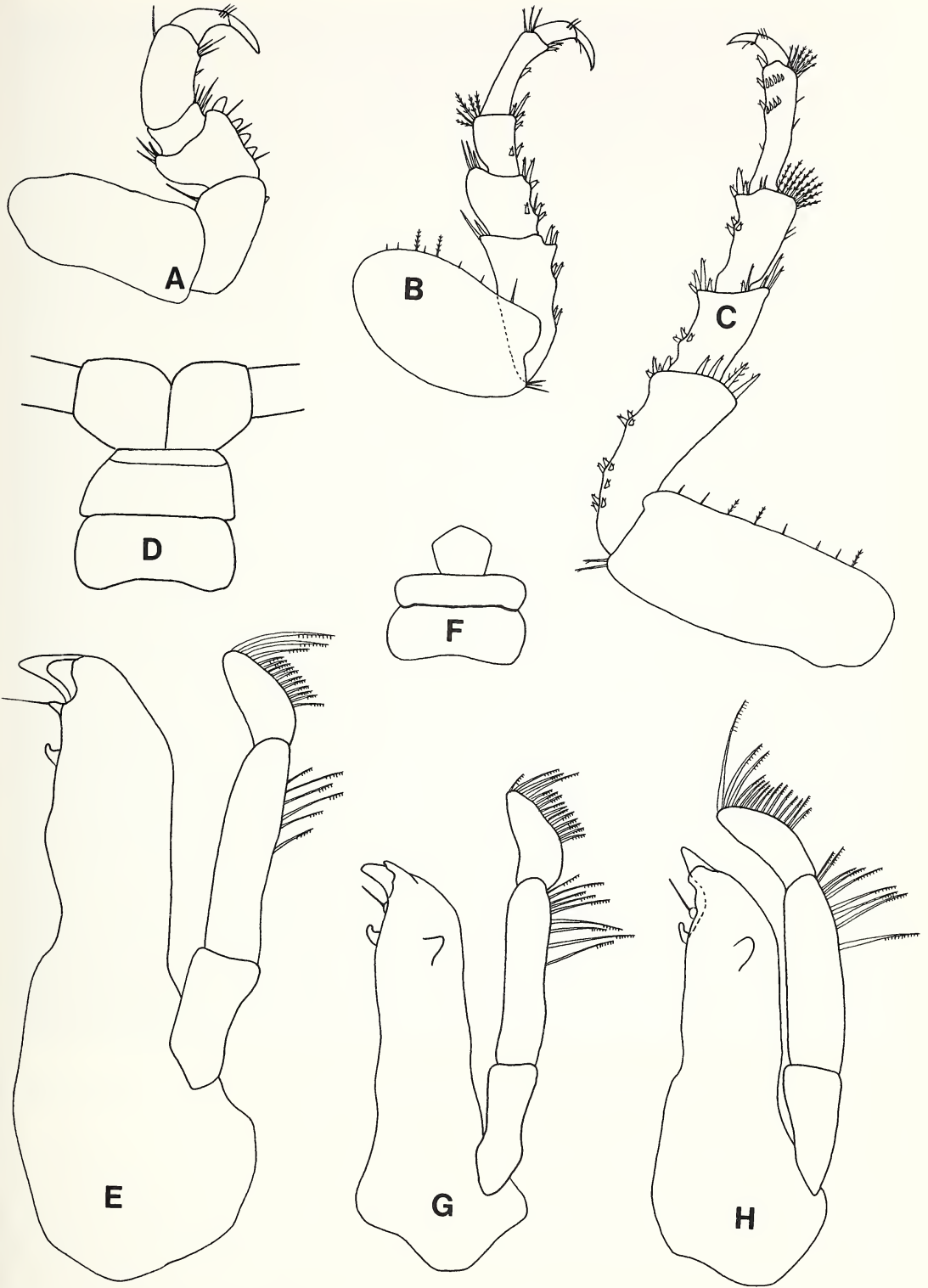


Figure 12. *Corallana* sp., USNM Acc. No. 142233, A-E: A, pereopod I; B, pereopod IV; C, pereopod VII; D, antennule bases, frontal lamina, clypeus, and labrum; and E, mandible. *Corallana nodosa*, USNM Acc. No. 107725, F-H: F, frontal lamina, clypeus, and labrum; G, right mandible; and H, left mandible.

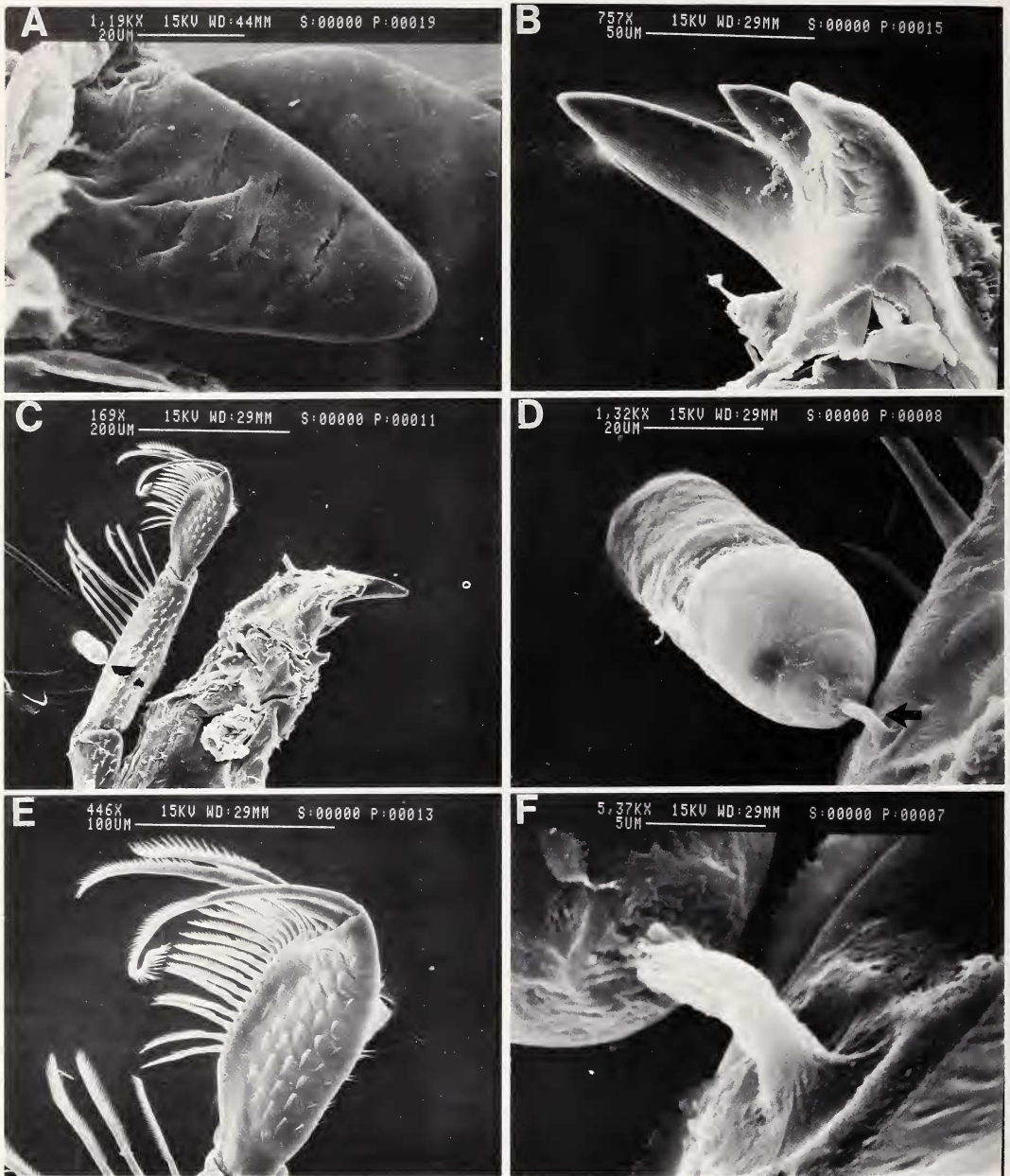


Figure 13. Scanning electron micrographs of *Corallana estuaria*, USNM Acc. No. 320977: A, apex of medial lobe of maxillule; B, mandible apex; C, mandible; D, parasitic protozoan on mandibular palp (arrow in C); E, distal article of mandibular palp; and F, detail of protozoan attachment to palp (arrow in D).

14) *Corallana estuaria* Jones et al., 1983:837, figures 1a-n.

**DISTRIBUTION.** Papua New Guinea and Queensland, Australia.

15) *Corallana bidentata* Jones et al., 1983:840, figures 2a-n.

**DISTRIBUTION.** Papua New Guinea.

16) *Corallana tridentata* Jones et al., 1983:842, figures 3a-n.

**DISTRIBUTION.** Papua New Guinea.

#### REMARKS

The genus *Corallana* was erected by Dana (1853) to house his new species *Corallana hirticauda*. Bruce (1982b) and Jones et al. (1983) noted the need for a thorough revision of *Corallana*. Both studies noted that a great deal of variation in the morphology of the mouthparts, frontal lamina, and clypeus exists in this genus. Variation is notably evident in the *Corallana* "sp." partly described but not named by Bruce (1982b). Some *Corallana* type material has been lost, and many of the earlier species

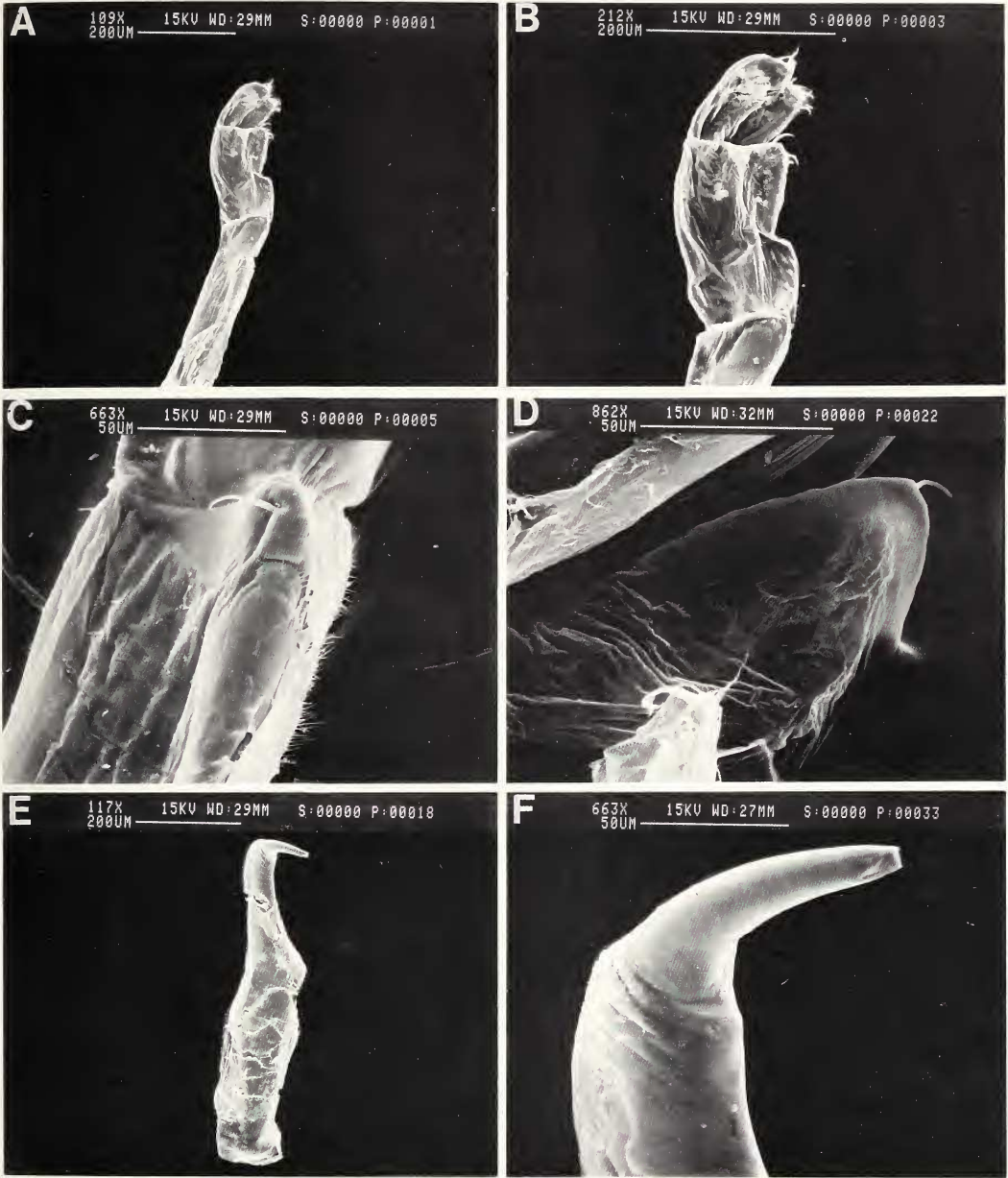


Figure 14. Scanning electron micrographs of *Corallana estuaria*, USNM Acc. No. 320977: A, maxilliped palp; B, detail of distal palp articles; C, detail of maxilliped basis; D, maxilla apex; E, maxillule; and F, maxillule apex.

descriptions are poor or incomplete; some lack any figures whatsoever.

In the description of *Corallana bidentata* Jones et al., 1983, the figures of the mandible, maxilliped, frontal lamina, clypeus, and labrum resemble those of *Tachaea*. The holotype was not examined by the present author, however, so this species must remain in *Corallana* for the present.

Sexual dimorphism in dorsal ornamentation exists in some *Corallana* species. As is usually the case in corallanid species, males often possess much more distinct tuberculation and ornamentation than do females, including cephalic, pereonal, and pleo-

nal tuberculation, and an upwardly produced basal article on the antennule peduncle. In some *Corallana* species, however, females are known to possess characters of ornamentation lacking in males. For example, in *C. furcilla* adult females have a pair of distinct apical processes or "prongs" on the pleotelson, which are apparently absent in males.

#### BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The 16 species of *Corallana* are restricted to marine and brackish- (low salinity) water habitats in the

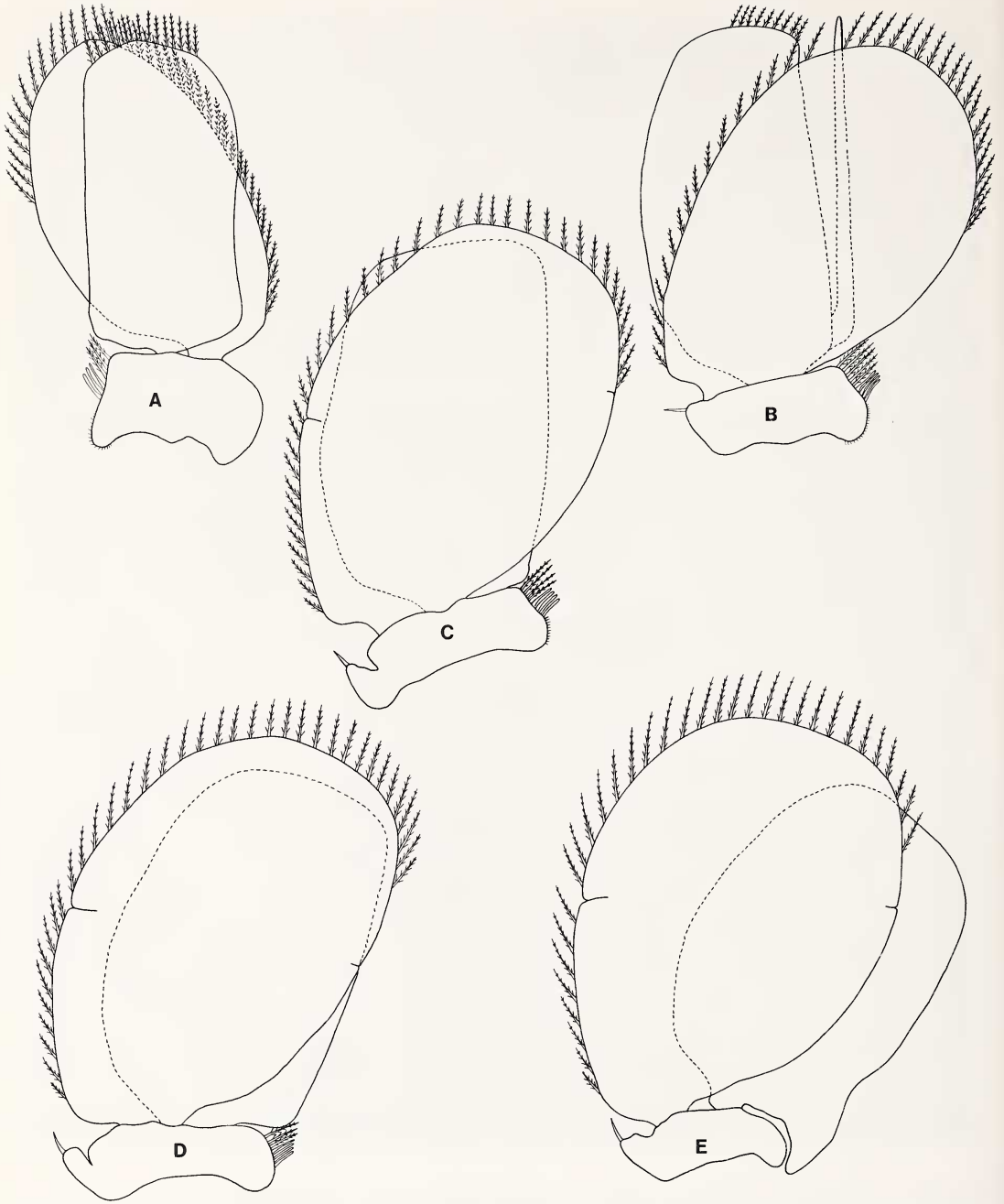


Figure 15. *Corallana* sp., USNM Acc. No. 142233: A, pleopod 1; B, pleopod 2; C, pleopod 3; D, pleopod 4; and E, pleopod 5.

Indo-West Pacific (Fig. 16) at depths ranging from the intertidal zone to 150 m. Six species are described as being “from wood” in estuarine or brackish-water habitats—either from rotting logs, mangrove prop roots, pier pilings, or treated wood test panels, in their own burrows or in those of other wood borers such as *Limnoria* sp., *Sphaeroma terebrans*, and *S. triste*. Wood used for burrowing by *Corallana* species includes *Avicennia eucalyptifolia*, *Rhizophora stylosa* (prop roots), and *Alstonia scholaris* (treated test panels) (see Jones et al., 1983).

Jones et al. (1983) discussed the wood-boring species of *Corallana* and noted that some of these *Corallana* species occurred in small colonies of about 20 individuals each in man-made wood structures and in larger colonies in mangrove stumps (*C. nodosa*), although *C. bidentata* occurred only singly or in pairs.

*Corallana* species have been reported from a variety of other hosts and substrates. *Corallana hirticauda* was found on dead coral (Dana, 1853); *C. bidentata* in the pneumatophores of *Sonneratia*

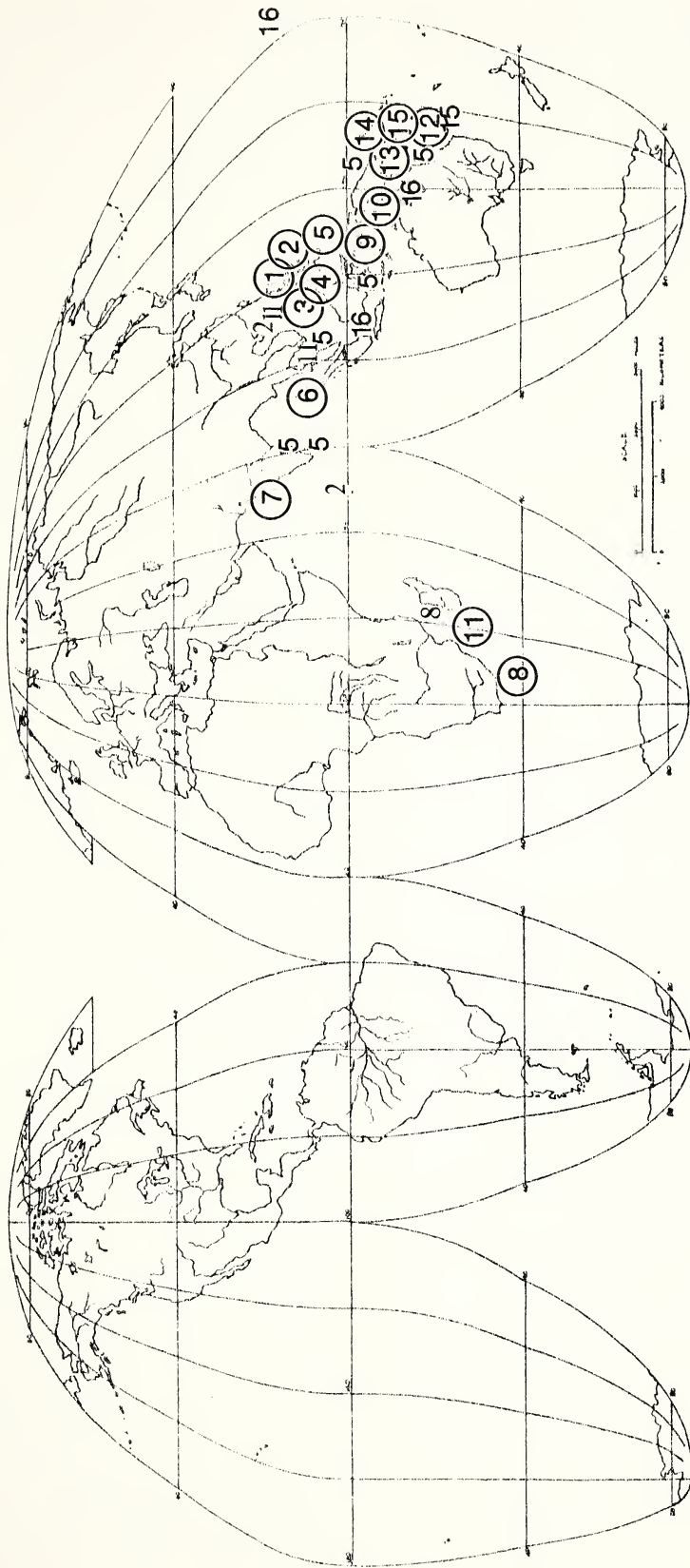


Figure 16. Distribution of *Corallaneta* species; type localities are circled. Species numbers are: 1, *C. hirticauda*; 2, *C. hirsuta*; 3, *C. collaris*; 4, *C. brevipes*; 5, *C. nodosa*; 6, *C. basalis*; 7, *C. sculpia*; 8, *C. africana*; 9, *C. glabra*; 10, *C. leopoldi*; 11, *C. furcilla*; 12, *C. kulai*; 13, *C. tridentata*; 14, *C. estuaria*; 15, *C. bidentata*; and 16, *C. sp.*

*alba* (Jones et al., 1983); and other *Corallana* species on rocks/mud, with sponge, algae, and coral, and in beam trawls over seagrass beds. *Corallana furcilla* has been collected as a "parasite" from *Chanos chanos* in a fishpond in the Philippines, *Corallana* sp. as a "parasite" from the fish *Puntius javanicus* in Siam, and *C. nodosa* "from prawn" at Lake Negombo, Sri Lanka.

### Genus *Excorallana* Stebbing, 1904a

*Excorallana* Stebbing, 1904a:13, 1904b:703; Lemos de Castro, 1960:64, 1964:3; Menzies and Glynn, 1968:42; Monod, 1969:48; Carvacho and Yanez, 1971:129; Delaney, 1982:273; Bruce et al., 1982:464; Delaney, 1984:1; Delaney and Brusca, 1985:728.

*Excorallana* Richardson, 1905:138 (*lapsus calami*).

### MATERIAL EXAMINED

*Excorallana acuticauda*: 1) South Atlantic Ocean, Hotspur Bank, BMNH 1880:30, holotype, H.M.S. *Alert*, depth 63 m, 17°32'S, 35°45'W, Leg. Lords of the Admiralty, 1 fe.; 2) Brazil, Alagoas, Maceio, USNM 25821, Branner-Agassiz Expedition, "from coral reef," 1 ma. and 1 fe.; 3) Florida, Loggerhead Key, N.W. of lighthouse, USNM (no Acc. No.), 4 Aug 1924, coll. W.L. Schmitt, depth 3–5 m, 1 ma.; 4) Florida, Loggerhead Key, USNM Acc. No. 68708, 1 ma.; 5) Florida, USNM Acc. No. 15488, Manter #778, from *Prianthus crenatus*, "dynamite," 1 fe. (gravid); 6) Brazil, Pernambuco, USNM 43676, 1 spec.; 7) Florida, Loggerhead Key, N.W. of lighthouse, USNM (no Acc. No.), 4 Aug. 1924, coll. W.L. Schmitt, depth 3–9 m, 1 ma.; 8) Florida, Tortugas, White Shoals, USNM Acc. No. 84129, Sta. 18, 1 fe.; 9) Florida, Tortugas, White Shoals, USNM Acc. No. 84129, col. W.L. Schmitt, Sta. 22, 1 fe.; 10) (as *Excorallana antillensis*), West Indies, St. Thomas, ZMUC syntype, 1 ma.; 11) (as *E. antillensis*), West Indies, ZMUC syntype, 1 fe.; 12) (as *E. antillensis*), West Indies, ZMUC syntype, 1 ma.; 13) West Indies, U.S. Virgin Islands, St. Croix, N.E. coast, 23 March 1982, KK-1982, coll. K. Kleeman, "taken at 10 m on forereef in empty bivalve burrows with other *Excorallana* species and unidentified cirolanids," 1 ma. and 1 fe.; 14) West Indies, U.S. Virgin Islands, St. Croix, 7 June 1983, ACM-1983, coll. A.C. Miller, "off rocks at 16 m depth," 1 ma.; 15) Florida, Biscayne Key, USNM 45956, 2 fe.; 16) West Indies, St. Thomas, USNM 87072, *Albatross*, Sta. 7667, 1 fe.; 17) Puerto Rico, Luis Pena Channel, USNM 406, coll. Johnson-Smithsonian Deep-Sea Expedition, "with 8' net and cargo light over ship's side," 3 fe.; 18) West Indies, Virgin Islands, St. Thomas, USNM 111384, 1 spec.; 19) Puerto Rico, Crashboat Basin, USNM 119486, "from stomach of *Odontoscion denter*, depth 3–4 m," 1 spec. *Excorallana tricornis tricornis*: 1) Florida, Tortugas, USNM 68375, "from red grou-

per *Epinephelus*," 6 ma. and 23 fe.; 2) West Indies U.S. Virgin Islands, St. Croix, N.E. coast, KK-1982, 23 March 1982, "taken at 10 m on forereef from empty bivalve burrows with other *Excorallana* spp. and cirolanids," coll. K. Kleeman, 8 ma. and 15 fe.; 3) West Indies, ZMUC syntypes, 305 spec.; 4) Central America, "Reialeio," ZMUC, 1 fe.; 5) West Indies U.S. Virgin Islands, St. Croix, ZMUC syntype, coll. Orsted, 1 fe.; 6) West Indies, ZMUC syntypes, 3 ma. and 2 fe.; 7) West Indies, St. Thomas, ZMUC syntypes, 2 fe.; 8) Florida, USNM Acc. No. 93400, Sta. 6, 1 ma. and 1 fe.; 9) Florida, USNM Acc. No. 93400, "living in tubular bryozoan from piles at Fort," 1 ma. and 1 fe.; 10) Florida, Tortugas, USNM Acc. No. 115488, "Night—found on table where Hartman was cutting up fish taken from trap on west side Loggerhead Key," 1 ma.; 11) Florida, Tortugas, Loggerhead Key, USNM (no Acc. No.), 1 ma., 1 fe., and 1 juvenile; 12) Florida, Tortugas, USNM (no Acc. No.), June 1925, "with polychaetes," coll. Dexter, 1 ma.; 13) Florida, Tortugas, Loggerhead Key, USNM (no. Acc. No.), 21 July 1924, "from rocks west of Lighthouse," coll. W.L. Schmitt, 1 fe.; 14) Florida, Tortugas, USNM Acc. No. 115488, "from outside head region and within buccal cavity of Nassau Grouper, taken in trap," 4 ma. and 10 fe.; 15) Florida, W. side of Bush Key Reef, near Long Key, USNM Acc. No. 84129, "from holes in rocks, 1 m depth," 1 ma.; 16) Florida, Tortugas, Loggerhead Key, off northern end, USNM Acc. No. 84129, 1 ma. and 1 fe.; 17) West Indies, USNM Acc. No. 208263, Sta. 106-56, 1 ma.; 18) Caribbean Sea, Saba Bank, USNM Acc. No. 208263, Sta. 106-56, "from princess rockfish *Mycteroperca bowersi* at 12.5 m depth," 12 spec.; 19) Puerto Rico, off Puntilla Point, USNM Acc. No. 142536, Sta. 19, depth 6–7 m, 5 spec.; 20) Puerto Rico, San Juan, USNM Acc. No. 142536, Sta. 21, "mangrove swamp," coll. Smithsonian-Hartford Expedition, 2 spec.; 21) Caribbean Sea, Isla Roatan, S.W. corner of island, RCB-1978, "living in yellow sponge, taken via SCUBA coll. on reef," coll. R.C. Brusca, 1 ma. *Excorallana tricornis occidentalis*: 1) Mexico, Gulf of California, Baja California Sur, Isla San Francisco, AHF 518-36, "with 3 *Excorallana houstoni*," coll. R/V *Velero III*, 1 ma.; 2) Mexico, Gulf of California, Baja California Norte, San Felipe, USNM Acc. No. 150937, 3 June 1934, "from holes in red beach sponges," 15 spec.; 3) Gulf of California, Baja California Norte, San Felipe, USNM Acc. No. 144660, "on gorgonians," 1 spec.; 4) Gulf of California, Baja California, Isla Tiburon, Bahia Red Bluff, USNM Acc. No. 150937, 75+ spec.; 5) Gulf of California, Baja California Sur, Isla Espiritu Santo, San Lorenzo Channel, USNM Acc. No. 139772, #60736, "corallines," depth 43 m, 1 ma.; 6) Gulf of California, Baja California Sur, Cabo San Lucas, USNM 86383, 19 July 1938, "from external and nostril of Gulf grouper, fish #1," 2 ma. and 19 fe.; 7) Gulf of California, Bahia Concepcion, USNM 86381, 1 fe.; 8) Ecuador, La Libertad, USNM 68438, Sta. 10-33, 1 fe. (cephalon damaged); 9) Mexico,

Jalisco, Bahia Coastocomate, 60 km N.N.W. of Manzanillo, Colima, USNM Acc. No. 28194, RAD-68-I, "inside empty *Gastrochaena* valves," depth 3–20 m, 20 spec.; 10) Mexico, Jalisco, Bahia Espiritu Santo, Playa Paraiso, USNM Acc. No. 281954, RAD-68-II, depth 5–10 m, 1 ma. and 3 fe.; 11) Mexico, Sonora, Puerto Penasco, AHF 1010-01, 2 fe.; 12) Costa Rica, Isla Cano, HG-1984, "with 280 micron dip net at 23:54 hours," coll. H. Guzman, Universidad de Costa Rica, 3 ma., 4 fe., and 2 mancas; 13) Costa Rica, Isla Cano, HG-1984, "with 280 micron dip net at 23:45 hours," coll. H. Guzman, Universidad de Costa Rica, 2 ma., 4 fe., and 5 mancas. *Excorallana houstoni*: 1) Galapagos Islands, Isla Santa Cruz, Academy Bay, Nelson's Landing, CAS 02544, "taken intertidally," 1 ma.; 2) Galapagos Islands, Isthmo Perry, Elizabeth Bay, Penguin Rocks, LACM (no Acc. No.), 23 May 1970, "intertidal rocks," coll. L.T. and V. Williams, 1 fe.; 3) Mexico, Gulf of California, Baja California Sur, Cabo San Lucas, Cabeza Ballena, AHF (no Acc. No.), 9 Nov 1946, Dawson Sta. 53, "at 7 a.m., water temp. 26.6°C," coll. E.Y. Dawson, 1 ma. and 1 fe.; 4) Mexico, Gulf of California, Baja California Sur, Isla San Francisco, AHF 518-36, "littoral—with 1 ma. *E. tricornis occidentalis*," coll. R/V *Veleo III*, 1 ma. and 2 fe.; 5) Galapagos Islands, Nameless Island, WDH-330765, Sta. 26A, 22 Feb 1978, "intertidal, with 25+ *Dynamenella* sp.," coll. W.D. Hope, 1 fe. *Excorallana bruscai*: 1) Mexico, Gulf of California, Baja California Sur, Isla Espiritu Santo, Bahia San Gabriel, USNM 144492, #634-37, "shore," 1 ma. and 3 fe. (2 gravid); 2) Mexico, Gulf of California, Sonora, Puerto Penasco, AHF 1006-01, "rocky intertidal," 1 ma.; 3) Mexico, Sonora, Puerto Penasco, AHF 1004-01, holotype 6611, "from sand beach in evening, using seine," 1 ma.; 4) Mexico, Sonora, Puerto Penasco, PMD-1981, 19 April 1981, "found inside white sponge *Leucetta losangelensis* with *Paracerceis sculpta*, in low intertidal," coll. P.M. Delaney, 1 ma.; 5) Mexico, Gulf of California, Baja California Sur, Bahia Concepcion, EWI-1980, "from subtidal coralline algae," coll. E.W. Iverson, 1 ma.; 6) Mexico, Sonora, Puerto Penasco, Cholla Bay, UA68-139, 1 ma.; 7) Mexico, Sonora, Puerto Penasco, Cholla Bay, AHF 1007-01, "on mud of low intertidal," 1 ma.; 8) Mexico, Sonora, Puerto Penasco, Station Beach, PP-ZI-129-21, 23 April 1979, "infauna of coquina reef," coll. P. Pepe, 4 ma. and 3 fe.; 9) Mexico, Sonora, Puerto Penasco, Station Beach, PP-ZII-51-83, "inside *Serpulorbis margaritaceus* tubes," coll. P. Pepe, 4 ma. and 1 fe. *Excorallana subtilis*: 1) West Indies, St. Thomas, ZMUC holotype, 1 juvenile; 2) Florida, Key West Harbor, USNM 13581, #614, 2 ma. *Excorallana truncata*: 1) Mexico, Baja California, Kellett Channel, S. of Cedros Island, LACM 71-159, "depth 36 m, pebbles and shale," R/V *Searcher*, 1 fe. (gravid); 2) Mexico, Gulf of California, Sonora, Puerto Penasco, PP-ZI-129-49, 26 Jan 1979, "cryptofauna of coquina reef," coll. P. Pepe, 1 ma. and 1 fe.; 3) California, Santa Monica

Bay, AHF 1636-1, Sta. 13, #1, "depth 64–66 m, coarse sand," 1 fe.; 4) Mexico, Baja California, Thurloe Head, USNM Acc. No. 128938, #283-34, "depth 14–18 m, dredging off Thurloe Pt.," 1 ma.; 5) California, Point Fermin, USNM Acc. No. 112912, #168, 1 ma.; 6) Mexico, Gulf of California, USNM (no Acc. No.), 25 March 1889, Sta. 3024, "depth 20 m," coll. R/V *Albatross*, 2 spec.; 7) Mexico, Baja California, Bahia San Quintin, USNM Acc. No. 139772, #488, "sand and seaweed," 1 ma.; 8) Mexico, Baja California, Isla Cerros, S. Bay, USNM Acc. No. 128938, "dredging at depth 18–26 m," 1 fe. *Excorallana berbicensis*: 1) Surinam (Dutch Guiana), Clevia Estate, USNM 60286, "from Clevia waterside," 1 ma. and 2 fe.; 2) British Guiana, Rio Berbice, USNM 50402 (types), Feb 1913, 2 spec. *Excorallana mexicana*: 1) Florida, Hillsborough Co., 104 km W. of Egmont Key, USNM 170833, Hourglass Cruises, Sta. 66-443, depth 55 m, coll. R/V *Hernan Cortez*, 1 ma.; 2) Florida, Hillsborough Co., 104 km W. of Egmont Key, USNM 330682, depth 55 m, coll. Hourglass Cruises, 1 fe.; 3) Florida, Hillsborough Co., 104 km W. of Egmont Key, Hourglass Cruises, Sta. 66-109, depth 55 m, 1 fe.; 4) Gulf of Mexico, USNM 9601, Sta. 2369-2374, depth 45–49 m, coll. U.S. Fish Commission Steamer *Albatross*, 3 ma.; 5) Gulf of Mexico, USNM 9601, Sta. 2406, coll. R/V *Albatross*, 1 ma.; 6) Gulf of Mexico, USNM 20479, Sta. 2405, coll. R/V *Albatross*, 2 spec.; 7) Gulf of Mexico, USNM 20478, Sta. 2369-74, R/V *Albatross*, 11 spec.; 8) Gulf of Mexico, USNM 9814, Sta. 2407, R/V *Albatross*, 2 ma.; 9) Dutch West Indies, Oranjestad, USNM Acc. No. 142536, Sta. 46, 1 ma.; 10) Northwest Atlantic Ocean, off Florida, USNM 211835, "by trawl at depth 53.7 m," 1 ma.; 11) Florida, between delta of Mississippi River and Cedar Keys, USNM 39420, Sta. 2369-74, depth 45–49 m, 11 ma. and 8 fe.; 12) Florida, between delta of Mississippi River and Cedar Keys, USNM 32074 (holotype), Sta. 2406, depth 47 m, coll. R/V *Albatross*, 1 ma. *Excorallana oculata*: 1) West Indies, ZMUC syntypes, 1 ma. and 1 fe.; 2) Brazil, off Cape St. Roque, USNM 43648, Sta. 2578, depth 36 m, coll. R/V *Albatross*, 1 ma.; 3) Brazil, off Cape St. Roque, USNM 32246, Sta. 2758, depth 36 m, coll. R/V *Albatross*, 1 ma. and 1 fe.; 4) West Indies, U.S. Virgin Islands, St. Croix, N.E. coast, KK-1982, 23 March 1982, "taken at 10 m depth on foreereef in empty bivalve burrows with other *Excorallana* spp. and cirrolanids," coll. K. Kleeman, 2 ma. and 1 fe. (gravid); 5) West Africa, Cameroon, S.W. of Annobon, near Fernando Poo Island, USNM 119468, Sta. 282, depth 18–38 m, coll. Pillsbury, 7 spec.; 6) West Indies, Barbados, English Harbor, USNM 53886, "taken using electric light," 1 ma.; 7) West Indies, Barbados, English Harbor, USNM 86377, #25289, "collected with electric light," 2 ma.; 8) Caribbean Sea, Puerto Rico, off Playa de Fajardo, USNM 90436, Sta. 358/67, "captured with circular net and electric cargo light at anchorage," coll. Johnson-Smithsonian Deep-Sea Expedition, 1

fe.; 9) West Africa, Congo, Ile. Annobon, ZMHUB, OM 29, "taken at 50–60 m with trawl or dredge," coll. A. Crosnier, 40+ spec. *Excorallana quadricornis*: 1) West Indies, St. Thomas, ZMUC syntypes, 1 ma. and 1 fe.; 2) West Indies, ZMUC syntype, 1 fe.; 3) Brazil, USNM 91435, #1.316, "Isopods from Museo Paulista, Brazil," 5 ma. and 10 fe.; 4) Puerto Rico, San Juan, USNM Acc. No. 142536, Sta. 21, "mangrove swamp," coll. Smithsonian-Hartford Expedition, 1 ma.; 5) West Indies, U.S. Virgin Islands, St. Croix, Mangrove Island, USNM Acc. No. 142536, Sta. 37, coll. Smithsonian-Hartford Expedition, 1 ma. and 2 fe.; 6) Jamaica, Montego Bay, Bogue Islands, USNM 52163, "from red sponge on mangrove roots," 3 ma.; 7) Jamaica, Montego Bay, Bogue Islands, USNM 41806, "from red sponge on mangrove roots," 33 spec.; 8) Venezuela, Isla Aves, USNM 154534, "isopods from fish or on copulatory scars of sea turtle *Chelonia mydas*," 1 ma. and 1 fe.; 9) No locality, USNM Acc. No. 283626, RAD-68-I, coll. G.E. Radwin, 1 ma. and 12 fe.; 10) West Indies, Martinique, St. Luce, USNM Acc. No. 277606, "parasites from *Harpe rata*," 1 ma., 2 fe., and 1 juvenile; 11) Jamaica, Montego Bay, Bogue Islands, USNM 41808, "orig. No. 26," "commensal on black ascidian on mangrove roots," 1 ma. and 1 fe. ( gravid). *Excorallana sexticornis*: 1) Puerto Rico, Caballo Blanco Reef, USNM 44243, coll. steamer *Fish Hawk*, 1 ma.; 2) Florida, Key West, USNM 13540 (types), 1 ma. and 8 fe. *Excorallana warmingii*: 1) Cuba, off southern coast, USNM Acc. No. 198858, #786, "dip net under night light," coll. R/V *Oregon*, 1 ma.; 2) Puerto Rico, Luis Pena Channel, USNM 90439, Sta. 79, #406, "taken with 8' net and cargo light over ship's side," coll. Johnson-Smithsonian Deep-Sea Expedition, 6 fe.; 3) Caribbean Sea, USNM 9590, Sta. 2365, coll. R/V *Albatross*, 1 fe. (most of pleon and pleotelson missing); 4) Atlantic Ocean, ZMUC holotype, 17°47'N, 35°16'W, 1 ma.; 5) Atlantic Ocean, ZMUC, 17°43'N, 64°56'W, "sta. 1281 X, 50 M.W., 11:30 p.m.," 1 ma.; 6) Florida, Loggerhead Key, USNM Acc. No. 68708, "off wharf," 1 fe.; 7) Florida, Tortugas, S. of Loggerhead Key, USNM Acc. No. 68708, "surface tow, 7 min. S. of wreck to wreck, 5 a.m.," 1 fe.; 8) Florida, Tortugas, Loggerhead Key, USNM Acc. No. 68708, "plankton, 5 a.m.," 1 fe. *Excorallana fissicauda*: 1) West Indies, ZMUC holotype, 1866, 1 fe.

## DIAGNOSIS

Antennule peduncle 2- or 3-articulate; basal article of peduncle expanded. Frontal lamina narrow, shape various; clypeus and labrum very broad and short. Mandible with elongate, falcate incisor; molar process and lacinia mobilis small or absent. Maxillule lateral lobe forming single large recurved spine; medial lobe simple, with bluntly rounded apex. Maxilla forming simple lobe with bi- or trifid apex. Maxilliped palp always 5-articulate, middle article elongate (length = 2 × width); maxilliped basis not

elongate. Anterior pereopods without serrate dactyli or propodi; carpi not produced.

## ADDITIONAL DESCRIPTION

Corallanidae with eyes well developed, often contiguous at midline of cephalon, or nearly so. Body often with dorsal setae, spines, tubercles, or carinae; dorsum often with setae in pits and globate sockets (Figs. 1D, 17, 18A–D). Ventral and medial surfaces of antennules, antennae, frontal lamina, clypeus, labrum, and mouthparts often with many comb- and scalelike cuticular structures of 5–10 micrometer dimensions (Figs. 17, 20–23). Antennule peduncle basal article enlarged (Figs. 17C, 19D, 20A, C). Antenna peduncle articles 4 and 5 elongate (Figs. 19E, 20A). Frontal lamina, clypeus, and labrum (Figs. 20A–D, 21G) visible anterior to mandibles, but may be partly obscured by same. Mandible palp 3-articulate, middle and distal articles with plumose marginal setae; left and right mandibles interdigitate (Figs. 20A, 21A, B, 22A–C). Maxillule lateral lobe forming single large recurved spine; medial lobe simple (Figs. 21C, 22A, C, 23A). Maxilla apex bi- or trilobed (Figs. 21E, 22A, 23A–D). Maxilliped palp middle article elongate (length = 2 × width) (Figs. 21D, 22A, D–F). Pereopods I–III subprehensile, with short blunt spines on posterior medial margins of meri and ischia (Figs. 18E, F, 19A). Pereopods IV–VII longer, ambulatory, with spines and setae; propodi not dilated as in *Tachaea* (Figs. 19B, C). Peduncles of pleopods 1–4 with 4–6 coupling spines on medial margin and group of plumose setae ventral to spines, lateral margins with simple spine (Figs. 24A–E). Peduncles of pleopods 2–5 often with small lobe on lateral margins. All rami of all pleopods setigerous. Male pleopod 2 with rodlike appendix masculina arising from proximal medial margin of endopod (Fig. 24B). Pleotelson with lateral incisions in many species (Fig. 1D).

## TYPE SPECIES

*Excorallana tricornis tricornis* (Hansen, 1890), originally described as *Corallana tricornis*, by designation (Delaney, 1984:2).

## DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

- 1) *Excorallana tricornis tricornis* (Hansen, 1890): 379, table VI, figures 4a–p, table VII, figures 1a–d; Lemos de Castro, 1960:61, 1964:4; Hutton, 1964:447; Menzies and Glynn, 1968: 11; Monod, 1969:50; Carvacho and Yanez, 1971:130; Moreira and Sadowsky, 1978:107; Menzies and Kruczynski, 1983:70; Kensley, 1984:33; Delaney, 1984:3.
- Excorallana tricornis tricornis* Richardson, 1905:139, 1912:188; Rouse, 1969:133 (*lapsus calami*).
- Corallana tricornis* Hansen, 1890:379; Stebbing, 1893:315; Richardson, 1901:517; Moore, 1902:169; Nierstrasz, 1917:101.



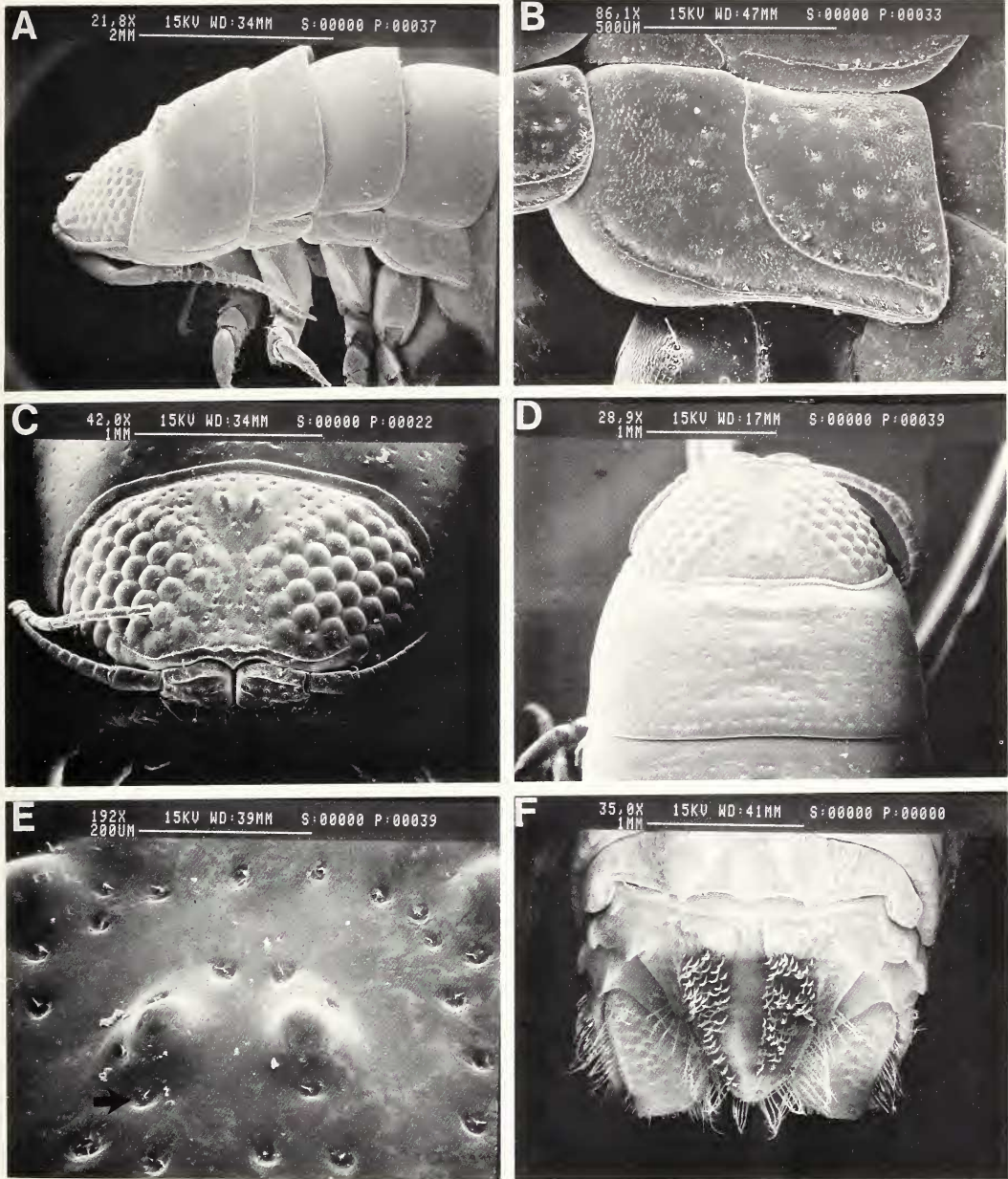


Figure 17. Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: A, anterolateral view; B, coxa IV; C, anterior view of cephalon; D, dorsal view of cephalon and pereonite I (arrow points to tubercle pair); E, tubercle pair (from D) surrounded by cuticular sensillae in "pits"; and F, dorsal setae and lateral incisions on pleotelson.

**DISTRIBUTION.** Gulf of Mexico and Caribbean.

- 2) *Excorallana houstoni* Delaney, 1984:11, figures 5-7, 20, 21.

**DISTRIBUTION.** Central Gulf of California, western Mexico, and Galapagos Islands.

- 3) *Excorallana bruscai* Delaney, 1984:5, figures 1-4, 14-17, 22.

**DISTRIBUTION.** Gulf of California.

- 4) *Excorallana acuticauda* (Miers, 1881):78, plate VII, figure 13; Lemos de Castro, 1960:61, 1964:3; Monod, 1969:48; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana acuticauda* Miers, 1881:78; Hansen, 1890:388; Nierstrasz, 1917:101.

*Excorallana antillensis* (Hansen, 1890):383; Lemos de Castro, 1960:61, 1964:4; Monod, 1969:48; Carvacho and Yanez, 1971:129; Menzies and Kruczynski, 1983:75; Delaney, 1984:3.

*Excorallana antillensis* Richardson, 1905:148 (*lapsus calami*).

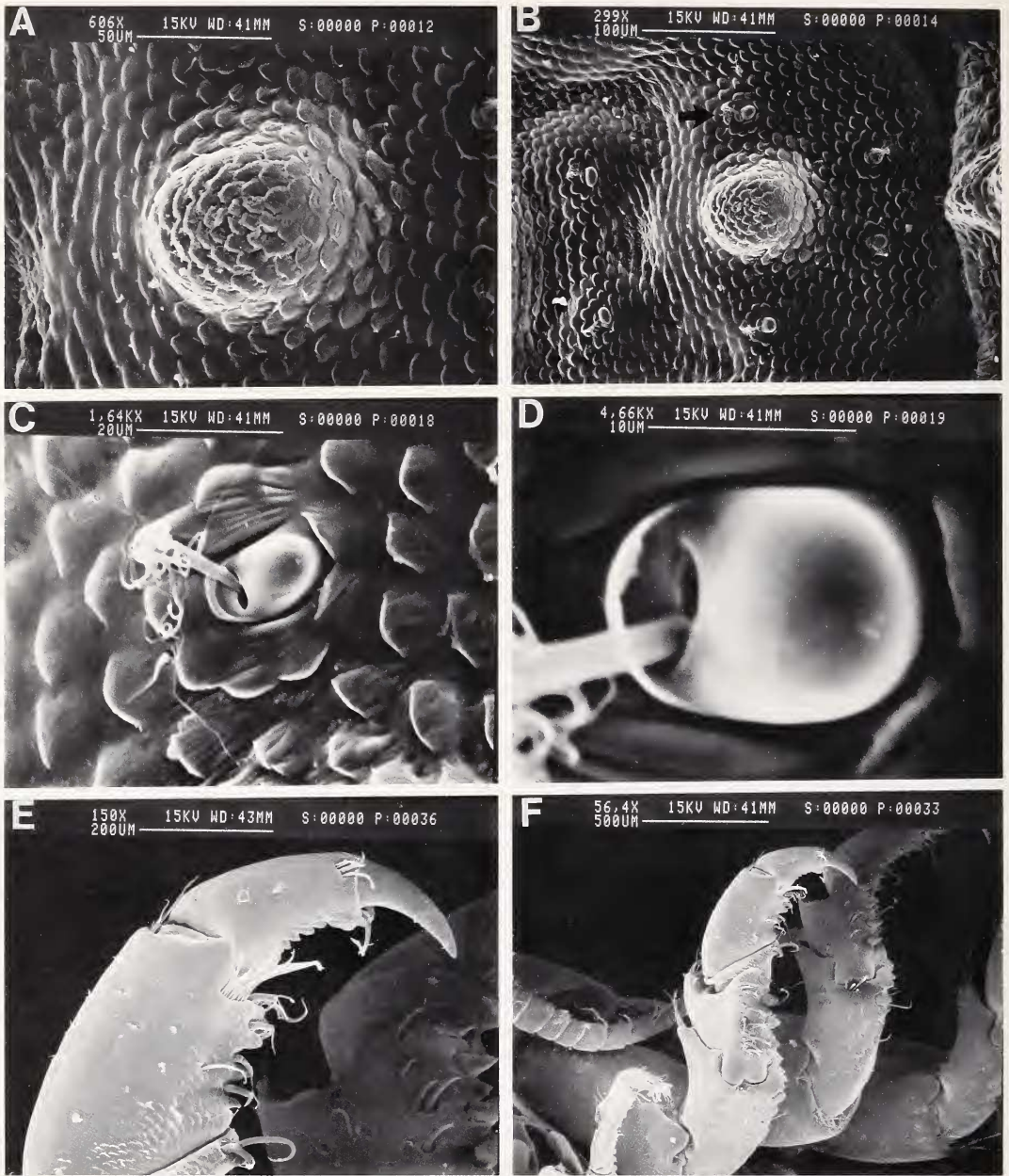


Figure 18. Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: A, median tubercle on pleonite 5; B, six cuticular structures around tubercle; C, one pleonal cuticular structure; D, detail of cuticular structure; E, pereopod I, propodus, and dactyl; and F, pereopod I.

*Corallana antillensis* Hansen, 1890:383; Richardson, 1901:517; Nierstrasz, 1917:101.

**DISTRIBUTION.** Caribbean and Brazil.

- 5) *Excorallana subtilis* (Hansen, 1890):382, table VII, figures 3a-e; Boone, 1921:93; Lemos de Castro, 1960:61, 1964:4; Miller, 1968:17; Monod, 1969:49; Carvacho and Yanez, 1971:130; Delaney, 1984:3.

*Excorallana subtilis* Richardson, 1905:146 (*lapsus calami*).

*Corallana subtilis* Hansen, 1890:382; Richardson, 1901:517; Nierstrasz, 1917:101.

**DISTRIBUTION.** Caribbean.

- 6) *Excorallana tricornis occidentalis* Richardson, 1905:141, no figures; Monod, 1969:50; Bowman, 1977:657; Delaney, 1984:13.

**DISTRIBUTION.** Southwestern Baja California, Gulf of California, and western Mexico south to Panama.

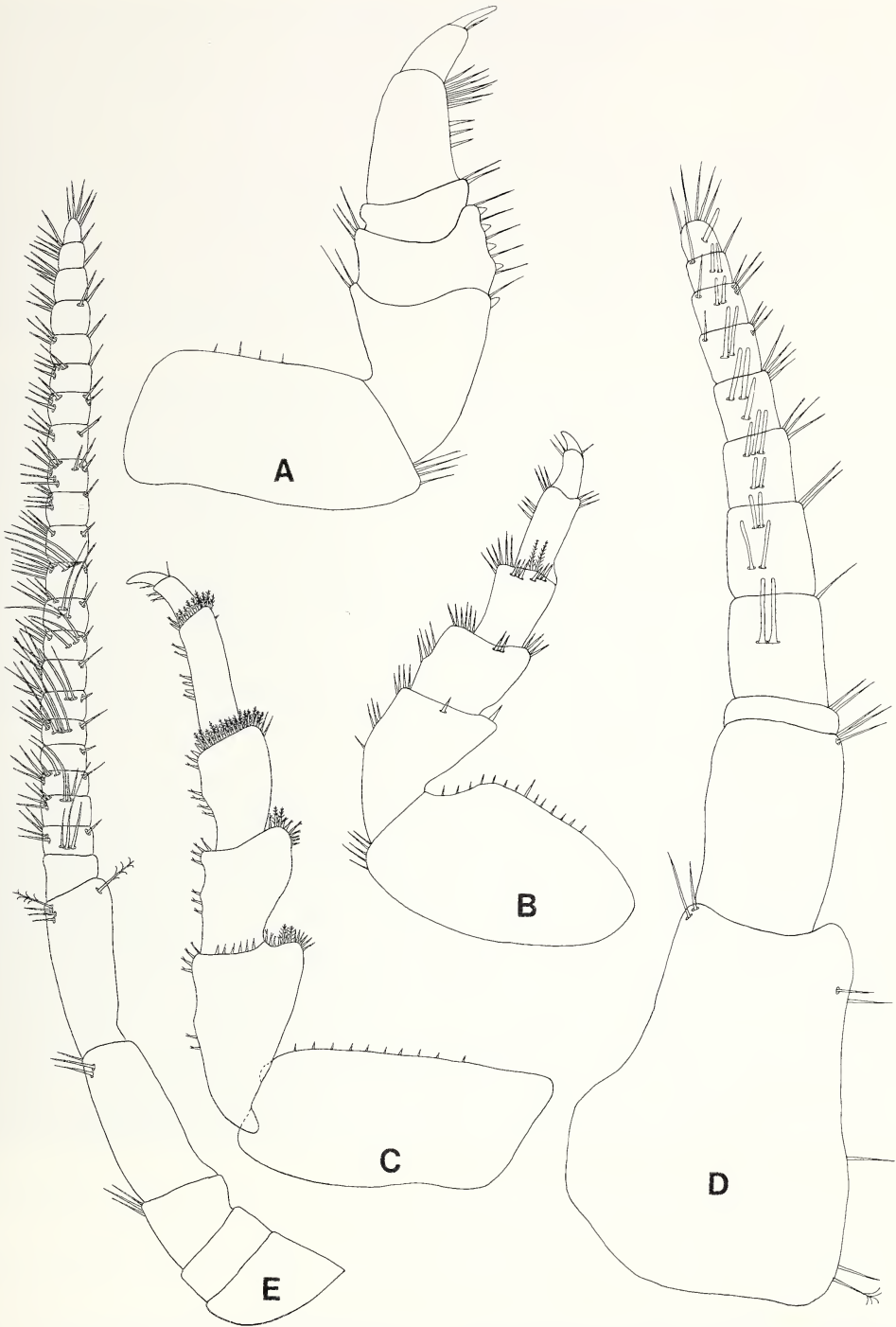


Figure 19. *Excorallana bruscai*, AHF holotype #6611: A, pereopod I; B, pereopod IV; C, pereopod VII; D, antennule; and E, antenna.

7) *Excorallana truncata* (Richardson, 1899a):825, figure 4; Nierstrasz, 1931:177; Lemos de Castro, 1960:61, 1964:4; Monod, 1969:50; Carvacho and Yanez, 1971:130; Delaney, 1982: 273, 1984:18.  
*Corallana truncata* Richardson, 1899a:825,

1899b:165, 1900a:217, 1901:517; Nierstrasz, 1917:101.  
*Excorallana truncata* Richardson, 1905:145 (*lapsus calami*).  
*Excorallana kathyae* Menzies, 1962b:345; Monod, 1969:50.

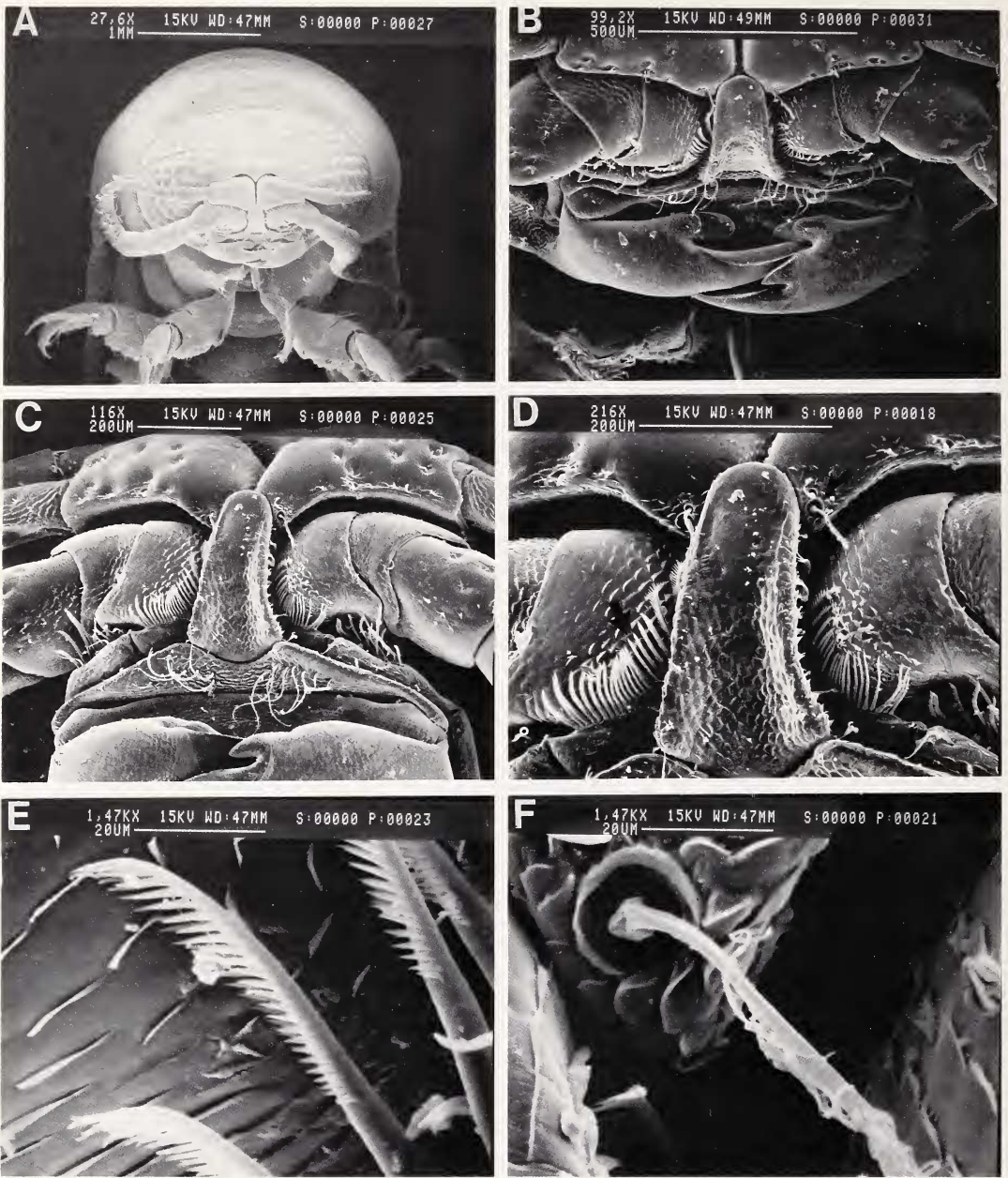


Figure 20. Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: A, anterior view of cephalon; B, detail of cephalon showing frontal lamina and mandibles; C, detail of frontal lamina and mandibles; D, frontal lamina; E, plumose seta at base of antenna (in D); and F, seta in pit on antennule peduncle (in D).

**DISTRIBUTION.** Point Conception, California to Galapagos Islands.

- 8) *Excorallana barbicensis* Boone, 1919:594, plate 92, figure 1; Van Name, 1925:471; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:50; Carvacho, 1977a:12; Delaney, 1984:3.

*Excorallana barbicensis* Carvacho and Yanez, 1971:129 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

- 9) *Excorallana longicornis* Lemos de Castro, 1960: 61, figures 1-10, 1964:5; Monod, 1969:50;

Carvacho and Yanez, 1971:130; Delaney, 1984:3.

**DISTRIBUTION.** Brazil.

- 10) *Excorallana mexicana* Richardson, 1905:142, figures 122, 123; Lemos de Castro, 1960:61, 1964:4; Monod, 1969:48; Carvacho and Yanez, 1971:129; Menzies and Kruczynski, 1983:72; Delaney, 1984:3.

*Excorallana mexicana* Richardson, 1905:142 (*lapsus calami*).

*Corallana mexicana* Nierstrasz, 1917:101.

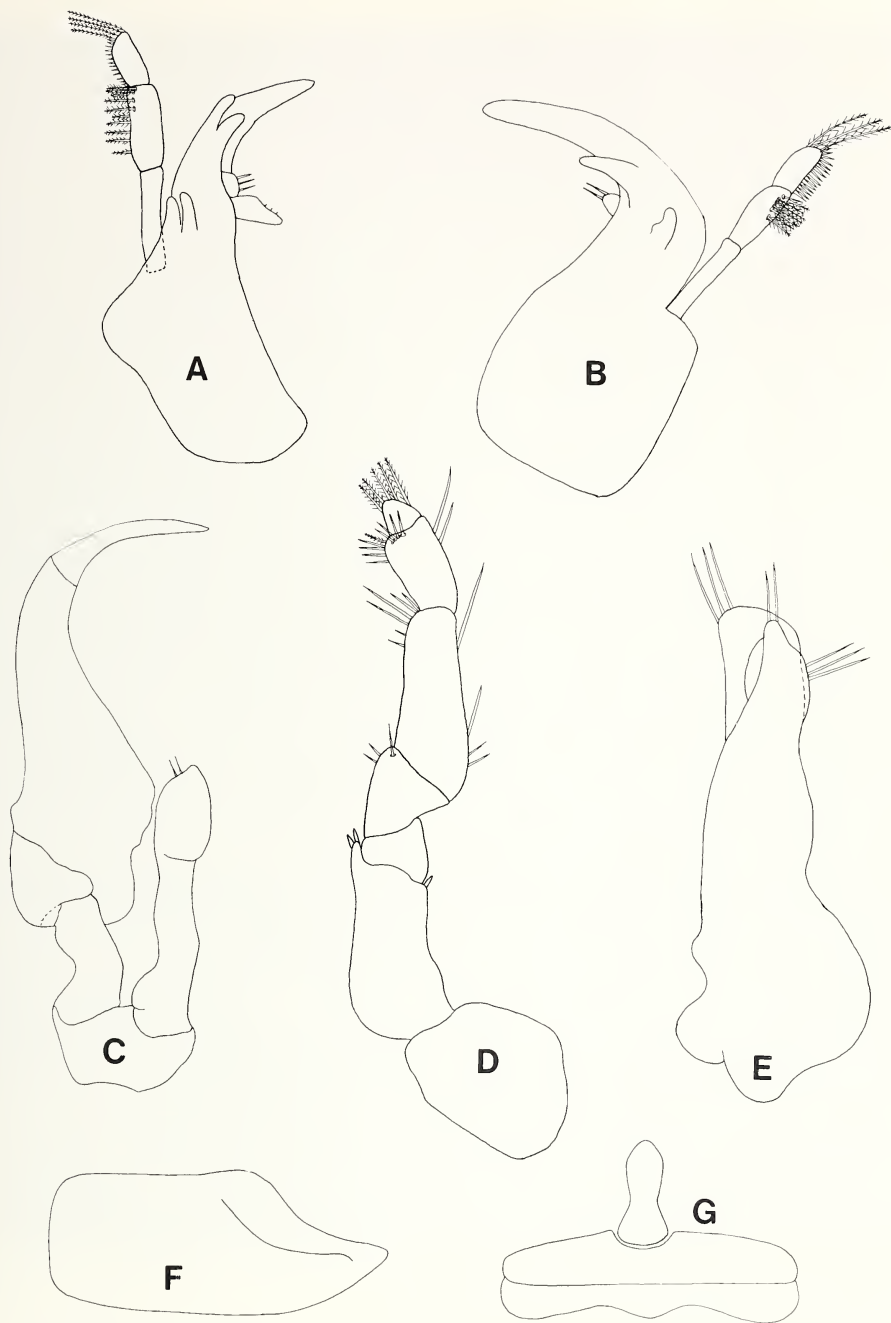


Figure 21. *Excorallana bruscai*, AHF holotype #6611: A, left mandible; B, right mandible; C, maxillule; D, maxilliped; E, maxilla; F, coxa VII; and G, frontal lamina, clypeus, and labrum.

**DISTRIBUTION.** Gulf of Mexico and Caribbean.

- 11) *Excorallana oculata* (Hansen, 1890):386, table VII, figures 6a, b; Boone, 1921:93; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana oculata* Hansen, 1890:386; Richardson, 1901:517; Nierstrasz, 1917:101.

*Excorallana oculata* Richardson, 1905:152 (*lapsus calami*).

**DISTRIBUTION.** Caribbean, Brazil, and West Africa (Isle Annobon).

- 12) *Excorallana quadricornis* (Hansen, 1890):382, table VII, figure 2; Lemos de Castro, 1960:61, 1964:1; Monod, 1969:50; Carvacho and Yanez, 1971:129; Carvacho, 1977a:11; Delaney, 1984:3.

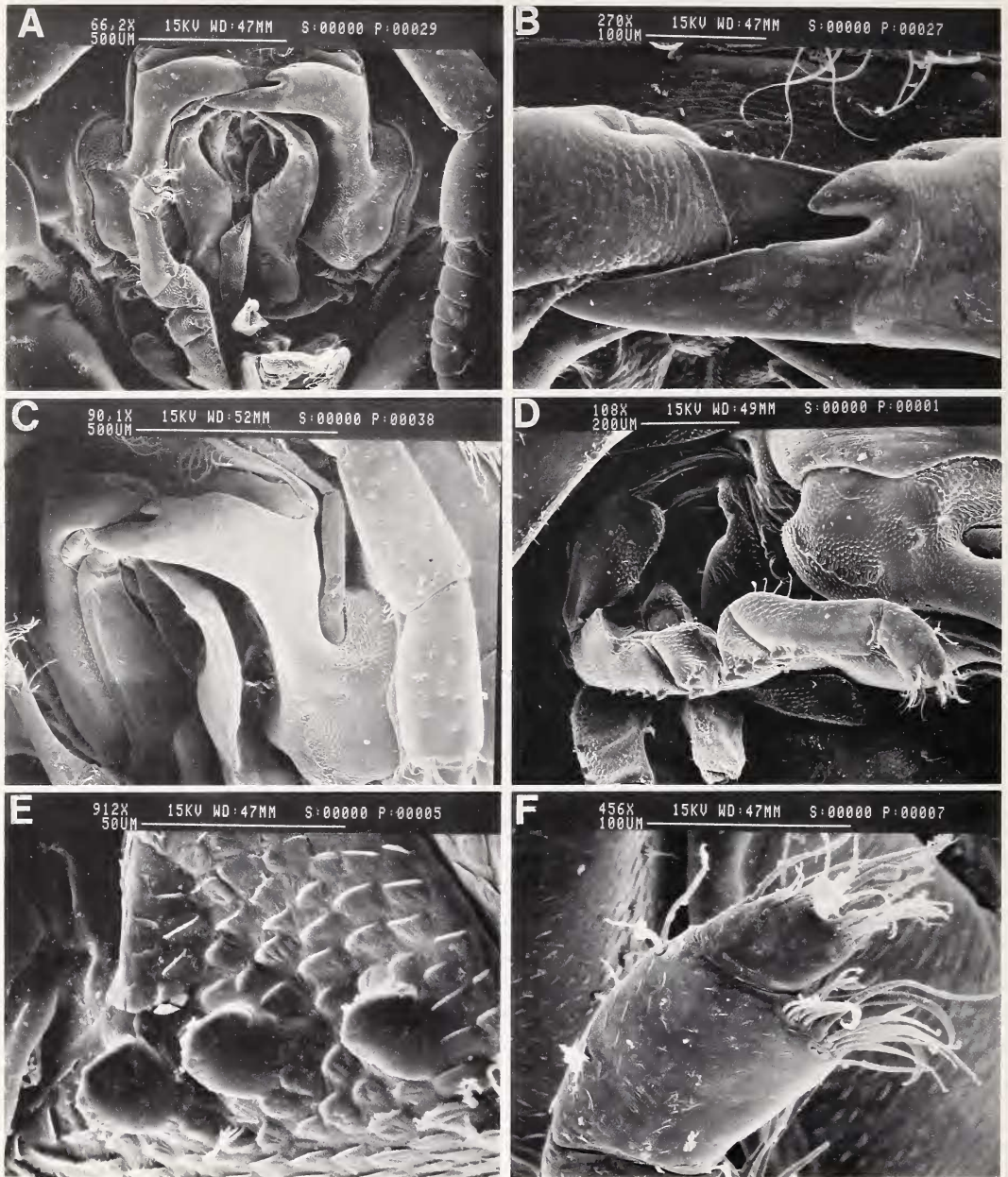


Figure 22. Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: A, buccal field; B, mandible incisors; C, lateral view of mandible and maxillule; D, maxilliped; E, tubercles on second article of maxilliped; and F, distal articles of maxilliped.

*Corallana quadricornis* Hansen, 1890:382; Richardson, 1901:517, 1902:290; Nierstrasz, 1917:101.

*Excorallana quadricornis* Richardson, 1905:144, 1912:188 (*lapsus calami*).

**DISTRIBUTION.** Caribbean and Brazil.

- 13) *Excorallana sexticornis* (Richardson, 1901): 518, figure 9; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana sexticornis* Richardson, 1901:518; Nierstrasz, 1917:101.

*Excorallana sexticornis* Richardson, 1905:143 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

- 14) *Excorallana warmingii* (Hansen, 1890):387, table VII, figures 7a-f; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:130; Schultz, 1979:224; Delaney, 1984:3.

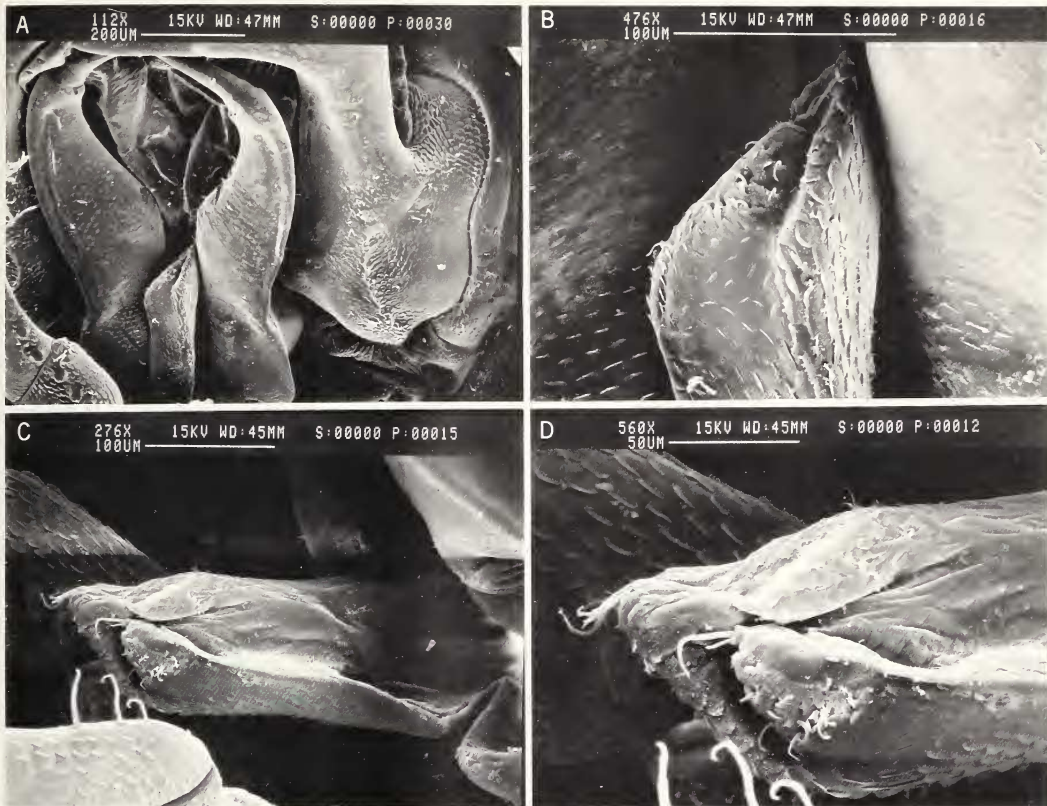


Figure 23. Scanning electron micrographs of *Excorallana* sp., USNM Acc. No. 128938: A, ventral view of maxilla, maxillule, and mandible base; B, maxilla apex; C, dorsal view of maxilla; and D, detail of maxilla apex (in C).

*Corallana warmingii* Hansen, 1890:387; Richardson, 1901:517; Nierstrasz, 1917:101.

*Excorallana warmingii* Richardson, 1905:154 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

- 15) *Excorallana fissicauda* (Hansen, 1890):385, table VII, figures 5a–d; Lemos de Castro, 1960:61, 1964:5; Monod, 1969:48; Carvacho and Yanez, 1971:129; Delaney, 1984:3.

*Corallana fissicauda* Hansen, 1890:385; Richardson, 1901:517; Nierstrasz, 1917:101.

*Excorallana fissicauda* Richardson, 1905:150 (*lapsus calami*).

**DISTRIBUTION.** Caribbean.

- 16) *Excorallana angusta* Lemos de Castro, 1960:63, figures 11–18, 1964:5; Monod, 1969:50; Carvacho and Yanez, 1971:130; Delaney, 1984:3.

**DISTRIBUTION.** Brazil.

- 17) *Excorallana richardsonae* Lemos de Castro, 1960:64, figures 19–27, 1964:4; Monod, 1969:50 (emendation).

*Excorallana richardsoni* Lemos de Castro, 1960:64, 1964:4; Carvacho and Yanez, 1971:130; Delaney, 1984:3 (*lapsus calami*).

**DISTRIBUTION.** Brazil.

- 18) *Excorallana costata* Lemos de Castro, 1960:66, figures 28–37, 1964:4; Monod, 1969:50; Carvacho and Yanez, 1971:130; Delaney, 1984:3.

**DISTRIBUTION.** Brazil.

- 19) *Excorallana meridionalis* Carvacho and Yanez, 1971:129, plates I, II; Carvacho, 1977b:27; Delaney, 1984:3.

**DISTRIBUTION.** Chile.

- 20) *Excorallana stebbingi* Lemos de Castro and Lima, 1976:75, figures 1–14.

**DISTRIBUTION.** Brazil.

#### REMARKS

Delaney (1984) reviewed the status of this genus and noted the need for a thorough revision. Previously, the most comprehensive treatments of this group have been Richardson (1905), Lemos de Castro (1960, 1964), Monod (1969), and Carvacho and Yanez (1971).

Sexual dimorphism in dorsal ornamentation is common. In many species males possess dorsal tu-

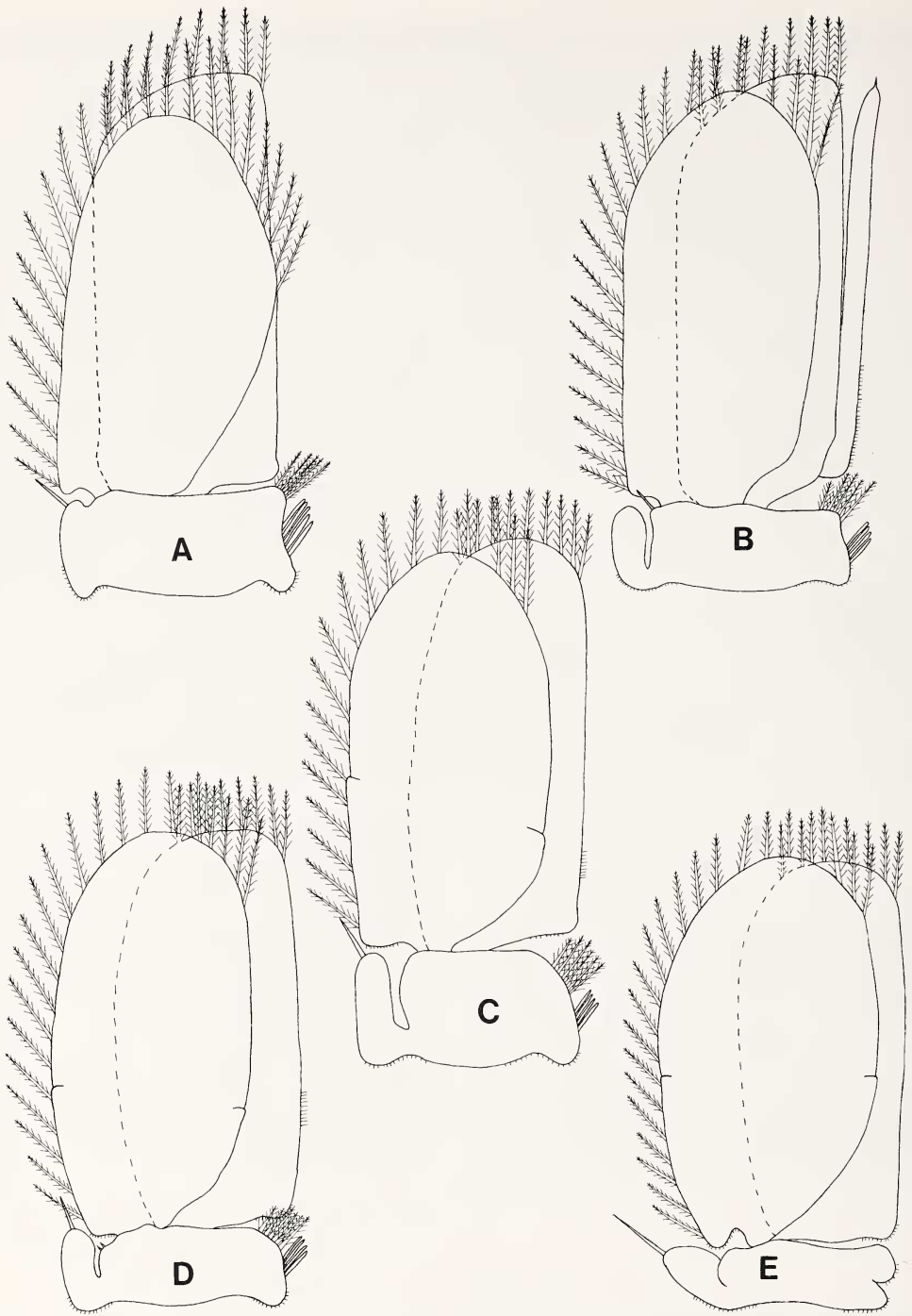


Figure 24. *Excorallana bruscai*, AHF holotype #6611: A, pleopod 1; B, pleopod 2; C, pleopod 3; D, pleopod 4; and E, pleopod 5.

bercles or "horns" on the cephalon and pereonite I, but in females these are usually lacking, or if present are generally reduced in size or number. Size of dorsal ornamentation may also be related to the age and maturity of the isopod.

Based upon examination of type-specimens of *Excorallana acuticauda* and *E. antillensis*, the lat-

ter is herein made a junior synonym of *E. acuticauda*. *Excorallana subtilis* is very similar to *E. acuticauda* and *E. richardsonae*, differing primarily in degree of dorsal setosity and the tuberculation of the pleon; herein I maintain it as a distinct species, but more specimens are needed to ascertain its true status.



*Excorallana* is the largest genus in the family Corallanidae. The genus is primarily confined to the New World tropics, between the latitudes of 40°N and 40°S (Fig. 25). One species, *Excorallana oculata*, has been collected from tropical west Africa. A number of Atlantic-Pacific "analog" or geminate species pairs exist, supporting the concept of a generalized trans-isthmian oceanic track connecting the eastern Pacific and Caribbean prior to the formation of the Panamanian isthmus (Woodring, 1966; Croizat et al., 1974).

*Excorallana* species probably emerge from cryptic habitats to temporarily parasitize fish or to prey on microcrustaceans and other invertebrates. Species in this group have been collected from depths of 183 m to the intertidal zone, and from a variety of habitats including coral reefs, limestone conglomerate (coquina) reefs, mangrove areas, andesite rock, and sand beaches. They have been collected as "commensals" of ascidians, calcareous sponges, and tube-building snails, as well as temporary parasites (or micropredators) of numerous fish species.

Menzies and Kruczynski (1983) presented evidence that some species of *Excorallana*, *Alcirona*, and *Lanocira* may partition their habitats by depth range in the Gulf of Mexico. Delaney (1984) found *E. bruscai* to exhibit an aggregated dispersion pattern as a cryptofaunal inhabitant of a limestone conglomerate reef at Puerto Penasco, Sonora, Mexico. The dispersion index was greatest in the upper (0' to +2') intertidal zone during January, but greatest in the lower zone (0' to -2') during April. This may indicate that some seasonal movement within the intertidal zone occurs in this species, perhaps related to the occurrence of gravid females (which were only found in April). *Excorallana tricornis occidentalis* is part of the demersal zooplankton at Isla Cano, Costa Rica, exhibiting definite nocturnal migration from the benthos to the water column. This species may prey on microcrustaceans such as mysids (Guzman et al., 1988). See Delaney (1984) and the Material Examined section of this study for extensive habitat and host data for other species in this genus.

### Genus *Lanocira* Hansen, 1890

*Lanocira* Hansen, 1890:395; Stebbing, 1893:315, 1904b:706, 1905:19, 1909:217; Moore, 1902:170; Richardson, 1910:8; Barnard, 1914:359, 1920:354, 1940:491, 1955:61; Nierstrasz, 1917:102, 1931:167; Monod, 1933:187; Pillai, 1954:7, 1967:272; Kensley, 1978:75; Bruce, 1980:315; Jones, 1982:65; Bruce et al., 1982:464; Delaney and Brusca, 1985:728.

*Nalicora* Moore, 1902:169; Richardson, 1905:164; Jones, 1982:72; Bruce et al., 1982:464; Menzies and Kruczynski, 1983:77.

*Corilana* Kossman, 1880:115; Nierstrasz, 1917:102,

1931:172; Monod, 1933:190; Bruce et al., 1982:464.

### MATERIAL EXAMINED

*Lanocira kroyeri*: 1) Brazil, Rio de Janeiro, ZMUC holotype, 1 fe., 3.8 mm. *Lanocira rotundicauda*: 1) Indonesia, Jakarta Bay, Seribu Islands, Pulau Edam, Java, CAS No. 025372, Quad. #R-082766, "sand and coral bottom," 2 fe., 6.6 and 6.6 mm, and 3 manca, all 2.4 mm. *Lanocira rapax*: 1) Gulf of Mexico, off Florida, USNM 11775, *Albatross*, Sta. 2369-74, 29°16'30"N, 85°32'W, depth 47 m, 34 spec.; 2) Gulf of Mexico, between delta of Mississippi River and Cedar Keys, Florida, USNM 46344, Sta. 2369-74, "out of USNM 39405," 5 fe. (gravid); 3) Puerto Rico, Mayaguez, north of Punta del Algarrobo, USNM 44279, coll. U.S. Fish Commission Porto Rico Expedition, 1898-1899, *Fish Hawk*, Sta. 138, 1 ma.; 4) West Indies, USNM Acc. No. 208263, Sta. 55-56, 1 fe. *Lanocira gardineri*: 1) Hong Kong, Ninepino, North Reef, AM No. P31524, "from sponge, 15 m," 1 fe., 6.4 mm; 2) Red Sea, Suez, ZMHUB No. 1314, 3 fe., 4.5, 5.2, and 5.8 mm, 5 ma., 3.4 (fragment), 4.0, 4.4, 4.9, and 5.6 mm, and 10 embryos, 1.0-1.25 mm; 3) Persian Gulf, Iraq, Khor Abdullah, near Um Quasor, ZMHUB, "11 a.m., sublittoral, depth 2m, water temp. = 25°C, taken with dredge," 1 fe., 6.8 mm, and 2 ma., 6.4 and 7.4 mm; 4) Philippines, Corregidor Straits, USNM 40956, R/V *Albatross*, Sta. D5108, depth 23 m, 5 fe. and 2 ma.; 5) West Pacific Ocean, Eniwetok Atoll, Runit Island, USNM Acc. No. 172586, "intertidal," 2 ma.; 6) Madagascar, Nossi-Be, Ankifi Beach, IIOE Program, SOSC, J. Rudloe, Ref. 54, Sta. JR-36, 13°31'S, 48°32'E, depth 0-0.2 m, 2 ma. and 4 manca; 7) Madagascar, Nossi-Be, Ankifi Beach, IIOE Program, SOSC, J. Rudloe, Sta. JR-22, 13°31'S, 48°32'E, depth 0-0.2 m, 1 ma. and 1 manca; 8) Madagascar, Nossi-Be, Ankifi Beach, IIOE Program, SOSC, J. Rudloe, Sta. JR-19/JR-4, 2 ma. and 3 manca; 9) Mozambique, Ponta da Barra Ralsa, USNM 40956, IIOE Program, R/V *Anton Bruun* Cruise 8, Sta. 400C, "GMST gear," 20°30'S, 35°43'E, depth 62 m, 2 fe., 3 ma., and 3 manca; 10) Philippine Islands, USNM, R/V *Albatross*, No. 2369-74, 1 fe. *Lanocira zeylanica*: 1) West Pacific Ocean, Bikini Island, USNM Acc. No. 176603, "from boat cradle, anchored in lagoon," 1 fe.; 2) West Pacific, Japtan Island, USNM Acc. No. 197874, H.S. Ladd, Sta. 1523, "seaward," 1 fe.; 3) East Pacific, Juan Fernandez Islands, Father Bay, USNM Acc. No. 93322, "given to S. Durand by fisherman," depth 54 m, 2 fe. and 1 ma.; 4) East Pacific, Juan Fernandez Islands, Santa Clara Island, USNM Acc. No. 93322, "collected from an antipatharian," 1 fe.; 5) Juan Fernandez Islands, Santa Clara Island, West Bay, USNM Acc. No. 93322, 36-45 m, 1 ma.; 6) Juan Fernandez Islands, Acla. Vaguena, USNM Acc. No. 93322, depth 32 m, 1 fe. and 2 ma.; 7) Juan Fernandez Islands, Carbojal Bay, USNM Acc. No. 93322, "dredged at 27-36

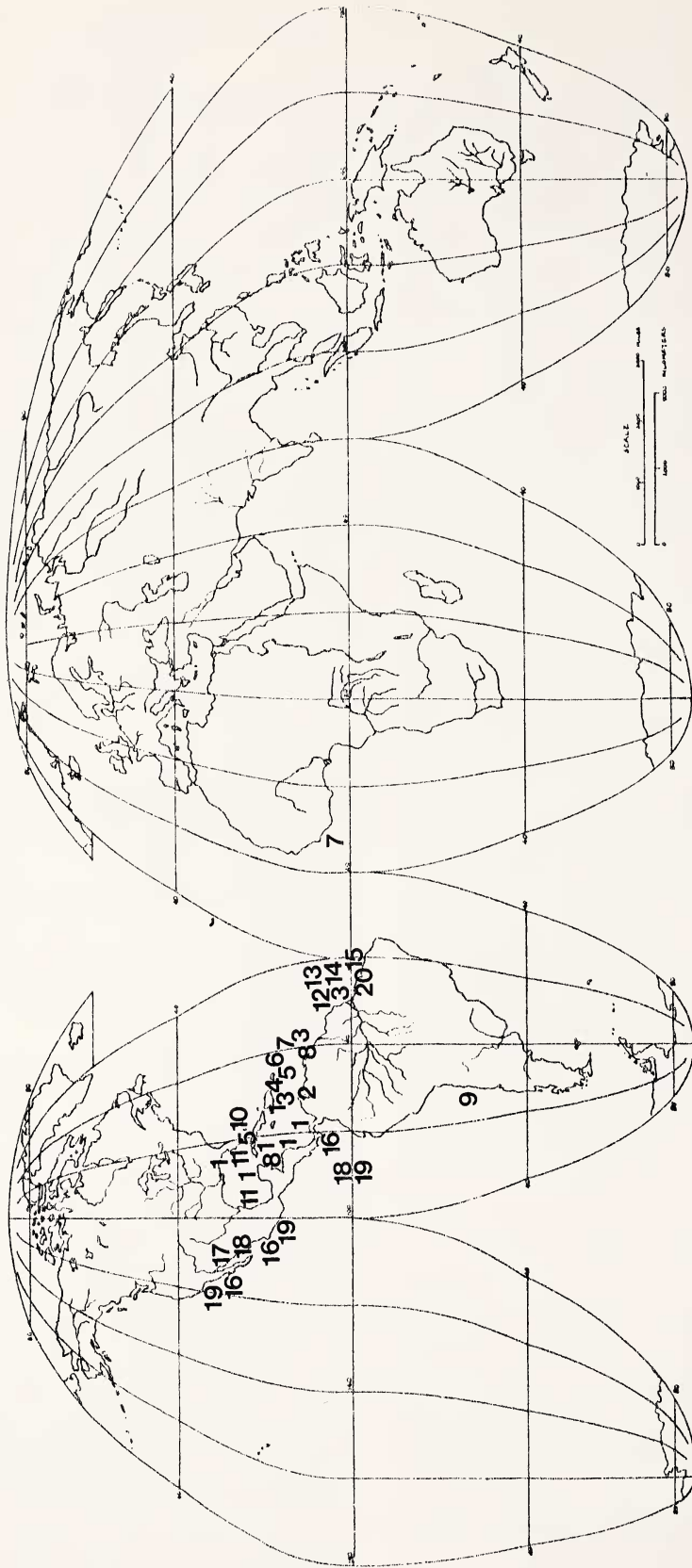


Figure 25. Distribution of *Excorallana* species; species numbers are: 1, *E. tricornis tricornis*; 2, *E. berbicensis*; 3, *E. quadricornis*; 4, *E. subtilis*; 5, *E. acuticauda*; 6, *E. fissicauda*; 7, *E. oculata*; 8, *E. warmingii*; 9, *E. meridionalis*; 10, *E. sexticornis*; 11, *E. mexicana*; 12, *E. longicornis*; 13, *E. costata*; 14, *E. angusta*; 15, *E. richardsonae*; 16, *E. tricornis occidentalis*; 17, *E. bruscai*; 18, *E. houstoni*; 19, *E. truncata*; and 20, *E. stebbingi*.

m.” 3 spec.; 8) Juan Fernandez Islands, Santa Clara Islands, off West Bay, USNM Acc. No. 93322, “from fisherman,” depth 45 m, 23 spec.; 9) Indian Ocean, Mahe’ Island, small baylet immediately south of north point on west side of island, just off the Fairhaven Hotel, USNM Acc. No. 276969, IIOE Program, Sta. F-35, depth 8–11 m, 1 ma.; 10) South Pacific Ocean, SEBOP Program, SOSOC, coll. R/V *Anton Bruun* Cruise 12, Sta. MV-65IV54, 33°38’S, 78°45’W, “otter trawl/benthic,” 1 fe., 1 ma., 1 juvenile, and 4 manca; 11) East Pacific Ocean, USNM, R/V *Anton Bruun* Cruise 12, Sta. 65256, Marsden Square, No. 415-2, “diving gear,” 1 ma.; 12) Indian Ocean, Seychelle Islands, Faon Island, off south shore, USNM Acc. No. 276969, IIOE Program, Sta. F-11, depth 11–15 m, 1 fe. *Lanocira latifrons*: 1) Mozambique, Ponta da Barra Ralsa, USNM 40956, IIOE Program, R/V *Anton Bruun* Cruise 8, Sta. 400C, “GMST gear,” 20°30’S, 35°43’E, depth 62 m, 1 ma.; 2) Red Sea, Suez, ZMHUB No. 13124, “from the umbrella of *Cassiopea andromeda* (Scyphozoa),” 1 fe., 4.6 mm (gravid with 5 embryos, 0.7–0.8 mm).

#### DIAGNOSIS

Antennule peduncle 2-articulate; basal article of peduncle narrow, not expanded. Frontal lamina narrow, pentagonal; clypeus broad, short; labrum small. Mandible with broad base, slender trunk and apex, and short incisor, with row of short recurved spines or dentate processes on lateral margin behind incisor; molar process usually small or absent, occasionally moderately sized, lacinia mobilis small or absent. Maxillule lateral lobe forming single large falcate spine; medial lobe simple, apically blunt. Maxilla 3- or 4-articulate, apical article sublinear, elongate, with two long apical setae. Maxilliped without endite; basis not elongate; palp broad, always 5-articulate, middle article not elongate. Anterior pereopods usually without serrate dactyli and propodi (except in *L. zeylanica* as figured by Monod, 1933:184); carpi not produced as in *Tachaea*.

#### ADDITIONAL DESCRIPTION

Corallanidae with well-developed eyes at anterolateral margin of cephalon. Dorsum often with tubercles or setae (Fig. 1E). Dorsum of some species densely covered with cuticular sensillae arising from pits or from globose sockets (Figs. 26C, E–F, 27). Antennule peduncle basal article not enlarged (Fig. 28A). Antenna peduncle articles 4 and 5 elongate (Fig. 26B). Clypeus much smaller relative to labrum than in *Alcirona* and *Argathona*; labrum small, but often conceals incisor of mandible (Figs. 26D, 28E). Mandible palp inserted near mandible base; 3-articulate, middle article longest, middle and distal articles with simple marginal setae, middle article with plumose setae (Figs. 28B, 29E, F). Maxillule lateral (outer) lobe forming single large falcate spine; medial margin with knoblike process in *L. rapax*; medial (inner) lobe simple with 0–2 small setae (Figs.

28H, 29D). Maxilla apical article sublinear, elongate, with 2 long apical setae (Figs. 28F, G, 29C). Maxilliped palp apical, lateral and medial margins with simple and plumose setae (Figs. 28C, 29A, B). Pereopods I–III subprehensile, meri with stout spines on posteromedial margins (Figs. 28D, 30A, 31A, B). Pereopods IV–VII longer, ambulatory, with simple setae and stout spines on posteromedial margins (Figs. 30B, C, 31C, D). Pleopod peduncles broader than long, with 3–5 coupling spines and groups of proximal plumose setae on medial margins, and with simple spine on lateral margins (Figs. 30D–H, 31E, F). Pleopod exopods broader and with more plumose marginal setae than endopods. Endopod of pleopod 5 naked, proximal medial margin produced, lobelike (Fig. 30H). Male pleopod 2 with rodlike appendix maculina, with simple apex, arising from proximal medial margin of endopod (Fig. 30E).

#### TYPE SPECIES

*Lanocira kroyeri* Hansen, 1890:396, plate VIII, figures 3a–l, by monotypy.

#### DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

- 1) *Lanocira kroyeri* Hansen, 1890:396, plate VIII, figures 3a–l; Stebbing, 1893:315, 1904b:707, 1905:20, 1909:218; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Jones, 1982:73.

DISTRIBUTION. Rio de Janeiro, Brazil.

- 2) *Lanocira rapax* (Moore, 1902):169, plate 9, figures 11–22; Richardson, 1905:164; Nierstrasz, 1917:102; Jones, 1982:72.  
*Nalicora rapax* Moore, 1902:169; Richardson, 1905:164; Menzies and Kruczynski, 1983:77.  
*Excorallana rapax* Schultz, 1969:211; Menzies and Kruczynski, 1983:77.

DISTRIBUTION. Puerto Rico, Florida, and Gulf of Mexico.

- 3) *Lanocira gardineri* Stebbing, 1904b:706, plate LI-a, 1905:19, 1909:218; Richardson, 1910:9; Barnard, 1914:359, 1920:354, 1940:491, 1955:61; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Pillai, 1954:7, 1967:274; Kensley, 1978:75; Bruce, 1980:316; Jones, 1982:72.

*Lanocira capensis* Barnard, 1914:359, plate 31A, 1920:354; Nierstrasz, 1931:169; Monod, 1933:188; Bruce, 1980:316; Jones, 1982:72.

DISTRIBUTION. Maldives, South Africa, Philippines, India, Kenya, Sri Lanka, Hong Kong, Persian Gulf, Mozambique, Madagascar, and Eniwetok Atoll.

- 4) *Lanocira rotundicauda* Stebbing, 1904b:707, plate L-a, 1905:19; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Pillai, 1967:272; Bruce, 1980:316; Jones, 1982:74.

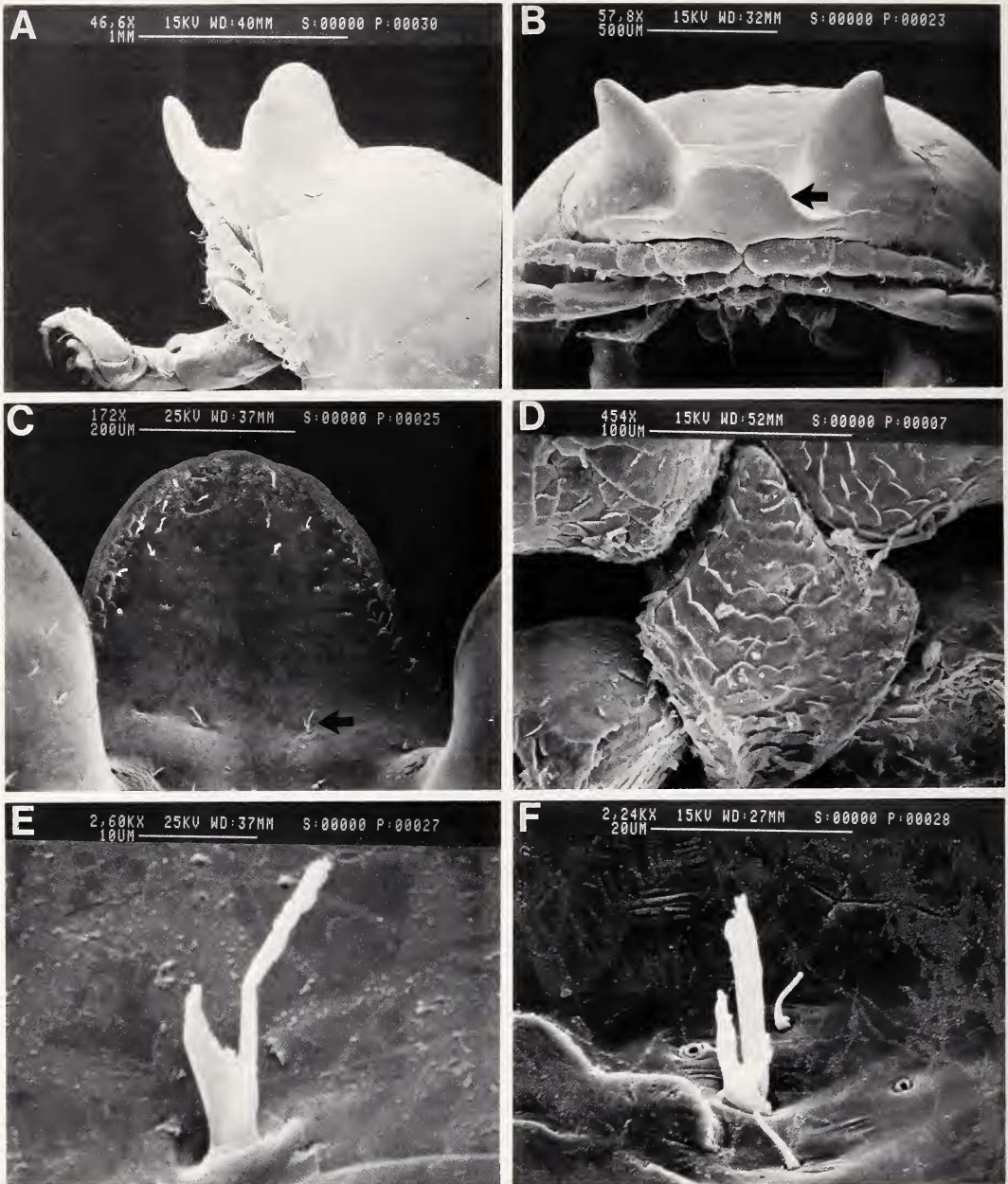


Figure 26. Scanning electron micrographs of *Lanocira gardineri*, USNM 40956: A, lateral view of cephalon and pereonite I; B, anterior view of cephalon and rostral process; C, posterior view of rostral process; D, frontal lamina; E, cuticular sensillum on rostrum (arrow in C); and F, cuticular sensillae on posterior cephalon.

**DISTRIBUTION.** Maldives, Sri Lanka, and Indonesia.

- 5) *Lanocira zeylanica* Stebbing, 1905:19, plate 5b, 1909:218; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Barnard, 1955:61; Pillai, 1967:272.

*Lanocira zeylandica* Jones, 1982:72 (*lapsus calami*).

*Lanocira hirsuta* Nordenstam, 1930:541.

**DISTRIBUTION.** Sri Lanka, Tanzania, Ken-

ya, Red Sea, Juan Fernandez Islands, Easter Island, Bikini Island, and Japtan Island.

- 6) *Lanocira latifrons* Stebbing, 1909:217; Nierstrasz, 1917:102, 1931:171; Monod, 1933:187; Barnard, 1955:61; Kensley, 1978:75; Jones, 1982:72.

**DISTRIBUTION.** South Africa, Mozambique, and Red Sea.

- 7) *Lanocira glabra* Jones, 1982:65.

**DISTRIBUTION.** Watamu, Kenya.

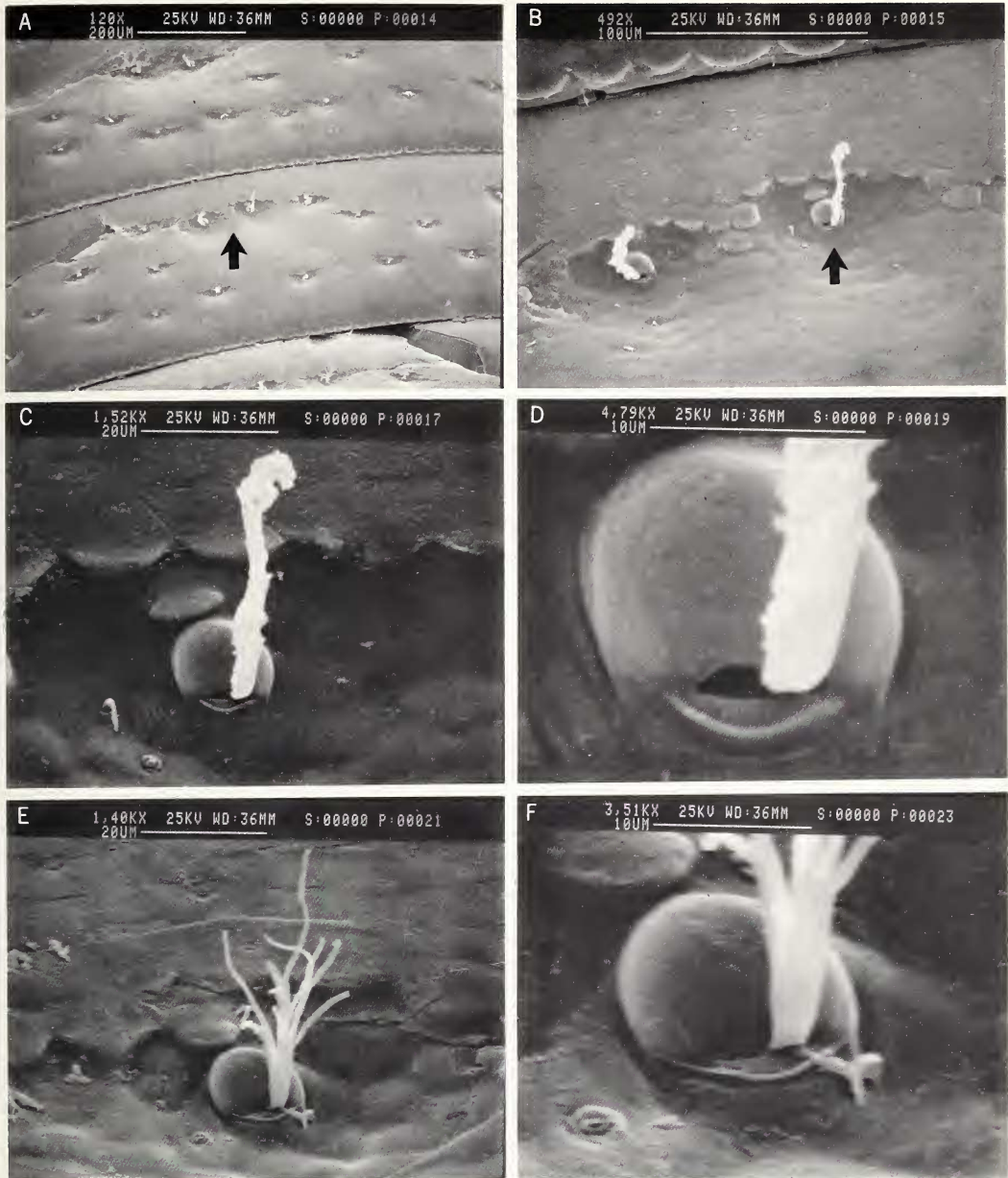


Figure 27. Scanning electron micrographs of *Lanocira gardineri*, USNM 40956: A, dorsal view of pereonite III; B, cuticular structures on pereonite III; C, one cuticular structure; D, detail of cuticular structure (in C); E, pleonal cuticular structure; and F, detail of pleonal cuticular structure (in E).

8) *Lanocira anasicula* Jones, 1982:68.

DISTRIBUTION. Watamu, Kenya.

REMARKS

The genus *Lanocira* was erected by H.J. Hansen in 1890 for his new species *Lanocira kroyeri*. Kossman (1880) proposed the new genus and species *Corilana erythraea*; this poorly defined genus was regarded as *genus et species inquirenda* by Monod (1933) and regarded as closest to *Lanocira* by Bruce

et al. (1982). Moore (1902) erected the genus *Nalicora* to house her new species *Nalicora rapax*, which she placed in the Alcironidae. Jones (1982) synonymized *Nalicora* with *Lanocira*.

The maxilla of *Lanocira* is 3- or 4-articulate, with a sublinear, elongate apical article and 2 long apical setae—a unique character state in the Corallanidae. The maxilla has been figured as 4-articulate by Hansen (1890), Moore (1902), Stebbing (1904a, b), and Richardson (1905), and as 3-articulate by Stebbing (1905), Barnard (1914), Monod (1933), and Jones

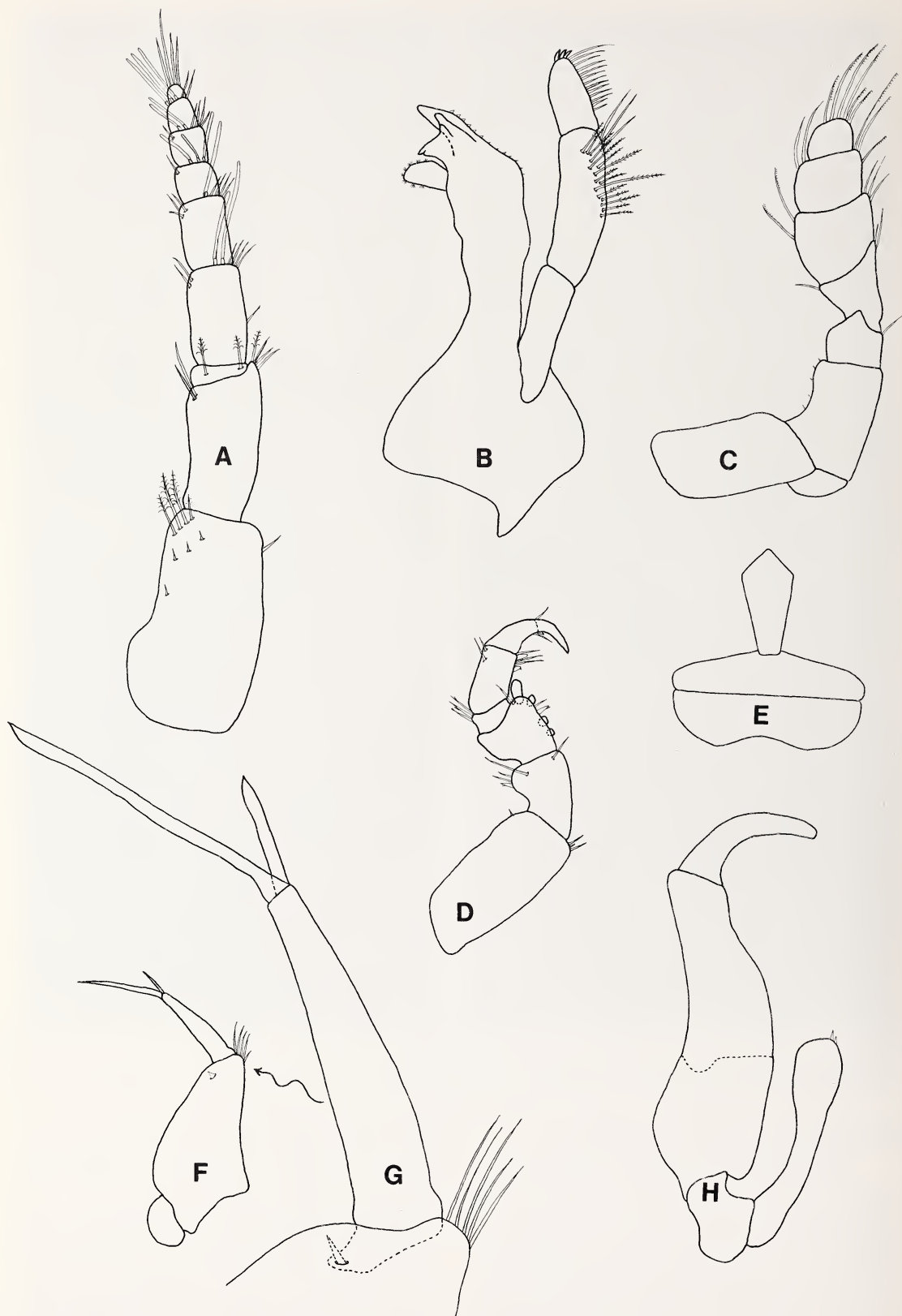


Figure 28. *Lanocira zeylanica*, USNM Acc. No. 93322: A, antennule; B, mandible; C, maxilliped; D, pereopod I; E, frontal lamina, clypeus, and labrum; F, maxilla; G, distal part of maxilla; and H, maxillule.

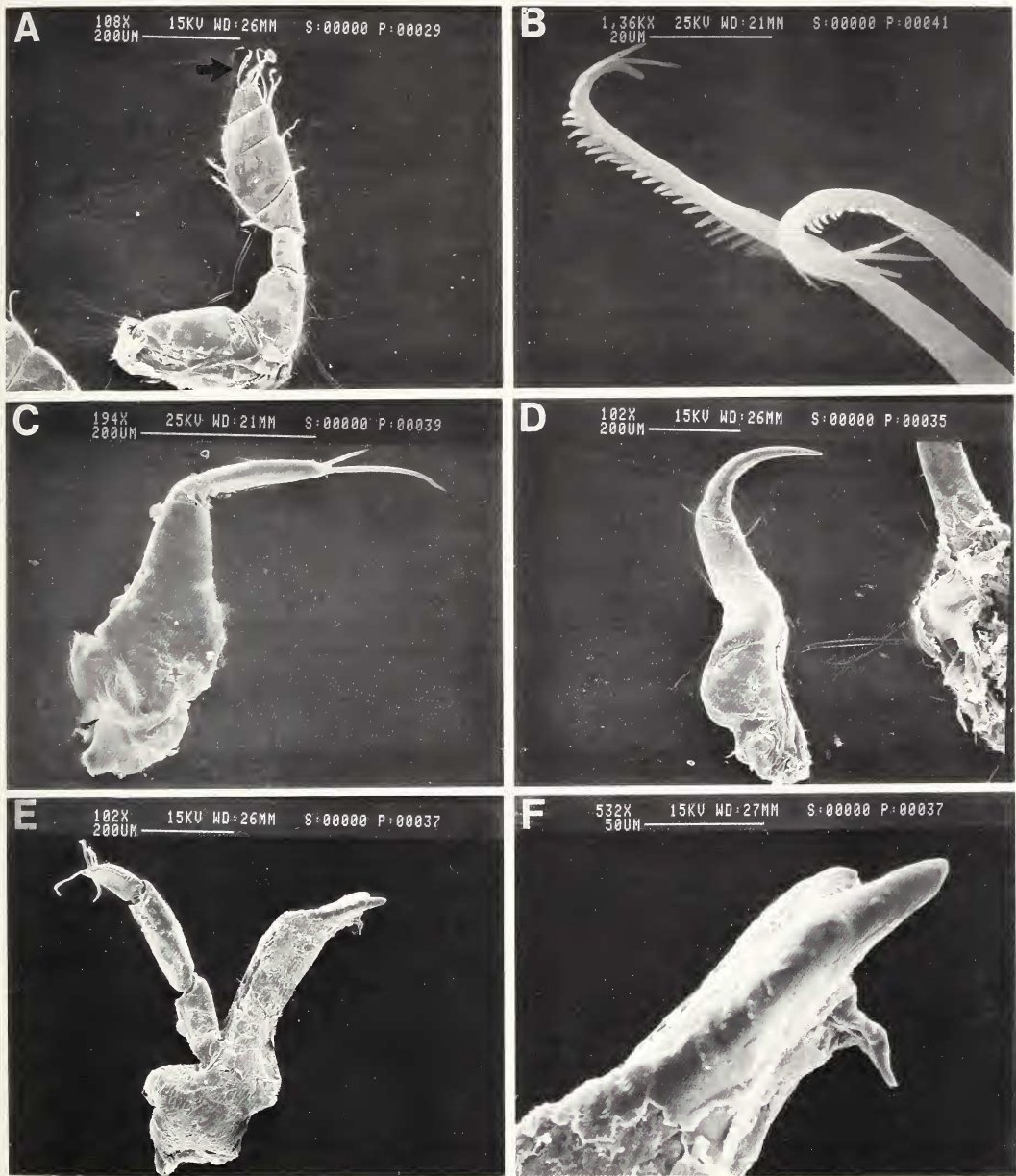


Figure 29. Scanning electron micrographs of *Lanocira zeylanica*, USNM Acc. No. 93322: A, maxilliped; B, apical setae on maxilliped; C, maxilla; D, maxillule; E, mandible; and F, mandible apex.

(1982). Although Hansen's (1890) maxilla figure was 4-articulate, he considered the maxilla as being 3-articulate "with the first segment subdivided." Jones (1982) figured the maxilla of *L. anasicula* as 3-articulate with a partial suture on the first article, indicating that some fusion of articles may have occurred.

Loss or fusion of maxilliped palp articles does not occur in *Lanocira* as in *Argathona* and *Tachaea*. Jones (1982) discussed the number of articles in the maxillipeds of various *Lanocira* species but did not distinguish between the palp of the maxilliped (always 5-articulate in this genus) and the

remainder of the maxilliped, i.e. the coxa and basis. Thus, Hansen (1890) and Moore (1902) were correct in describing maxilliped palps as 5-articulate but figuring maxillipeds with 7 articles in their species descriptions.

Some sexual variation is evident in the dorsal ornamentation of *Lanocira* species, as all other corallanid genera. Jones (1982) noted that females often lack the rostral process characteristic of male *L. gardineri*, *L. latifrons*, and *L. anasicula*. Thus, care should be taken when identifying females of those species.

Bruce (1980) noted that some authors have con-

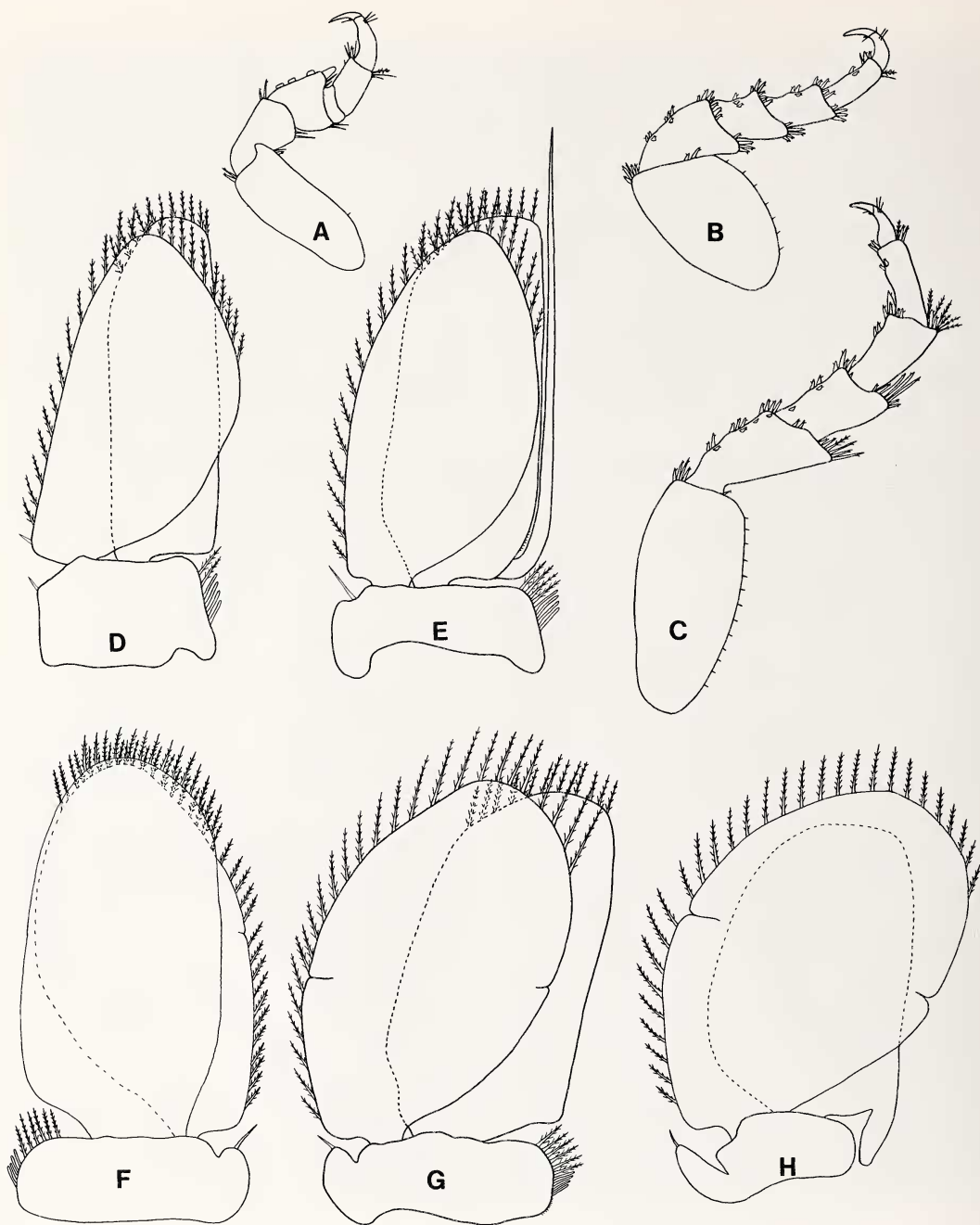


Figure 30. *Lanocira zeylanica*, USNM Acc. No. 93322: A, pereopod I; B, pereopod IV; C, pereopod VII; D, pleopod 1; E, pleopod 2; F, pleopod 3, G, pleopod 4; and H, pleopod 5.

sidered *Lanocira rotundicauda* a possible synonym of *L. gardineri* (Stebbing, 1905; Monod, 1933), but Pillai (1967) and Jones (1982) maintained them as distinct species. Barnard (1955) mentioned the possibility that *L. latifrons* is only the fully adult male of *L. gardineri* but maintained them as separate species (as did subsequent authors).

#### BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The eight species of *Lanocira* are usually found in tropical/subtropical marine habitats. Five of the

species are to be restricted to the Indo-West Pacific (*L. gardineri*, *L. rotundicauda*, *L. latifrons*, *L. glabra*, and *L. anasicula*). *Lanocira zeylanica* has the widest distribution in the genus, being known from throughout the Indo-West Pacific as well as from the Juan Fernandez Islands and Easter Island in the eastern South Pacific. *Lanocira rapax* and *L. kroyeri* are restricted to the Caribbean/Gulf of Mexico and Western Atlantic (Brazil) regions, respectively (Fig. 32).

*Lanocira* species have been found from the intertidal to depths of 120 m from substrates includ-



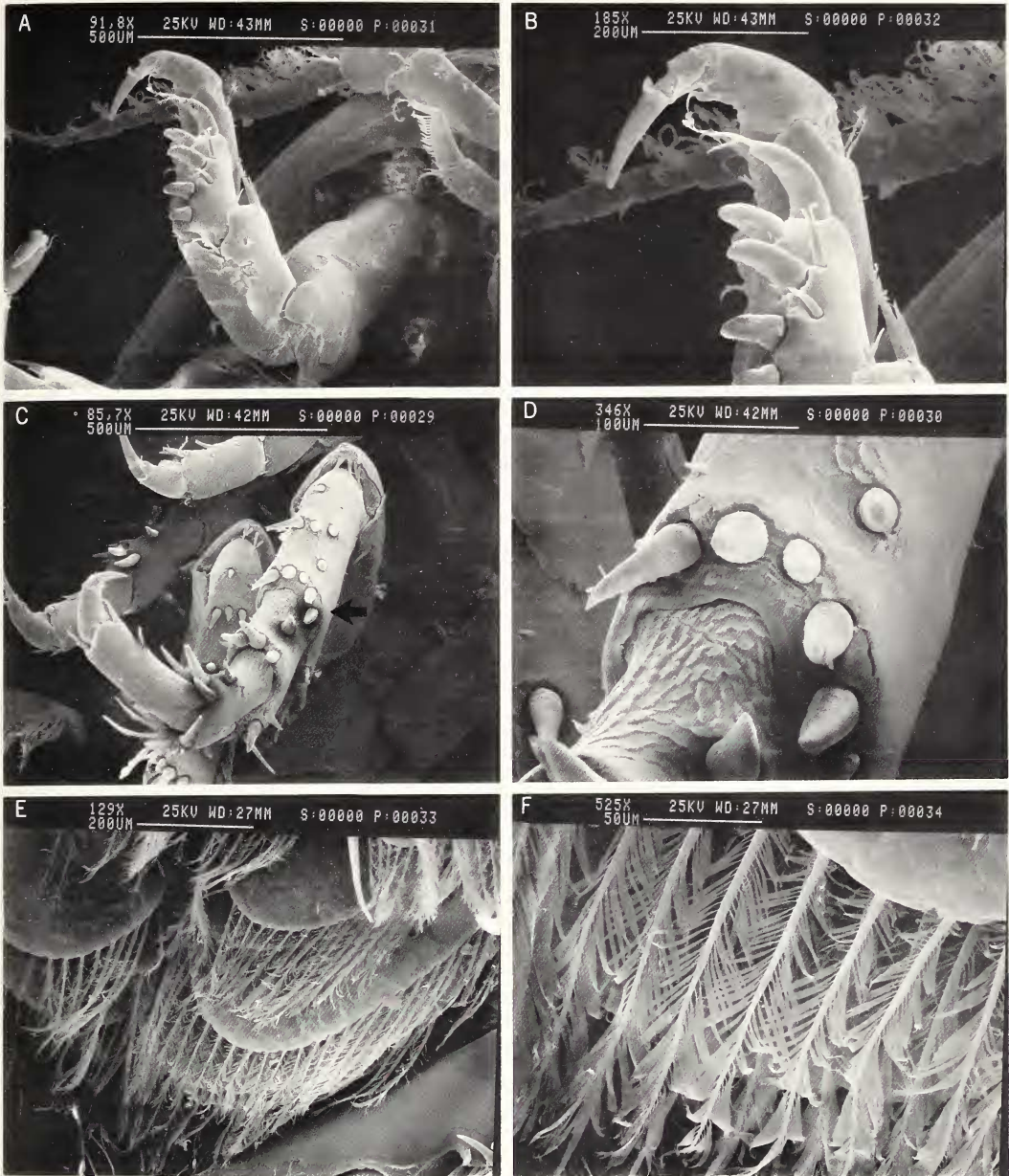


Figure 31. Scanning electron micrographs of *Lanocira gardineri*, USNM 40956: A, pereopod I; B, propodus and dactyl of pereopod I; C, pereopod VI; D, spines on ischium of pereopod VI; E, apex of pleopods 4 and 5; and F, plumose marginal setae on pleopod 5.

ing live and dead corals, coral rubble, and sand. There is only one record (this study) of an unidentified *Lanocira* species collected as a “temporary parasite” of a fish (*Variola louti*), but there are a variety of “commensal” associations reported. *Lanocira gardineri* has been collected from sponges (Barnard, 1920; Bruce, 1980), from among the tubes of the worm *Sabellaria capensis* (Barnard, 1914), with ascidians (Stebbing, 1905), and from corals (Jones, 1982). *Lanocira zeylanica* has been collected from sponges (Monod, 1933) and from corals (Monod, 1933; Jones, 1982). *Lanocira latifrons*

has been reported from “the umbrella of *Cassiopea andromeda* (Scyphozoa)” (this study). *Lanocira glabra* has been collected as an associate of algae and marine angiosperm rhizomes (Jones, 1982). *Lanocira anasicula* has been collected from *Montipora* corals (Jones, 1982).

Jones (1982) noted that many *Lanocira* species seem limited to hard substrates and may be restricted to cryptic habitats in sheltered waters, especially the crevices of live and dead corals. He also noted the absence of *Lanocira* from his plankton tows at Watamu, Kenya, and suggested that

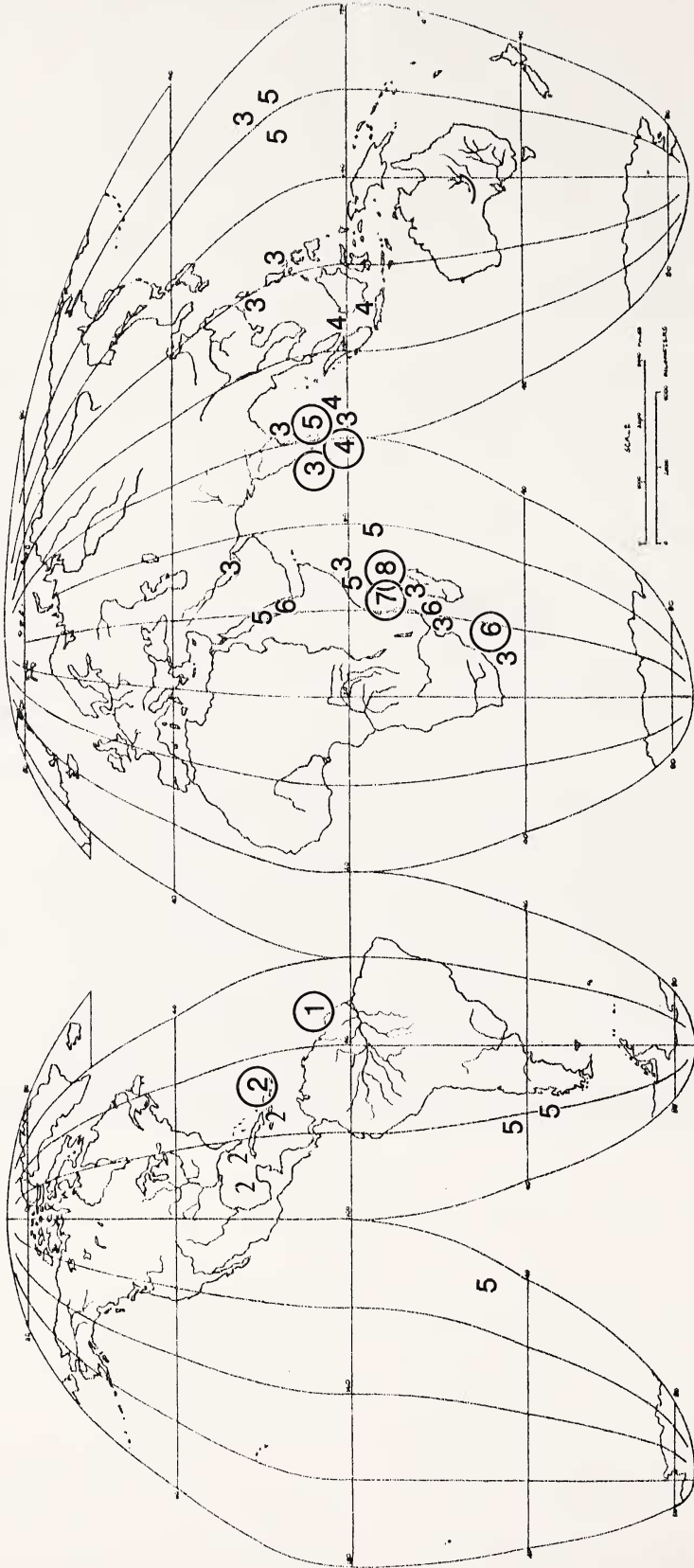


Figure 32. Distribution of *Lanocira* species; type localities are circled. Species numbers are: 1, *L. kroyeri*; 2, *L. rapax*; 3, *L. gardineri*; 4, *L. rotundicauda*; 5, *L. zeylanica*; 6, *L. latifrons*; 7, *L. glabra*; and 8, *L. anasicula*.

this absence, along with the morphology of the mandibles, implied omnivorous or herbivorous habits for *Lanocira*. The scarcity of fish "parasite" records gives some support to the contention of omnivorous habits for this genus.

Barnard (1920) noted that one specimen of *Lanocira capensis* (a synonym of *L. gardineri*) was parasitized by two cryptoniscan larvae, which he attributed to the genus *Clypeoniscus*.

## Genus *Tachaea*

Schioedte and Meinert, 1879

*Tachaea* Schioedte and Meinert, 1879:284; Hansen, 1890:239; Weber, 1892:551; Stebbing, 1893:315, 1904a:14, 1904b:703, 1907:39, 1908:107; Thielemann, 1910:18; Tattersall, 1921:419; Shen, 1936:17; Nierstrasz, 1917:102, 1931:172; Nierstrasz and De Mares van Swinderen, 1931:397; Bruce, 1982b:248; Bruce et al., 1982:464; Delaney and Brusca, 1985:729.

*Austroargathona* Riek, 1953:259, 1967:176; Bruce et al., 1982:464; Delaney and Brusca, 1985:729. *Icochaeta* Caldwell, 1879:38 (*lapsus calami*). *Icochaes* Shen, 1936:17 (*lapsus calami*).

### MATERIAL EXAMINED

*Tachaea crassipes*: 1) no locality data, ZMUC, 1 spec., 4 mm (cephalon missing); 2) (as *Tachaea incerta*, type) ZMUC, 1 spec., 6.8 mm. *Tachaea lacustris*: 1) Java, ZMHUB No. 23023, "FF4d," Sunda Expedition, 3 fe., 8.9, 8.4, and 9.6 mm; 2) East Java, Lake Klakah, ZML No. 1288, Deutsch Limnologische Sunda Expedition, 1 ma., 10.1 mm, and 2 fe., 9.2 and 7.6 mm; 3) Java, Lake Klakah, USNM Acc. No. 100460, >20 spec. *Tachaea spongillicola*: India, Calcutta, BMNH syntypes, 1907-10-19-4, "In canals of *Spongilla carteri*," 2 spec., 5.2 and 2.8 mm (cephalon and pleon missing). *Tachaea chinensis*: 1) Siam, Huai Nam Puat, USNM 142208, "HGD 114," 1 fe.; 2) Thailand, Ratchathani Province, Ubon Ubon, at morning market, USNM Acc. No. 309712, Smithsonian Institution, WBD-Mekong Program, Sta. T-1079, 15°13'30"N, 104°52'E, 1 spec.; 3) China, Hong Kong, USNM Acc. No. 312185, "Associated with oysters," 2 ma.; 4) China, Fukien, Haiteng, USNM Acc. No. 161481, 1 fe.; 5) Japan, Yokohama, ZMHUB, "From a pool with *Palaemon*," 1 fe., 5.3 mm; 6) Japan, Tokyo, ZMHUB No. 6922, 1 fe., 6.6 mm; 7) China, Peking, ZMUC, 1 fe., 5.3 mm; 8) Malaya, Johore, Gunong Pulai, BMNH 1961-8-25-24-25, "On *Macrobrachium* sp.," 2 fe., 4.5 and 2.9 mm; 9) Japan, Honshu, Mie Prefecture, ZML, "Mouth of small stream near Toba, Kii Peninsula, brackish water," 2 fe. spec., 8.4 and 7.4 mm; 10) Japan, Tokyo, ZMHUB No. 6967, 1 fe., 6.3 mm. *Austroargathona caridophaga*: 1) Australia, Queensland, Conondale River, ZML No. 1715, paratypes, "Parasitic on *Macrobrachium*," 2 fe., 9.0 and 6.6 mm; 2) Aus-

tralia, Queensland, AM slides of holotype and allotype appendages. *Austroargathona picta*: 1) Australia, New South Wales, AM slides of holotype appendages. *Austroargathona* sp.: 1) Thailand, 3300 m N. of Udorn Thani, BMNH 1977-325-2, "Found on *Macrobrachium lanchesteri* in a rice field," 2 fe., 4.6 and 4.8 mm. *Tachaea* sp.: 1) New Guinea, Papua, Bootless Bay, Motupore Island, Port Moresby, USNM Acc. No. 320977, 1 fe.; 2) Undescribed species, NTM slides of ma. (N.L. Bruce.)

### DIAGNOSIS

Antennule peduncle 2-articulate; basal article expanded. Frontal lamina quadrangular, elongate, length = 2.0–3.0 times width; rounded anteriorly, narrowing posteriorly. Clypeus short, broad; labrum small. Mandible with small, monocuspid incisor; lacinia mobilis and molar process small or absent. Maxillule lateral lobe forming single large curved spine; medial lobe simple, with bluntly rounded apex. Maxilla short, 2- or 3-articulate, ending in rounded lobe. Maxilliped without endite; basis elongate, length = 1.5–2.0 times width; palp 3-, 4-, or 5-articulate, middle article not elongate. Anterior pereopods with carpi strongly produced on posteromedial margins; without serrate dactyli and propodi.

### ADDITIONAL DESCRIPTION

Eyes small, widely separated. Body occasionally with dorsal tubercles and setae (Figs. 1F, G). Antennule peduncle basal article expanded (Fig. 33F). Antenna peduncle articles 4 and 5 elongate (Fig. 33E). Frontal lamina, clypeus, and labrum visible anterior to mandibles; labrum may cover distal region of mandibular incisor. Clypeus sometimes encompassing lateral margins of labrum (Fig. 34A). Mandible molar process, when present, represented by small 3-spined lobe; lacinia mobilis represented by 1–3-spined lobe. Palp inserted near mandible base, 3-articulate, middle article longest, with simple marginal setae; distal article with plumose marginal setae and often with comblike cuticular structures (Figs. 33C, H, 35D, 36C–F). Maxillule lateral (outer) lobe forming single large curved spine, occasionally with 1 minute straight spine at base (in *T. picta*); medial (inner) lobe with single apical seta (Figs. 33I, 35G, 37C, F, 36A, B). Maxilla with 0–4 apical setae (Figs. 33D, J, 35E, 37C, E). Maxilliped palp distal articles with simple marginal setae (Figs. 33A, B, G, 35A–C, 37A, B, D). In gravid females, oostegites cover buccal field, and large epipods, with plumose marginal setae, arise from maxilliped bases (Fig. 35A). Pereopods I–III short, prehensile; with short bifid spines, simple spines and setae on posteromedial margins (Fig. 34B, C, 35F). Pereopods IV–VII longer, ambulatory, with spines and setae on posteromedial margins, and long propodi (Fig. 34D). Pleopod peduncles wider than long, with 4–5 cou-

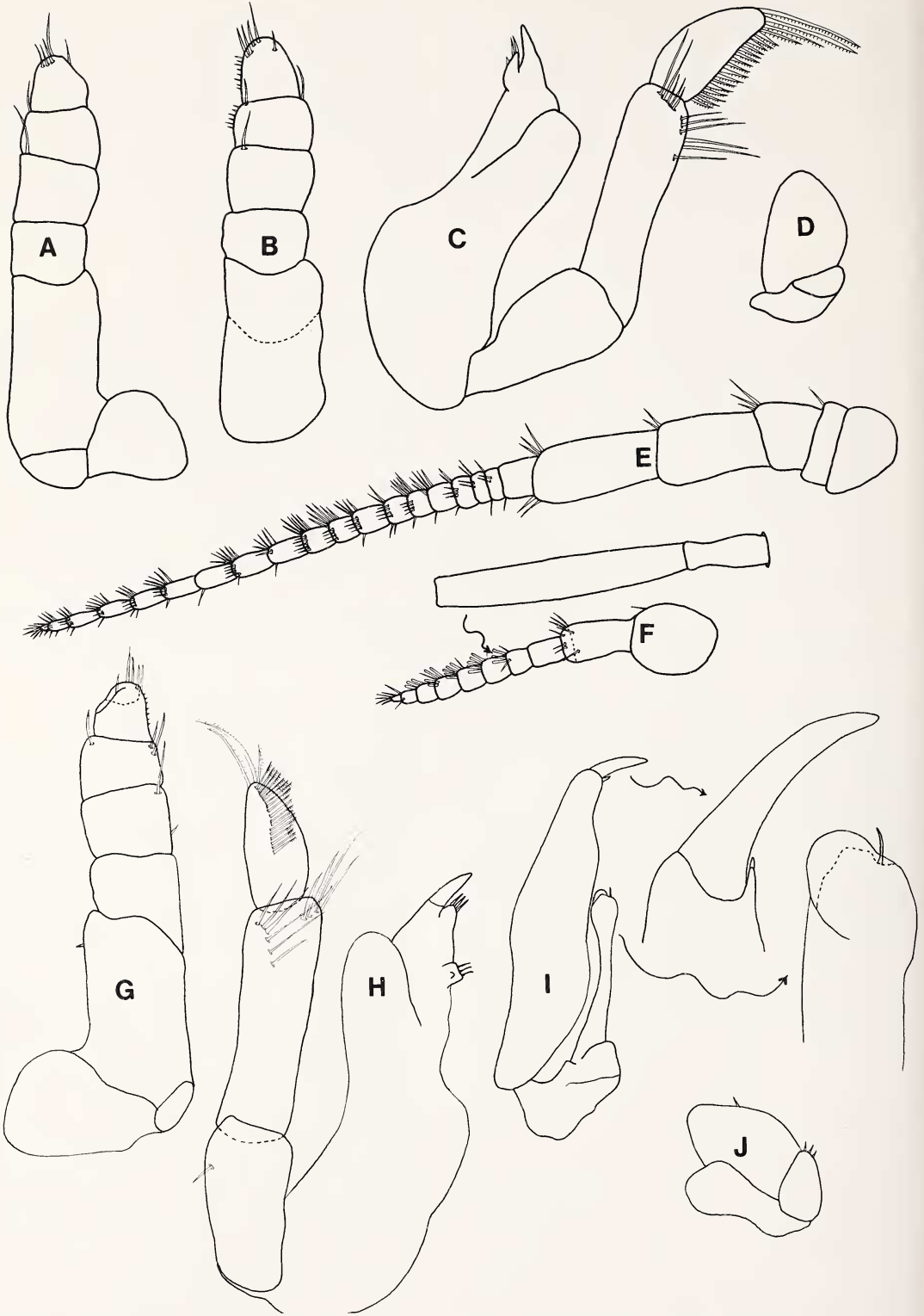


Figure 33. *Tachaea* sp., NTM, male one, A-F: A, left maxilliped; B, right maxilliped; C, left mandible; D, right maxilla; E, antenna; and F, antennule. Male two, G-J: G, left maxilliped; H, right mandible; I, left maxillule; and J, right maxilla.

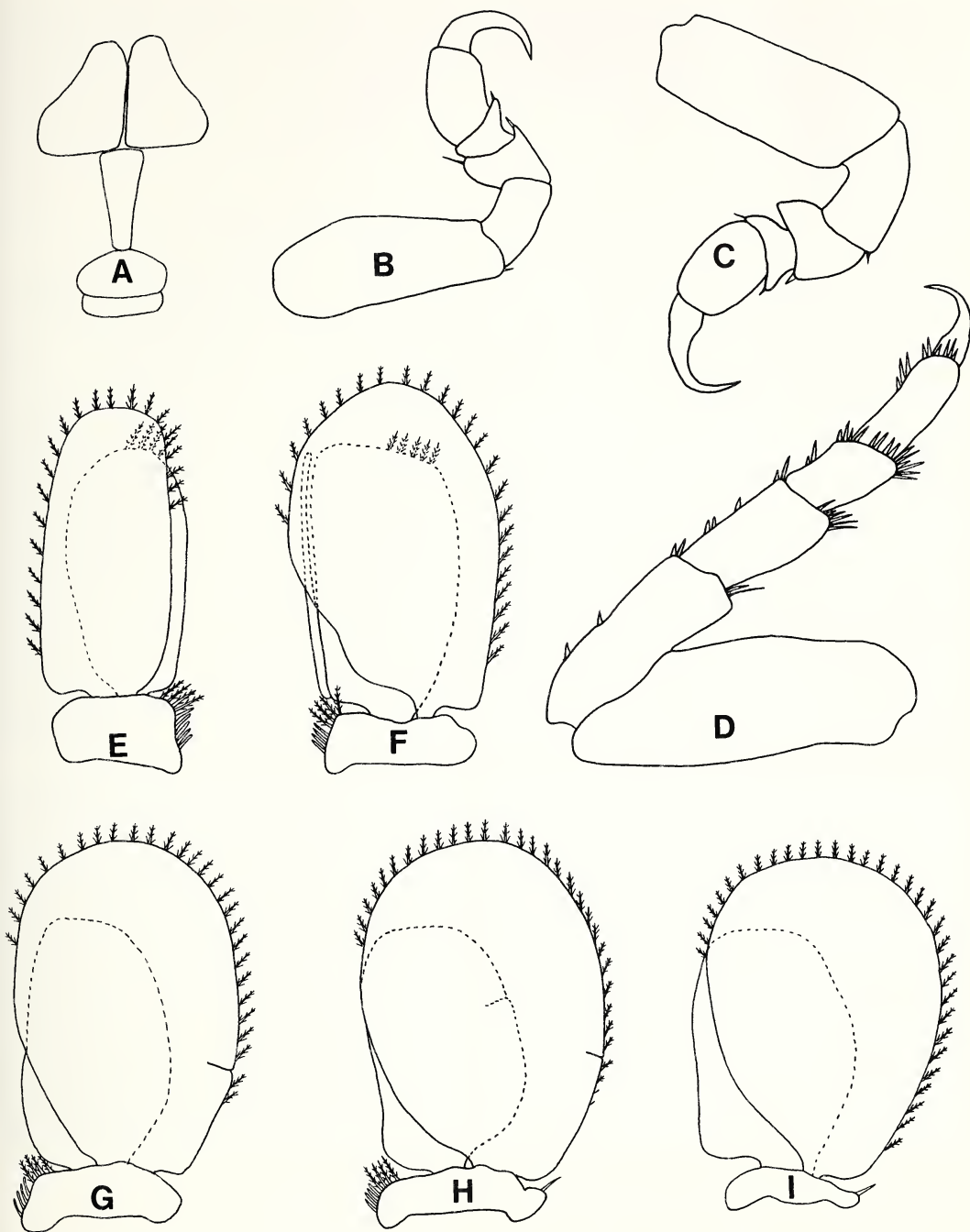


Figure 34. *Tachaea chinensis*, USNM 312185: A, antennule bases, frontal lamina, clypeus, and labrum. *Tachaea lacustris*, USNM Acc. No. 100460, B-I: B, pereopod I; C, pereopod III; D, pereopod VII; E, pleopod 1; F, pleopod 2; G, pleopod 3; H, pleopod 4; and I, pleopod 5.

pling spines and groups of proximal setae on medial margins, lateral margins often with simple spine (Figs. 34E-I). Exopods of pleopods broader, longer, and with more plumose marginal setae than endopods; endopod of pleopod 5 naked, endopods of 1-4 naked or with sparse setation. Male pleopod

2 with rodlike appendix masculina arising from proximal medial margin of endopod (Fig. 34F).

#### TYPE SPECIES

*Tachaea crassipes* Schioedte and Meinert, 1879, by monotypy.

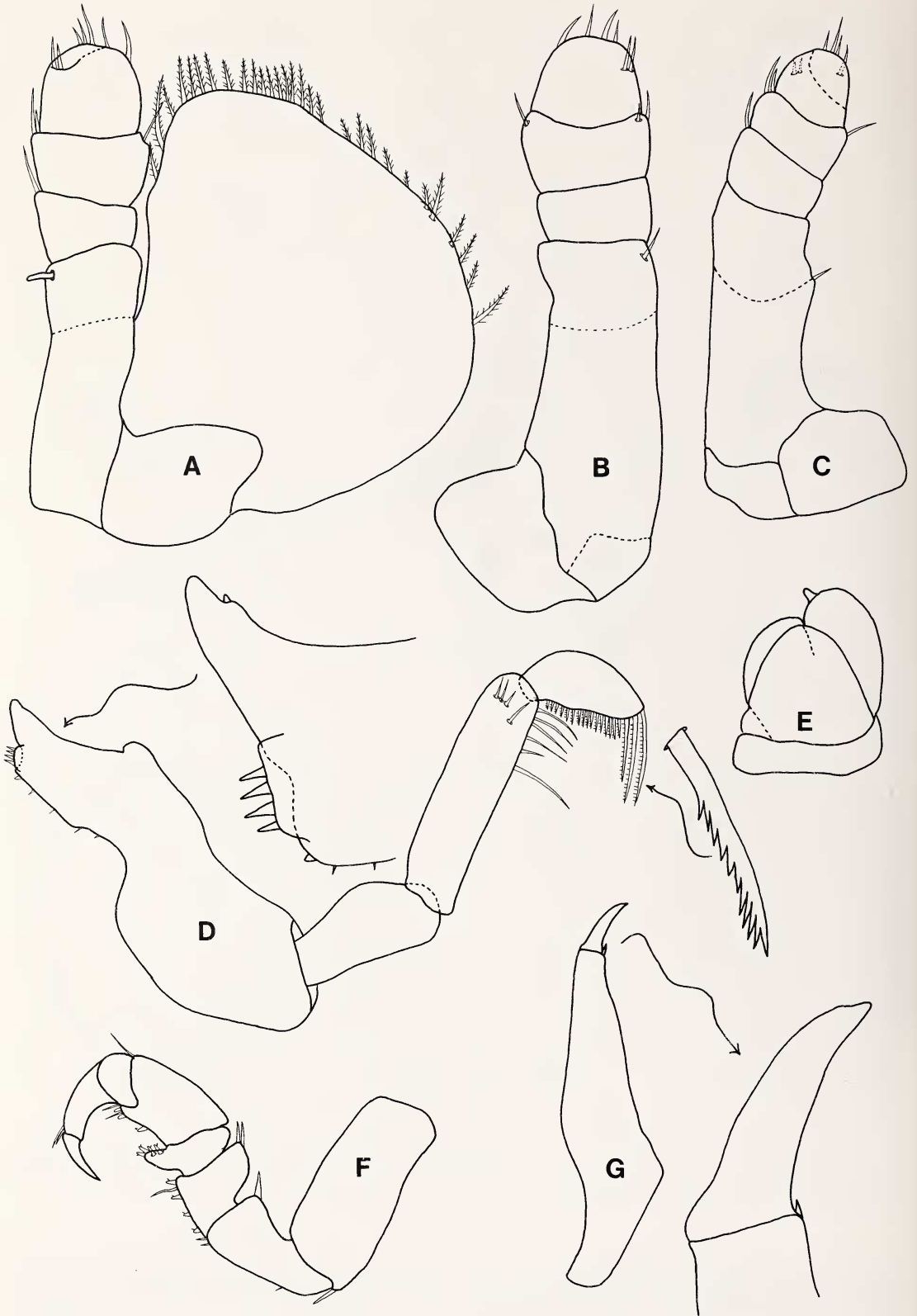


Figure 35. *Tachaea picta* (ex *Austroargathona*), AM holotype female, C-G: A, *T. caridophaga* (ex *Austroargathona*), holotype female, left maxilliped; B, *T. caridophaga*, allotype male, right maxilliped; C, right maxilliped; D, left mandible; E, left maxilla; F, pereopod I; and G, right maxillule.

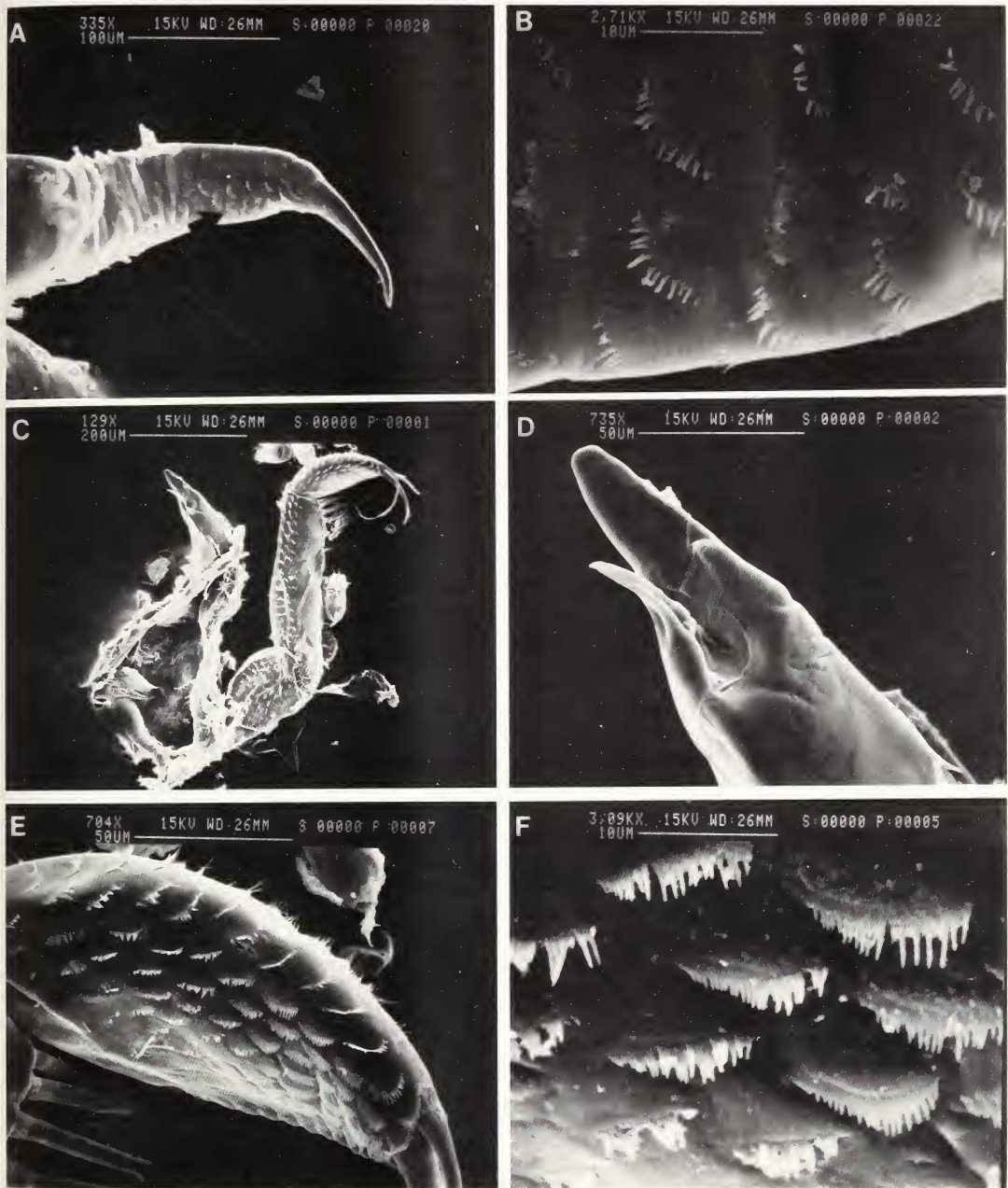


Figure 36. Scanning electron micrographs of *Tachaea lacustris*, USNM Acc. No. 100469: A, maxillule, lateral lobe; B, detail of maxillule (in A); C, mandible; D, mandible apex; E, distal article of mandibular palp; and F, comblike cuticular structures on distal article of mandibular palp.

#### DESCRIBED SPECIES, WITH SYNONYMS AND DISTRIBUTIONS

- 1) *Tachaea crassipes* Schioedte and Meinert, 1879: 285, table IV, figures 2–7; Hansen, 1890:398; Weber, 1892:552; Stebbing, 1893:315, 1907:41; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:419; Nierstrasz and De Marees van Swinderen, 1931:399; Shen, 1936:17.

*Tachaea incerta* Hansen, 1890:400, table IX, figures 2a, b; Weber, 1892:552; Stebbing, 1893:315, 1907:41; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Nierstrasz and De Marees van Swinderen, 1931:398.

*Ichochaes crassipes* Shen, 1936:17 (*lapsus calami*).

**DISTRIBUTION.** Singapore.

- 2) *Tachaea lacustris* Weber, 1892:551; Stebbing,

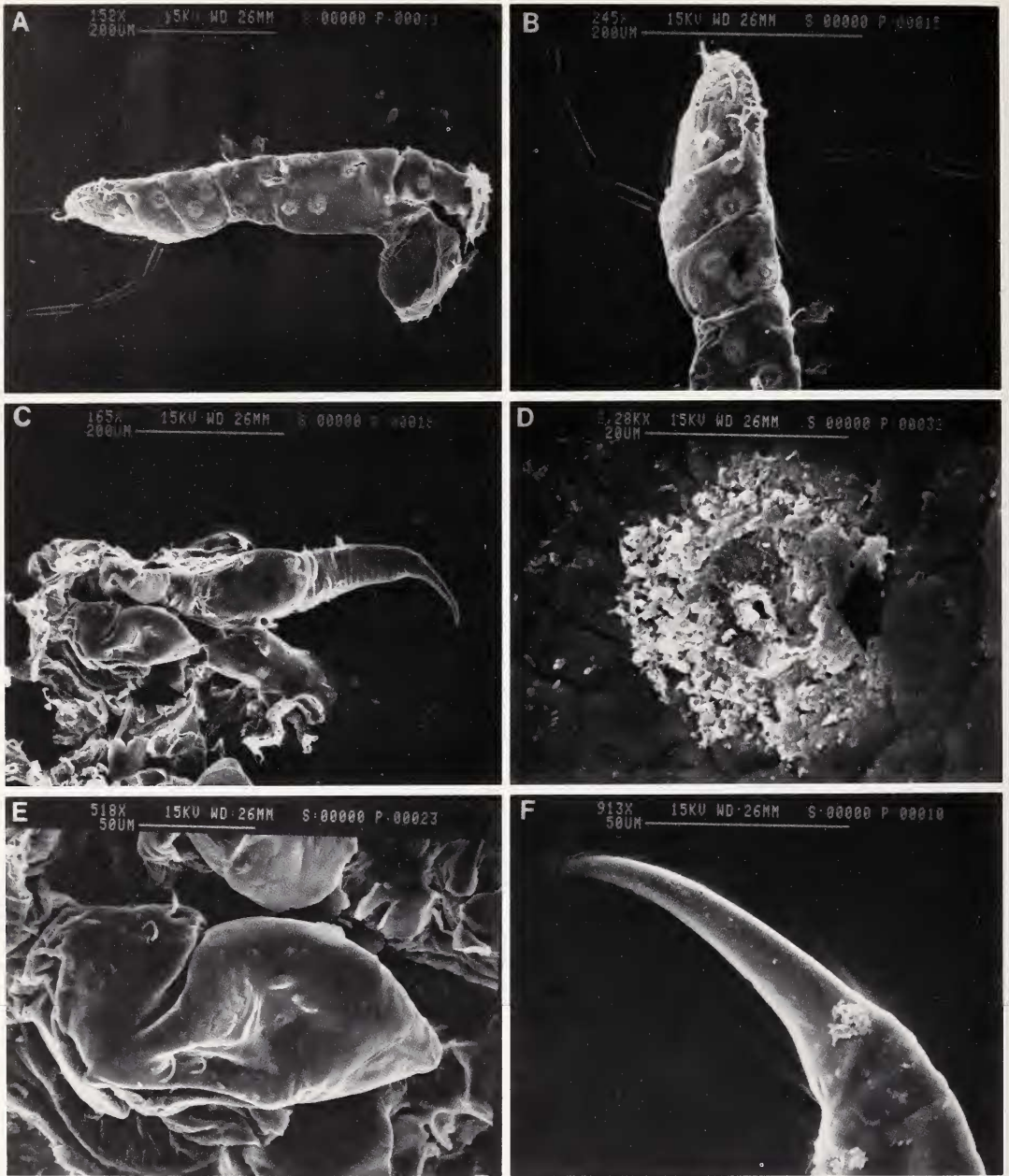


Figure 37. Scanning electron micrographs of *Tachaea lacustris*, USNM Acc. No. 100469: A, maxilliped; B, maxilliped palp; C, maxilla and maxillule; D, surface detail of maxilliped (arrow in B); E, maxilla; and F, maxillule apex.

1908:107; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:420; Nierstrasz and De Marees van Swinderen, 1931:397; Shen, 1936:17.

**DISTRIBUTION.** Sumatra and Java.

- 3) *Tachaea spongillicola* Stebbing, 1907:40, plate 6, 1908:107; Thielemann, 1910:21; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:419; Nierstrasz and De Marees van Swinderen, 1931:398; Shen, 1936:17.

**DISTRIBUTION.** India.

- 4) *Tachaea chinensis* Thielemann, 1910:19, figures 12–20; Nierstrasz, 1917:102, 1931:172; Tattersall, 1921:420; Nierstrasz and De Marees van Swinderen, 1931:399; Shen, 1936:17.

**DISTRIBUTION.** China, Japan, Thailand, and Malaya.

- 5) *Tachaea caridophaga* (Riek, 1953):259, figures 1–7.  
*Austroargathona caridophaga* Riek, 1953:259.

**DISTRIBUTION.** Queensland, Australia.



- 6) *Tachaea picta* (Riek, 1967):176, figures 1–6.  
*Austroargathona picta* Riek, 1967:176.

**DISTRIBUTION.** Queensland and New South Wales, Australia.

## REMARKS

The genus *Tachaea* was established in 1879 by Schioedte and Meinert for their *Tachaea crassipes*.

The genus *Austroargathona* was erected by Riek in 1953 for his species *Austroargathona caridophaga* and was placed by him in the Corallanidae. A second species, *Austroargathona picta*, was added by Riek in 1967.

The validity of the genus *Austroargathona* has been suspect for some time, as was noted by Bruce et al. (1982). The 2 existing species of *Austroargathona* have morphological features typical of *Tachaea* species, including features of the antennules, antennae, mouthparts, and pereopods. Examination of type and non-type specimens, and comparison of morphological characters, has indicated to me that *Austroargathona* should be synonymized with the *Tachaea*, the latter having priority.

Although Riek (1953) did not mention the obviously similar *Tachaea* when comparing his new genus *Austroargathona* to other corallanid genera, the absence of molar process and lacinia on the mandible, the 3-articulate maxilliped palp, and the nonexpanded propodi of pereopods I–III were the only characters indicated that might distinguish *Austroargathona* from *Tachaea*.

The presence or absence of a molar process and lacinia mobilis on the mandible varies among species of *Tachaea*. Absence of a mandibular molar process has been noted in certain species of *Excorallana* (Richardson, 1905; Delaney, 1982, 1984) and *Alcirona* (Richardson, 1905; Hale, 1925; Menzies and Glynn, 1968; Menzies and Kruczynski, 1983).

From examination of *Tachaea* and *Austroargathona* specimens I have found that the number and extent of maxilliped article fusion/loss may vary within species (as in *T. chinensis*, see Thielemann, 1910, and Shen, 1936) as well as among species. The second corallanid species described by Riek (1967), *Austroargathona picta*, possesses a 4-articulate maxilliped palp. Apparent fusion or loss of maxilliped articles is known in various *Tachaea* species such as *Tachaea crassipes* Schioedte and Meinert, 1879 (in Hansen, 1890), *T. spongillicola* Stebbing, 1907, and *T. chinensis* Thielemann, 1910. Tattersall (1921) noted that various degrees of maxilliped fusion have been described in *Tachaea*: fusion of 2nd and 3rd articles (by Hansen, 1890); 6th and 7th articles (by Stebbing, 1907); 2nd–3rd and 6th–7th articles (by Thielemann, 1910); and no fusion or loss of articles at all (Shen, 1936). Tattersall (1921) also noted that fusion may be incomplete, as evidenced by partial suture lines on the maxillipeds of *T. chinensis* Thielemann. Loss or fusion of maxilliped palp articles is also recorded in certain

species of *Argathona* (Stebbing, 1905, 1911; Hale, 1925; Monod, 1933, 1975; Barnard, 1936; Pillai, 1967; Bruce, 1982b). Loss and/or fusion of maxilliped palp articles also commonly occurs in many other families of isopods.

Lastly, the carpi of pereopods I–III are produced in both *Tachaea* and *Austroargathona*.

The name *Icochaeta crassipes* was published in the *Zoological Record* for 1879 (Caldwell, 1879: 38) and attributed to Schioedte and Meinert, but does not appear in either of their publications that year. Shen (1936) misspelled the name as *Icochaes crassipes* but indicated that it and *Tachaea incerta* should be regarded as junior synonyms of *T. crassipes*. *Icochaeta* and *Icochaes* should be regarded as incorrect subsequent spellings (*lapsus calami*) of the correct genus name *Tachaea*.

Sexual dimorphism exists in the dorsal ornamentation of some *Tachaea* species, as in all other genera of the Corallanidae and Tridentellidae. In *Tachaea lacustris* males have a pair of anterior cephalic tubercles as well as large tubercles on the posterior pereonites; these structures are lacking in females (see Nierstrasz and De Marees van Swinderen, 1931:398).

Stebbing (1907) noted that in *Tachaea spongillicola* the pleotelson is broadly rounded in females but is apically truncate in males. Based on this information he synonymized *T. incerta* Hansen with *T. crassipes* Schioedte and Meinert. Stebbing distinguished *T. spongillicola* from *T. crassipes* by the apical article of the maxillipeds as well as the decreased spination of the pereopods and the shorter pleon (relative to pereon length) in the former species.

Nierstrasz and De Marees van Swinderen (1931) redescribed *Tachaea lacustris* Weber and noted much variation in the number of antenna flagellar articles, pleotelson spination, and pleotelson shape, which they found to vary from rounded to “somewhat pointed.”

*Tachaea leopoldi* Nierstrasz, 1930, was removed to the genus *Corallana* by Bruce (1982b).

*Tachaea picta* Riek, 1967, is very similar to *T. caridophaga* Riek, 1953, and may prove to be a junior synonym. However, until more specimens can be examined they must remain separate species.

## BIOGEOGRAPHIC AND ECOLOGICAL NOTES

The six described species of *Tachaea* show a range in habitat and distribution that is more restricted than that of any other genus in the family Corallanidae, being confined mainly to tropical/subtropical freshwater habitats in the Indo-Pacific region (Fig. 38). One species, *T. crassipes*, has been reported as marine (from coral reefs, Singapore), while the other five species, from freshwater ponds, lakes, and rivers, have been reported as “ectoparasites” of fish (*Culter brevicauda*, “Cyprinoiden” fish, and “catfish”) and various shrimp species (*Ca-*

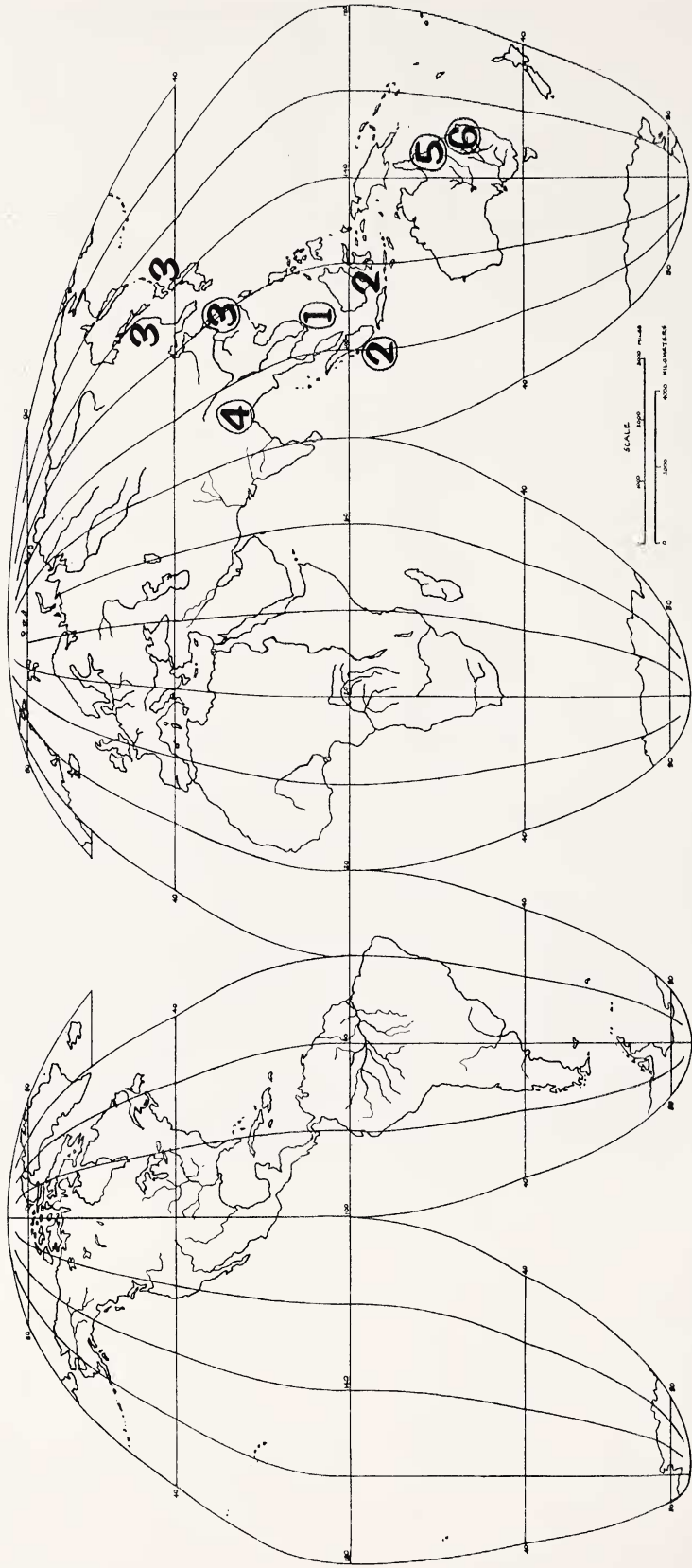


Figure 38. Distribution of *Tachaea* species; type localities are circled. Species numbers are: 1, *T. crassipes*; 2, *T. lacustris*; 3, *T. chinensis*; 4, *T. spongillicola*; 5, *T. caridophaga*; and 6, *T. picta*.

*ridina nilotica gracilipes*, *Caridina denticulata*, *Palaemonetes sinensis*, *Leander paucidens*, *Macrobrachium australiense cristatum*, *Macrobrachium lanchesteri*, *Macrobrachium* sp., *Palaemon* sp., and *Paratya* sp.). Other *Tachaea* species have been collected as "commensals" of freshwater sponges (*Spongilla carteri* or *Spongilla lacustris*) and as associates of oysters, hydroids, and the burrows of larval *Povilla corporaali*.

## CLADISTIC ANALYSIS

### MATERIALS AND METHODS

#### General Methods

Cladistic relations between the six currently recognized genera of the isopod family Corallanidae and the outgroup families Tridentellidae and Cirolanidae were determined by analyzing sets of morphological character states using the PAUP computer program of Dr. David Swofford (Version 2.4) and the PHYLIP package of Dr. Joseph Felsenstein (Version 2.7), as adapted and compiled for IBM personal computers by Dr. George D.F. Wilson. The philosophical methods used in this study were largely summarized in three recent texts (Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981).

Nomenclature and terminology were taken from current literature on the families Corallanidae, Tridentellidae, and Cirolanidae (see Delaney and Brusca, 1985). Characters used in the analysis were mostly traditional characters used to define corallanid genera (see Bruce et al., 1982), such as morphology of the mouthparts and pereopods, as well as additional characters of antennules, eyes, pleotelson, and frontal laminae. Character states were determined by examining type-species and type-specimens whenever possible, but all materials examined were used to diagnose the characters for each corallanid genus. Fifty trees resulting from PAUP and PHYLIP were compared for topology and tree length. Homoplasy statistics, if provided by the program, were also compared. Each tree is referred to by the program that generated it and by number. For example, the PAUP tree in Figure 39 is referred to as PAUP 1 in the text and Table 4, and the DOLLOP tree 17 is called DOLLOP 17 in Table 4. The object of this analysis was to find the tree that was the most parsimonious in terms of minimum tree length (= number of character state changes) and minimum homoplasy (= number of convergences and reversals required for the construction of the particular tree), as well as being the tree most corroborated by topologies produced from the other cladistic algorithms.

#### Character Coding

The numerical coding of characters is an extremely important part of cladistic analysis. The coding procedure requires the systematist to convert his knowledge of the variation within and between

taxa into numerical format. This almost always involves some subjectivity on the part of the systematist, whether acknowledged or not.

Some features of corallanid genera were easier to code than others, and these have straightforward character state descriptions. However, some characters required more ambiguous character state descriptions. For example, many *Alcirona* species possess serrated dactyli on pereopod I, yet not all species in that genus do. Therefore, the character state description (see Appendix II) for that character reads "without serrate dactyli" for genera in which the condition has never been observed, and "with serrate dactyli in some species" for genera where this state has been observed, though not necessarily in all species. I consider this a valid way of including characters that are variable within a genus and yet contain useful phylogenetic information.

#### Out-groups and Character State Ordering

The polarity of transformation series of character states were initially established by out-group analysis, using two related flabelliferan families, the Cirolanidae and Tridentellidae (for methods see Eldredge and Cracraft, 1980; Watrous and Wheeler, 1981; and Maddison et al., 1984). The Cirolanidae includes approximately 35 genera, while the Tridentellidae is monogeneric (*Tridentella*). Analyses with PAUP were done using these polarized ("ordered") multistate characters and with unpolarized characters (see Appendices II and III for character list and data matrices). These multistate characters were then recoded into binary character state data using the FACTOR program in PHYLIP. This binary state character set was analyzed with the PHYLIP programs WAGNER, DOLLOP, PENNY, MIX (parsimony optimization), and CLIQUE (compatibility optimization) for comparison to PAUP-generated trees. The evolutionary assumptions in PAUP and PHYLIP algorithms are compared in Table 2.

#### Methods Used with the PAUP Program

PAUP trees were produced from an 8-taxon, 21-character multistate data matrix. Both "directed" and "undirected" analyses were performed. In the "directed" analysis, the families Cirolanidae and Tridentellidae were the designated out-groups used to polarize character states. Each of the two out-groups were used in turn to root the tree. However, trees of similar topology, identical length, and consistency index were produced each time. Subsequently, "undirected" analyses were performed in which the "unordered characters" option was used.

The "Alltrees" option was used; this is the exhaustive search option evaluating all possible tree topologies, computing the length of each and finding the absolute shortest, most parsimonious tree.

#### Methods Used with the PHYLIP Programs

The set of multistate characters used in the PAUP analysis was recoded into binary characters using

**Table 2. Comparison of different cladistic programs used in this study.**

Program	Function
PAUP	Unrestricted parsimony method = reversals and parallelism/convergences equally probable in explaining synapomorphy distributions.
PHYLIP	A package of cladistic programs (as follows).
WAGNER	Unrestricted parsimony = reversals and convergences equally probable.
DOLLOP	Restricted parsimony = allows one forward character change plus as many reversals as necessary.
PENNY	Unrestricted parsimony = WAGNER parsimony with "branch and bound" tree search method.
CLIQUE	Character compatibility method = seeks groups of mutually compatible characters to explain maximum number of synapomorphies.
MIX	Restricted Camin-Sokal parsimony = allows forward character changes but not reversals.
ITERMIX	Generates data sets with the order of taxonomic units randomized.
FACTOR	Recodes multistate characters using additive binary coding.

the FACTOR program in PHYLIP as follows. Each multistate character to be factored was described by a list of pairs of character states that are adjacent to one another on a hypothesized character state tree. An ancestral state was not designated for any of the recoded characters. However, FACTOR requires that character states be coded as transforming from one particular state to another—a hy-

pothesis of character state evolution (a character state tree). The result was an 8-OTU, 32-character data set (Appendix III); the recoding of multistate characters into binary ones produced an additional 11 characters.

Unlike PAUP, some programs in PHYLIP are known to be sensitive to order of OTUs in the data set. Therefore, 10 versions of the binary data set, with the order of the OTUs randomized, were constructed using the ITERMIX program in PHYLIP. These randomized versions were each analyzed with WAGNER, DOLLOP, and MIX (Camin-Sokal parsimony option) but not with PENNY or CLIQUE, as according to Felsenstein (1984) these latter two are not sensitive to the input order of OTUs, making multiple runs of the data set unnecessary.

## RESULTS AND DISCUSSION

Table 3 summarizes the results from various cladistic programs used in terms of: number and type of characters used; number of trees produced per iteration; length of trees and associated statistics such as consistency index (C.I.) and F-values, if such were given by the program. The program results are compared below.

### PAUP and PHYLIP Parsimony Analyses

The tree produced by the unordered PAUP analysis (Fig. 39) was generated from a completely "unordered" matrix of character states—no direction of evolutionary transformation was presumed for any character or used to impose a particular order on the cladogram. This topology was subsequently rooted using the designated out-groups to produce the directed tree PAUP 1. Meacham (1984) presents arguments supporting initial use of "undirected characters" in cladistic analyses and the subsequent directing of the undirected tree. PAUP 1 (Fig. 39) was the shorter tree (length = 32), had a higher consistency index (C.I. = 1.0), and was less ambigu-

**Table 3. Cladistic analysis of Corallanidae: results from different programs.**

Program	Characters	Trees produced	Comments
PAUP	21, multistate	1 tree, length = 32, C.I. = 1.0	"unordered," unrestricted parsimony
PAUP	21, multistate	5 trees, length = 39, C.I. = 0.821, F-values = 28.0-48.0	"ordered," unrestricted parsimony
WAGNER*	32, binary	5 trees, length = 39 (10 iterations: data input order randomized)	unrestricted parsimony
DOLLOP*	32, binary	1 tree, length = 41 (10 iterations: data input order randomized)	restricted parsimony
PENNY*	32, binary	5 trees, length = 39	unrestricted parsimony (branch and bound method)
CLIQUE*	32, binary	9 cliques/trees, 25 characters, length = 25	character compatibility analysis
MIX*	32, binary	4 trees, length = 40 (10 iterations: data input order randomized)	restricted Camin-Sokal parsimony

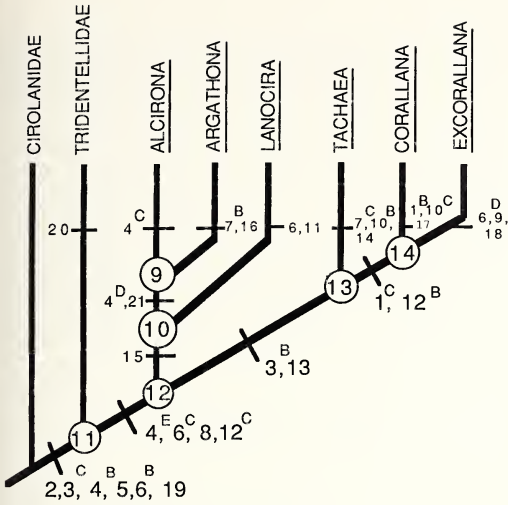
\* Programs from the PHYLIP package.

## CLIQUE (PHYLIP) Analysis of Character Compatibility

Seventy-eight percent (25/32) of all characters were included in at least one of the nine cliques produced by this analysis; 66% (21/32) of all characters in the original data set were common to all nine cliques, indicating some character congruence. Eighty-four percent (21/25) of characters found in cliques were common to all cliques. Binary characters 5 and 15 were excluded from all of the nine cliques. These are binary characters recoded from multistate characters, meaning that some character states of certain multistate characters were excluded from cliques while others were not.

Thirty-four percent of the characters in the data set were "new" ones resulting from binary recoding. None of the cliques included all the binary characters produced from all the multistate characters.

As noted by Felsenstein in the documentation to PHYLIP 2.7, cliques of characters found by CLIQUE are cliques of two-state characters. If these are "binary-factors" recoded from multistate characters (by additive binary coding), some of the two-state characters from one multistate character may be involved in a clique and others *not involved*. For example, the two multistate characters of maxilla and maxillule morphology, when recoded into binary, made eight binary characters; in only one clique do all eight appear. As previously noted, binary characters 5 and 15 (each previously a part of a multistate character) do not appear at all. It is quite possible that this skews the meaning of "compatibility" for characters recoded in such a fashion and may be responsible for some of the differences in the nine cliques produced in this analysis. The creation of binary characters from multistate characters may weight those multistate characters in the analysis, and this implies that fundamental differences may exist between multistate and recoded, non-multistate trees.



PAUP 2.4 CLADOGRAM  
LENGTH = 32  
CONSISTENCY INDEX = 1.0

**Circled numbers are nodes,  
other numbers are characters,  
letters are character states.**

Figure 39. PAUP tree 1, produced from unordered characters.

ous (one tree) than those PAUP trees resulting from ordered characters (length = 39, C.I. = 0.821, five trees), as well as the trees produced from the WAGNER, DOLLOP, PENNY, and MIX (Camin-Sokal option) algorithms in PHYLIP (Table 3). The PAUP 1 tree (Fig. 39) was not only shorter than all other trees produced from programs using the entire data matrix (i.e. excluding compatibility analysis—CLIQUE), it was also corroborated by trees and cliques from more algorithms than any other PAUP or PHYLIP topology (Table 4).

Table 4. Corroborating trees and cliques for variant PAUP topologies.\*

PAUP topologies and statistics	Corroborating trees and cliques	Number of supporting trees/programs
PAUP 1 (length = 32, C.I. = 1.0, no F-value)	PAUP 6; WAGNER 9, 10; PENNY 27; CLIQUE 35, MIX 43, 45, 46, 49	9/5
PAUP 2 (length = 39, C.I. = 0.821, F-value = 48.0)	WAGNER 7; DOLLOP 17-26; PENNY 29	12/3
PAUP 3 (length = 39, C.I. = 0.821, F-value = 40.0)	WAGNER 8, 15, 16; PENNY 28; CLIQUE 32, 33	6/3
PAUP 4 (length = 39, C.I. = 0.821, F-value = 28.0)	WAGNER 11, 12, 14; PENNY 31; CLIQUE 40; MIX 50	6/4
PAUP 5 (length = 39, C.I. = 0.821, F-value = 28.0)	WAGNER 13; PENNY 30	2/2

\* Program name and number indicate individual trees.

## Choice of Final Cladogram

Comparison of the results produced by PAUP and PHYLIP shows the PAUP tree produced from unordered characters (and subsequently rooted with the designated out-groups), PAUP 1 (Fig. 39), is the most highly corroborated cladistic relationship for the genera of Corallanidae. PAUP 1 is supported by trees and cliques from more different programs than any other topology (Table 4). Other variant topologies are represented by the ordered PAUP trees (PAUP 2–5), which are also supported by trees or cliques from various PHYLIP programs, but not to the extent of PAUP 1, especially considering its length and consistency index. PAUP 1, constructed using the unrestricted parsimony criterion, minimized homoplasy and tree length and maximized the amount of information about cladistic relations in the Corallanidae, while avoiding unwarranted assumptions about evolutionary rates and the probabilities of different kinds of events (as in some PHYLIP programs which prefer reversals over convergences, etc.).

In addition to providing maximum parsimony and corroboration, PAUP: 1) allowed multistate character descriptions, which corresponded to the biological reality of corallanid genera (i.e. the evolutionary differentiation of some structures has produced more than two character states); 2) was an unrestricted parsimony method, i.e. it did not force assumptions about whether character reversals or independent acquisitions (convergence/parallelism) were more probable; 3) allowed the use of “unordered” characters, removing at least some bias towards polarization of character states; 4) provided character state data and statistics useful in choosing between trees; and 5) produced the shortest tree (excluding CLIQUE, which did not utilize the entire data set), with the highest consistency index. Accordingly I offer PAUP 1 (Fig. 39), rooted with Tridentellidae as the sister-group, as the best estimate of cladistic relations among the genera of Corallanidae.

## General Character Trends in the Final Cladogram

In the final (rooted) PAUP cladogram (PAUP 1), most of the now-polarized character changes involve reduction and simplification of cephalic appendages, tending to follow Brown's (1965) “Rule of Evolutionary Reduction.”

Simplification and reduction of appendages in the Corallanidae from cirolanid/tridentellid morphologies involve the following character state transitions. The antennule peduncle is reduced from 3- to 2-articulate, and the basal article is expanded. The broad, short-incisored cirolanid mandible is transformed to a more slender-trunked, long-incisored mandible (such as in *Excorallana*) with reduction in size and spination of the molar process and with reduction or loss of the lacinia mobilis. The apex of the lateral lobe of the maxillule under-

goes reduction of spine number, but an increase in size of one to two unique spines; the medial lobe likewise undergoes simplification of the apex, with loss of robust circumplumose spines and greatly reduced setation. The maxilla loses an entire lobe (becoming uniramous) and has the apex of the remaining lobe variously modified, but is always simplified, with reduced setation. The maxillipeds lose the endite, undergo fusion or loss of palp articles several times, and gain an elongate basis or elongate middle article in the palp. The pereopods, eyes, and pleotelson show unique modifications in various corallanid genera.

## Specific Character State Changes in the Cladogram

The following is a step-by-step discussion of the cladogram (Fig. 39) chosen as the one most representative of true cladistic relations between the corallanid genera and two out-groups, the Cirolanidae and Tridentellidae, for the reasons discussed above. Numbers in parentheses correspond to character apomorphies in the cladogram, and letters are character states.

The Tridentellidae and the Corallanidae are distinguished from the out-group Cirolanidae by the following characters: (2) mandible with molar process reduced in spination or size, or absent (3C) mandible with lacinia mobilis absent; (4B) maxillule lateral lobe apex with 3–5 stout hooked spines and several smaller subapical spines; (5) maxillule medial lobe with simple apex, without 3–4 robust, circumplumose spines; (6B) maxilla uniramous (i.e. without medial and lateral lobes); and (19) frontal lamina always flat, not projecting.

Synapomorphies uniting the corallanid genera and distinguishing them from the tridentellids are as follows: (4E) maxillule with single large falcate spine; (6C) maxilla forming a short, rounded lobe; (8) maxilliped without endite; and (12C) antennule peduncle 2-articulate.

The synapomorphy separating “Lineage A”—*Lanocira*, *Alcirona*, and *Argathona*—from cirolanids, tridentellids, and the other corallanid genera (“Lineage B”—*Tachaea*, *Corallana*, and *Excorallana*) is (15) first pereopod dactylus with serrations or dentate processes on margin.

Within Lineage A, *Lanocira* is differentiated from *Argathona* and *Alcirona* by these autapomorphies: (6) maxilla 3–4-articulate, apical article sublinear/elongate; and (11) mandible with row of dentate processes behind incisor.

The genera *Argathona* and *Alcirona* are distinguished from *Lanocira* by possession of (4D) maxillule lateral lobe apex with 1 large falcate spine and 1–3 smaller, hooklike, subapical spines (*Lanocira* having a single large falcate spine and no small accessory spines), and (21) medial lobe of maxillule distally expanded, with truncate apex.

*Argathona* is distinguished from *Alcirona* by the following synapomorphies: (7B) maxilliped palp 4–

5-articulate (versus always 5-articulate in *Alcirona*); and (16) eyes divided by unpigmented, transverse band in some species.

*Alcirona* is distinguished from its sister-group *Argathona* by (4C) maxillule medial lobe apex with 2 large falcate spines and 0–3 small accessory spines between the large ones.

Lineage B is separated from Lineage A by having (3B) a small lacinia mobilis on the mandible (apparently lost in the tridentellids and Lineage A, but regained here), and (13) basal article of antennule peduncle expanded.

Within Lineage B, *Tachaea* is distinguished from *Corallana* and *Excorallana* by: (7C) maxilliped palp 3–5-articulate; (10B) maxilliped basis elongate (length = 1.5–2.0 times width) (but not narrow as in *Corallana*); and (14) inner angle of pereopod I carpus produced.

*Corallana* and *Excorallana* are separated from *Tachaea* by the following synapomorphies: (1C) mandible with incisor elongate; (12B) antennule peduncle 2–3-articulate (versus 2-articulate in all other corallanid genera).

*Corallana* has the following apomorphies: (1B) mandibular incisor either short or long (several *Corallana* species show this condition, while most others have much shorter mandibular incisors; it is always long in *Excorallana*); (10C) maxilliped slender, basis narrow and very elongate (length = 2.0–4.0 times width); and (17) frontal lamina sometimes reduced or absent.

*Excorallana* is distinguished from *Corallana* by the following autapomorphies: (6D) maxilla with apex bi- or trilobed; (9) maxilliped palp with middle article elongate; and (18) many species in genus with lateral incisions in pleotelson.

## BIOGEOGRAPHY AND PHYLOGENY

### INTRODUCTION

As noted by McDowall (1978) and Brusca (1984), one can never know with certainty whether any given generalized biogeographic track is the product of a single vicariant event or numerous dispersal events. It is possible to narrow the search for pertinent vicariant events using knowledge of cladistic (sister-group) relationships and distribution patterns of endemic taxa. The existence of both vicariant and dispersal phenomena in the real world is certain, thus the task in this analysis was to decide which of these phenomena was most likely responsible for the biogeographic patterns seen in the genera of the Corallanidae today. Simpson (1980) summed up this philosophy neatly: "A reasonable biogeographer is neither a vicarist nor a dispersalist but an eclecticist."

This study uses some cladistic biogeographic methods, although problems exist with the methodology, as follows: 1) possible errors in the character cladogram could result in errors in the taxon-area cladogram; 2) the method cannot positively distinguish between vicariance and concordant dis-

persal; 3) geological hypotheses are narratives, but they must be in geographic cladogram form to be easily compared with taxon-area cladograms; 4) the method acknowledges the utility of fossils but sometimes downplays their importance; 5) as used by some authors, the method is two-dimensional in its thinking, that is, the vertical displacements of land masses or ocean levels are often ignored; 6) the method is based on comparisons of groups of three or more endemic taxa; it de-emphasizes widespread taxa (which are used at a different level in the hierarchy in a manner analogous to the use of symplesiomorphies in a character cladogram); and 7) attempts to find congruent vicariant patterns require character cladograms for many different taxa, and these simply have not yet been constructed.

### METHODS

Organization of this study is as follows: 1) the geographic distribution patterns among and within corallanid genera (particularly endemism) are considered; and 2) a general descriptive synthesis of corallanid isopod distributions is made, with hypotheses to explain those distributions in light of cladistic analyses, geologic history, and other data.

This study uses cladistic biogeographic methods, wherein a character cladogram of corallanid genera is used to construct a taxon-area cladogram for comparison to a geographic cladogram. The methods used largely follow those detailed in the recent texts by Eldredge and Cracraft (1980), Nelson and Platnick (1981), Wiley (1981), and Humphries and Parenti (1986) and use the hypotheticalo-deductive method primarily as discussed by Morse and White (1979) and Brusca (1984), where "no paradigm is assumed to be of overriding importance, but rather an attempt is made to interpret the patterns of characters and the geographic distributions of taxa in the most biologically parsimonious fashion" (Brusca, 1984:102).

### Distribution Maps

The distribution maps of corallanid genera are based upon specimens I examined (see taxonomy section for complete list) and upon those reported in the literature. Map localities were plotted as accurately as possible, but the diameter of the symbols used to indicate species localities covers a radius of approximately 100–200 km on the maps. Usually, no attempt was made to verify identifications or locality records taken from the literature unless there was some reason to doubt their validity (e.g. suspicious presence or absence of a particular taxon from an area).

### Terminology

Lithospheric plate designations and plate boundaries are from the maps in Springer (1982). Abbreviations for lithospheric plates and for world oceans are noted in the various tables in which they appear.

Table 5. Number and percent of corallanid species found in various world oceans.\*

Isopod genus	Ocean					
	EP	WP	EI	WI	EA	WA
<i>Alcirona</i>	2/33	5/83	1/17	0/0	1/17	1/17
<i>Argathona</i>	0/0	10/83	3/25	4/33	0/0	0/0
<i>Corallana</i>	0/0	13/81	2/13	5/31	0/0	0/0
<i>Excorallana</i>	5/25	0/0	0/0	0/0	1/5	15/75
<i>Lanocira</i>	1/13	3/38	3/38	6/75	0/0	2/25
<i>Tachaea</i>	0/0	5/83	2/33	0/0	0/0	0/0
<i>Tridentella</i> (Tridentellidae)	4/31	7/54	0/0	0/0	0/0	2/15

\* EP = East Pacific, WP = West Pacific, EI = East Indian, WI = West Indian, EA = East Atlantic, WA = West Atlantic. Number of species reported is followed by percent of total species per genus (rounded to nearest whole number). Note that percentages may add up to >100% because some species are found in more than one ocean region.

In the following discussion, a distinction is made between species occurring in an ocean area and species occurring in the waters over a lithospheric plate.

### Taxon-Area Cladograms

These were constructed by placing the geographic (ocean) area occupied by a taxon in place of the taxon name on the cladogram resulting from the cladistic analysis (Fig. 39). Simplified (reduced) taxon-area cladograms were made by deleting unique, noncongruent areas from three-taxon statements in the area cladograms. These reduced taxon-area cladograms were compared to a geographic cladogram of ocean areas for congruence.

### Geographic Cladogram

This was constructed from the scenarios of earth history found in Dietz and Holden (1970), Briden and Smith (1977), Hallam (1981), Barron (1987), and others.

## RESULTS AND DISCUSSION

### Distribution of the Corallanidae

The Corallanidae are primarily a tropical/subtropical family of shallow-water isopods. The geographic distributions of species within each genus are shown on the maps in Figures 6, 10, 16, 25, 32, and 38 and Table 5. The number of endemic species per genus and percent of total species per genus found in various ocean regions are given in Table 6. All the genera except *Excorallana* attain their highest species diversity in the Indo-West Pacific region (Table 5). *Excorallana* is generally restricted to the New World, with 70% of its species endemic to the West Atlantic and 25% endemic to the East Pacific. *Argathona*, *Corallana*, and *Tachaea* are restricted to the Indo-West Pacific. The two remaining genera, *Alcirona* and *Lanocira*, are almost circumtropical in distribution, with only two to three species in each genus occurring in the New World.

Two species are known from both the Caribbean and the East Atlantic (*Alcirona krebsii* in Lineage A and *Excorallana oculata* in Lineage B). These are the only records of corallanids from the East Atlantic and probably represent either a simple dispersal from the New World or a reduced element of a West Atlantic-East Atlantic generalized track.

Table 7 shows that the majority of mobile animal hosts used by corallanid genera are fish, but turtles, shrimp, and scyphozoans have also been exploited as temporary hosts. Although this type of association is limited in duration, the possibility exists that some dispersals may have occurred via such "hosts."

The sister-group to the Corallanidae is the monogeneric Tridentellidae (*Tridentella*), which has 11 species, is found in tropical, temperate, and cold-temperature waters and is known from the West Atlantic, East Pacific, West Pacific, and Northwest Pacific. The other family used in the cladistic analysis, the Cirolanidae, is circumoceanic in distribution.

### Biogeographic Relationships of Sister-Groups

Two clear areas of corallanid endemism are evident in the taxon-area cladogram (Fig. 40) and in Table 6, corresponding to the Indo-West Pacific (Old World) and the West Atlantic-East Pacific (New World). Both corallanid lineages have some genera present in each of these areas of endemism.

In Lineage A, both *Alcirona* and *Lanocira* are represented in the New World (East Pacific and West Atlantic) by two to three species each, although each of these genera attains its highest species diversity in the Indo-West Pacific. The third Lineage A genus, *Argathona*, is endemic to the Indo-West Pacific. Lineage A contains relatively fewer species (25) than Lineage B (42) but is much more widely distributed, with all of its genera being exclusively marine. *Lanocira* and *Alcirona* are each present in five different ocean regions, and *Argathona* in three ocean areas (Tables 5, 6). *Alcirona* and *Lanocira* share West Atlantic, East Pacific, and West Pacific



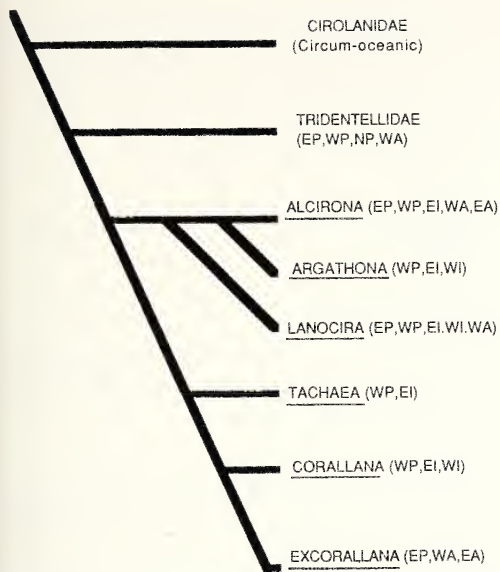


Figure 40. Taxon-area cladogram for the genera of Corallanidae.

areas with the sister-group Tridentellidae. *Argathona*, the endemic in Lineage A, shares West Pacific and Indian Ocean areas with each of the other two genera.

In Lineage B, *Tachaea* and *Corallana* are both endemic to the Indo-West Pacific, and *Excorallana*

is primarily restricted to the New World. Lineage B is more speciose than Lineage A, with more species in "specialized," non-marine habitats. *Tachaea* is known mainly from freshwater ponds, lakes, and streams (as temporary parasites of certain shrimp and fish species—see Table 7). *Corallana* has 40% of its species described from estuarine or brackish habitats, many with wood-boring habits. One *Excorallana* species, *E. berbicensis*, has been reported from freshwater (Rio Berbice). Lineage B is more geographically restricted than Lineage A. *Tachaea* and *Corallana* are found in two or three areas in the Old World, and *Excorallana* in two ocean regions in the New World (excluding one species known from the East Atlantic, see above). *Corallana* and *Tachaea* share West Pacific and Indian Ocean areas, while *Excorallana* shares the East Pacific and West Atlantic areas with the sister-group Tridentellidae and the two widely distributed genera of Lineage A (Fig. 40).

### Comparison of Taxon-Area and Ocean-Formation Cladograms

Hypothesized relationships of ocean areas are depicted in Figure 41, a proposed cladogram of tropical ocean areas. This cladogram has somewhat ambiguous dates for earth history events, reflecting the controversy surrounding the dating of the various geotectonic events, as discussed by Dietz and Holden (1970), Briden and Smith (1977), Hallam (1981), Barron (1987), and others.

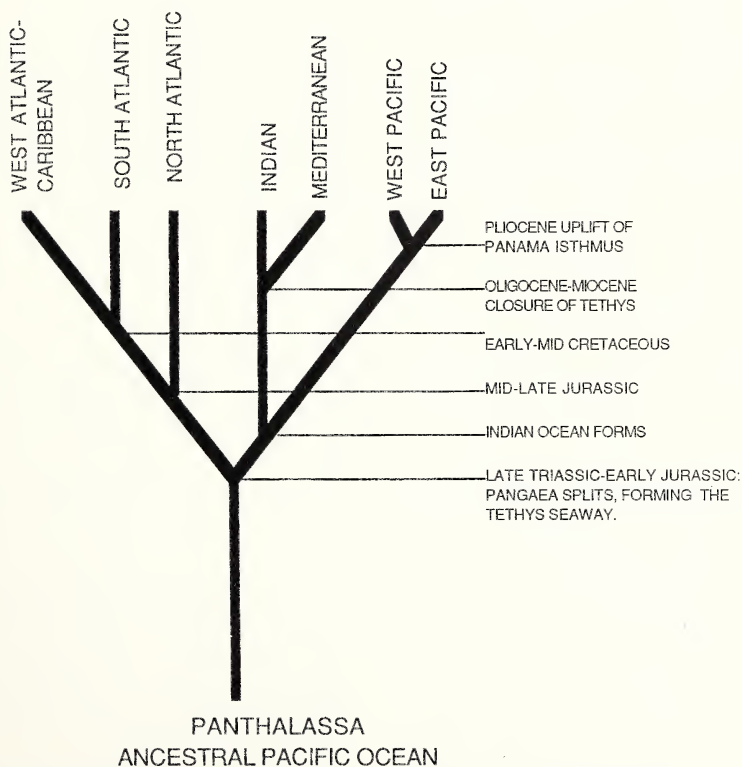


Figure 41. Proposed geographic cladogram depicting the opening of the tropical oceans.

Table 6. Number and percent of corallanid species endemic to various world oceans.\*

Isopod genus	Ocean					
	EP	WP	EI	WI	I	WA
<i>Alcirona</i>	1/17	3/50	0/0	0/0	0/0	0/0
<i>Argathona</i>	0/0	8/67	0/0	1/8	2/17	0/0
<i>Corallana</i>	0/0	10/63	1/6	2/13	3/19	0/0
<i>Excorallana</i>	5/25	0/0	0/0	0/0	0/0	14/70
<i>Lanocira</i>	0/0	0/0	0/0	3/38	3/38	2/25
<i>Tachaea</i>	0/0	4/67	1/17	0/0	1/17	0/0
<i>Tridentella</i> (Tridentellidae)	4/31	7/54	0/0	0/0	0/0	2/15

\* EP = East Pacific, WP = West Pacific, EI = East Indian, WI = West Indian, I = Indian (total), WA = West Atlantic. Number of endemic species is followed by percent species per genus (rounded to nearest whole number). Note that percentages may add up to >100% because some ocean regions include smaller ocean regions.

Limited congruence exists between the simplified (reduced) taxon-area cladogram (Fig. 42A) and the reduced geographic cladogram of tropical ocean areas (Fig. 42B). The fact that both corallanid lineages share Pacific, Atlantic, and Indian Ocean areas, while the sister-group Tridentellidae shares only Pacific and Atlantic Ocean areas, was taken as support for the hypothesis that the divergence of the Corallanidae and the Tridentellidae was related to the opening of the Indian and Atlantic Oceans.

Of the later events pictured on the geographic cladogram, the opening of the North and South Atlantic Oceans can be excluded from the analysis. Corallanids are not known from these areas. The remaining events on the cladogram are those in-

volving paleo-epicontinental seas, the closure of Tethys (creating the Mediterranean), and the uplift of the Panamanian isthmus.

### Phylogeny of the Corallanidae

This scenario is based on the above comparison of the taxon-area cladogram and ocean-formation cladogram, as well as other biological data.

The taxa cladogram resulting from cladistic analysis (Fig. 39) is interpreted as depicting the Corallanidae and Tridentellidae evolving from some common ancestral "cirolanoid-like" stock and also indicates two lineages within the Corallanidae. Lineage A consists of *Alcirona*, *Argathona*, and *Lanocira* and Lineage B includes *Tachaea*, *Corallana*, and *Excorallana*.

It may be hypothesized that the modern genera within the Tridentellidae and Corallanidae evolved from common ancestors present in Panthalassa (the ancestral Pacific Ocean) or later in the cosmopolitan warm-water Tethyan biota discussed by Brusca (1984) and Hallam (1981). There is evidence for the progressive divergence of some elements of the Tethyan fauna, such as rudistid bivalves and large benthic foraminiferans between the Caribbean and Mediterranean regions (Coates, 1973; Kauffman, 1973). Heck and McCoy (1976) claimed that the modern distributions of corals, seagrasses, seagrass-associated foraminiferans, and mangroves support the concept that a circumglobal Tethyan-track fauna existed at one time. The distribution of modern circumtropical coastal faunas, including the Corallanidae, can be hypothesized to be due at least partially to the fragmentation of this tropical Tethyan track.

Divergence of the Corallanidae from the Tridentellidae was probably related to the opening of the Atlantic and Indian Oceans in the late Triassic or early Jurassic (Fig. 43). This would explain the fact that *Lanocira* attains its highest species diversity in the Indian Ocean, as well as being one of the older, widely distributed genera.

The two lineages within the Corallanidae must have diverged from each other prior to the closure

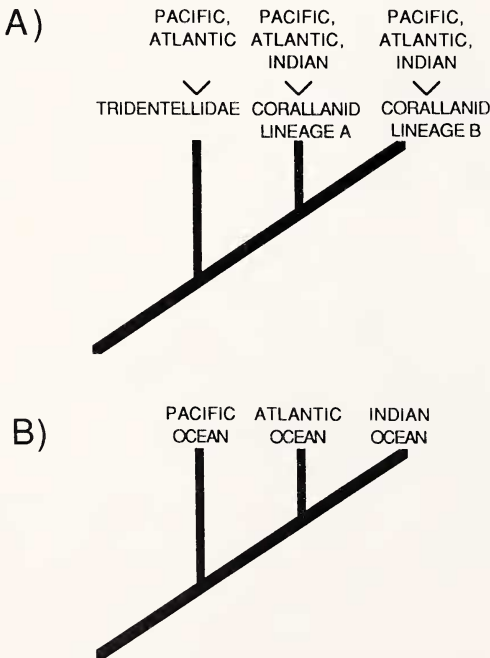


Figure 42. A, Reduced taxon-area cladogram for the Corallanidae. B, Reduced geographic cladogram of tropical oceans.

Table 7. Genera of temporary hosts for corallanid isopod genera.\*

Isopod genus	Temporary host genus	Family
<i>Alcirona</i>	<i>Pseudoscarus</i>	Scaridae
	<i>Priacanthus</i>	Priacanthidae
	<i>Scarus</i>	Scaridae
	<i>Echidna</i>	Muraenidae
	<i>Amphacanthus</i>	Acanthuridae
<i>Argathona</i>	<i>Epinephelus</i>	Serranidae
	<i>Diagramma</i>	Serranidae
	<i>Pseudolabrus</i>	Labridae
	<i>Cromileptes</i>	Serranidae
	<i>Lutjanus</i>	Lutjanidae
	<i>Plectropomus</i>	Serranidae
	<i>Tetraodon</i>	Tetraodontidae
	<i>Variola</i>	Serranidae
	<i>Muraena</i>	Muraenidae
	<i>Chelonia</i> (turtle)	
	<i>Corallana</i>	<i>Chanos</i>
	<i>Puntius</i>	Cyprinidae
<i>Excorallana</i>	<i>Mycteroperca</i>	Serranidae
	<i>Epinephelus</i>	Serranidae
	<i>Priacanthus</i>	Priacanthidae
	<i>Lachnolaimus</i>	Labridae
	<i>Ocyurus</i>	Lutjanidae
	<i>Sparisoma</i>	Scaridae
	<i>Neomaenis</i>	Lutjanidae
	<i>Caranx</i>	Carangidae
	<i>Haemulon</i>	Pomadasyidae
	<i>Sphyræna</i>	Sphyrænidae
	<i>Scarus</i>	Scaridae
	<i>Diodon</i>	Diodontidae
	<i>Aetobatus</i>	Myliobatidae
	<i>Dasyatis</i>	Dasyatidae
	<i>Lycengraulis</i>	Engraulidae
	<i>Chelonia</i> (turtle)	
<i>Lanocira</i>	<i>Cassiopea</i> (scyphozoan)	
	<i>Variola</i>	Serranidae
<i>Tachaea</i>	<i>Culter</i>	Cyprinidae
	<i>Caridina</i> (shrimp)	
	<i>Palaemon</i> (shrimp)	
	<i>Palaemonetes</i> (shrimp)	
	<i>Paratya</i> (shrimp)	
	<i>Leander</i> (shrimp)	
	<i>Macrobrachium</i> (shrimp)	

\* Mobile animal hosts only; all temporary host genera listed are fish except as indicated in parentheses; family names given for fish genera only. Records were taken from specimen labels or from the literature.

of the Tethys seaway at its eastern end, in the late Oligocene or early Miocene, because both Old World (Indo-West Pacific) and New World (East Pacific-West Atlantic) endemic genera are present in Lineage B. To assume otherwise requires invoking multiple dispersals, either across the Pacific Ocean or through nontropical waters; neither of these possibilities is convincingly supported by corallanid distribution patterns.

Eustatic transgression and regression of epicontinental seaways separating Asia and Europe in the late Jurassic and North America in the mid-Cretaceous (Kauffman, 1973; Cox, 1974; Hallam, 1981)

may also have contributed to the divergence of these lineages by allowing Lineage B to exploit new habitats. Lineage A is exclusively marine, has two genera that are almost circumtropical, and has the least derived morphology; whereas Lineage B, with three endemic genera, has two genera that have exploited brackish, estuarine, and freshwater habitats, and shows the most derived states of the Corallanidae's character transitions towards reduction and simplification of appendages.

The existence of East Pacific-West Atlantic geminate species in *Excorallana* (see Delaney, 1984) indicates that modern corallanid genera probably

Table 8. Number of corallanid species endemic to various lithospheric plates.\*

Isopod genus	Lithospheric plate										
	P	N	C	NA	A	IA	E	PH	AR	CO	SA
<i>Alcirona</i>	0	1	0	0	0	1	2	0	0	0	0
<i>Argathona</i>	0	0	0	0	0	5	3	1	0	0	0
<i>Corallana</i>	0	0	0	0	1	7	3	1	0	0	0
<i>Excorallana</i>	1	1	3	2	0	0	0	0	0	0	4
<i>Lanocira</i>	0	0	0	0	2	0	0	0	0	0	1
<i>Tachaea</i>	0	0	0	0	0	3	3	0	0	0	0
<i>Tridentella</i> (Tridentellidae)	4	2	0	2	0	2	1	0	0	0	0

\* Lithospheric plates (after Springer, 1982) are designated as follows: P = Pacific, N = Nazca, C = Caribbean, NA = North American, A = African, IA = Indian-Australian, E = Eurasian, PH = Philippine, AR = Arabian, CO = Cocos, SA = South American. Two *Tridentella* species from New Zealand are not included above, because they are considered to be on two lithospheric plates (IA and P).

existed prior to the Pliocene. These geminates are still identifiable despite the passage of millions of years since the Pliocene uplift of the Central American isthmus. This may indicate a relative speciation rate for corallanid isopods.

The pre-Pliocene existence of corallanid genera, together with the limited congruence between the

reduced cladograms (Figs. 42A, B), establishes a relative timescale for divergence of modern genera within Lineage B. These genera probably diverged after Tethys closure in the late Oligocene or early Miocene, but prior to the Pliocene. It is hypothesized that the closure of Tethys was associated with the divergence of *Excorallana* and *Corallana*. These

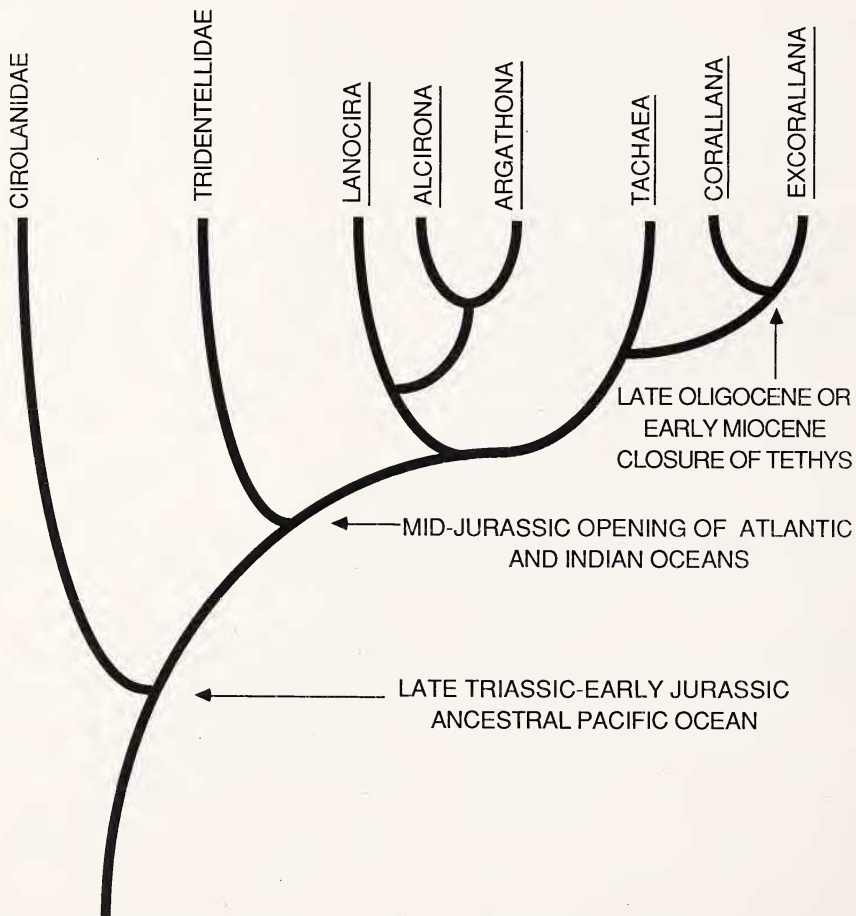


Figure 43. Proposed phylogeny for the genera of Corallanidae, derived from Figures 40-42 and other data.

genera are sister-groups (Fig. 39), yet are restricted to the New and Old Worlds, respectively.

Table 8 indicates the affinities of corallanid and tridentellid species to various lithospheric plates. Note that corallanid genera are only marginally represented on the Pacific plate, in contrast to shorefishes and some invertebrate taxa (Springer, 1982); there are no corallanid genera endemic to the Pacific plate, and only one endemic corallanid species. Although more corallanid species doubtlessly will be described from the vast Pacific area, the paucity of species from the Pacific plate leads one to dismiss use of the two alternate geotectonic theories of earth evolution, "Pacifica" (Nur and Ben-Avraham, 1977; Ben-Avraham, 1981) and "earth expansion" (Carey, 1976, 1983; Pitman et al., 1974). Both of these theories would require distributions of corallanid isopods in and around the Pacific Basin that are unsupported by collection data or would require multiple dispersals to explain present distributions. The classic continental drift and plate tectonic theories (Dietz and Holden, 1970; Briden and Smith, 1977; Hallam, 1981; Barron et al., 1987; and others) are more parsimonious than other earth history theories in explaining the phylogeny of the Corallanidae (Fig. 43).

Paleontological records of isopods are relatively scarce; fossil flabelliferans are known from the Triassic of Germany, Jurassic of Britain and Central Europe, and Cretaceous of Brazil (Schram, 1986: 151). Many flabelliferan families are distinguished by appendage morphology, which is usually poorly preserved in isopod fossils. Thus, there are no fossil corallanids or tridentellids known that might corroborate either out-group or biogeographic relations.

Various physical and biological processes were responsible for the evolution of the Corallanidae and for the biogeographic distributions of its genera. Vicariant events were influenced by physical processes resulting from geotectonic, eustatic, paleoclimatic, and oceanographic conditions. Biological factors included dispersals, extinctions, and developmental mode. The evolutionary effect of these processes on the Corallanidae has apparently been: 1) the development of "temporary parasitism," 2) the adaptation of appendages toward an increasingly parasitic lifestyle, and 3) the ecological radiation of corallanid genera in marine, brackish, and freshwater habitats.

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## APPENDIX I: INVALID CORALLANID NAMES

### INVALID CORALLANID GENUS NAMES

- Austroargathona* Riek, 1953 (now *Tachaea*)  
*Brotherus* Budde-Lund, 1908 (now *Argathona*)  
*Gurida* Budde-Lund, 1908 (now *Argathona*)  
*Icochaeta* Caldwell, 1879 (*lapsus*) (now *Tachaea*)  
*Icochaes* Shen, 1936 (now *Tachaea*)  
*Nalicora* Moore, 1902 (now *Lanocira*)  
*Orcilana* Nierstrasz, 1931 (now *Argathona*)

### INVALID CORALLANID SPECIES NAMES

- Alcirona hirsuta* Moore, 1902 (now *Alcirona krebsii*)  
*Alcirona insularis* Hansen, 1890 (now *Alcirona krebsii*)  
*Alcirona macronema* (Bleeker, 1857) (now *Argathona macronema*)  
*Alcirona maldivensis* Stebbing, 1904 (now *Alcirona krebsii*)  
*Alcirona pearsoni* Monod, 1926 (now *Argathona rhinoceros*)  
*Alcirona tuberculata* Richardson, 1910 (now *Cirolana tuberculata*)

- Argathona longicornis* (Budde-Lund, 1908) (now *Argathona macronema*)  
*Argathona reidi* Stebbing, 1910 (now *Argathona rhinoceros*)  
*Argathona similis* Richardson, 1910 (now *Argathona macronema*)  
*Austroargathona caridophaga* Riek, 1953 (now *Tachaea caridophaga*)  
*Austroargathona picta* Riek, 1967 (now *Tachaea picta*)  
*Brotherus longicornis* Budde-Lund, 1908 (now *Argathona macronema*)  
*Corallana acuticauda* Miers, 1881 (now *Excorallana acuticauda*)  
*Corallana antillensis* Hansen, 1890 (now *Excorallana acuticauda*)  
*Corallana fissicauda* Hansen, 1890 (now *Excorallana fissicauda*)  
*Corallana macronema* Miers, 1881 (now *Argathona macronema*)  
*Corallana mexicana* Nierstrasz, 1917 (now *Excorallana mexicana*)  
*Corallana oculata* Hansen, 1890 (now *Excorallana oculata*)  
*Corallana quadricornis* Hansen, 1890 (now *Excorallana quadricornis*)  
*Corallana sexticornis* Richardson, 1901 (now *Excorallana sexticornis*)  
*Corallana subtilis* Hansen, 1890 (now *Excorallana subtilis*)  
*Corallana tricornis* Hansen, 1890 (now *Excorallana tricornis tricornis*)  
*Corallana truncata* Richardson, 1899 (now *Excorallana truncata*)  
*Corallana warmingii* Hansen, 1890 (now *Excorallana warmingii*)  
*Excorallana antillensis* Lemos de Castro, 1960 (now *Excorallana acuticauda*)  
*Excorallana kathyae* Menzies, 1962 (now *Excorallana truncata*)  
*Excorallana rapax* Schultz, 1969 (now *Lanocira rapax*)  
*Gurida coelata* Budde-Lund, 1908 (now *Argathona rhinoceros*)  
*Icochaes crassipes* Shen, 1936 (now *Tachaea crassipes*)  
*Lanocira capensis* Barnard, 1914 (now *Lanocira gardineri*)  
*Lanocira hirsuta* Nordenstam, 1930 (now *Lanocira zeylanica*)  
*Nalicora rapax* Moore, 1902 (now *Lanocira rapax*)  
*Orcilana hanseni* Nierstrasz, 1931 (now *Argathona macronema*)  
*Tachaea incerta* Hansen, 1890 (now *Tachaea crassipes*)  
*Tachaea leopardi* Nierstrasz, 1930 (now *Corallana leopardi*)

## APPENDIX II: CHARACTERS USED IN THE CLADISTIC ANALYSIS

Multistate characters used in this analysis follow, with alphanumeric designations, the character state descriptions, and the numeric code assigned to each state.

- 1) a—Mandible incisor short (0)
- b—Mandible incisor short or long (1)
- c—Mandible incisor long (2)

- 2) a—Mandible molar process large, robustly spined (0)
- b—Mandible molar process reduced (in spination and/or size) or absent (1)
- 3) a—Mandible with robust lacinia mobilis (0)
- b—Mandible with small lacinia mobilis (1)
- c—Mandible without lacinia mobilis (2)
- 4) Maxillule lateral lobe apex:
  - a—with 11–14 spines (0)
  - b—with 3–5 stout hooked spines and smaller subapical spines (1)
  - c—with 2 large falcate spines, 0–3 smaller spines between them (2)
  - d—with 1 large falcate spine, and with 1–3 hooklike subapical spines (3)
  - e—with 1 large falcate spine only (4)
- 5) Maxillule medial lobe:
  - a—with 3–4 robust, circumplumose spines (0)
  - b—with simple apex, without robust plumose spines (1)
- 6) Maxilla:
  - a—with medial and lateral lobes (0)
  - b—uniramous, stout, 2-articulate, with conical apex (1)
  - c—uniramous, short, rounded lobe (2)
  - d—uniramous, with apex bi- or trilobed (3)
  - e—uniramous, 3–4-articulate, apical article sublinear and elongate (4)
- 7) Maxilliped palp:
  - a—5-articulate (0)
  - b—4- or 5-articulate (1)
  - c—3- or 5-articulate (2)
- 8) Maxilliped basis:
  - a—forming an endite (0)
  - b—not forming an endite (1)
- 9) Maxilliped palp middle article:
  - a—not elongate (0)
  - b—elongate (1)
- 10) Maxilliped basis:
  - a—not elongate (0)
  - b—elongate (1)
  - c—basis very elongate, maxilliped slender (2)
- 11) Mandible:
  - a—without row of denticles behind incisor (0)
  - b—with row of denticles behind incisor (1)
- 12) Antennule peduncle:
  - a—3-articulate (0)
  - b—2–3-articulate (1)
  - c—2-articulate (2)
- 13) Antennule peduncle:
  - a—basal article not expanded (0)
  - b—basal article expanded (1)
- 14) Pereopod I carpus:
  - a—inner angle not produced (0)
  - b—inner angle produced (1)
- 15) Pereopod I dactylus:
  - a—without serrated margin (0)
  - b—with serrated margin (in some species) (1)
- 16) Eyes:
  - a—not divided by unpigmented, transverse band (0)
  - b—divided by unpigmented, transverse band (in some species) (1)
- 17) Frontal lamina:

- a—present, not reduced (0)
- b—occasionally reduced or absent (1)
- 18) Pleotelson:
  - a—without lateral incisions (0)
  - b—with lateral incisions (in some species) (1)
- 19) Frontal lamina:
  - a—always flat, not projecting (0)
  - b—projecting ventrally in some species (1)

- 20) Maxilla apex:
  - a—without dentate, scalelike spines (0)
  - b—with dentate, scalelike spines (1)
- 21) Maxillule medial lobe:
  - a—apex simple in shape, rounded or narrow (0)
  - b—apex truncate and expended distally (1)

**APPENDIX III:  
DATA MATRICES USED IN  
PAUP AND PHYLIP**

**PAUP:**

Taxa	Characters 1-21
<i>Corallana</i>	1 1 1 4 1 2 0 1 0 2 0 1 1 0 0 0 1 0 0 0 0
<i>Alcirona</i>	0 1 2 2 1 2 0 1 0 0 0 2 0 0 1 0 0 0 0 0 1
<i>Argathona</i>	0 1 2 3 1 2 1 1 0 0 0 2 0 0 1 1 0 0 0 0 1
<i>Lanocira</i>	0 1 2 4 1 4 0 1 0 0 1 2 0 0 1 0 0 0 0 0 0
<i>Excorallana</i>	2 1 1 4 1 3 0 1 1 0 0 1 1 0 0 0 0 1 0 0 0
<i>Tachaea</i>	0 1 1 4 1 2 2 1 0 1 0 2 1 1 0 0 0 0 0 0 0
Tridentellidae	0 1 2 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
Cirolanidae	0 1 0 0

**PHYLIP:**

Taxa	Characters 1-32
<i>Alcirona</i>	0 0 1 1 1 1 1 0 0 1 1 1 0 0 0 0 1 0 0 0 0 1 1 0 0 1 0 0 0 0
<i>Argathona</i>	0 0 1 1 1 1 1 1 0 1 1 1 0 0 1 0 1 0 0 0 0 1 1 0 0 1 1 0 0 0
<i>Corallana</i>	1 0 1 1 0 1 1 1 1 1 1 1 0 0 0 0 1 0 1 1 0 1 0 1 0 0 0 1 0 0
<i>Excorallana</i>	1 1 1 1 0 1 1 1 1 1 1 1 1 0 0 0 1 1 0 0 0 1 0 1 0 0 0 0 1 0
<i>Lanocira</i>	0 0 1 1 1 1 1 1 1 1 1 1 1 1 0 0 1 0 0 0 1 1 1 0 0 1 0 0 0 0
<i>Tachaea</i>	0 0 1 1 0 1 1 1 1 1 1 1 0 0 1 1 1 0 1 0 0 1 1 1 1 0 0 0 0 0
Tridentellidae	0 0 1 1 1 1 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Cirolanidae	0 1