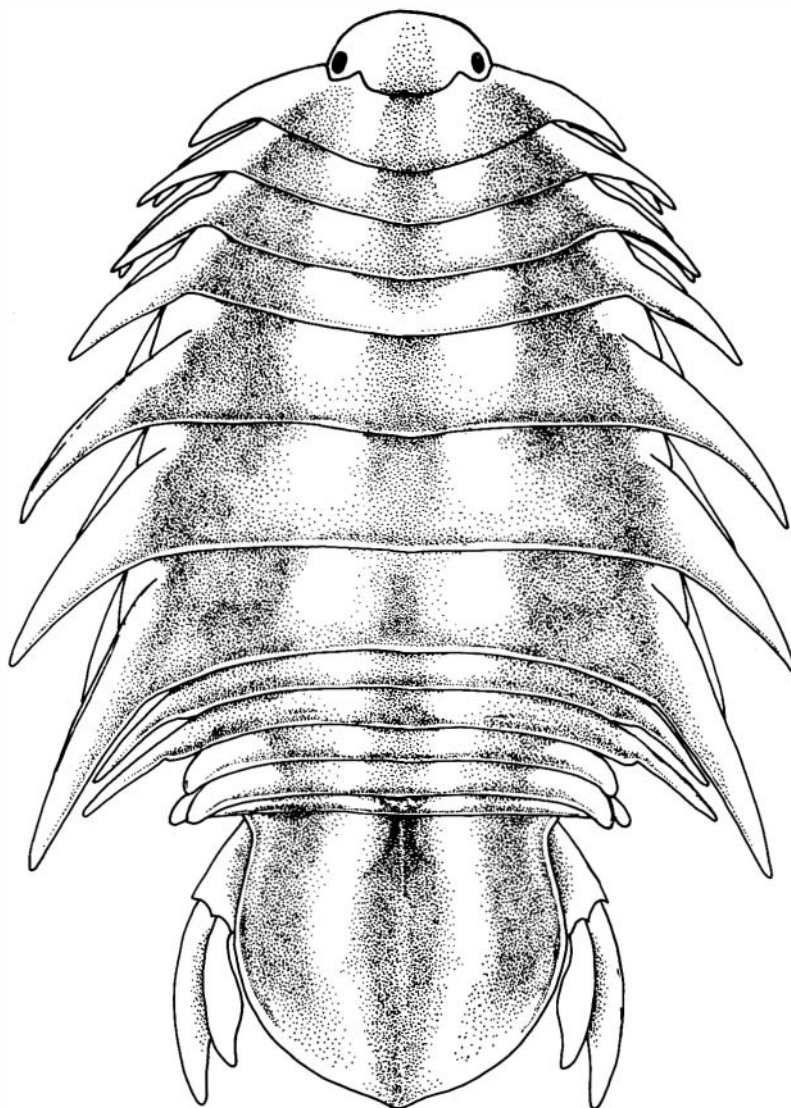


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# A Guide to the Marine Isopod Crustacea of Pacific Costa Rica



Richard C. Brusca  
Ernest W. Iverson

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**Abstract:** The marine isopod crustaceans known from, or expected to occur on Pacific Costa Rican shores are presented. Keys, diagnoses, synonymies and figures are given for 37 species, in 14 families. Five previously undescribed species are included, three of which are formally named and described: *Metacirrolana costaricensis* n. sp., *Rocinela murilloi* n. sp., and *Cyathura guaroensis* n. sp.

A general overview of oceanographic aspects of Pacific Costa Rican waters is given, as well as a brief review of biological studies that have been published concerning Costa Rican shores. An introduction to the anatomy and general biology of isopods is presented, which includes a somewhat detailed discussion of head appendages.

## INTRODUCTION

For numerous reasons, Costa Rica has become the most accessible area in all of Central America for tropical biologists to conduct field work. The last decade has seen a slow but steady increase in interest by both American and European scholars of Costa Rican marine (and terrestrial) biology. Yet, little is known regarding the natural history of Costa Rican shores, and no field identification guides have yet been written to the common invertebrates, fishes or algae of this or any other Central American coast. Costa Rica extends in a NW-SE direction for nearly 500 km, between 11° and 8° N latitude. It boasts every imaginable tropical coastal marine habitat, from rocky shores and sandy beaches, to mangrove lagoons and coral reefs. Those individuals fortunate enough to conduct field work along the shores of Costa Rica are unanimous in their enthusiasm for the area (Fig. 1).

The marine fauna of Pacific Costa Rica belongs to the tropical Panamic Province, of the warm-water Eastern Pacific Zoogeographic Region (Fig. 2). Knowledge of the biota of Pacific Costa Rican shores is of value to a great many scientists working in a variety of disciplines in tropical and subtropical regions of the New World. Further, Costa Rica comprises a geographic portion of the modern descendant

biota of the important "Tertiary Caribbean Province" of Woodring, 1966 (the "Panamanian Track" of Croizat, *et al.*, 1974).

We were prompted to write this handbook by the presence of ever increasing numbers of biologists and environmentalists studying Costa Rican shores. Isopod crustaceans occur in virtually every habitat in this region. Yet, until now no source of identification, keys or collected illustrations were available to aid either the specialists or nonspecialist in the identification of these important components of coastal marine communities.

The purpose of this guide is to introduce both the working naturalist and the coastal environmentalist to the shallow-water isopods of Pacific Costa Rica. With this goal in mind, we have presented both background material and simplified keys for the various isopod taxa. We hope that this work is usable (and used) by both the specialist and the generalist, and that it provides the incentive to consider this important group of crustaceans in future coastal and benthic ecological studies. Isopods pay no heed to international boundaries and a number of species not yet taken from Costa Rican waters proper are known from areas immediately to the north and south. For all of the above reasons, we have included some species that have not been collected in Costa Rica proper, but in all probability occur there. We have also chosen to provide readers with a

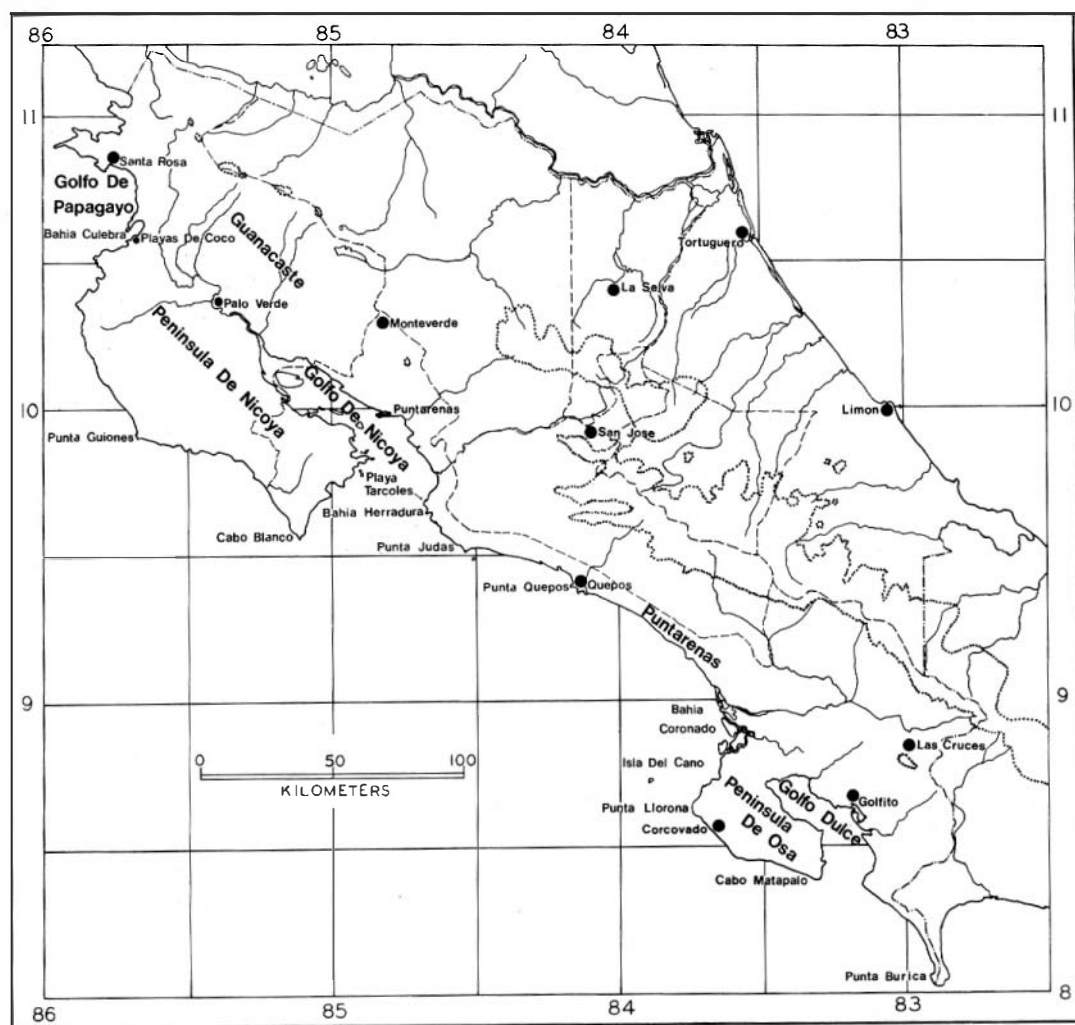


Figura 1

## Costa Rica.

brief review of coastal oceanography and a summary of published studies on littoral biology for the region. It is recognized that in many ways this work is incomplete. In particular, it does not adequately treat the minute species (those less than 5 mm in length), nor have we attempted to study the fauna of the continental shelf. Hopefully, this preliminary study will stimulate others to examine and describe that fauna.

## ACKNOWLEDGMENTS

A great many people assisted in the field work that led to this publication. Most important were Jay Savage (of the University

of Miami), who first introduced the senior author to Costa Rica; and Manuel M. Murillo (of the Universidad de Costa Rica), who went far beyond the usual wonderful courtesies of *ticos* to assist us in countless ways. Many others contributed directly and indirectly to the success of this project and we want to extend our most sincere appreciation to them all. We especially thank Bill and Myrna Bussing, Ana Dittel and José Vargas, whose friendship and assistance made the time spent in Costa Rica not only profitable but very special. A great deal of field assistance was also provided by the senior author's graduate students: Diane Perry, Phil Pepe, Paul Delaney and Carol Stepien. All of the field work was accomplished

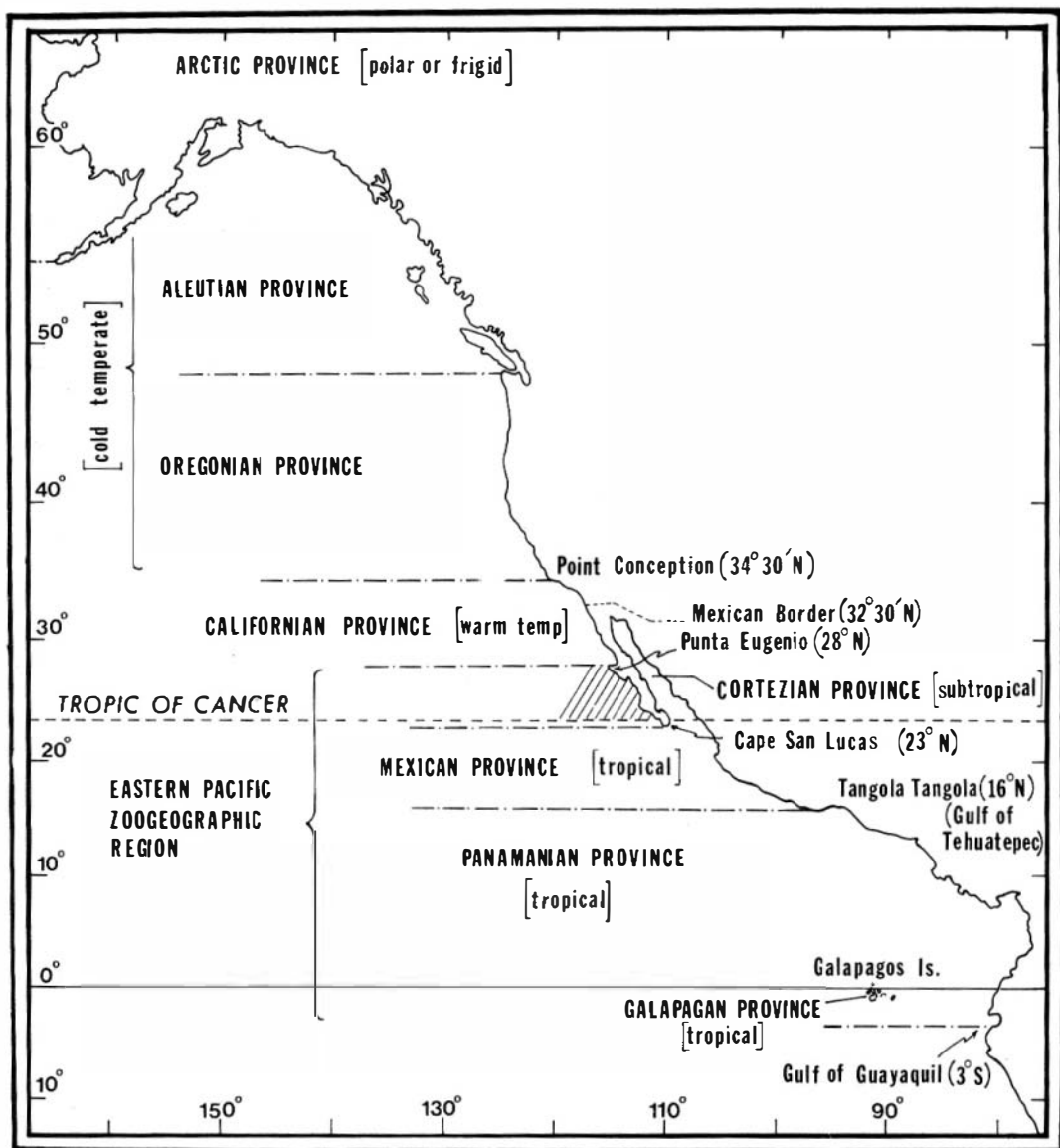


Figura 2

Biogeographic provinces of the northeast Pacific.

with the invaluable assistance of Anna Mary Mackey, who also acted as principal editor during the preparation of the manuscript. This project was funded by the generous support of the Universidad de Costa Rica, the National Science Foundation (INT 78-21363 and DEB 78-03150), and the Charles A. Lindberg Foundation. The art work is primarily that of the talented Frances Runyan, although some of the drawings are also by the authors. Lastly we thank Peter Glynn for the hospitality he

provided in Panama and for sharing his vast knowledge of tropical eastern Pacific coastal ecology with us, and the Costa Rica offices of O.T.S. (Organization for Tropical Studies) for their continued assistance.

#### GENERAL OCEANOGRAPHIC ASPECTS OF PACIFIC COSTA RICAN SHORES

Numerous reports on the physical oceanography of Pacific Central American waters have

been published; many of these are cited in Hickey (1979), Brusca and Wallerstein (1979b), and Brusca (1980). Of particular importance are: Sverdrup (1947), U.S. Dept. Commerce (1952), Schaefer *et al.* (1958), Reid (1960), Renner (1963), Bennett (1963), Wooster and Reid (1963), Wyrski (1964; 1965a; 1965b; 1966), Saur and Stewart (1967), Forseberg (1969), Thomas (1977), and Patzert (1978). Fewer studies on the biological oceanography of this region have been published, although important information can be found in Holmes *et al.* (1957), Forseberg (1963; 1969), Forseberg and Joseph (1964), Broenkow (1965), Blackburn (1966; 1968), Blackburn *et al.* (1970), Owen and Zeitzschel (1970), and various reports of the Bulletin of the Inter-American Tropical Tuna Commission.

Surface circulation in the eastern equatorial Pacific varies considerably in response to the shifting of the major wind systems. Further, the west coast of Central America is the meeting place of two great Pacific currents, the California Current and the Equatorial Countercurrent, as well as remnants of the Peru Current. This region is also the place of origin of the Northern Equatorial Current. For these reasons and others, the Pacific coast of Costa Rica experiences seasonally variable oceanographic conditions. In general, the Costa Rican Coastal Current (the "Central America Current" of some authors) flows northwestward along the coast from the Gulf of Panama, to near the mouth of the Gulf of California. As this current moves northward, north of the Gulf of Tehuantepec, it is forced increasingly offshore and westward. Here it melds with the south-eastward flowing "Mexican Current", composed of remnants of the California Current and waters leaving the Gulf of California, to join in the formation of the Northern Equatorial Current. The Costa Rican Coastal Current is itself derived primarily from the Equatorial Countercurrent, plus minimal input from seasonally variable coastal waters of Panama and Colombia.

During most of the year, a large divergence occurs off the Osa Peninsula of Costa Rica, where waters of the Equatorial Countercurrent split to turn north and south (about 8°N). The northern branch forms the Costa Rican Coastal Current, but the southern branch circulates clockwise in a giant cell or gyre that extends south all the way to the Azuero Peninsula of

Panamá and many miles offshore. During the summer and fall this clockwise gyre breaks down and much of its former southward displacement enters the Gulf of Panama. The overall result of this process is a northward flowing coastal current north of Punta Judas, a southward flowing current south of the Osa Peninsula, and variable currents in between. Wyrski (1965b; 1966) provides an excellent summary of surface circulation and general oceanography of the eastern equatorial Pacific. Peterson (1960) has provided a general summary of oceanographic conditions of the Gulf of Nicoya.

Monthly charts of sea surface temperature for the eastern equatorial Pacific region have been issued since 1969 by the Bureau of Commercial Fisheries, San Diego, California, and average monthly charts for the coastal region as well as monthly anomaly charts as far back as 1947 are also available (e.g. Johnson, 1961; Renner, 1963). Wyrski (1965b) has published accurate and detailed monthly charts of sea surface temperature, and charts showing the change of surface temperature from month to month for this area.

The coastal waters of Pacific Costa Rica belong to Wyrski's (1966) "Tropical Surface Water" category, described as follows.

*Tropical Surface Water* is found in regions where sea surface temperature is high and its seasonal variation small, and where salinity is low due to an excess of rainfall over evaporation. In the eastern tropical Pacific this water can be identified by the area where surface temperature is always about 25°C. Within this area, salinity is usually less than 34.0‰, due to an excess of rainfall over evaporation, which, according to Dietrich (1957) is greater than 50 cm/year. The southern boundary of tropical surface water runs from Ecuador to north of the Galapagos Islands and continues west at about 4°N where it coincides approximately with the southern boundary of the Countercurrent. The water carried east with the Countercurrent as well as that carried west in the southern parts of the North Equatorial Current is tropical surface water. The northern boundary of the tropical surface water can be identified approximately with the 25°C isotherm which lies near 15°N and fluctuates during the year by about 5°

of latitude. Lowest salinities within this water are found in the Gulf of Panama and off the coast of Colombia, where salinity varies from 34‰ to less than 30‰ at the end of the rainy season (Bennett, 1965). Except along the southern boundary of the Countercurrent, where it can be as much as 100 m deep, the vertical extent of the water is limited to the shallow mixed layer, usually only 20-50 m thick. Temperature decreases and salinity increases within the sharp discontinuity layer below this mixed layer.

Overall, nearshore sea surface temperature along Pacific Costa Rica varies little, ranging from winter lows of 24° - 25°C to summer highs of 27° - 28°C. Of course, on tidal flats, backwaters of estuaries and tidal pools temperatures often climb as high as 35°C or more. Due to the mountainous terrain of Costa Rica, the trade winds are greatly diminished along most of the Pacific coast, although during winter and spring limited upwelling does occur as surface waters are moved offshore. Trade winds move across the Nicaraguan-Costa Rican isthmus for only about 4 1/2 months, during the dry season of December to May. In the Golfo de Papagayo, and to a limited extent also Bahía de Salinas, pronounced dry season upwelling can drive sea surface temperatures down to 18° - 19° C. By March, as winds are subsiding, sea surface temperatures begin to rise slowly. By April, upwelling has gradually ceased along most of the Costa Rica - Panama coast.

A permanent shallow thermocline is characteristic for the entire tropical eastern Pacific region. This permanent thermocline occurs at progressively greater depths as one moves offshore, and is typically quite deep over the outer shelf. Unlike the Subtropical regions to the north and south of Central America, where seasonal variation in surface temperature becomes appreciable, a separate (additional) shallow summer thermocline rarely forms off Costa Rican shores.

In the area of 7° - 12°N, 89° - 100°W, there exists a large region of upwelling, approximately 200 - 400 km in diameter. The area is situated at the eastern end of the thermocline ridge associated with the Equatorial Countercurrent, and in this region the thermocline often reaches within 10 m of the sea's surface, forming a domelike feature referred to by oceanographers

as the Costa Rican Dome. The cyclonic circulation in the Dome is thought to be the result of three currents—the Equatorial Countercurrent to the south, the Costa Rican Coastal Current to the east, and the North Equatorial Current to the north—which come together off Costa Rica to form a large cyclonic gyre. A recent study postulates the Dome to be a region of localized upwelling produced by wind stress curl (Hofmann *et al.*, 1981), although at certain times of the year the intensity of the upwelling is probably enhanced by the eastward flow of the Equatorial Countercurrent. The important eastern tropical Pacific tuna fishery is presumably closely linked to this large upwelling phenomenon

## BIOLOGICAL STUDIES OF PACIFIC COSTA RICAN SHORES

Studies of intertidal community structure and/or trophic relationships along eastern Pacific tropical shores are few in number. At the time of this writing, there existed only a handful of published studies dealing with noncoral littoral community ecology, specifically in Costa Rica. Paine (1966) wrote a brief description of a rocky shore habitat based on 5 day's observation near Mata de Limon, in the Golfo de Nicoya. Paine's site was a protected rocky coast shore, in a region that is predominantly a mangrove-bay environment. Dexter (1974) studied the macroscopic infaunas of several sandy beaches in Pacific (and Atlantic) Costa Rica. Spight (1976; 1977) published a comparative study of temperate (Washington) and tropical (Costa Rica) gastropod "communities" (or guilds). Bakus (1968) studied the diversity and intertidal zonation of gastropods at a number of sites on Pacific and Atlantic shores. In addition to these studies, Fischer has published a series of papers on the phenomenon of bioerosion on Pacific Costa Rican shores (Fischer, 1979; 1980; 1981a; 1981b), which include limited data on vertical zonation of abundant invertebrates. Also, Villalobos (1979a; 1979b; 1980a; 1980b), published studies on population structure in the barnacle *Tetracita stalactifera* on Costa Rican shores.

Those few ecological studies that have been accomplished in intertidal areas peripheral to Costa Rica were summarized by Bakus (1969) and Brusca (1985). Important, noncoral, intertidal studies subsequent to these reviews are



as follows: Bertness' studies on hermit crab ecology, primarily in Panama (Bertness, 1980; 1981a; 1981b; 1981c; 1981d; 1981e; 1981f; 1981g; Bertness and Cunningham, 1981, Bertness *et al.*, 1981); a study of the mangrove clam *Geloina inflata*, including data on Pacific Costa Rican mangrove environments in general (Castaing *et al.*, 1980); Menge, Lubchenco and Gaines' studies on community structure and plant-herbivore interactions in rocky intertidal habitats of Pacific Panama (Menge and Lubchenco, 1981; Lubchenco and Gaines, 1981; Gaines and Lubchenco, 1982); and, Lessios' (1981) study of reproductive patterns in Panamanian urchins (both coasts). In addition, there are several Ph.D. theses dealing with aspects of tropical eastern Pacific coastal ecology.

The only current study of coastal community ecology being undertaken in Pacific Costa Rica is a large baseline study of benthic soft-bottom communities of the Golfo de Nicoya, under the direction of Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica.

In addition to the above intertidal investigations, Glynn, Porter and others have accomplished considerable work on the coral biotope of Pacific Central America (see Literature Cited for key references), and Glynn has long-term studies in progress that include coral communities of Pacific Costa Rica. Isolated coral reefs occur all along Pacific Costa Rican shores, particularly in sheltered habitats, but are concentrated mainly in the Golfo de Papagayo and Golfo Dulce regions. Good reef development is also present on Isla del Caño. Numerous dead reefs, as well as considerable coral rubble and debris are common in some areas of the Golfo de Papagayo (e.g. the Bahía Culebra area). Considerable interest has been given to the taxonomy of coastal invertebrates of Pacific Central America, as evinced by the large series of systematic papers resulting from the expeditions of the Allan Hancock Foundation, the New York Zoological Society and others (see Brusca, 1980 for an extensive bibliography to these works).

## INTRODUCTION TO THE ISOPOD CRUSTACEANS

**General external morphology:** The Order Isopoda Latreille, 1817, is distinguished from

the other six orders of Peracarida by the following combination of characters:

First thoracomere fused to cephalon, and rarely the second as well. No carapace. Body usually dorsoventrally depressed. Pleon short, in many with various segments fused; telson nearly always fused with last pleonite to form a pleotelson. First and second antennae almost always uniramous; with a minute scale or "squama" in a few taxa; some anthurids have a short multi-articulate "accessory flagellum" on second antennae. Eyes sessile. Mandible usually with a multiarticulate palp (the reduced endopod) and a multidentate incisor process; left and right lacinia often differ; molar process highly variable. Pereopodal coxae more-or-less fused with body somites to form lateral extensions on pereonites (coxal plates). First thoracopods modified as maxillipeds; with a short coxa (often divided); a short lamellar epipod (not enclosed in a branchial chamber); basis flattened and produced into a bladelike "endite"; palp of up to 5 articles (the reduced endopod). Second thoracopods modified as maxillipeds only in Gnathiidae. Pleopods biramous, flattened, specialized for respiration; second pair usually with stylets in males ("appendix masculina"). Heart located primarily in pleon; usually with 2 pairs of ostia and 5 pairs of lateral arteries. Maxillary glands usually present in adults. Young leave marsupium before appearance of last pair of pereopods (as "manca").

The generalized isopod body plan is diagrammed in Figure 3. The body is divided into three regions: the *cephalon* ("head"), *pereon*, and *pleon* ("abdomen"). Strictly speaking the cephalon of an isopod is actually a cephalothorax, as it is always fused with the first thoracomere (and also the second in the Gnathiidae). However, by convention the cephalothorax of isopods is referred to simply as the cephalon (or head). The term pereon refers, as in all Crustacea, to those thoracomeres (thoracic somites) that are NOT fused with the head.

The head bears the following sets of paired appendages, from anterior to posterior (Figures 4, 5): *antennae one* (occasionally referred to as the antennules, inner, superior, or upper antennae); *antennae two* (the outer, inferior of

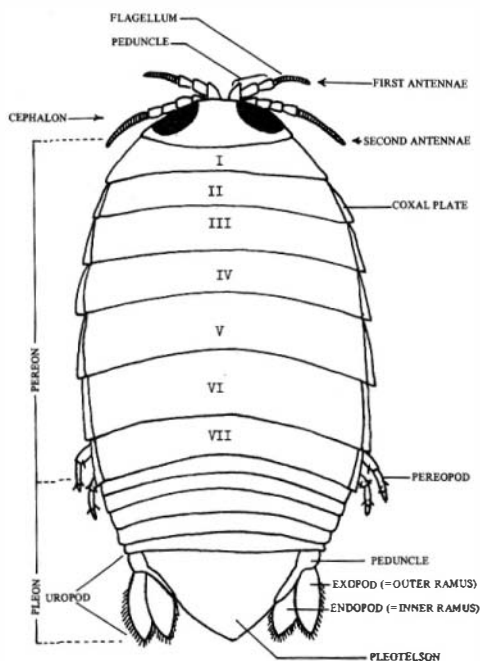


Figura 3

The generalized isopod body plan.

lower antennae); *mandibles*; 2 pair of *maxillae* (maxilla 1 and maxilla 2); and the *maxillipeds*. Gnathiids have two pair of maxillipeds; all other isopods have a single pair. The first antennae usually have a *peduncle* of 3 (occasionally 2 or 4) stout articles, and a *flagellum* of several to many smaller articles. The articles of the first antennae often bear modified setae called *aesthetascs* (= *esthetes*), that are olfactory (chemosensory) in function. The second antennae are usually considerably longer than the first, have 5 (occasionally 4 or 6) discernible peduncular articles, and generally numerous flagellar articles. The second antennae are generally tactile structures. Fusion of the flagellar articles with a corresponding reduction in their overall number is a common phenomenon in several taxa. For example, several epicarid genera have the antennae greatly reduced or even entirely absent; many idoteid genera have the flagella of the second antennae reduced to one or only a few articles. Only a few genera, mostly asellotes, retain a remnant of the exopod of the

second antennae, represented by a small, articulated and generally setose antennal scale.

The mandibles usually bear a 1 to 3 jointed *palp* (representing the remaining articles of the endopod), a heavily sclerotized *incisor process* (the "pars incisiva" of some authors), an articulated *lacinia mobilis*, and a *molar process* (the "pars molaris" of some authors). There is also often a *setal row* (= *spine row*) located between the incisor and molar process. In many taxa, some or all of these mandibular structures may be reduced or even absent. The molar process, for example, is wanting in the following families: cymothoidae, Aegidae, Limnoriidae, some Idoteidae, some Sphaeromatidae, Oniscoidae, and Armadillidiidae. It is vestigial or wanting in the Corallanidae. Further, it is not uncommon for only one of the mandibles (usually the right) to possess a weakly developed *lacinia mobilis*, or to lack the *lacinia* altogether. Because of this and other structural modifications, both mandibles should always be examined (Fig. 4). The *lacinia mobilis* is closely associated with the incisor and spine row, and was probably originally derived from the latter. The *lacinia* was long considered unique to the Peracarida, however, *lacinia*-like structures have recently been discovered in the larvae of several eucarid species and perhaps in some adult syncarids. The anatomical variability of the *lacinia mobilis* through the various groups that possess it is strikingly great. Dahl and Hessler (1982) and Brusca (1984) provide some recent comments on this morphological structure.

Maxilla 1 (sometimes called the maxillule) is usually composed of two lobes, a smaller *inner lobe* and a larger *outer lobe*. The inner lobe is generally sensory in function, the outer lobe masticatory or biting. Maxilla 2 is generally also composed of an *inner lobe* and an *outer lobe*, the latter usually being partly or entirely bifurcate. The lobes of the first and second maxillae articulate on a *protopod* (= *sympod*). The nature (phylogenetic and ontogenetic origins) of the lobes of the first and second maxillae has yet to be satisfactorily described for isopods, or the peracarids in general. Most authors consider them to be modified endites, the endopod and exopod being absent. Some workers have considered the inner lobe to be a modified endopod, the outer lobe the modified (reduced) exopod. The nature of the basal articles (protopod) of these appendages is also

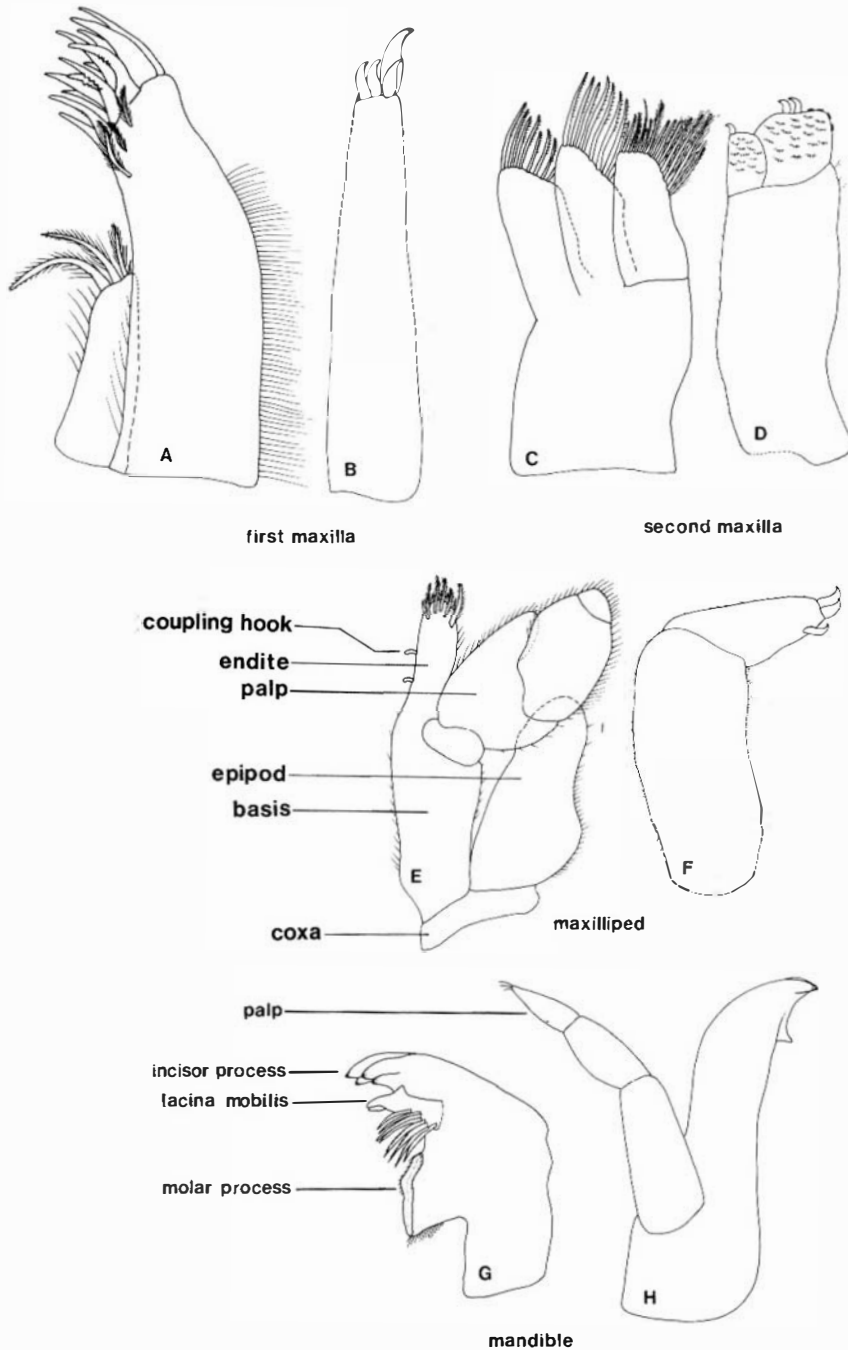
uncertain. If a majority opinion exists, it is probably in agreement with Hansen (1890; 1897) and Sheppard (1933; 1957) (also see Jackson, 1926). These workers consistently produced some of the most detailed and accurate studies of isopod morphology yet to be published. They viewed the maxillae to be composed of 3 articles, 2 small basal articles and a third larger article that we recognize as the outer lobe. Whether this outer lobe is a true article or merely an endite of the second basal article has not been settled. The inner lobe is viewed as an endite of the small first or proximal article. The "biramous" outer lobe, or endite(s), of maxilla 2 is probably the product of an evolutionary trend that began with a simple apical cleft and has progressed in many isopod groups to a completely bilobed structure. Unfortunately, the minute basal articles (the protopod) of the maxillae are difficult to remove and very rarely illustrated in publications. Considerable uncertainty exists regarding these two appendages and readers are referred to the above papers for more details. Adding to the confusion is the fact that in nearly all suborders one finds taxa in which the maxillae have been variously modified, reduced, specialized or even entirely lost.

The maxillipeds are, as the name implies, primitively derived from the first thoracopods, whose body somite (thoracomere one) became fused with the cephalon in the evolutionary past of this group. The gnathiids have two pair of maxillipeds (hence only 6 pereonites); all other isopods have a single pair of maxillipeds (and 7 pereonites). The second pair of maxillipeds in the gnathiids (those of the second thoracomeres) are generally called *pylopods* (or "gnathopods"). The maxillipeds consist of a basal part, the *coxa* (occasionally incorrectly called the "basis"), from which arise the inner and outer lobes. The coxa is often divided into 2 pieces, each bearing a separate lobe (though not always). The outer lobe is the *epipod* (also referred to as the *exite* or *epignath*). The inner lobe is composed of the modified articles of the endopod, consisting of a large basis upon which arises a number of smaller articles. If all the original articles of the endopod are present (basis, ischium, merus, carpus, propus, dactylus) the palp is composed of 5 articles (e.g. Sphaeromatidae, Corallanidae, Anturidae, Limnoriidae, etc.). However, often

a number of these articles is missing, due either to loss or fusion of adjacent articles, to present a palp of 2, 3 or 4 articles (e.g. Serolidae, Aegidae, Anthuridae, etc.). The enlarged basis of isopod maxillipeds forms a *blade* or *endite*, upon which one to several *coupling hooks* may occur. Coupling hooks (retinacula), when present, occur on the inner margin of the blade and serve to lock the two maxillipeds together, allowing them to function as a single unit.

Almost all isopods have *compound eyes*, composed of numerous *ommatidia* which create a mosaic image. Species in the family Trichoniscidae (Oniscidea) lack compound eyes, instead having groups of *ocelli* (simple eyes). There is a tendency for deep-sea, interstitial and cave-dwelling species to undergo loss of the eyes. This may take the form of a simple pigment loss or actual loss of the ommatidia (in part or in their entirety). Degenerate eyes are occasionally covered by a noticeably thickened cuticle. In some groups the eyes appear to degenerate with age (e.g. some species of Cymothoidae). For recent studies on the fine structure of mysid and tanaidacean compound eyes see Hallberg (1977), Elofsson and Hallberg (1977), Anderson, *et al.* (1978) and Hallberg and Anderson (1978).

Although not true appendages, the mouth field bears two additional sets of unpaired structures, loosely referred to as the upper and lower lips. Between the bases of the antennae there arises a *frontal lamina* (Fig. 5). The frontal lamina of isopods is probably homologous to the *epistome*, a plate formed of the antennal sterna and common to all groups of Crustacea. Various authors have proposed different names for this plate or sclerite, and even designated various regions of it by different names. Thus, the *profrons*, *postfrons*, and *frontal lamina* of Jackson (1926; 1928) are all parts of the epistome proper. Similarly, the *frontal process* of the Idoteidae is but the lower region of this epistomal plate or sclerite, which in some groups happens to project outward to become visible in the dorsal aspect (Fig. 5 a,b). Posterior to and borne upon the frontal lamina is the "upper lip" or *labrum*. In most (but not all) isopods the labrum consists of two pieces, the anteriormost (proximal) referred to as the *clypeus*, the posteriormost (distal) as the labrum proper. Whether or not the labrum and clypeus should be considered part of the epistome is perhaps a moot point; and one not

**Figura 4**

Appendages of the head. A,B maxilla one (A, Idoteidae; B, Cymothoidae). C,D maxilla two (C, Idoteidae; D, Cymothoidae). E,F maxilliped (E, Idoteidae; F, Cymothoidae). G,H mandible (G, Idoteidae; H, Cymothoidae). Note that the cymothoid mouth parts show considerable reduction or specialization for the parasitic lifestyle (e.g. maxilliped reduced to a 2-3 jointed palp; mandible without lacinia or molar process). Species of the family Idoteidae lack a palp on the mandible.

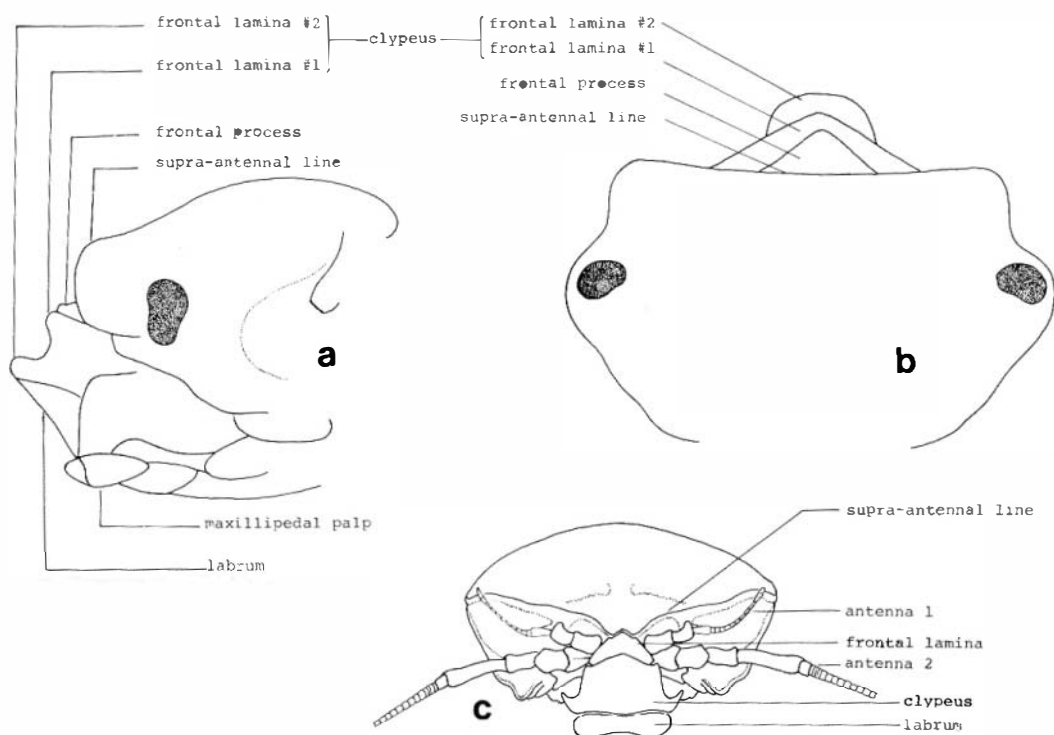


Figura 5

**Nomenclature of the isopod head. a,b cephalon of an idoteid isopod, lateral and dorsal views (after Menzies, 1950). c, cephalon of a cirolanid isopod.**

easily answered. In the Idoteidae the lower margin of the clypeus projects forward to become visible in the dorsal aspect, and in this taxon it is hence referred to as *frontal lamina 2* (Fig. 5 a,b). Separating these structures from the upper surface of the cephalon itself is the *frontal line* (also referred to as the *frontal margin*, or *supraantennal line*). Note that the frontal line is quite different, both in placement and origin, from the frontal lamina and frontal process. Readers are warned that past authors have often confused these structures in the literature. The rostrum of some isopod species (e.g. *Excirrolana*, some *Aega*) is formed from the frontal line (i.e., the frontal margin of the cephalon), NOT the frontal process as is often stated.

The posterior border of the buccal field is formed by the lower lip, or *labium*. The labium is usually produced and cleft into a large bilobed structure, and hence more commonly referred to as the *paragnath* (= hypostome, metastome, hypopharynx).

The thoracomeres not fused with the head comprise the pereon, its segments being the *pereonites* (in this text numbered with roman numerals). The paired, uniramous legs of each pereonite are the *pereopods* (also numbered with roman numerals). In all marine groups except the Gnathiidae, certain anthurid genera, the genus *Harponyx* (Cymothoidae), and many of the epicarids there are 7 pairs of pereopods. The pereopods may be ambulatory, natatory, subchelate, or "prehensile" (Fig. 6). True chelipeds do not occur in the Isopoda. Ambulatory pereopods are simple, not strongly recurved, and used primarily for walking. Natatory pereopods have the distalmost articles flattened into swimming paddles. In "prehensile" pereopods the terminal article, the *dactyl* (= dactylopod) is as long or longer than the penultimate article (propus), strongly developed and recurved, and used for clinging or grasping. Although the articles of the pereopods normally number seven, variations occasionally occur. Pereopod morphology is illustrated in

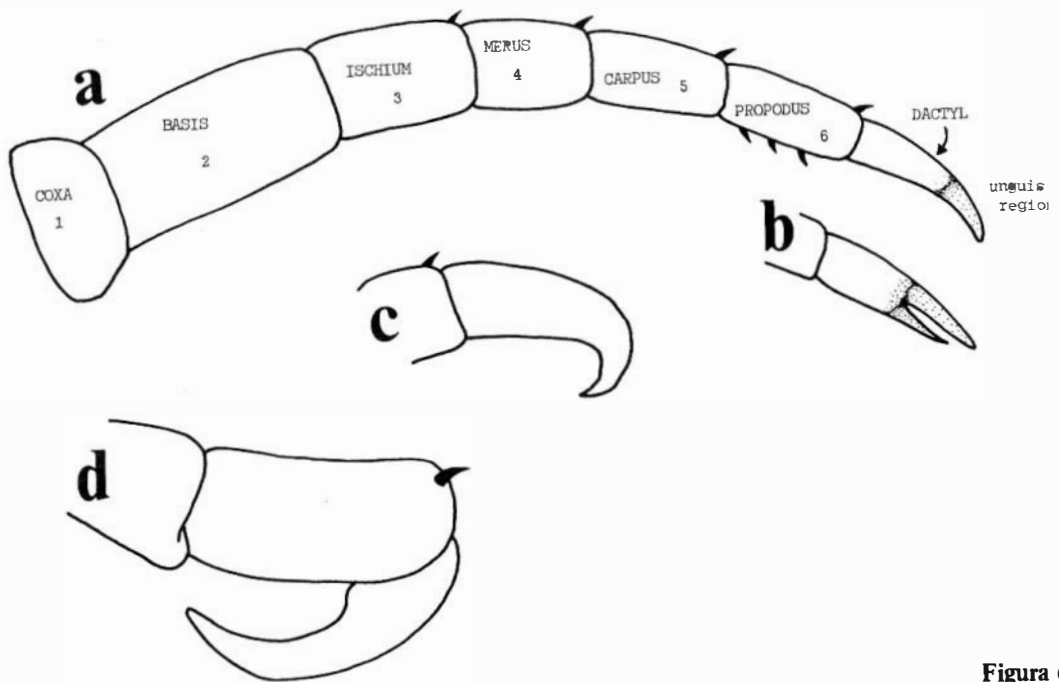


Figure 6

Nomenclature of the isopod pereopod. a, a generalized isopod pereopod. b, a bifid (biungulate) dactyl. c, a "prehensile" dactyl. d, a subchelate dactyl.

Figure 6. The tip of the dactyl (referred to as the *unguis*) may be simple, bifid or trifid. The basal-most article of the pereopods (the *coxa*-*podite*, or simply *coxa*) forms two important structures. It develops an outward expansion that may fold up to fuse completely, or in part, with the lateral margin of its respective pereonite. This structure is termed the *dorsal coxal plate*. It is important to note that true coxal plates occur only in the isopods and amphipods; the similar appearing pereonal *epimeres* of other crustacean taxa are formed by outgrowths of the lateral margin of the sternites or tergites (of the body segments), rather than the coxae of the thoracopods. For this reason these structures should be referred to in isopods and amphipods as coxal plates (not as epimeres). Pereonite I in isopods almost invariably has the dorsal coxal plate entirely fused to the body somite. Only in a few groups (i.e. many asellotes, some epicarids, most Phreatoicidae, the Plakarthriidae, *Bathynomus*) do the pereopodal coxae remain small and not fused to the lateral body margin. In the Idoteidae, *ventral coxal plates* may also form, extending ventromedially to obscure the sternites.

In female isopods (except the Gnathiidae) several coxae also expand medially, forming thin lamellate plates loosely covering the ventral surface of the pereon. These are the *oostegites*, which form the brood pouch or *marsupium* of the females. Most taxa form oostegites on the anterior 4 or 5 pairs of pereopods, but some species use 6 or 7 pairs. Gravid females of some species develop oostegite-like lamellae on the maxillipeds.

The abdomen is referred to as the *pleon*, its segments being the *pleonites* (numbered with arabic numerals). Each pleonite bears a pair of biramous, lamellate appendages termed the *pleopods* (also numbered with arabic numerals). In some groups the pleopods are enclosed by an operculate covering, formed from the uropods (valviferans) or certain of the anterior pleopods themselves. The pleopods typically serve as gills and swimming appendages, and are often modified in this regard (e.g. with plumose marginal setae in most families; with brushlike attachments in *Bathynomus*; branched in epicarids and some cymothoids, etc.). The ventral (= anterior when unfolded) pleopodal lamellae are the *exopods*; the dorsal (= posterior

when unfolded) the endopods. The isopod abdomen probably primitively consisted of six pleonites and a terminal telson. However, all known isopods have the sixth pleomere fused with the telson, to form a *pleotelson*. In the anthurideans the fusion is often incomplete and a line of demarcation may be visible in the dorsal aspect. The anus opens subterminally on the pleotelson. Several anthuridean genera possess statocysts at the base of the pleotelson. The pleotelson bears a pair of *uropods*, representing the appendages of the fused sixth pleonite. Each uropod bears an inner and outer ramus, the *endopod* and *exopod* respectively, arising from the *protopod* or *peduncle* (also referred to as the basis or sympod). The uropods of isopods differ greatly from one suborder to another and often between families within a suborder, and are used extensively in the classification of the higher taxa.

Much of the frustration beginning students of the Isopoda experience stems from inconsistent use of morphological terminology in the literature. A particularly good example is the term "prehensile". The strict definition of this term implies a structure that is adapted for grasping or clinging. As such, this is a functional term (not a morphological one) and this definition, when applied to an appendage, allows for a variety of interpretations. This circumstance has led to considerable confusion, as one worker may consider the slightly recurved dactyl of a *Cirolana* pereopod as "prehensile", while another worker may not (reserving the term for such highly developed and strongly recurved dactyls as those seen in the Cymothoidae and Aegidae). In the present paper, we restrict the term "prehensile" to those pereopods in which the dactyl is as long, or longer than, the propus (e.g. pereopods I - VII of Cymothoidae; I - III of Corallanidae and Aegidae). We urge users of this handbook or any other literature to be thoroughly familiar with the correct or preferred definitions of terms used in describing the morphology of the Isopoda, as well as variations on these definitions.

**Sexual dimorphism:** The only groups which show a truly marked sexual dimorphism are the gnathiids, sphaeromatids and parasitic taxa (primarily the epicarids and cymothoids). However, in all groups subtle dimorphism is evident between gravid and nongravid females

and males, due to the presence or absence of the secondary sex characters (appendix masculina, penes and oostegites). Gravid females having the marsupium swollen with developing embryos, tend to become noticeably broader across the midline (pereonites II-VI).

In the suborder Epicaridea the males are usually 4-5 times smaller than the females, to which they are generally attached. The small males usually retain a distinct bilateral symmetry, whereas the females are usually distorted, often possessing no remnants whatsoever of bilateral symmetry. In some species, females are so asymmetrical that they are difficult to recognize as isopods at all. In certain genera of the family Sphaeromatidae the males develop characteristics of the pleotelson and uropods that differ markedly from the females. In the suborder Gnathiidae the males develop huge mandibles that project forward from the head, reminiscent of certain ant or termite castes. Female gnathiids lack mandibles altogether. Similarly, mature female gnathiids have an enormous rotund pereon that is lacking in the normally contoured males.

**Reproduction:** Isopods are dioecious, relying on copulation and internal fertilization. However, in several groups of Flabellifera, Epicaridea and Anthuridea, protogynic or protandric hermaphroditism has evolved. In the species thus far studied, it has been shown that the same primordial gonadal mass develops into either testes or ovaries. The gonads are paired organs lying on either side of the pereonal cavity, opening by means of ducts, usually at the base of the fifth pair of legs in the female and the posterior sternal margin of pereonite VII in males. The male genital structures are the *penes* (the *genital papillae* or *genital apophyses*). In the gnathiids, many valviferans and most terrestrial forms, the penes are completely fused; in most other groups two distinct finger-like structures (often fused only at their bases) are usually evident. Size and development of the penes differs greatly among the various taxa, from the simple swellings or bumps of cymothoids to the well-formed structures of most other flabelliferans. The second pair of pleopods of males, in most isopods, are modified as gonopods, upon which are borne the *appendix masculina* (sing., appendix masculinum); also occasionally referred to as "stylets". These structures

generally consist of an elongated stylet or palplike organ on the median edge of the endopod. The appendix masculinum generally originates at the base of the endopod, but in a few species it arises midway up the lamella (e.g. *Cleantoides occidentalis*, *Paracerceis*, *Discerceis*, *Paraleptosphaeroma glynni*, and others). In some cases this structure is ornately sculptured, while in others it is so simplified as to appear non-functional. Gnathiids, epicarids, and some species of Flabellifera lack appendix masculina altogether. In most asellotes, the first two pleopods function together for sperm manipulation. The appendix masculina are presumed to function in the transfer of the spermatophore from the male penes to the female oviductal openings (*Limnoria* apparently does not form spermatophore packets). This precise behavior has not, however, been well documented in isopods. In at least two groups, appendix masculina also occur on the first pair of pleopods: most oniscoideans and all of the Valvifera except the Idoteidae and Holognathiidae. In some species seminal receptacles have been found in females (most oniscoideans, *Asellus*, *Jaera*); in others they apparently do not exist (*Limnoria*, *Sphaeroma*). In terrestrial species with seminal receptacles, a single copulation is sufficient for at least two broods.

Males are known to carry females for some time prior to copulation and, at least in some cases, wait for her to molt before attempting insemination. Although actual insemination has not been observed directly in any species, several copulatory behavior patterns have been documented. The male generally holds the female beneath him, so the two lie male venter to female dorsum. Some species situate head to head, while others arrange themselves "head to tail". Insemination apparently takes place during a brief period when the male slides to one side of the female and then the other, so that his venter temporarily lies against her right or left side, his pleon folding slightly under her body. Females generally carry the developing eggs in a ventral brood pouch formed from the overlapping oostegites. Some species, however, brood embryos in the oviducts, which become enlarged to function as uteri (*Excirologa*). Others brood embryos in special chambers formed by paired invaginations of the thoracic sterna (most Sphaeromatidae; gnathiids, which lack oostegites altogether; the epicaridean genus

*Hemioniscus*). Several genera are known to form male-female pair bonds (e.g. *Paracerceis*, *Sphaeroma*, most cymothoids and epicarideans).

Isopods follow a typical crustacean developmental scheme, with the well-known peracaridean specializations. From a few to hundreds (cymothoids), or even thousands (bopyrids) of eggs may be produced in a single brood. The egg is centrolecithal, large and yolky. It is enclosed by two membranes, the chorion and the vitelline membrane. Development is direct within the marsupium. The usual cleavage pattern is nuclear division and migration to form a periblastula. Cleavage is holoblastic and nearly equal but there is little evidence of a spiral pattern. The embryo is generally organized in such a way that its entoderm is in close association with the yolk. As external signs of segmentation begin to appear, the mesoderm (arranged in bands) breaks into serially aligned packets. Appendicular musculature and the circulatory system start to form, and rudimentary coelomic pouches develop. These pouches eventually become associated with the reproductive and excretory systems, and true coelomic spaces do not persist; the adult body cavities are almost entirely hemocoelic in nature.

In most taxa there is no major metamorphosis, the young resembling the adults but with the last pair of legs undeveloped. These young hatchlings are referred to as *manca stage*. The manca molt a few times to become juveniles (sexually immature), and the juveniles eventually become mature adults. Exceptions are certain epicarid groups, particularly the cryptoniscids, in which considerable morphogenesis occurs and several distinct "larval" stages are recognizable. Oniscoideans usually leave the marsupium with only 6 pereonites, adding the seventh at the first molt, then adding the seventh pair of legs at the next molt. Most littoral species that have been studied appear to have a lifespan of 1-2.5 years.

**Excretion:** Little is known about organs concerned with excretion in isopods. Both nephrocytes and a pair of maxillary glands are present. Marine species tend to have considerably shorter nephroducts (of the maxillary glands) than fresh water species.

**Digestion:** The alimentary system typically consists of a long straight gut (which, as in



other crustacea, is almost entirely ectodermal in origin) with 1-3 pairs of long *midgut caeca*. These caeca have been variously referred to in the literature as "hepatic caeca", "hepatopancreas" or "liver". The caeca are endodermal in origin and arise near the small stomach, which is situated in the cephalon and anterior pereonites. Their functions are to produce the majority of the digestive enzymes, provide space for digestion and absorption, store various energy reserves, and perhaps store certain calcium salts for use during the molting cycle. The stomach is a very small region, usually in the form of a chitinous "gastric mill" or *proventriculus*. Holdich and Ratcliffe (1970) have shown that all but a very small section of the post-proventricular region of the gut is lined with a chitinous intima and a peritrophic membrane, and should therefore be considered as a proctodaeum, or hindgut (i.e. ectodermal in origin). Some species form well defined fecal pellets, particularly terrestrial species, while others do not. Plant burrowers (i.e. *Limnoria*, *Cylisticus corvexus*, and perhaps some *Oniscus*) typically lack any signs of intestinal flora or fauna, suggesting that they may some day be sources of new classes of antibiotics (Boyle and Mitchell, 1978).

**Nervous system:** The nervous system is on the typical arthropod plan and consists principally of a "brain" or a pair of *cephalic ganglia* and a double ventral nerve cord, connected by partially fused, paired ganglia. The cephalic ganglia are simple and often reduced, especially in the relatively secretive terrestrial genera (which show a corresponding reduction in eye and antennal size and function). The tritocerebrum is best developed and is associated with the large second antennae; ganglia of the mouth parts form a loosely fused subesophageal mass. The pereonal ganglia form the easily identified ventral nerve cords, while the pleonal ganglia are more-or-less coalesced (especially in terrestrial genera). The paired ventral nerve cords generally lie so close together as to appear as a single cord through the dissection microscope.

Sense organs of isopods include a wide variety of setal types, particularly on the antennae and mouth parts. Sessile compound eyes are present in most species (excepting some Oniscoidea, cave forms, parasites, and deep sea species), and statocysts occur in a few taxa

(particularly the Anthuridae). Aesthetascs (flattened club-shaped setae that function as chemoreceptores) are largely restricted to the first antennae. A variety of microscopic cuticular structures occur on the surfaces of isopods. These are difficult to see without scanning electron microscopy and are very poorly documented. Shaeromatids have the dorsal surface covered with an array of pitlike structures which typically house a central rod of either glandular or nervous function (Iverson, unpub. data).

**Isopod taxonomy and identification:** The taxonomy of the Isopoda historically has been based largely upon the morphology of the cephalon, pereonites, pereopods, coxal plates, pleotelson, uropods and (to a limited extent) mouth parts. Recent studies on isopod development and natural history have revealed that there exists a considerable degree of variation in many of these structures. For example, the number of antennal articles and the shape of the pleotelson and cephalon may vary with age, sex, or predator damage, while the morphology and visibility of the coxal plates and the general body shape often vary greatly within a single population. Mouth parts and pleopods, both rarely described in the older literature, are becoming increasingly important as bearers of reliable taxonomic information.

Isopod taxonomists have typically referred to the coxal plates (or coxae) in the context of McCormick's (1969) definition: the lateral expansion of a pereopodal coxa jointed broadly to the lateral margin of the tergite. However, as Sheppard (1957) and Brusca and Wallerstein (1979a) have pointed out, in some groups, the coxae may also be expanded ventrally to form ventromedial plates (i.e. the *Valvifera*). Brusca and Wallerstein (1979a) present a general discussion on the use of coxal plates (with particular reference to idoteid taxonomy) and Brusca (1981) discusses these characters with regards to the cymothoidae.

Taxonomic criteria and characters useful in distinguishing species in the various genera are presented in their respective position in this text. All of the morphological structures that need be examined in using the following keys are easy to locate, even those requiring dissections (the mouth parts, pereopods, and pleopods). All that is usually needed is a dis-

secting microscope, two pairs of good forceps (jeweler's forceps are excellent) and a thin probe (an insect pin stuck through the eraser end of a pencil makes an excellent probe for microscopic work). If you prefer to mount an appendage on a slide, do so in glycerine, with a coverslip, and when finished with your observations replace it in alcohol. We do not recommend the use of commercial mounting media as they make manipulation of the appendages impossible, lack long-lasting optical clarity and do not preserve crustacean material properly. Keep the appendages in small vials (labeled), stoppered with cotton, in the same jar with the specimen from which they came. In most cases stains are not required and good transmitted (substage) lighting will bring out all the features necessary for proper identification. If a stain is needed, borax carmine or fast green with lactic acid are good, as the material can be destained in low grade alcohol until the proper color is achieved for optimal observation.

To use the keys, begin at couplet number one, with the animal to be identified in front of you, under a dissecting microscope. After reading each choice of the first couplet, decide which set of characters applies to the specimen you are identifying. Look at the number following the description fitting your animal and go to the couplet with that number. Continue going from couplet to couplet, each time making the choice of which of the two sets of characters applies to your animals. Eventually you will reach a name instead of a number, and that is the taxon to which your animal belongs. Beginning students should start with the key to the suborders on page 17, and continue from there to the family keys and species keys as appropriate. After the completion of each key identification, be certain to read the diagnosis provided for that taxon. Never rely on the keys alone for an identification; always double check yourself with the diagnoses and figures. Great care has been taken to present up-to-date diagnoses of every taxon covered in this handbook. All of the keys in this book are phyletic. That is to say, in almost all cases they should lead one to the proper taxon, or to no clear identification at all.

Like amphipods, marine isopods do not readily autotomize. Most specimens can be placed directly in a 70 percent solution of

alcohol (preferably ethanol), with a small amount of glycerine added, for storage. As with most animals, isopods tend to change or lose their color in alcohol. Color, however, is rarely used as a taxonomic character in this group, although in some species, in a few groups (anthurids, etc.), chromatophore PATTERNS have been shown to be reliable features to aid in identification. For this reason, should a distinct color pattern be evident, descriptive notes should be made prior to preservation. It is important that these, and any small crustaceans, not be allowed to dry out. Should this occur your material can be rehydrated by soaking it in a 0.5 % solution of trisodium phosphate for 2-3 days, and then washing it in water before transferring back to alcohol. Fragile species, such as *Ligia*, some of the small anthurids and asellotes, the interstitial forms, arcturids, etc., may be relaxed prior to killing. This can be accomplished by any of several standard methods including the use of chlorotone, added slowly to the small container housing the specimens. Lack of immediate response to physical prodding indicates the isopod is relaxed and ready to be fixed. Large numbers of individuals, or lots, can be stored in individual vials, stoppered with cotton, and placed together (upside down) in larger screw-top or bail-top jars.

Proper examination of isopods requires the use of a low-power, binocular, dissecting microscope (approximately 5-60X magnification) and ideally a high-power compound microscope. Best results are obtained with a dissecting microscope that has both substage and reflected light sources, and maximum viewing success is attained by use of high intensity fiber optics light sources.

## METHODS

Collections were made by the senior author and A. M. Mackey during three field excursions in spring, 1979, winter and spring, 1980, and summer 1981, at selected coastal sites in Costa Rica. Additional material from Costa Rica and other Central and South American localities was examined from the collections of the Allan Hancock Foundation, Scripps Institution of Oceanography, the Universidad de Costa Rica, and the United States National Museum (Smithsonian Institution). Collections were also made by Brusca, Mackey and Iverson in Panama and

Guatemala during the summers of 1979, 1980, and 1981.

Collections were made in two ways. First, in order to assure collection of a wide range of species from a variety of habitats, formalin washes were made of rocks, driftwood, mud, algae, etc. Washed material was screened through a 0.5 mm mesh sieve. Secondly, discrete samples were taken from various selected microhabitats (e.g. on and under rocks, in sand, in dead barnacle shells, on mangrove roots, etc.).

All material was stored in 70% ethyl alcohol, and examined with compound and dissecting microscopes either at the Universidad de Costa Rica or the Allan Hancock Foundation.

Nomenclature generally follows that of the authors' previous publications. Familial, generic and species diagnoses are based upon the most recent published data and our own observations; diagnoses of all taxa treated are applicable for those taxa regardless of geographic locality. Synonymies are given for all species, either complete or subsequent to a recent, thorough, published treatment; when no synonymy is indicated, there have been no published references to that species (other than the original description). The abbreviation AHF stands for: Allan Hancock Foundation, University of Southern California. Holotypes of all new species are deposited at AHF; additional material is deposited at AHF and the Zoological Museum of the Universidad de Costa Rica.

## THE ISOPODS OF PACIFIC COSTA RICA

Only two papers have been published dealing specifically with the marine isopod fauna of Pacific Costa Rica. Dexter (1974) compared the sandy-beach fauna of Atlantic, and Pacific Costa Rica and Colombia, reporting on the abundances of the isopods *Exosphaeroma* sp. (as *E. diminutum*) and *Excirrolana braziliensis* (as *Cirrolana salvadorensis*). Glynn *et al.* (1975) clarified the taxonomic status of *Excirrolana braziliensis* and discussed the zonation and distribution of this important sandy-beach inhabitant. Other Pacific-Central American isopod studies include: Hansen (1890: 1897), Richardson (1914), Schuster (1954), Bott (1954), Dexter (1977; 1979), Kensley and Kaufman (1978), Glynn (1968; 1976b), and Glynn and Glynn (1974). Because many Costa

Rican isopods range north to western Mexican shores, the following references are also germane to their study: Richardson (1901; 1905), Boone (1918), Menzies (1962a), Schultz (1973; 1977), Pennak (1958), Bowman (1977), Nunomura (1978), Dexter (1972; 1976), Brusca (1977, 1978a; 1978b; 1980; 1981; 1983a; 1983b; 1984), Brusca and Wallerstein (1977; 1979a, 1979b), Wallerstein and Brusca (1982), Thun and Brusca (1980), Bruce *et al.* (1982), and Brusca and Gilligan (1983).

Only three papers have been published on the terrestrial isopods of Costa Rica. Richardson (1910a) discussed three species: *Coxopodias tristani* Richardson, *Metoponorthus pruinosis* (Brandt), and *Philoscia musconum* (Scopoli). We have found the latter to be quite common in leaf litter in the Monteverde area (specimens collected by Dr. S. Anderson). Richardson (1913) described *Pentoniscus pruinosis*. Schultz (1969) removed the latter species to the genus *Philoscia* and discussed its morphological variability (also see Richardson, 1910b; Van-Name, 1925; 1926, and Schultz, 1974).

The present paper includes 37 species of marine isopods, in 14 families. The most abundant isopod in Pacific Costa Rica is probably *Excirrolana braziliensis*, which occurs on both sandy and rocky beaches. Also common are the small anthurid *Cyathura guaroensis* n. sp., and the sphaeromatids *Exosphaeroma* sp. and *Ancinus panamensis* Glynn and Glynn. Nearshore fishes are not uncommonly infested with the cymothoids *Nerocila acuminata*, *Cymothoa exigua* or *Lironeca vulgaris*. Bottom trawlers in shallow subtidal depths commonly collect the aegid *Rocinela signata*.

The following key defines all nine suborders of Isopoda, although only five of these are included in this paper. The Phreatoicidea is a freshwater taxon known only from the Southern Hemisphere. The Oniscidea are entirely terrestrial. No Asellota or Microcerberidea were recovered during this study; the latter being minute interstitial forms, the former being primarily offshore forms. Only a single asellote has been recorded from off Pacific Costa Rica, the deep-water *Storhyngura pukhra*. Those species of Asellota that might inhabit the littoral regions of Costa Rica are probably too small to have been captured in the 0.5 mm mesh sieves used during our field collecting. The Epicaridea are all parasitic on other crustaceans. No epicarids have been

reported in the literature from Costa Rican shores, and none were collected during our field work. Only a single specimen of Gnathiidae was recovered during our field work. Like the

asellotes, most species of tropical gnathiids are very small and easily overlooked. Also like asellotes, gnathiids reach their greatest diversity in offshore benthic habitats.

#### Key to the suborders of isopods (of the world)

1. Parasitic on other crustaceans; female much larger than male and with slightly to highly distorted bilateral symmetry; pereopods and pleopods present, absent or reduced . . . . . *Epicaridea*
1. Not parasitic on crustaceans; females more-or-less the same as males, with clear bilateral symmetry; pereopods and pleopods always well developed . . . . . 2
2. With 6 free pereonites and 5 pairs of pereopods; 2 pairs of maxillipeds (the second pair being the flattened pylopods); mandibles of males grossly enlarged and extended beyond front of cephalon; mandibles absent in females (Fig. 21) . . . . . *Gnathiidea*
2. With 7 free pereonites, and 6-7 pairs of pereopods; 1 pair of maxillipeds; mandibles not as above . . . . . 3
3. Body more-or-less compressed from side to side (as in gammarid amphipods); freshwater (known only from So. Hemisphere) . . . . . *Phreatoidea*
3. Body flattened dorsoventrally, or tubular; freshwater, marine, estuarine or terrestrial . . . . . 4
4. Primarily terrestrial; first pair of antennae minute, rudimentary; pleopods tracheate . . . . . *Oniscidea*
4. Aquatic; first pair of antennae may be small, but never rudimentary; pleopods not tracheate . . . . . 5
5. Uropods modified into a pair of covers folded under the pleon and covering the pleopods (Fig. 17 c,d) *Valvifera*
5. Uropods not as above (lateral or terminal) . . . . . 6
6. Body elongate, length greater than 6 times width; body tends to be tubular . . . . . 7
6. Body not elongate, length less than 4 times width; body dorsoventrally flattened . . . . . 8
7. Length usually greater than 4 mm; uropods folded up and partially over the pleotelson (Fig. 19) . . . *Anthuridea*
7. Length usually less than 3 mm; uropods not as above, terminal; minute interstitial forms . . . . *Microcerberidea*
8. Uropods lateral, hinged at sides of pleotelson to form a "tail fan"; first or second pleopods almost never form operculate covers for remaining pleopods (Figs. 7-16) . . . . . *Flabellifera*
8. Uropods terminal or nearly so (hinged on the posterior margin of pleotelson), minute and usually styliform; first or second pleopod often modified into thin opercular plates covering remaining pleopods in female (Fig. 20) . . . . . *Asellota*

#### Checklist of Pacific Costa Rican isopods

NOTE: Species marked with an asterisk (\*) have not yet been collected from Costa Rican shores, but are expected to occur there.

#### ORDER ISOPODA

##### SUBORDER FLABELLIFERA

##### Family Sphaeromatidae

*Ancinus* sp.

*Ancinus panamensis* Glynn & Glynn

*Dynamenella josephi* Glynn

\* *Dynamenella setosa* Glynn

*Paraleptosphaeroma glynni* Buss & Iverson

\* *Striella balani* Glynn

*Exosphaeroma* sp.

*Sphaeroma peruvianum* Richardson

##### Family Cirolanidae

*Cirolana parva* Hansen

*Metacirolana costaricensis* n. sp.

\* *Natatolana californiensis* (Schultz)

*Exciorolana braziliensis* Richardson

*Eurydice caudata* Richardson

##### Family Corallanidae

\* *Excorallana tricornis occidentalis* Richardson

##### Family Aegidae

*Aega acuminata* Hansen

*Aega plebia* Hansen

*Rocinela murilloi* n. sp.

\* *Rocinela signata* Schioedte & Meinert

## Family Cymothoidae

*Nerocila acuminata* Schioedte & Meinert*Nerocila excisa* (Richardson)\* *Anilocra meridionalis* Richardson*Lironeca vulgaris* Stimpson\* *Lironeca convexa* Richardson\* *Lironeca bowmani* Brusca*Cymothoa exigua* Schioedte & Meinert\* *Idusa carinata* Richardson\* *Ceratothoa gaudichaudii* (Milne Edwards)

## SUBORDER GNATHIIDEA

*Gnathia* sp.

## SUBORDER FLABELLIFERA

The largest of the isopod suborders, flabelliferans are primarily littoral or shallow benthic in habit although a variety are also known from deeper waters of the continental slope and basins. Freshwater, cave and hot springs species are also known. About 3,000 species, in 175 genera, have been described. Seven of the 12 flabelliferan families are herein reported from Pacific Costa Rica.

The body of most flabelliferans is distinctly depressed and possesses well-developed eyes, antennae, coxal plates, and walking legs, although loss of sight and antennal reduction occasionally occur in deep benthic, parasitic, and cave dwelling species. Members of this suborder are quickly recognized by the morphology of the uropods, which are flattened, arise laterally at the base of the pleotelson, and usually forming a "tail fan". The penduncles of the second antennae are of 5 or 6 articles, the mouth parts are well-developed for biting, chewing, slicing or piercing. Maxilla 1 is usually biramous; maxilla 2 is usually triramous. The pereopods lack subchelae, except in the Serolidae and the sphaeromatid genus *Ancinus*, but may be distinctly prehensile. The pleon often consists of 5 free segments plus the pleotelson, although fusion may reduce the pleon to any number of "segments"; all 5 pairs of pleopods generally persist.

## SUBORDER VALVIFERA

## Family Idoteidae

*Cleantioides occidentalis* (Richardson)\* *Cleantioides planicauda* (Richardson)

## SUBORDER ANTHURIDAE

## Family Anthuridae

*Cyathura guaroensis* n. sp.

## SUBORDER ASELOTA

## Family Munnidae

\* *Munna*

## Family Ianiiridae

\* *Ianiropsis*

## Family Jaeropsidae

\* *Jaeropsis*

## Family Eurycopidae

*Størthyngura*

## Key to the families of flabellifera known from Pacific Costa Rica

1. Uropods greatly reduced, with very small, often clawlike exopod; body less than 3 mm long; burrowing in wood or algal holdfasts . . . . . *Limnoriidae*
1. Uropods not greatly reduced; body rarely less than 3 mm in length; rarely burrowing in wood or algae\* . . . . . 2
  2. Pleon composed of 3 or fewer visible free segments, plus the pleotelson . . . . . 3
  2. Pleon composed of 4-5 free visible segments, plus the pleotelson . . . . . 4
3. Pleon composed of 3 free "segments", plus pleotelson; cephalon fused medially with pereonite I; pleopods 1-3 small and natatory, basis elongated; pleopods 4-5 large, broadly ovate, suboperculiform; body strongly depressed, flat in cross-section . . . . . *Serolidae*
3. Pleon composed of 1-2 dorsally visible, free "segments", plus pleotelson; cephalon not fused medially with pereonite I (except in *Ancinus* and *Bathycopea*); pleopods subequal, of modest size, basis not elongated, 4-5 ovate but not operculiform; body ovate in cross-section, dorsum convex . . . . . *Sphaeromatidae*

\* A few species of Sphaeromatidae are known to burrow into coastal wood structures.

4. Pereopods IV-VII prehensile (dactyls longer than propi); antennae reduced, without clear distinction between peduncle and flagellum; maxillipedal palp of only 2 articles . . . . . *Cymothoidae*
4. Pereopods IV-VII ambulatory (dactyls shorter than propi); antennae normal, with clear distinction between peduncle and flagellum; maxillipedal palp of 2, 3, or 5 articles . . . . . 5
5. Mandible without lacinia mobilis or molar process; maxilla 1 reduced to a single slender stylet, with apical recurved spines; maxilliped, first and second maxillae with stout, recurved, apical spines . . . . . *Aegidae*
5. Mandible with or without lacinia mobilis and molar process; maxilla 1 not as above, bilobed (although outer lobe MAY form a single large spine); maxilliped and second maxilla without stout, recurved, apical spines . . . . . 6
6. Mandible with distinct, large, bladelike molar process; pereopods I-III ambulatory or only weakly prehensile (dactyls always shorter than propi); maxilla 1 simple, never with outer lobe as below . . . . . *Cirolanidae*
6. Mandible with lacinia and molar process absent or reduced (vestigial); pereopods I-III usually prehensile; maxilla 1 outer lobe may or may not form a large recurved spine . . . . . *Corallanidae*

### Family Sphaeromatidae

Mandibles stout; lacinia mobilis and molar process usually well developed (except in *Ancinus*, *Bathycopca*, and *Tecticeps*); palp of 3 articles. Maxillipedal palp of 5 articles. Antennae 1 peduncle of 3 articles; antennae 2 peduncle of 5 articles. Pleon comprising an anterior and posterior part; anterior part of 5 variably fused pleonites (1-4 pleonites indicated dorsally by lateral incisions); posterior part forming vaulted pleotelson. Uropods lateral; exopod free when present; endopod fused with peduncle. Sexual dimorphism often pronounced.

Members of this large family differ from all other marine isopods in several regards. Perhaps the most obvious characteristic observed when handling living specimens is their ability to either roll up into a sphere (conglobate), or fold over on themselves (cephalon to pleotelson). The ability to roll into a sphere is shared with several genera of terrestrial isopods. Unlike most other isopods, the fertilized eggs of most sphaeromatids are withdrawn into invaginations on the ventral surface of the pereon, where the embryos are brooded. Another difference is the presence of a tubular channel on the ventral side of the pleotelson, related to the passage of the respiratory current from the pleonal vault.

Sphaeromatids are common intertidal and shallow-water forms which occur in all of the world's oceans in almost every habitat, including the deep sea and land-locked thermal hot springs. The vast majority of species are marine with only a few species known from fresh water. Terrestrial forms are unknown in this family. Sphaeromatids are rather small isopods, adults ranging in size from about 2.5 to 15 mm.

Many species are excellent swimmers, entering the water column for brief periods (often on a diurnal cycle; e.g. Fincham, 1974). Other species (e.g. *Paraleptosphaeroma* and *Ancinus*) are poor swimmers and probably enter the water column only infrequently, if ever. Feeding strategies, like most aspects of sphaeromatid biology, have not been well studied. Undoubtedly, a number of different strategies are employed in this large family. Some species are known to eat algae, bryozoans, conotrich protozoans, and foraminiferans, while others (e.g. *Ancinus*) ingest sand grains (presumably for the attached bacteria and diatoms). The anterior pereopods of some species (e.g. *Sphaeromaj*) are abundantly supplied with long, plumose setae which act as filter feeding structures (Rotramel, 1975).

Sphaeromatids are typically crevice animals, and are especially common under rocks and in association with other organisms such as algae, encrusting sponges, barnacles (both living and dead), chitons and bryozoans. Other species burrow into wood, soft rock, or mud. Several species are euryhaline, and have been the subject of intensive study in this regard. Little is known about reproduction and growth of sphaeromatids. Holdich (1968a; 1968b; 1969; 1970; 1971) and Holdich and Ratcliffe (1970) have studied species of *Dynamene* in some detail on European shores, while Buss and Iverson (1982) examined several aspects of the biology of *Paraleptosphaeroma glynni* from Panama. Bowman and Kuhne (1974) discussed the mating behavior of the Australian species *Cymodetta gambosa*. Kerambrum and his colleagues have produced a large series of papers treating the ecology of three species of

*Sphaeroma* in French waters (see Kerambrum 1970a; 1970b; 1971; 1972; 1973; 1974; 1975a; 1975b; 1975c and references included therein). Carlton and Iverson (1981) discussed the natural history and biogeography of *Sphaeroma walkeri* Stebbing. Leboeuf and Howe (1981) discussed the role of color change in the ecology of the east American species *Sphaeroma quadridentatum* Say.

The family Sphaeromatidae presently comprises about 75 genera in 5 subfamilies: Ancininae, Cassidininae, Dynameninae, Sphaeromatinae, and Tectiptinae (see Iverson, 1982 for a review of the family classification and a list of genera in each subfamily). We have collected 6 species of sphaeromatids from Pacific Costa Rica, and include two others in the key and descriptions that are expected to occur here.

#### Key to the Species of Pacific Costa Rican Sphaeromatidae

1. Uropods uniramous; pereopod I subchelate; pereopod II subchelate in male only; cephalon medially fused to first pereonite (Figs. 7-8) . . . . . 7
1. Uropods biramous; pereopods I-II ambulatory, never subchelate; cephalon not medially fused to first pereonite . . . . . 2
  2. Body strongly depressed; pleopods 4-5 without fleshy transverse folds . . . . . 3
  2. Body not depressed; transverse fleshy folds on at least the exopod of pleopods 4-5 . . . . . 4
3. Two proximal articles of first antennae expanded anteriorly into flat plates (Fig. 10) . . . . . *Paraleptosphaeroma glynii*
3. First antennae normal, proximal articles not expanded into flat plates (Fig. 10) . . . . . *Striella balani*
  4. Pleopods 4-5 with fleshy transverse folds on both rami (exopod & endopod); pleotelson apex entire or with a notch or foramen . . . . . 5
  4. Pleopods 4-5 with transverse fleshy folds only on endopods; pleotelson apex usually entire, without a notch or foramen . . . . . 8
5. Pleotelson evenly convex, posterior margin without foramen or notch (Fig. 9) . . . . . *Dynamenella josephi* (♀)
5. Pleotelson convex anteriorly, posteriorly somewhat flattened; males with posterior foramen . . . . . 6
  6. Pleonal suture line composed of single, short incision; male with transverse pleotelson foramen; body not heavily setose (Fig. 9) . . . . . *Dynamenella josephi* (♂)
  6. Pleonal suture line composed of 2 incisions forming a "Y"; male with circular pleotelson foramen; body very setose (Fig. 9) . . . . . *Dynamenella setosa*
7. Pleotelson with transverse depression near posterior apex; lateral margin of rostrum straight, not anteriorly expanded; male pereopod II dactyl closing midway on propus; small, adults less than 4.5 mm in length (Figs. 7, 8) . . . . . *Ancinus panamensis*
7. Pleotelson without transverse depression near posterior apex; rostrum anteriorly expanded; male pereopod II dactyl reaching proximal end of propus; larger, adults to 7.0 mm in length (Fig. 7) . . . . . *Ancinus* sp.
  8. Dorsal surface of pleotelson smooth; outer margin of uropodal exopod evenly crenulate; uropodal rami do not extend beyond apex of pleotelson . . . . . *Exosphaeroma* sp.
  8. Dorsal surface of pleotelson with prominent tubercles; outer margin of uropodal exopod with 2-3 large teeth; uropodal rami extend somewhat beyond apex of pleotelson . . . . . *Sphaeroma peruvianum*

#### *Ancinus* Milne Edwards, 1840

**Diagnosis:** Body markedly depressed. Cephalon medially fused to first pereonite. Mandibles lacking a molar process; inner lobe of first maxilla degenerate; second maxilla with 2 lobes. First pereopod subchelate; male second pereopod prehensile; female second pereopods ambulatory. Coxal plates distinct in lateral view, not markedly expanded laterally

in dorsal view. Pleon with an oblique suture line (incision) near lateral margins. Pleopod 1 uniramous, lacking endopod. Pleopod 2 operculate. Pleopod 3 exopod uniarticulate. Pleopods 4 and 5 lack transverse fleshy folds. Uropods uniramous, lacking exopod; endopod long, slender and styliform.

**Remarks:** This genus is restricted in distribution to temperate and tropical waters

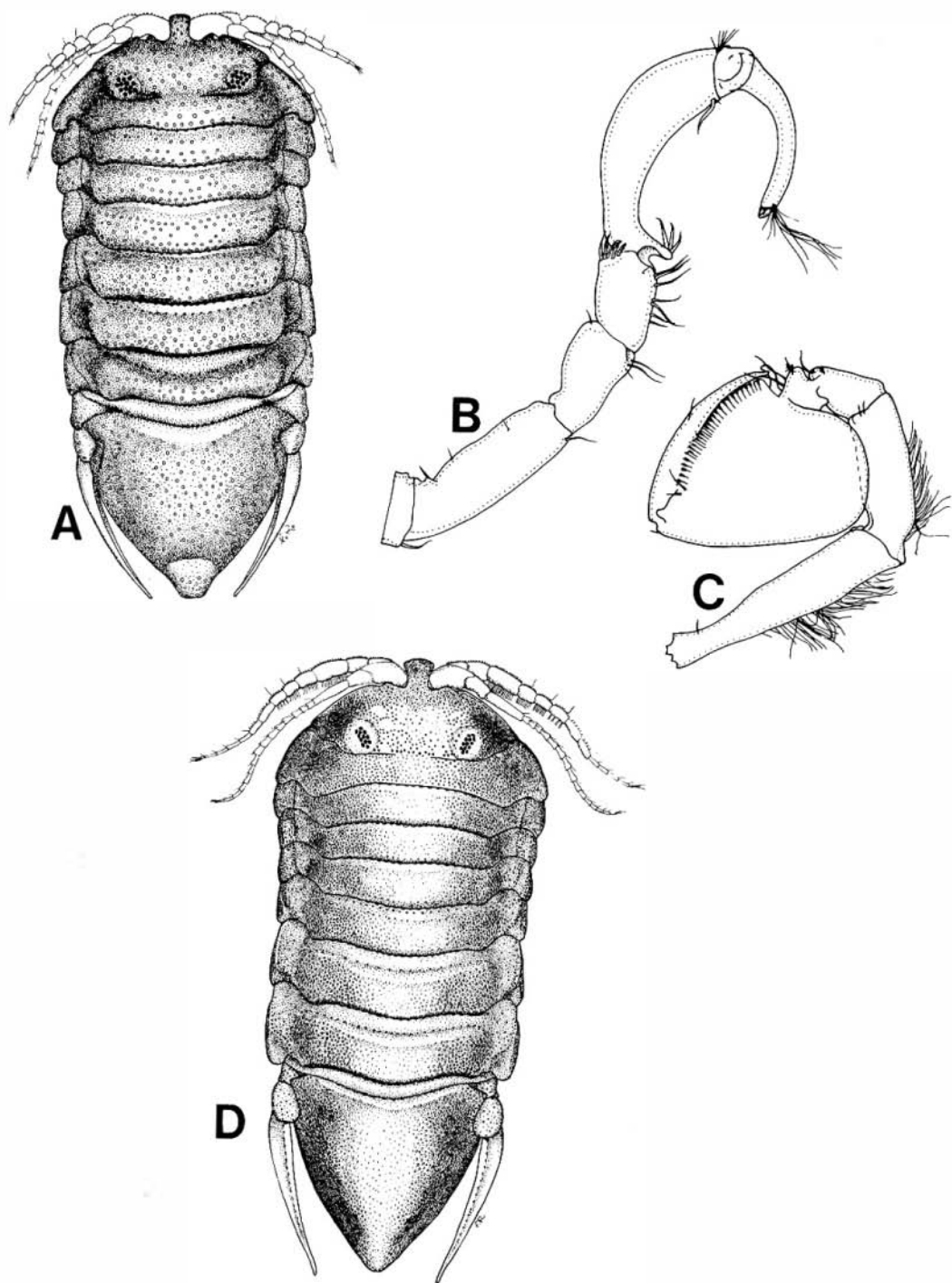


Figura 7

*Ancinus panamensis*: A, dorsal view; B, pereopod I; C, pereopod II. *Ancinus sp.*: D, dorsal view. (a-c from Glynn and Glynn, 1974).



of the New World. Due to the subtle differences between some species, the systematics of this genus is confused. Important references include: Loyola e Silva (1971), Glynn and Glynn (1974); a key to the known species is given in the latter paper. The genus is currently in the process of being revised by E.W. Iverson, including the description of several new species.

*Ancinus panamensis* Glynn and Glynn, 1974  
Figs. 7, 8

**Diagnosis:** Dorsal surface smooth, lacking obvious sculpturing, lateral margins of body concave, narrowest at pereonite IV. Rostrum truncate anteriorly; dorsal surface slightly concave. Dactyls of male second pereopod short, closing near middle of propus. Pleopods 4-5 lack transverse fleshy folds. Pleopod 5 exopod with 3 squamiferous protuberances. Pleotelson length less than width (measured at posterior edge of uropod peduncle); dorsum arched anteriorly; posteriorly with a distinct transverse depression three-quarters of the distance to apex (best viewed laterally). Dorsal color patterns highly polymorphic.

**Remarks:** This species can be easily recognized by its small size, distinctive flattened body, and styliform uropods. Adult males measure less than 4.5 mm; females less than 3.0 mm. In juveniles, the uropods fall short of the pleotelson apex; in adult males they are extended slightly beyond the pleotelson apex.

Glynn and Glynn (1974) reported their specimens from sandy beaches of Pacific Panamá and Colombia. We have collected *A. panamensis* from only one locality, Parque Nacional Santa Rosa, where a juvenile specimen was taken from intertidal rocks embedded in sand and mud adjacent to a stretch of sandy beach.

**Distribution:** *Ancinus panamensis* is now known to range at least from Pacific Costa Rica south to Colombia.

*Ancinus* sp.  
Fig. 7

**Diagnosis:** Dorsal surface smooth, lacking obvious sculpturing. Lateral margins of body concave, narrowest at pereonite V. Rostrum anteriorly inflated; dorsally concave. Dactyl of

male second pereopod long, closing on proximal end of propus. Pleopod 5 exopod with 5 squamiferous protuberances, proximal protuberance minute; endopod with single subapical squamiferous patch. Pleotelson triangular; 0.75 times longer than wide; posteriorly without a distinct transverse depression three-quarters of the distance to apex (best viewed laterally).

**Remarks:** Adult specimens of this species are easily distinguished from *A. panamensis* by their larger size, features of the rostrum, and lack of a transverse depression on the pleotelson. Adults are usually greater than 5 mm in length. This and other New World *Ancinus* will be fully described and figured in a forthcoming paper by E. Iverson.

**Distribution:** Although we have not collected this species ourselves, we have examined specimens from Bahía Salinas, in the northernmost region of the Guanacaste Province of Costa Rica, and from Bahía Chamela, Jalisco, México.

Genus *Dynamenella* Hansen, 1905

**Diagnosis:** Cephalon not medially fused with pereonite I. Molar process of mandible present. Pereopods I and II ambulatory, never prehensile. Pleopod 2 normal, not operculate. Pleopod 4 with both rami lacking transverse pleats or folds; exopod unjointed. Pleopod 5 with both rami lacking transverse pleats or folds and without setae; exopod with low subapical squamiferous protuberances. Uropods biramous. Antennular peduncle article 1 not extended anteriorly as a plate. Both sexes with pereon and pleon lacking dorsal processes, and with both rami of uropod lamellar, the endopod being greater than half the length of the exopod. Pereopod 1 markedly more robust than other pereopods. All pereopods with simple, not bifid, accessory unguis. Exopod of pleopod 3 with or without articulation. Sexual dimorphism obvious. Appendix masculina of males arise from near base of endopod of pleopod 2 and extend to or beyond apex of endopod. Posterior region of Pleotelson in males with dorsally directed foramen connected to apex by narrow slit. Females with apex of pleotelson various; bearing slight notch, simple groove, or foramen

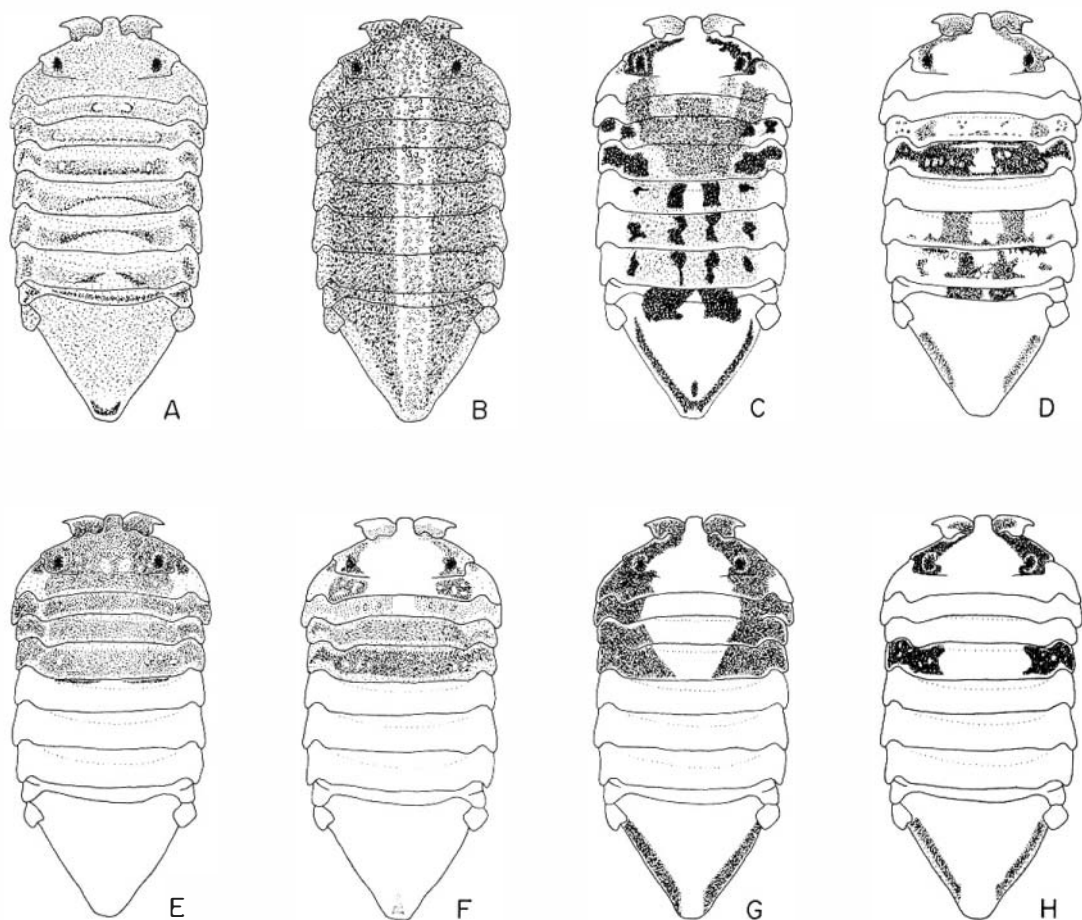


Figura 8

*Ancinus panamensis*, color polymorphism. (from Glynn and Glynn, 1974).

connected to apex by narrow slit. Brood pouch of females lacking oostegites, formed from two opposing ventral pockets covering entire ventral pereon and opening in midline between fourth pereopods.

**Remarks:** Species of *Dynamenella* vary in the presence or absence of an articulation on the exopod of pleopod 3, and in the shape of the pleotelsonic foramen. According to Harrison and Holdich (1982), excepting *D. platyura*, the Old World species lack an exopodal articulation, while the New World species possess one. The genus is primarily tropical/subtropical in distribution. Like *Exosphaeroma*, *Dynamenella* has long been a “catch-all” taxon—a convenient place to put a number of closely related, but difficult to separate species. This

genus has recently been revised (Harrison and Holdich, 1982).

*Dynamenella josephi* Glynn, 1968

Fig. 9

**Diagnosis:** Penes long, 1-1/2 times length of pleopod 2; tenuiform; fused basally over 1/8 of length. Pleonal suture line with a single, forwardly-directed incision. Appendix masculinum of male long, nearly twice length of pleopodal endopod. Exopod of pleopod 4 with cleft on upper, lateral margin; endopod with apical setae. Exopod of pleopod 5 with 3 prominent, squamiferous probuberances. Sexes dimorphic in pleotelson; mature male with slit and transverse foramen on posterior border of pleotelson; female with smooth, ovate border

or at most with faintly perceptible indentation. Anterior border of pleotelson with 2 small pairs of tuberculate ridges; posterior half of pleotelson with single pair of elongate, tuberculate ridges (lateral to midline), these ridges smooth and rounded in females but irregular and ragged in males. Tuberculate carina on midline of pleotelson, extending forward about half its length.

**Remarks:** Glynn (1968) described *D. josephi* from specimens collected in the high intertidal region of Naos, Tórtola, and Perico Islands, Panama. The isopods were found living in the empty tests of, and crevices between, the barnacles *Tetraclita squamosa panamensis* and *Chthamalus* sp. Until now, this species had not been reported since its original description, although it is apparently fairly common at the type locality. We have collected *D. josephi* from the rocky intertidal zone of Playas del Coco, Playa Tárcoles and Parque Nacional Santa Rosa, where it lives on barnacle-covered rocks in sand and mud substrates. Its small size (2.5-3.5 mm), and its secretive habits suggest that it is easily overlooked. Sexual dimorphism is exceptionally pronounced in this species. Females have a very inflated and rounded pleotelson, which might suggest that they belong to another species, or perhaps even a new genus. However, characteristic dorsal sculpturing on the pleotelson and pleonal suture lines serve to unite males and females of this species. As noted by Glynn (1968), pleotelson sculpturing is rather low and broadly rounded, making it difficult to see.

**Distribution:** This species is known from Naos, Tórtola, and Perico Islands in the Gulf of Panama, as well as coastal northern and central Pacific Costa Rica.

*Dynamenella setosa* Glynn, 1968

Fig. 9

**Diagnosis:** Body covered with dense growth of long setae. Pleonal suture leading forward for about half its length then curving medially; a second, shorter incisor joins main cleft at point of flexure. Penes long (exceeding length of pleopod 2); tenuiform; fused at base. Appendix masculinum long, nearly twice the length of endopod, tapering to narrowly rounded apex. Exopod of pleopod 5 with 3

squamiferous protuberances; one located laterally and 2 apically. Posterior border of pleotelson denticulate, with a narrow slit connecting to a circular foramen. Central portion of pleotelson inflated. Uropods large, serrate and extended well beyond posterior border of pleotelson.

**Remarks:** Glynn (1968) described *D. setosa* from specimens collected in the high intertidal region of Naos and Tórtola Islands, Panama. The isopod was associated with the barnacle *Tetraclita squamosa panamensis*. *Dynamenella setosa* has not been reported since its original description and we have not yet recovered it from Costa Rican shores, although its occurrence here is anticipated.

**Distribution:** Known only from Naos and Tórtola Islands, Gulf of Panama.

*Sphaeroma* Latreille, 1802

**Diagnosis:** Maxillipedal palp with last 3 articles poorly developed or rudimentary. Pereopods I-III with long, plumose setae on articles 3-4. Posterior margin of pleotelson without a notch or foramen; pleopod 3 outer ramus unsegmented. Mature males with well developed appendix masculina on pleopods 2. Sexes similar.

**Remarks:** Estevez and Simon (1974) claimed that of the 130 described species assigned to this genus, less than 35 were valid. Of these, at least 8 are known or suspected borers, although only 3 have been reported from mangroves: *S. terebrans* Bate, 1866; *S. destructor* Richardson, 1897, and *S. peruvianum* Richardson, 1910. Most authors have considered the former two to be synonymous (e.g. Pillai, 1955), and use the senior synonym *S. terebrans*. Richardson (1905) did not agree with this synonymy.

*Sphaeroma peruvianum* Richardson, 1910

**Diagnosis:** Body covered with small granules, becoming larger posteriorward and being mixed with prominent tubercles on the last pereonite and pleon. Front of cephalon produced into a small point. Flagellum of first antennae comprising about 11 articles, extending to

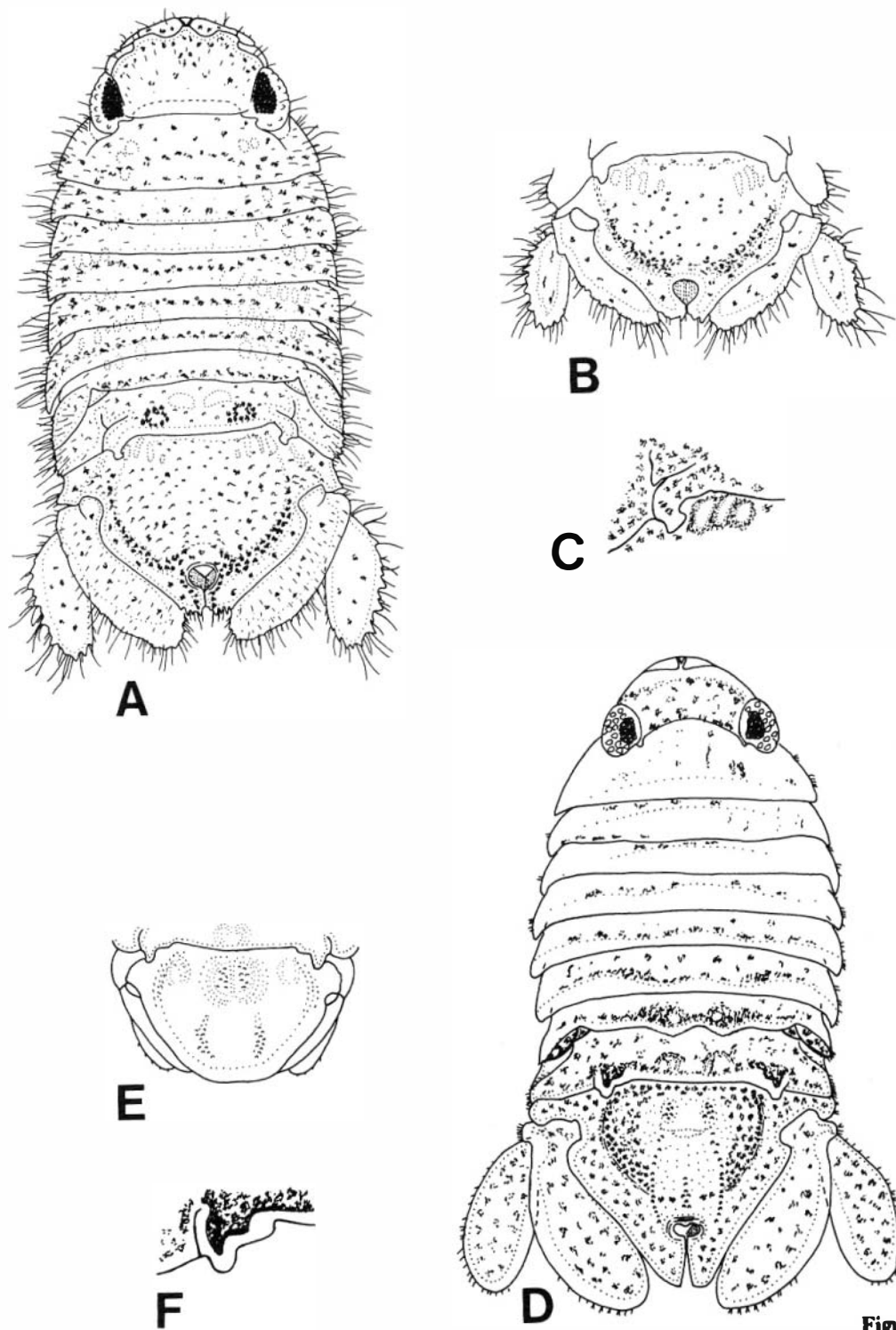


Figura 9

*Dynamenella setosa*: A, dorsal view, male; B, pleotelson, female; C, enlarged view of pleonal suture. *Dynamenella josephi*: D, dorsal view, male; E, pleotelson, female; F, enlarged view of pleonal suture. (from Glynn, 1968).

middle of pereonite I; flagellum of second antennae comprising about 14 articles, extending to posterior margin of pereonite II. Mandible with 3-pointed incisor process. Pereonites with transverse tuberculate ridge; pereonite VII with 4 large tubercles in a transverse line. Pleon of 2 pieces; anterior "segment" with 6 large tubercles, 3 each forming triangles either side of the midline; pleotelson with 6 large tubercles, 4 in an anterior row and 2 below those; posterior margin broadly rounded, slightly turned upwards along edge; with a thick tuft of long setae near insertion of uropods. Uropodal rami subequal in length, extending just beyond apex of pleotelson; endopod pointed and smooth-edged; exopod with 2-3 teeth on outer margin.

**Remarks:** *Sphaeroma penuvianum* was described from a collection given to Richardson by R.E. Coker, taken from the roots of red mangroves at Matapalo (near Capón), Peru. It was mentioned by Estevez (1978) and was apparently the species discussed by Simberloff, *et al.* (1978) (as *Sphaeroma* sp.). Like *S. terebrans* and *S. destructor*, *S. penuvianum* is an obligate commensal with *Rhizophora mangle*, the red mangrove. Nothing is known concerning the ecology of this species, although at the time of this writing an investigation of its biology had been initiated by Dr. D. Perry (working in the Gulf of Nicoya). The other two species of mangrove-boring *Sphaeroma* have enjoyed some studies (see Estevez, 1978 and Estevez and Simon, 1974, for references). There is some debate as to whether these isopods damage the mangroves by weakening the root structure (Rehm and Humm, 1973), or actually are beneficial to the mangroves by stimulating the production of new prop roots (Simberloff, *et al.*, 1978). Evidence to date indicates that mangrove-boring sphaeromatids do not actually ingest the wood they destroy, but rather sit in their burrow filtering particulate matter out of a feeding respiratory current with their setose pereopods and pleopods.

Although we have collected *S. penuvianum* only at Punta Chomes, in the Gulf of Nicoya, it probably ranges throughout Pacific Costa Rica and south as far as *Rhizophora* can be found (Peru).

*Exosphaeroma* Stebbing, 1900

**Diagnosis:** Maxillipedal palp articles 2-4 medially produced into lobes. Pereopods

without long plumose setae. Pereonites VI-VII lacking a large medial process. Brood plates small, not reaching midline. Second pleonal "segment" composed of 3 medially fused somites, but only the most anterior somite reaches lateral margin. Pleonal suture line incisions widely separated at base of pleotelson. Penes not basally fused; generally short; not sharply pointed. Appendix masculinum of male second pleopod long and slender. Pleopod 3 exopod biarticulate. Pleopods 4-5 exopods only with transverse fleshy folds. Apex of pleotelson without terminal notch. Uropodal exopod smooth or crenulate, without large dentitions or teeth.

**Remarks:** The genus *Exosphaeroma* is a large, possibly polyphyletic taxon which has in the past been used as a convenient collecting place for a number of related species. Further study will undoubtedly reveal several new genera within *Exosphaeroma*. Sexual dimorphism is often very pronounced (e.g. *E. amplicauda* from California). Only a single species is known from Pacific Central American shores.

*Exosphaeroma* sp.

Fig. 10 b-d

*Exosphaeroma diminutum* (Pacific records only), Dexter, 1972: 425; 1974: 54; 1979: 547

**Diagnosis:** Dorsal surface of body smooth, without sculpturing. Clypeus elongate; anterior portion longer than posterior arms; roughly diamond shaped; apex truncate. Maxillipedal palp articles 2-3 without an elongate seta at distal lateral margin; articles 3-4 with a minute seta at distal lateral margin. Inner margin of pereopods I to VII weakly armored, with only a few, stout, bifid setae. Pereopod VII much longer than pereopod I, propodus longer than either carpus or merus, which are subequal in length. Coxal plate suture lines not visible in adult males; present on pereonites II - VII of females and juvenile males. Penes about 3 times longer than broad; apex rounded; widely separated at base. Appendix masculinum about 1/3 longer than endopod; tapering to a narrowly rounded tip; inner margin scalloped along midlength. Pleotelson moderately produced posteriorly, apex broadly rounded; lateral margin straight; dorsal 2/3 raised into a dome, posterior 1/3 somewhat flattened (in

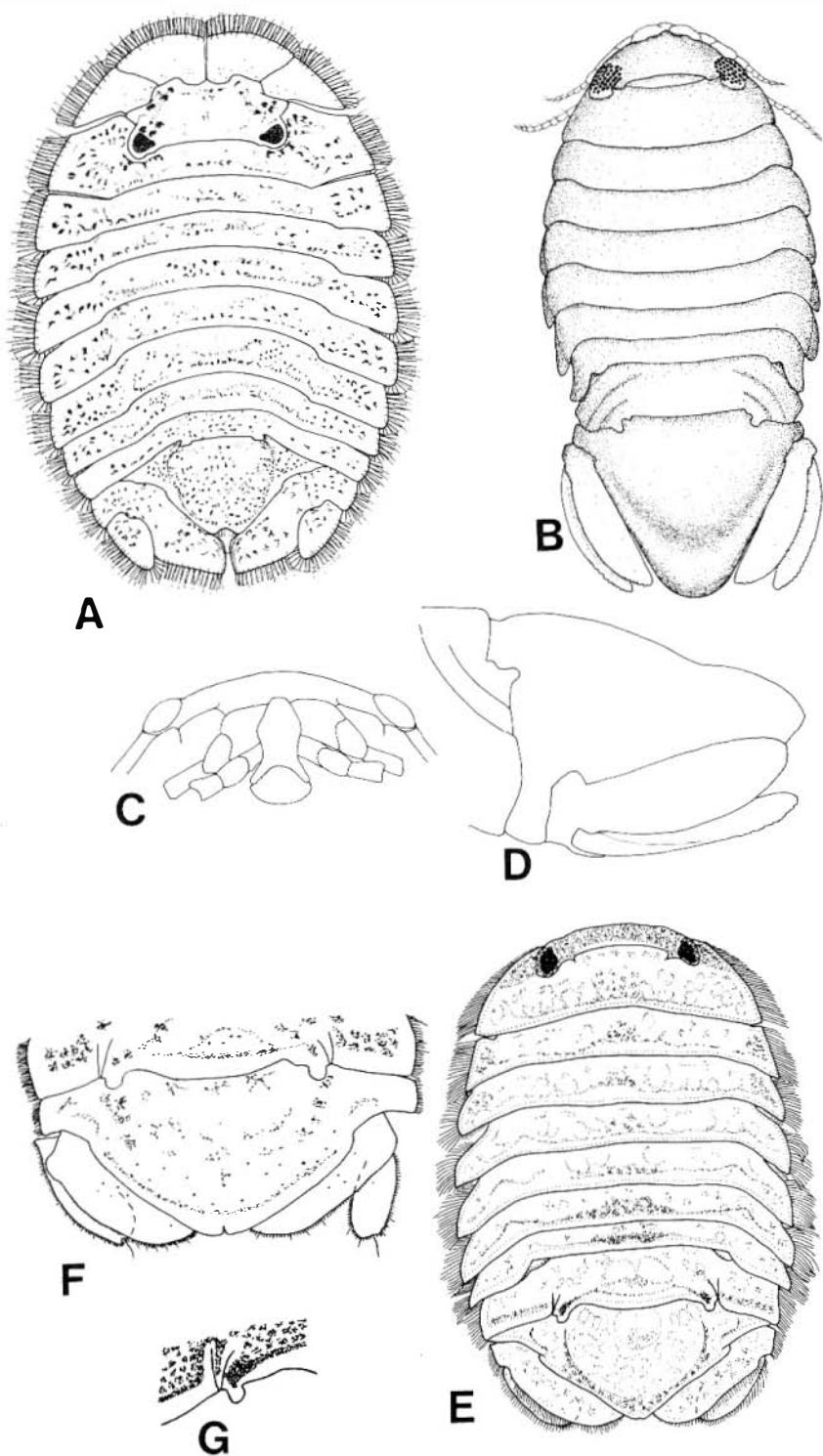


Figura 10

A, *Paraleptosphaeroma glynni*. B, *Exosphaeroma* sp., dorsal view. C, *Exosphaeroma* sp., ventral view of frontal lamina and clypeus. D, *Exosphaeroma* sp., lateral view of pleotelson and uropod. E, *Striella balani*, dorsal view, male. F, *S. balani*, pleotelson, female. G, *S. balani*, enlarged view of pleonal suture. (A from Buss and Iverson, 1981; E-G from Glynn, 1968).

lateral view, a distinct obtuse angle is formed). Uropods similar in both sexes; exopod crenulate.

**Remarks:** *Exosphaeroma* sp. apparently ranges at least from the northern Gulf of California to the Bay of Panama. It was a common species on the sandy beaches of Costa Rica, Panama and Colombia studied by Dexter (see synonymy), wherein it was reported as *Exosphaeroma diminutum* Menzies and Frankenberg, 1966. The latter species is a common inhabitant of sandy beaches throughout the Caribbean and southeast coasts of the U.S. Whether the Pacific and Atlantic forms are distinct species or simply polymorphic variants of *E. diminutum* has not yet been established, however, distinct differences are present to distinguish the two from one another. *Exosphaeroma* sp. (Pacific form) has a distinctly shaped clypeus and an anteriorly inflated pleon. Further, *E. diminutum* tends to roll into a spherelike ball when it conglobates, whereas *E. sp.* tends to simply fold in the midline, with the pleotelson apex failing to reach the mouth field.

In the northern Gulf of California *Exosphaeroma* sp. is commonly collected under shell fragments on sandy stretches of tidal flats. In Costa Rica, at Parque Nacional Santa Rosa, we collected it in formalin washes of rocks embedded in sand, adjacent to a long sandy stretch near the opening of a mangrove lagoon. Dexter's (1974) records are also from sandy beaches, ranging considerably in topography and including calcareous sands, quartz/feldspar sands, and volcanic sands (median grain sizes ranged from 137  $\mu\text{m}$  to 283  $\mu\text{m}$ ). See Dexter (1974) for additional data on abundances and distribution.

**Distribution:** Known records are from the northern Gulf of California, Costa Rica, Panamá and Colombia. Dexter (1974) reported it from 7 localities in Pacific Costa Rica: Playita Blanca Coco; Tamarindo; Sámara; Boca de Barranca; Jacó; Playa Cocal, Quepos; and Playa Espadilla, Quepos. We have collected it, in addition, at Parque Nacional Santa Rosa (Guanacaste).

*Paraleptosphaeroma* Buss and Iverson, 1981

**Diagnosis:** Body oval, strongly depressed, fringed with translucent *membrana cingula*.

Two proximal articles of first antennae expanded anteriorly into flat plates which completely enclose anteriormargin of cephalon. Rostrum short; clypeus not visible dorsally. Inner margin of maxillipedal palp articles 2-4 not markedly produced into lobes. Mandible with strongly developed molar process and elongate, toothed incisor. Coxal plates broadly expanded laterally. Pleon dorsally fused into a single piece. Penes considerably longer than wide, fused basally. Pleopod I without an endopod. Endopod reduced on pleopod 2; appendix masculinum attached near apex. Pleopods 4 and 5 lacking transverse folds. Pleotelson completely enclosed by expanded endopods of uropods; exopod short, fitting into lateral margin of endopod. Protogynic hermaphrodites; sexual dimorphism not evident in dorsal view, excepting size.

**Remarks:** *Paraleptosphaeroma* is a monotypic genus which shows remarkable similarity in body morphology to the Japanese genus *Leptosphaeroma* Hilgendorf, 1885, and to the Australian genus *Amphoridella* Baker, 1908. The genus *Amphoridella* differs from the other two genera by having transverse folds on both the exopod and endopod of pleopods 4 and 5, plus having pereonite 1 modified into a gnathopod. In *Leptosphaeroma* the anterior "segment" of the pleon is composed of 3 medially fused pleonites, each reaching the lateral body margin. In *Paraleptosphaeroma*, the anterior "segment" of the pleon lacks all traces of any partially fused somites. The unique arrangement of the appendix masculinum on the endopod of pleopod 2 serves to separate the one species assigned to this genus from all other sphaeromatids.

The *membrana cingula* present around the lateral body margin of this species is composed of an upper row of widely separated setae, and a lower row of evenly spaced setae-like structures embedded in a membranous sheet. Like other modifications for a limpet-like body plan, the *membrana cingula* probably assists the animal from being washed off its substratum by wave action.

*Paraleptosphaeroma glynni* Buss and Iverson, 1981

Fig. 10

**Diagnosis:** Body without obvious dorsal sculpturing. Antennae 1 short, reaching middle

of pereonite 1; antennae 2 long, extended beyond posterior margin of pereonite 1. Molar process of mandible strongly developed, with numerous cusps. Penes long, tapering to narrowly rounded apices. Pleopods 1-2 exopods at least twice as long as wide. Appendix masculinum of male pleopod 2 inserting near apex of endopods; apex of appendix masculinum broadly rounded and curved towards lateral margin of endopod. Pleopod 4 without transverse folds; outer margin of exopod inflated; exopod with a single, short apical, plumose seta. Pleopod 5 without transverse folds or plumose marginal setae; outer margin of rami inflated; endopod with 2 squamiferous patches. Pleotelson wider than long; anterodorsal surface with a slight longitudinal swelling (best seen in lateral view) along midline; posterodorsal surface with 2, submedian, low, longitudinal swellings. Pleotelson apex somewhat upturned and ventrally grooved. Uropodal endopod long; inner margin somewhat thickened and bifurcated by a longitudinal groove into which the lateral margin of the pleotelson fits. Anterior to insertion of exopod, lateral margin of pleotelson broad.

**Remarks:** One of the more interesting aspects of the biology of this species is the occurrence of sequential hermaphroditism. Although present in several other families of marine isopods, hermaphroditism in the Sphaeromatidae has been reported only from this species (Buss and Iverson, 1981). *Paraleptosphaeroma glynni* is a protogynic hermaphrodite, individuals first being females and later transforming into males. Copulatory behavior is equally unique in this species. Unlike any other isopod known to us, except perhaps some Cymothoidae, copulation in this species takes place ventor to ventor.

Interspecific interactions have been studied in detail by Buss and Iverson (1981). In Panamá, this species lives on cobbles encrusted with the bryozoans *Antropora tinctoria* and *Onychocella alula*, plus the coralline alga *Neogoniolithum rugulosum*. Competition for space among these various encrusting organisms is regulated by the presence or absence of the isopod. Like *Ancinus panamensis*, *Paraleptosphaeroma* seems to avoid swimming. In fact, it has been shown experimentally that it will starve itself rather than swim a few centimeters to a new cobble

stone with an abundant food supply (Buss and Iverson, 1981). We have collected this isopod only at Playa Tárcoles, from formalin washes of intertidal rocks.

**Distribution:** Currently known from Costa Rica to the Pacific entrance of the Panamá Canal.

*Striella* Glynn, 1968

**Diagnosis:** Body oval, strongly depressed and fringed with a dense setose growth. Antennae 1 with proximal articles not expanded anteriorly into flat plates or readily visible in dorsal view. Maxillipedal palp articles 2-4 not produced into lobes on inner margin. Mandible with strongly developed molar process and elongate, toothed incisor. Pereopods I-VII with natatory setae. Penes long, tenuiform and fused only basally. Pleopod 1 endopod elongate, about 3 times longer than wide. Appendix masculinum on pleopod 2 proximally inflated, narrowly rounded distally, and extending slightly beyond apex of endopod. All pleopods unjointed; pleopods 4-5 without transverse fleshy folds. Pleotelson terminating posteriorly in a blunt point; minute incision faintly visible terminally.

**Remarks:** Although resembling *Paraleptosphaeroma* in possession of a depressed body and lack of folding on the fourth and fifth pleopods, this genus lacks the anteriorly enlarged proximal articles of the first antennae, which quickly distinguishes *Paraleptosphaeroma*. *Striella* shares many features with other genera, but not to the degree which would allow assignment to any specific one (Glynn, 1968).

*Striella balani* Glynn, 1968

Fig. 10

**Diagnosis:** Pleotelson essentially smooth, with slightly raised, hemispherical area at midline near anterior border. Pleonal suture lines short, V-shaped. Lateral edge of body fringed with setae (best developed in larger individuals). Maxillipedal palp articles 2-4 not markedly expanded into lobes. Appendix masculinum of pleopod 2 inflated at base, apex narrowly rounded and extended slightly



beyond tip of endopod; with minute spines in couplets along medial border. Endopod of pleopod 4 with a single apical seta. Pleopod 5 with 3 squamiferous protuberances; upper pair of protuberances capped with minute, horny spines.

**Remarks:** Like most tropical sphaeromatids, *Striella* is a small species, adult males reaching only about 3 mm in length, while females are a little smaller. Glynn (1968) reported this species from the high intertidal zone of Naos Island, Panama, where it was associated with barnacles. It has not been reported since.

**Distribution:** This isopod is known only from Naos Island, Panama. Its presence in Pacific Costa Rican waters is anticipated.

#### Family Cirolanidae

Body sleek and symmetrical, with distinct coxal plates on pereonites II-VII. Pereopods ambulatory, although the first 3 pairs often tend towards a prehensile form; dactyls of I-III not manifestly larger than those of IV-VII, and never as large and recurved as in the Cymothoidae or Aegidae. Pleon usually with 5 distinct pleonites, plus the pleotelson. Uropods with both rami well developed, forming distinct tail fan with pleotelson; pleotelson and uropods with marginal setae and/or spines. Peduncle of antenna 2 of 4-5 distinct articles. Mandible usually with lacinia mobilis and well developed molar process, the latter being an expanded and

flattened saw-toothed structure; palp of 3 articles. Maxilliped with palp comprised of 4-5 setose articles; never with hooked or recurved spines.

The majority of the cirolanids are free living predators or meat eating scavengers. The mandibles are well adapted for biting and chewing, and many can inflict a reasonably painful bite on swimmers. One species, (*Natatolana borealis* Lilljeborg) occasionally infests the gills and hearts of various species of sharks and rays in the Atlantic, apparently boring right through the host's skin. Some burrow in sand or live under rocks, others spend much of their lives in algal and animal turfs, mussel beds, or kelp holdfasts. Most are graceful swimmers, entering the water column at various times. They are most common in shallow-water habitats, where they are often abundant, and are easily captured by hand, formalin washes of algal turfs, or trapping (e.g. with dead fish as bait). Many are known to have endogenous activity rhythms (see Hastings, 1981 for an introduction to that literature). A number of species are troglobitic (at least 20 in North America), while others occur in the deep sea. In both of these latter cases, the animals are usually without pigmentation and are blind. The family contains about 300 valid species worldwide. Of the 44 currently recognized genera of Cirolanidae, 5 are known from the tropical Eastern Pacific at this time: *Cirolana*, *Excirrolana*, *Eurydice*, *Natatolana*, and *Metacirolana*.

#### Key to the Species of Pacific Costa Rican Cirolanidae

1. Cephalon with spatulate rostral process extending forward to separate bases of antennae; lateral margins of pleonite 5 not overlapped and hidden by pleonite 4; dorsum of pleotelson usually with a pair of mediolateral depressions (Fig. 11a) ..... *Excirrolana braziliensis*
- Cephalon without a spatulate rostral process; lateral margins of pleonite 5 almost always overlapped and hidden by pleonite 4; pleotelson not as above ..... 2
2. Basal articles of antennae 1 slender and very close together, exiting from head straight forward, the second articles then forming a sharp right angle to extend the antennae laterally; peduncle of antennae 2 of 4 articles; peduncle of uropods with inner angles not markedly produced and acute (Fig. 11b) ..... *Eurydice caudata*
- Basal articles of antennae 1 normal, not as above; peduncle of antennae 2 of 5 articles; peduncle of uropods with inner angles markedly produced ..... 3
3. Without eyes, or eyes unpigmented; frontal margin of cephalon evenly convex; frontal lamina very narrow throughout, apex not dilated; pleotelson margin with 8-12 spines; uropods without apical notch; rarely taken in depth less than 50 meters (Fig. 11e) ..... *Natatolana californiensis*
- Never blind; frontal margin of cephalon with acute frontal process; frontal lamina broad, at least for some portion; pleotelson margin with 2 or 8 spines; uropods with apical notch; rarely taken in depths greater than 50 meters ..... 4

4. Lateral margins of cephalon form acute angles at level of eyes; antenna 2 with 8-12 flagellar articles; frontal lamina narrow posteriorly, expanded anteriorly into rounded plate that meets with frontal process of cephalon; pleotelson margin with 2 spines (Fig. 11d) . . . . . *Metacirolana costaricensis* n. sp.
- Lateral margins of cephalon not as above; antennae 2 with 22-29 flagellar articles; frontal lamina not as above; pleotelson margin with 8 spines (Fig. 11c) . . . . . *Cirolana parva*

### Genus *Exciorolana* Richardson, 1912

**Diagnosis:** Cephalon with well-developed rostral process, usually expanded distally into a spatulate shape and produced to separate bases of first antennae. Frontal lamina robust. Maxillipedal palp of 5 articles. Pleon of 5 free segments, plus pleotelson; pleonite 5 not markedly reduced, lateral margins not covered by pleonite. 4. Pleopods 1 and 2 similar to each other; long and slender. Uropods inserted laterally; inner angle of peduncle strongly produced; exopod and endopod usually with marginal spines. Dorsum of pleotelson usually with a pair of depressions, one on either side of midline.

**Remarks:** Members of this genus appear to be ovoviviparous, the large yolk-filled eggs being deposited in the enlarged paired oviducts, which function as uteri (in the female). Here the eggs remain throughout gestation. The oostegites are much reduced and form a genital operculum rather than a brood pouch. Klapow (1970) theorized that this alteration of brooding strategies is an adaptation to the sandy beach habitat in which members of this genus are almost invariably found. Internal retention of the developing embryos is said to provide protection against the physical stresses of the environment, particularly scouring by the constantly moving sand grains. The appearance of an *Exciorolana* zone appears to be a common feature of wave-washed sandy beaches in the tropics, subtropics, and warm-temperate regions of the world (Dahl, 1953; Gauld and Buchanan, 1956; Brusca and Brusca, 1978; Brusca 1980). One species that appears to be an exception to this is *E. kumari* Bowman, 1971, a tubicolous species that burrows in the mangrove swamps of Malaysia. *Exciorolana kumari* is also the only species of the genus that exhibits a marked sexual dimorphism and lacks marginal spines on the uropods.

Species of *Exciorolana* typically live buried in the sand during low tide, and emerge during the

high tide periods to swim about and feed on both live and dead fishes and invertebrates. They will also emerge at low tide when freshly killed animal matter is available. They may thus be considered micropredators and carrion scavengers. A few recently discovered species live in mangrove habitats, perhaps inhabiting insect burrows in mangrove roots (Bowman, 1971; 1977; Jones and Icely, 1981). The correct generic placement of these mangrove dwelling species needs further study. Species of *Exciorolana* rarely live in depths much below O-tide level, and are easily collected by sifting the sand during low tide periods, or by use of a night-light and dip net during high tides. For further references see: Dana (1853), Hansen, (1890), Ives (1891), Richardson (1905; 1912), Thielmann (1910), Hatch (1947), Fee (1926), Lemos de Castro (1969), Glynn *et al.* (1975), Dexter (1977), and Bruce and Jones (1981), Klapow (1972a; 1972b).

### *Exciorolana braziliensis* Richardson, 1912

Fig. 11a

For synonymy see Glynn *et al.*, 1975.

**Diagnosis:** Small, to about 7.5 mm in length; most individuals 2-5 mm. Dorsum with numerous, distinct, punctate to dendritic chromatophores. Antennae long, extended at least to pereonite IV. Articles of maxillipedal palp with long setae; endite with 3-6 large, plumose setae. Pleopods 1-2 endopods with plumose marginal setae; 3-5 endopods without plumose marginal setae. Pleotelson with 10-30 plumose marginal setae, but no marginal spines; with a distinct, double-crested depression (see generic diagnosis). Uropodal exopod much longer than endopod.

**Remarks:** Glynn *et al.* (1975) stated: "We have found the antennae of Pacific individuals to vary as follows: Ant<sup>1</sup> is shorter (with 6-12 flagellar articles) than Ant<sup>2</sup> (10-12 articles) up to a body length of 3-4 mm; between 3-5 mm

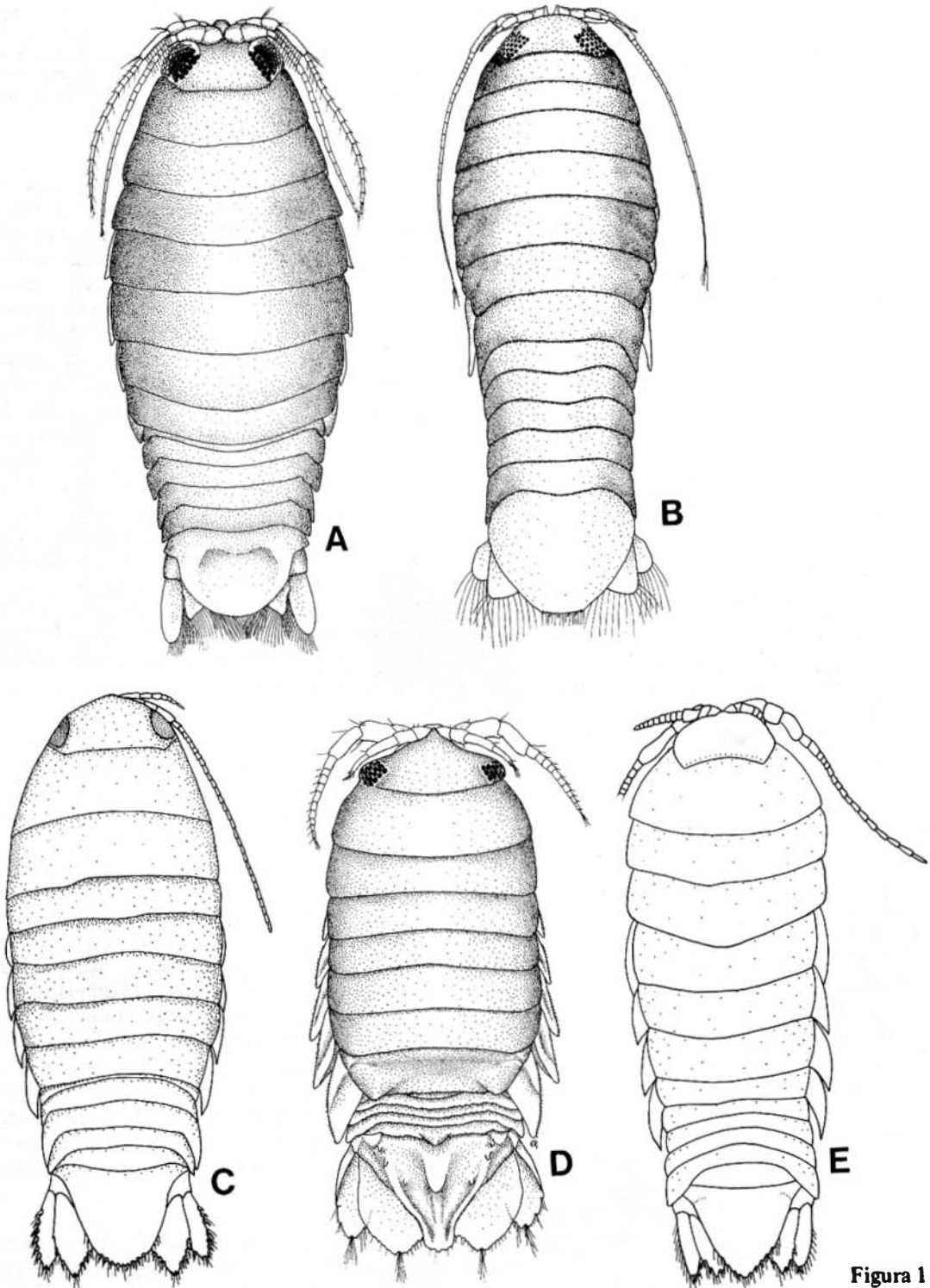


Figura 11

Cirolanidae. A, *Excirolana braziliensis*. B, *Eurydice caudata* (Nicaraguan specimen). C, *Cirolana parva*. D, *Metacirolana costaricensis* n.sp. E, *Natatolana californiensis*.

body length the antennae are commonly subequal in size. In large individuals, exceeding about 5 mm in length,  $Ant^1$  is longer (15-20 articles) than  $Ant^2$  (11-16 articles). In some small individuals (2.5-4.0 mm), the antennae were also found to be quite variable in length with  $Ant^1$  longer, shorter, or equal to  $Ant^2$ ." These authors discuss several other aspects of the morphology of *E. braziliensis* in detail. *E. braziliensis* closely resembles *E. mayana* (Ives, 1891), a Caribbean species that was claimed by Richardson (1905) to occur in Baja California, Mexico (Bahía San Francisco, *sic*). *E. mayana* may be distinguished from *E. braziliensis* by examination of the pleon; in *E. mayana* the uropodal endopod is only slightly shorter than the exopod, the pleotelson is about 2/3 as long as wide at the base (but less the 1/2 as long as wide in *E. braziliensis*), its posterior margin is armed with spines as well as setae, and it lacks the transverse depression typical of most species in the genus. We have not recorded *E. mayana* from the Pacific.

The younger growth stages of *E. braziliensis* were described by Bott (1954) and Schuster (1954) as new species (*Cirolana koepckeii* and *C. salvadorensis*, respectively). Dexter (1972) misidentified *E. braziliensis* as the similar *Excirolana* (= *Cirolana*) *mayana*, and recorded it as *Cirolana salvadorensis* in her Costa Rican and Colombian studies (Dexter, 1974).

*Excirolana braziliensis* may be the most ubiquitous species of intertidal invertebrate along the sandy beaches of tropical America (Glynn *et al.*, 1975). It occurred on 90% of the sandy beaches examined by Dexter (1972, 1974, 1976). Of the 45 Pan-American beaches examined by Dexter (1977), *E. braziliensis* was most dense at Naos Island, in Pacific Panama, where mean densities in excess of 6,000/m<sup>2</sup> were recorded in some samples. Dexter presented considerable data on the littoral distribution, population structure, and reproductive biology of this species. She found *E. braziliensis* to be characterized by continuous reproduction, rapid growth and population turnover, high tolerance to changes in the physical environment, and near ubiquitous occurrence on sandy beaches. Further, she found abundance not directly related to wave action, type of sediment or beach slope. All of these features are attributes of opportunistic species. While *E. braziliensis* produces relatively small broods (4-17 per brood, depending on female size), a

population may turn over as frequently as every four months, resulting in a high yearly population.

*Excirolana braziliensis* has been recorded from a wide variety of sand substrates, including quartz, calcareous, volcanic, igneous, and mixed, with median grain size ranging from 20-431  $\mu$ m<sup>2</sup>.

We found this species at every sandy beach site we collected, including Bahía Culebra (Guanacaste), Parque Nacional Santa Rosa (Guanacaste), and Tárcoles (Puntarenas). At the latter two sites we collected it both on the sandy beach itself, as well as in rocky shore habitats where the rocks were embedded in considerable sand. Quantitative samples taken by M. Murillo and A. Dittel from Bahía Culebra showed *E. braziliensis* to occur in upper, mid and lower tidal samples, predominantly in sands with a composition of 50% 20-40  $\mu$ m: 50% 40-130  $\mu$ m grains. Densities ranged from a mean of 24 isopods/1000 cc sand sampled in the high intertidal ( $n = 4$ ), to 8.1 isopods/1000 cc sand in the mid-intertidal ( $n = 3$ ), to 5.2 isopods/1000 cc sand in the low intertidal ( $n = 2$ ). The largest individuals collected were taken from the lowest samples; the smallest individuals from the highest samples.

Dexter (1974) recorded *E. braziliensis* from all eight of her Pacific Costa Rica sampling localities, including Playita Blanca (Coco), Tamarindo, Sámara, Puntarenas (La Punta), Boca de Barranca, Jacó, Playa Cocal (Quepos), and Playa Espadilla (Quepos).

Brusca (1980) described the feeding behavior of *E. braziliensis* as follows: "It has two rather different and distinct feeding behaviors. The first occurs during the high tides. The isopod patiently waits for the tide to begin to flow. . . whereupon it emerges from its seclusion to swim freely about in the water column, seeking a passing fish. When a prey fish is located, the isopod grabs ahold and rides about for a few minutes while taking its meal. The mandibles are powerful and strongly fitted for chewing and biting. The other feeding behavior occurs primarily during the low tides, when this isopod becomes an important beach scavenger. A dead fish washed ashore on a sandy beach. . . will quickly be reduced to a mere skeleton as literally thousands of these crustaceans emerge from the sand to consume the refuse".

**Distribution:** *Exciorolana braziliensis* is a wide-ranging species on both coasts of tropical and subtropical America (and warm-temperate South America). In the eastern Pacific, it ranges from the head of the Gulf of California, as far south as Guanaqueros, Chile, and is the predominant macrofaunal invertebrate on most sandy beaches throughout this range.

Genus *Eurydice* Leach, 1815

**Diagnosis:** Rostral process of cephalon minute or absent; frontal lamina not obvious. Antenna 1 with first articles thin and extending straight in front; second articles affixed at a right angle to the first, thus directing the antennae laterally. Antennae 2 much longer than antennae 1; peduncle of 4 articles. Maxillipeds without coupling hooks on endites. Mandibles with broad, tridentate incisor; lacinia mobilis and molar process well-developed. Pleon of 5 segments, plus pleotelson; pleonite 5 not markedly reduced, lateral margins not covered by pleonite 4. Pleopods 1 and 2 similar to one another. Uropods inserted somewhat ventrally on pleon; inner angle of peduncle only weakly produced.

**Remarks:** Species in this genus are similar in appearance to *Cirolana* species, but may be quickly distinguished by their unusual antennal arrangement and other characters (see key). Only one species of *Eurydice* is known from the eastern Pacific, *E. caudata*; its ecology is largely unknown. Eleftherion and Jones (1976) have reviewed the systematics and ecology of the Indian *Eurydice*; Jones (1974) has discussed the ecology of Saudi Arabian *Eurydice*; Singarajah (1966), Knight-Jones and Qusim (1967), Jones and Naylor (1970), Jones (1968; 1970a; 1970b), Salvat (1966), Alheit and Naylor (1976), and Soika (1955) have studied the ecology of European species. About 25 species of *Eurydice* have been described in the world literature, all are apparently predators and carnivorous scavengers.

Most are sand beach and shallow subtidal dwellers. Fish (1970) and Fish and Fish (1972) reported fortnightly movement of *E. pulchra* up and down the slope of sand beaches, following the tidal cycle as Klapow (1970; 1971; 1972a; 1972b) has reported for *Exciorolana chiltoni*.<sup>\*</sup> Fish and Fish (1972), Alheit and Naylor (1976), Jones and Naylor (1970), Hastings (1981), and others have reported on fortnightly swimming-feeding cycles for *E. pulchra* that are closely tied to nocturnal ebbing high tide cycles. We have captured *E. caudata* with regularity throughout southern California and western Mexico, by night lighting over shallow sandy bottoms.

*Eurydice caudata* Richardson, 1899

Fig. 11b

For synonymy see Bowman, 1977.

**Diagnosis:** Eyes very large. First antennae short, of 7-8 articles; extended about to beginning of flagellum of antennae 2; 4th article elongated. Second antennae long, with flagellum of more than 18 articles; extended to at least pereonite V or VI. Pleotelson broader than long, posterior margin broadly rounded or truncate, with 4 articulated spines and several long setae set between a pair of large marginal teeth. Uropods attach ventrally; short, not quite reaching posterior margin of pleotelson; exopod and endopod truncate, heavily setose. Appendix masculina of pleopod 2 (males) inserted slightly distal to proximal 1/4 of medial margin of endopod; extending well beyond apices of pleopodal rami.

**Remarks:** *Eurydice branchiopus* was described from southern California by Menzies and Barnard (1959), but reduced to a synonym of the Atlantic *E. littoralis* (Moore) by Menzies and Glynn (1968). Bowman (1977), however, removed *E. branchiopus* from *E. littoralis*, placing it in synonymy with *E. caudata*.

*E. caudata* is most often taken by night-lighting off ships anchored over shallow soft bottoms. In California and western Mexico, we have recorded it from coarse sands to silts, in depths of 5 to 100 m. This isopod is common and abundant throughout its range.

**Distribution:** Southern California southward, throughout western Mexico and Central

\* Caution must be used when interpreting Klapow's studies as he apparently was not thoroughly familiar with the relevant literature: further, Bruce and Jones (1981) recently synonymized 3 other species of *Exciorolana* into *E. chiltoni* (*E. Kincaidi* [Hatch, 1947], *E. vancouverensis* [Lee, 1926], and *E. japonica* Richardson, 1912). Both *E. Kincaidi* and *E. linguifrons* (Richardson, 1899) have been reported from Klapow's study area.

America, to the Golfo de Guayaquil, and including the islands of Revillagigedos, Socorro, Clarion, Tres Marías, and Cocos. We have examined hundreds of specimens from mainland shores of Mexico, Guatemala, Ecuador and Nicaragua. *Eurydice caudata* was taken at numerous Costa Rican localities by the Templeton Crocker expedition of the California Academy of Sciences in 1932 (by night-lighting off the R/V *Zaca*).

#### Genus *Cirolana* Leach, 1818

**Diagnosis:** Rostral process of cephalon minute or absent. Frontal lamina robust. Peduncle of second antenna of 5 articles. First and second peduncle articles of antennae 1 do not form right angles to one another (as in *Eurydice*). Maxilliped usually with 1-3 coupling hooks (occasionally more) on inner margin of endite. Mandible with broad tridentate incisor; lacinia mobilis and molar process well-developed. Pleopods 1 and 2 similar to each other. Uropods inserted laterally; peduncles with inner angles strongly produced; rami with or without plumose marginal setae. Five pleonites, the fifth usually being considerably smaller than the preceding four and with its lateral margins generally (but not always) covered by pleonite 4; pleonite 1 often concealed by pereonite VII.

**Remarks:** Cirolanids are common and often abundant in many shallow-water marine habitats and several species inhabit the abyssal environment. Most are predacious opportunistic scavengers and several have been recorded as attacking live fish and hence been referred to as parasites. However, in most of these associations no permanent attachment takes place and these are best labeled as micropredation. In at least one related species, however, true (though nonobligatory) parasitism may occur—*Natatona borealis* is an amphi-Atlantic species recently shown to attack the gills of sharks along the Florida coast, occasionally burrowing all the way into the pericardial cavity. Destruction blamed on this isopod resulted in the closing of the only large commercial shark fishery on the Florida east coast (at Cape Canaveral) in 1978 (Bird, 1981). The ecology of the species of the Indian Ocean has been discussed by Jones (1976); Johnson (1974, 1976) has published on the ecology of the California species *C. harfordi*.

#### *Cirolana parva* Hansen, 1890

Fig. 11c

For synonymy see: Bowman, 1977; Bruce and Bowman, 1982.

**Diagnosis:** Small, to 7.8 mm in length. Dorsum of cephalon with faint anterior interocular carina, and faint but entire transverse furrow running between the dorsomedial margins of each eye. Eyes well-developed. Anterior margin of cephalon with a short rostral process. Antenna 1 with 7-12 flagellar articles; antenna 2 with 22-29 flagellar articles. Frontal lamina broad, pentagonal, tapering to a triangular apex where it meets with (and is somewhat overlapped by) the down-curved rostral process; clypeus short, narrow. Maxilliped with 2 coupling hooks on endite. Pereopod I with simple setae projecting from distal margins of all articles; merus armed with series of blunt robust spines on outside margin. Pleonite 1 partly concealed by pereonite VII. Pleotelson triangular, with plumose marginal setae and 8 marginal spines; without carinae. Uropods with serrate margins and a deep apical notch on each ramus; marginal spines and simple setae on both rami; endopod slightly longer than exopod; extending slightly beyond apex of pleotelson.

**Remarks:** A common and often abundant species on tropical and subtropical coasts around the world. In the eastern tropical Pacific it is one of the most common isopods found between the tides. In this regard, it appears to be the southern ecological equivalent (replacement) of the common temperate *C. harfordi* (Lockington).

*C. parva* has a predilection for coral crevices, sponge interstices and algal turfs, although they apparently leave these refugiums on a regular basis as they are not uncommonly collected in plankton tows, particularly at night. Specimens have been collected from depths as great as 145 m. We have collected *C. parva* from the algal mats of Parque Nacional Santa Rosa where they co-occured with *Metacirolana costaricensis* n. sp.

**Distribution:** Until recently, considered to be a eurythermal circumtropical and warm temperate species; in the eastern Pacific, it probably ranges from Mexico at least to Costa

Rica, although we have definite records only from Costa Rica. In the Indian Ocean (Jones, 1976), Puerto Rico (Menzies and Glynn, 1968) and Gulf of California (Brusca, 1980) it has been reported as the most common species of *Cirolana* found. However, Bruce and Bowman (1982) have recently raised the probability that what has passed for *C. parva* in the past has in fact been a "complex" of several closely related (sibling) species. Upon examination of type material of *C. parva*, plus additional material from various localities throughout the world, Bruce and Bowman concluded that the only reliable records that exist are for the Caribbean and the Gulf of Mexico; all other records, they feel, need confirmation. Our Costa Rican specimens, however, appear to be *C. parva* (*sensu* Bruce and Bowman, 1982).

#### Genus *Metacirolana* Nierstrasz, 1931

**Diagnosis:** Rostral process of cephalon present, short and acute or of modest size; frontal lamina dilated anteriorly, freely projecting; clypeus triangular, projecting freely downwards. Peduncle of antenna 2 of 5 articles. Maxilliped slender, endite with one or several coupling hooks. Mandible with broad tridentate incisor; molar process (and usually lacinia) present and well-developed. Pleopods 1 and 2 similar to each other. Uropods with inner angle of peduncle not produced. Pleon with 5 free pleonites; lateral margins of pleonite 5 usually not covered by pleonite 4.

**Remarks:** This genus was resurrected by Bruce (1981) to house a group of about 15 reasonably distinctive cirolanid species, including *M. joanneae* (Schultz, 1966) of California waters and *M. sphaeromiformis* (Hansen, 1890), a Caribbean species that Menzies and Glynn (1968) have suggested may be circumtropical.

*Metacirolana costaricensis* n. sp.

Fig. 11d

**Diagnosis:** Small, less than 3 mm in length. Cephalon short, with lateral margins forming subacute angles at level of eyes; with transverse bar of dark chromatophores between eyes; with acute rostral process directed between bases of antennae 1, where it meets the expanded

frontal lamina. Antenna 1 short, reaching posterior margin of cephalon; flagellum of 3 articles. Antenna 2 reaching pereonite II with 8-12 flagellar articles. Frontal lamina narrow posteriorly, inflated and rounded anteriorly. Lacinia mobilis of mandible greatly reduced. Coxal plates V-VII very large, posteriorly directed, carinate, and extended well beyond margins of their respective pereonites. Pleotelson with midlongitudinal carina; flanked by submedian longitudinal carinae; posterior margin with 2 apical spines and a few scattered setae. Rami of uropods with setae and spines; both rami with shallow apical notch, from which a tuft of long setae arises; endopod much larger than exopod; neither rami extend beyond pleotelson margin.

**Remarks.** *M. costaricensis* is at first easily mistaken for an *Excirolana* because of the unusual arrangement of the rostral process and frontal lamina, the former being acute and the latter being anteriorly (dorsally) rounded, the two together at first resembling the spatulate rostrum of excirolanids.

*Metacirolana costaricensis* was collected at Parque Nacional Santa Rosa. Surf temperature at the time of collection was cool for the latitude, 26°C in April, suggesting that some upwelling may occur at that locality. The isopods were living in the short algal turf covering the rocks. *Excirolana braziliensis* co-occurred with *M. costaricensis* at this locality, but the former was restricted to the under-rock and between-rock habitats, where fine sands and coarse muds occurred. The snapping shrimp *Alpheus leviusculus* Dana and a small brittle star (*Ophiophragmus* sp.) were also common in the algal turf from which *M. costaricensis* was taken. Several specimens were also taken at Parque Nacional Playa Manuel Antonio, Quepos, on sandy shores.

**Type deposition:** Holotype, AHF No. 8011; Costa Rica, Guanacaste Province, Parque Nacional Santa Rosa, from rocky shore outside mangrove estero; water temp. 26°C; Coll. R.C. Brusca, A.M. Mackey, M.M. Murillo, & A. Dittel.

**Distribution:** *M. costaricensis* is so far known only from the Pacific shores of Costa Rica (Parque Nacional Santa Rosa, Guanacaste; Parque Nacional Playa Manuel Antonio, Quepos).

#### Genus *Natatolana* Bruce, 1981

**Diagnosis:** Rostral process of cephalon wanting; frontal lamina narrow, 3-4 times longer than broad. Peduncle of antenna 2 of 5 articles. Maxillipedal endite with multiple coupling hooks. Mandible with broad tridentate incisor; lacinia mobilis and molar process well-developed. Pereopods V-VII with bases markedly flattened and provided with long natatory setae. Pleopods 1 and 2 similar to each other. Uropods with inner angle of peduncle not produced posteriorly. Pleon with 5 free pleonites; pleonite 1 partially concealed by pereonite VII; pleonite 5 overlapped by pleonite 4.

**Remarks:** Bruce (1981) recently established this genus to house the 30 or so known species of "swimming cirolanids". The genus is immediately separated from all others in the family by the presence of a flattened basis on pereopods IV-VII and by the narrow frontal lamina.

#### *Natatolana californiensis* (Schultz, 1966)

Fig. 11e

For synonymy see Brusca and Ninos, 1978 (as *Cirolana californiensis*).

**Diagnosis:** Eyeless or eyes without pigmentation. Anterior margin of cephalon evenly convex, without rostral process; cephalon deeply immersed into pereonite 1. Antenna 1 with 8-12 flagellar articles; antenna 2 with 10-21 flagellar articles. Frontal lamina very narrow; clypeus short. Pleotelson triangular, with 8-12 small marginal spines and long plumose setae; margin smooth except for shallow notches where spines and setae insert. Uropods with marginal spines and long plumose setae; endopod and exopod lack distinct apical notch; endopod slightly longer than exopod. Seventh pereopods occasionally abruptly smaller than all other pairs.

**Remarks:** The most striking features that distinguish *N. californiensis* from all other tropical eastern Pacific species are the lack of eyes (or if ommatidia are present, they lack pigmentation), the very narrow frontal lamina, the occasionally reduced seventh pereopods, and the deeply immersed (in pereonite 1) cephalon. Brusca and Ninos (1978) synonymized *N. californiensis* (as *Cirolana californiensis*) with *Cirolana deminuta* Menzies and George, 1972. The latter was described from the Peru-Chile Trench.

This species has most often been reported from depths between 700 and 2,000 m, although a few collections have been from depths as shallow as 40 m. All records have been from fine sands or sand-clay mixtures, usually reported as gray-green sandy-mud or olive-brown silty sand.

**Distribution:** *N. californiensis* has not yet been reported from Costa Rica. However, we have examined specimens from throughout southern California and western Mexico, as well as the type material from the Peru-Chile Trench. Its occurrence in Costa Rican waters is anticipated, and it may eventually be found in the deeper areas of the Golfo de Nicoya, as well as in offshore waters.

#### Family Corallanidae

Body symmetrical; dorsum moderately arched; often with dorsal setae, spines and/or tubercles. Eyes usually large. Antenna 1 with 2- or 3-articulate peduncle; antenna 2 with 5-articulate peduncle; flagella of both antennae distinct and multi-articulate. Frontal lamina present, narrow; clypeus generally wide; labrum often narrower than clypeus. Mandible with narrow 2- or 3-dentate incisor; lacinia mobilis reduced or absent; molar process rarely present, often vestigial and represented by a small fleshy lobe; palp 3-articulate. First maxilla with outer lobe simple or falcate, with 1 to several terminal spines; inner lobe small, simple. Second maxilla reduced, 1- or 2-lobed, without stout spines. Maxilliped without endite (except for *Tnødentella*); palp slender, composed of 4 or 5 articles. Pereopods I-III usually prehensile (dactyl as long, or longer than propus), occasionally ambulatory (dactyl shorter than propus); pereopods IV-VII always ambulatory. Coxal plates distinct on pereonite



II-VII. Pleopods biramous, all lamellar; coupling hooks present on medial margin of pleopod peduncles 1-4. Uropods inserted at anterolateral margins of pleotelson; both rami articulate.

Corallanidae has had a long and complicated taxonomic history that has only recently been clarified (Bruce *et al.*, 1982). As it currently stands, this family houses 7 recognized genera, including the genus *Excorallana* (formerly in its own family). Members of the Corallanidae superficially resemble 3 other flabelliferan families (Cirolanidae, Aegidae, Cymothoidae), although they can usually be quickly distinguished from these in the field by the presence of their large eyes, distinctly visible coxal plates, and often present heavy setosity or dorsal tuberculation. Although no corallanids have yet been reported from Pacific Costa Rica, we have included the amphi-American *E. tricornis* in anticipation of its discovery in these waters.

#### Genus *Excorallana* Stebbing, 1904

**Diagnosis:** Eyes well-developed, often contiguous or nearly so. Body often with dorsal setae, spines, tubercles or carinae. First antennae with 2-3 peduncular articles, basal article enlarged; second antennae with 5 peduncular articles, articles 4 and 5 elongate. Frontal lamina, clypeus and labrum visible anterior to mandibles, but may be partly obscured by same; frontal lamina narrow; clypeus and labrum very broad and short. Mandible with elongate incisor; molar process and lacinia small or absent; palp of 3 articles. Left and right mandibles tend to interdigitate. Maxilla 1 with outer lobe forming a single, large, recurved spine; inner lobe simple. Maxilla 2 apex bilobed, spinose. Maxilliped with 5-articulate palp, middle (antepenultimate) article elongate, often with length twice width. Pereopods I-III subprehensile or prehensile, with short blunt spines on posterior medial margin of merus and ischium; pereopods IV-VII ambulatory. Peduncles of pleopods 1-4 with 4-6 coupling spines on medial margin and a group of plumose setae ventral to spines. Peduncles of pleopods 2-5 often with small lobe on lateral margin. All rami of all pleopods setigerous. Male pleopods 2 with rod-like appendix masculina arising from proximal medial margin of endopod.

**Remarks:** Neither Stebbing (1904a; 1904b), Richardson (1905) nor any subsequent author designated a type species for *Excorallana*. *Excorallana tricornis tricornis*, originally described as *Corallana tricornis* by Hansen (1890), has been designated the type of the genus by Delaney (1984). The most comprehensive treatments of the genus *Excorallana* were provided by Richardson (1905), Lemos de Castro (1960; 1964), Monod (1969) and by Carvacho and Yáñez (1971), and Delaney (1984). The genus is distinguished from other genera of Corallanidae by the morphology of the mouthparts and pereopods. Species of *Excorallana* have been collected at depths ranging from the intertidal zone to 183 m. The genus is primarily a warm-water group, no species having been found in latitudes higher than 40°N, and only one species (*E. meridionalis*) has been reported from south of the Equator. There are currently 19 species and subspecies described in *Excorallana*; all are New World forms. A key to the species of this genus, as well as zoogeographical and ecological discussions, can be found in Delaney (1984).

#### *Excorallana tricornis occidentalis*

Richardson, 1905

Fig. 12

See Bowman (1977) and Delaney (in press) for synonymy.

**Diagnosis:** Body narrow and rather elongate, length about 3X width. Cephalon about twice as wide as long; with 3 large horns, 1 rostral and 2 posterolateral (between eyes); frontal lamina longer than wide and with anterior margin produced into a median point. Antennae 1 with 3 peduncular and 4-7 flagellar articles; antennae 2 with 16-21 flagellar articles. Pereonite I with 2 small anterior tubercles; pereonites II-VII without dorsal setae or tubercles. Pleonites 2-5 with tuberculate posterior margins. Pleotelson triangular; apex acutely rounded; with lateral incisions. Uropods slightly longer than pleotelson, fringed with long setae.

**Remarks:** Richardson (1905) distinguished *Excorallana tricornis occidentalis* as a subspecies distinct from the west Atlantic *E. tricornis tricornis* based on specimens from the Gulf of California. Bowman (1977) amplified

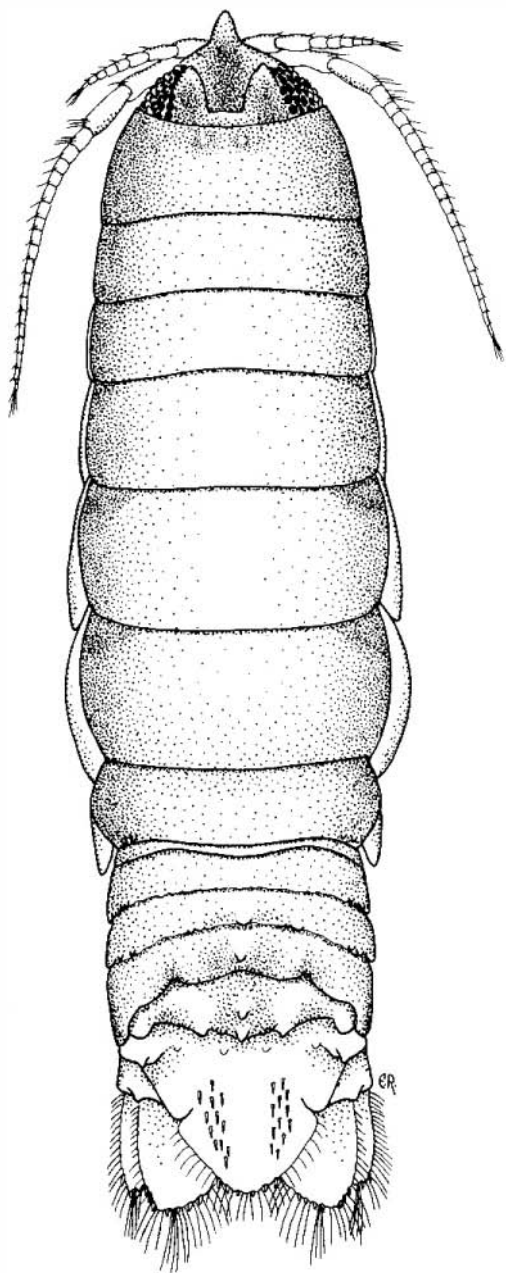


Figura 12

*Excorallana tricornis occidentalis* (from the holotype).

the descriptions of these subspecies, pointing out that the lateral incisions in the pleotelson of *E. t. occidentalis* are not separated by a gap as in *E. t. tricornis* (as well as several other characters). Although we have not yet found *E. tricornis occidentalis* on Pacific Costa Rican shores, its presence here is anticipated; we have

examined specimens from Panama and throughout western Mexico. It has been collected from depths ranging from the intertidal zone to 138 m, on rocks, sandy beaches and in mangrove habitats. It has also been taken from the body of various fishes, upon which it no doubt feeds in a micropredaceous fashion.

### Family Aegidae

Body cirolanidlike, but usually quite large and robust. Peduncle of both pairs of antennae stout and well-defined; flagella multiarticulate. Eyes large and well-developed, or occasionally absent. Mandible without molar process or lacinia mobilis; palp of 3 articles. Maxillipedal palp of 2, 3 or 5 articles; distalmost articles with strong, often recurved spines. Maxilla 1 consists of a single, slender stylet, with stout apical spines. Maxillae 2 bilobed, with stout apical spines. Pereon with well-defined coxal plates on II-VII. Pereopods I-III distinctly prehensile, dactyls longer than propi and somewhat recurved. Pereopods IV-VII not prehensile; slender; dactyls not longer than propi. Four or five free pleonites, plus pleotelson. Pleotelson and uropods with marginal setae and/or spines; peduncle of uropod with inner margin produced into an acute process. Most or all pleopods with plumose marginal setae. Little sexual dimorphism.

Members of the family Aegidae are active predators on fishes, and may be classified as "micropredators" or "temporary parasites". They cling tenaciously to their prey (or "host fish") while taking a meal, but are not known to display host specificity. They may also feed in a scavenging mode, consuming dead fishes that settle to the benthos. When not feeding, aegids lie on the substratum where they are often picked-up in benthic trawls and grabs. They are occasionally taken with plankton nets. Brusca (1981) described the evolutionary relationship of the family in relation to other flabelliferan taxa.

There are 5 valid genera of Aegidae in the world, of which three are known to occur in the eastern Pacific (*Aega*, *Rocinela*, *Syscenus*). Although about 22 species in these 3 genera have been reported from the eastern Pacific, only 9 have been recorded from the Tropical Eastern Pacific Region. Of these 9, only one has previously been reported from Costa Rican waters (*Aega plebia*, from south of Cocos

Island). Three species have been reported from the vicinity of the Galapagos Islands (*Aega acuminata* Hansen, 1897; *Aega longicornis* Hansen, 1897; and *Aega plebia*). Coventry (1944) reported the Caribbean *Aega ecarinata* Richardson, 1898, from off Acapulco (central west Mexico). Two species have been reported from Pacific Panama (*Rocinela modesta*

Hansen, 1897 and *Aega maxima* Hansen, 1897). *Rocinela laticauda* Hansen, 1897 has been reported from western Canada to Acapulco and the Tres Marias Islands. *Rocinela tuberculosa* Richardson, 1898, *R. laticauda*, and *R. signata* Schioedte and Meinert, 1897 all occur in the Gulf of California (west Mexico), the latter also being recorded from Panama.

#### Key to the Species of Pacific Costa Rican Aegidae

1. Maxillipedal palp of 2-3 articles; articles 1 and 2 of antennae 1 not expanded; frontal lamina small, narrow and indistinct (visible in ventral aspect) . . . . . 3
- Maxillipedal palp of 5 articles; articles 1 and 2 of antennae 1 more-or-less expanded; frontal lamina large, broad and distinct (visible in ventral aspect) . . . . . 2
2. Rostrum well-developed, extended ventrally to separate first antennae; articles of maxillipedal palp not lobed; propus of pereopod I not lobed (Fig. 13a-c) . . . . . *Aega plebia*
- Rostrum short, not extended ventrally between first antennae; articles 2-3 of maxillipedal palp lobed; propus of pereopod I with strong lobe (Fig. 13d-f) . . . . . *Aega acuminata*
3. Pleotelson with W-shaped pigment pattern on dorsum; propus of pereopod I unarmed and not lobed, carpus unarmed, merus with 1 large and 2 small spines on inner margin (Fig. 14 k,l) . . . . . *Rocinela signata*
- Pleotelson without a W-shaped pigment pattern on dorsum, but with a pair of submedian pits; propus of pereopod I with 4-5 large spines on a large lobe, carpus and merus with 1 spine each (Fig. 14a-j) . . . . . *Rocinela murilloi* n. sp.

#### *Aega* Leach, 1815

**Diagnosis:** Body compact; pleon not much narrower than pereon. Eyes present, usually large, occasionally contiguous. Anterior margin of cephalon often produced into a short rostrum, folded ventrally to more-or-less separate bases of first antennae. Frontal lamina large and distinct, projecting between bases of second antennae. Antennae 1 rather short, with first 2 articles of peduncle more-or-less expanded. Maxilliped with a 5-articulate palp. Coxae thick, usually sculptured laterally with oblique curved ridges; produced posteriorly into acute or subacute angles. Pereopods I-III usually with simple cylindrical propi, rarely expanded into a spinose lobe. Pereopods IV-VII increasing in length posteriorly, with short, simple propi; usually with many slender spines on most articles. The genus *Aega* has been recently reviewed by Brusca (1984), who proposed 2 subgenera, *Aega* and *Rhamphion*.

*Aega* (*Aega*) *acuminata* Hansen, 1897

Fig. 13 d-f

See Brusca (1984) for synonymy.

**Diagnosis:** Large, to at least 50 mm in length. Eyes very large and well-pigmented, ap-

pearing rust colored in alcohol. Rostrum acute and short, not extended between antennae. Frontal lamina large, raised, and shield-shaped. Peduncle of antenna I middle article with distal process. Maxillipedal palp with middle articles produced into strong distal lobes. Pereopod I propus with large distal lobe. Pleotelson with posterior margin strongly acuminate; uropods extended beyond pleotelson margin; exopod ovate, endopod falcate.

**Remarks:** This species had not been reported since its original description, based on a single male specimen (incorrectly labeled a female by Hansen) collected by the U.S. Fish Commission steamer *Albatross* near the Galapagos Islands, from a depth of 768 m. Hansen (1897) described the eyes as being "dark grayish, almost black" – this was presumably from a live or freshly preserved specimen. We have recovered a second specimen (a female) from the collections of the Scripps Institution of Oceanography Benthic Invertebrate Collections, from off "Cabo Blanea" [probably Cabo Blanco], Costa Rica (09°23'N, 65°06'W; April 22, 1973; 1353 m; free vehicle trap. R/V *Agassiz*).

**Distribution:** *A. acuminata* is presently known from only two deep water localities, one off Pacific Costa Rica and the other off the

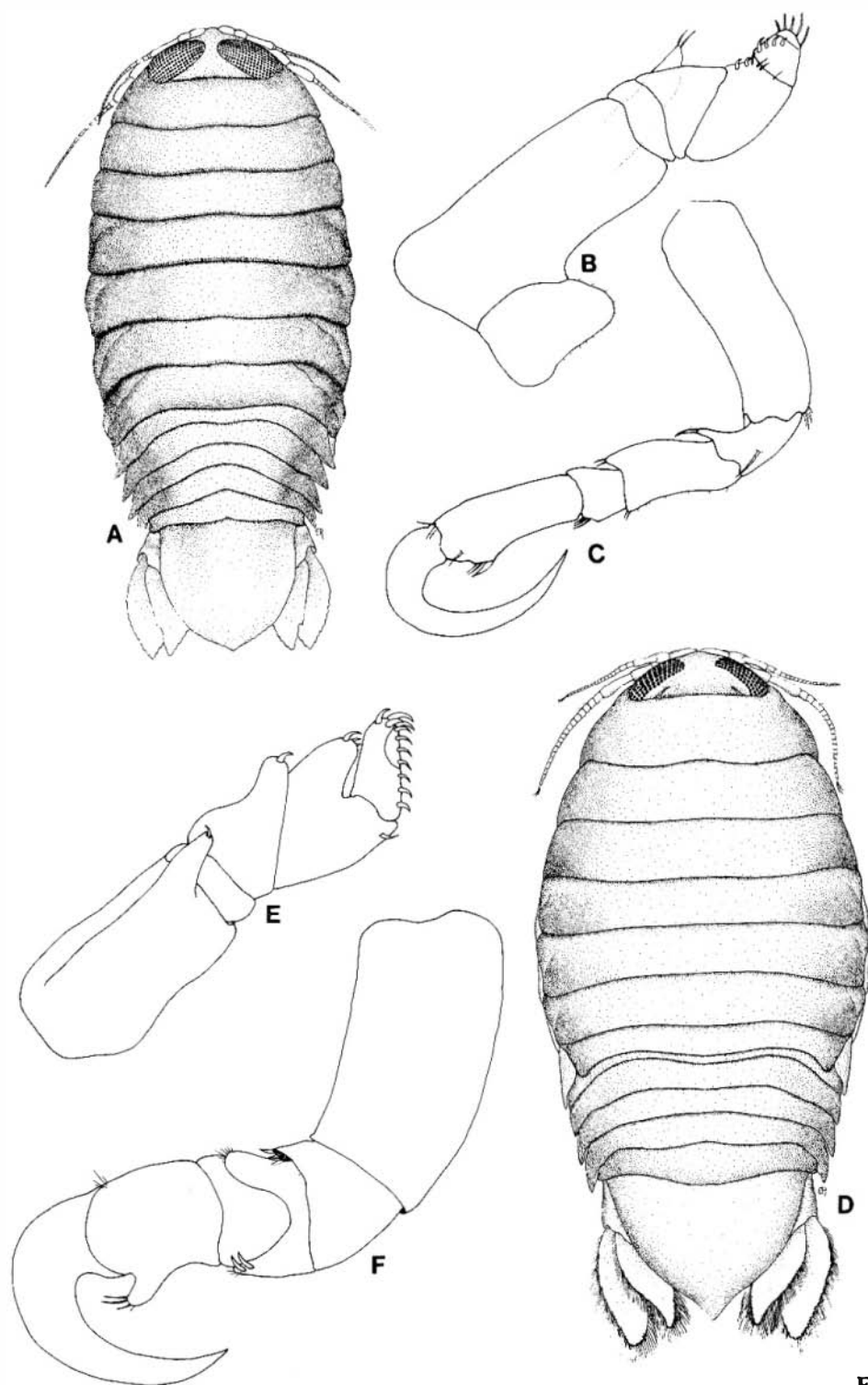


Figura 13

*Aega plebia*: A, dorsal view (from a syntype; female); B, maxilliped; C, pereopod I. *Aega acuminata*: D, dorsal view (from the type; female); E, maxilliped; F, pereopod I.

Galapagos Islands. These records suggest that this species is primarily a deep-living offshore form, whose distribution may range greatly beyond its currently recorded range.

*Aega (Rhamphion) plebia* Hansen, 1897

Fig. 13 a-c

See Brusca (1984) for synonymy.

**Diagnosis:** Moderately large, to at least 37 mm in length. Eyes very large, well-pigmented, nearly touching in midline. Rostrum well-developed, extended ventrally to form an acute projection separating first antennae. Frontal lamina large, raised, and shield-shaped. Peduncle of antenna 1 with middle article normal; distal article about twice length of second. Maxillipedal palp with proximal and distal articles quite small, medial 3 articles larger but not produced into acute lobes as in *A. acuminata*. Pereopod I propus not produced into a distal lobe, but with a raised subapical plate bearing a single robust spine. Pleotelson shield-shaped, posterior margin subacuminate; uropods extend about to posterior margin of pleotelson; exopod and endopod ovate.

**Remarks:** Hansen (1897) described *A. plebia* from six specimens collected during the 1891 eastern Pacific expedition of the U.S. Fish Commission Steamer *Albatross*. All were taken from the vicinity of Cocos Island, from depths of 842 m to 1956 m. Birstein (1973) synonymized *A. magnoculis* Richardson, 1910 with *A. plebia*; however, he did not examine type material, basing the synonymy solely on the original published descriptions. Brusca (1984) agreed with the synonymy. We have not personally collected this species in Costa Rican waters; our diagnosis and figures are based upon the type material.

**Distribution:** Tropical eastern Pacific records are from the region of Cocos Island (Costa Rica), off Panama, and off Peru; northwest Pacific records are from the Bering Sea. *A. plebia* has been taken from depths of 688 to 2534 m.

*Rocinela* Leach, 1818

**Diagnosis:** Body usually less compact and more depressed than in *Aega*. Eyes well-

developed. Anterior margin of cephalon often extended to form a short rostrum covering all or part of first two articles of antenna 1. Mandibles with apex narrow, not denticulate; palp of 3 articles, middle article subequal or barely longer than first, which is greatly elongated. Frontal lamina small, narrow, usually indistinct. Antennae 1 much shorter than antennae 2; basal articles of 1 not expanded. Maxilliped with a 2- or 3- articulate palp. Pereopods I-III usually (but not in all species) with propi expanded into a spine-bearing lobe. Coxae thin, especially on II-III. Pleon not much narrower than pereon.

*Rocinela signata* Schioedte and Meinert, 1879

Fig. 14 k-l

See Bowman, 1977, for synonymy.

**Diagnosis:** Body smooth, without dorsal tubercles. Cephalon twice as wide as long, with front produced over basal articles of first antennae. Flagellum of antenna 1 of about 4 articles; flagellum of antenna 2 of about 10-11 articles. Eyes large, dark, widely separated. Pereopods I-III with ventral margin of propus unarmed, or with a single, strong, recurved spine; no spines on carpus; 3 spines on merus. Dorsum of pleotelson with two distinct semilunar bands of pigment, these usually being fused to form an inverted W-shaped figure.

**Remarks:** A rather small aegid, reaching lengths of 10-15 mm. Richardson (1912) remarked on specimens from Jamaica (presumably live material): "The color is beautifully variegated in delicate shades of brown, pink and grey" and "The eyes [are] light pink". Preserved specimens are drab and uncolored. Hansen (1897: 109) reported a similar species, *Rocinela modesta*, described from a single mutilated specimen (length 23.5 mm), from outside the Gulf of Panama; it has not been recorded since. *R. modesta* differs from *R. signata* and *R. murilloi* in having 4 very weak spines on the propus of pereopod 1, and 3-4 spines on the merus.

*Rocinela signata* has been reported from a broad spectrum of "host" fishes, and is found attached to the general body surface as well as the gills. It has been reported from at least one shark (from the gills of nurse sharks, Gulf of

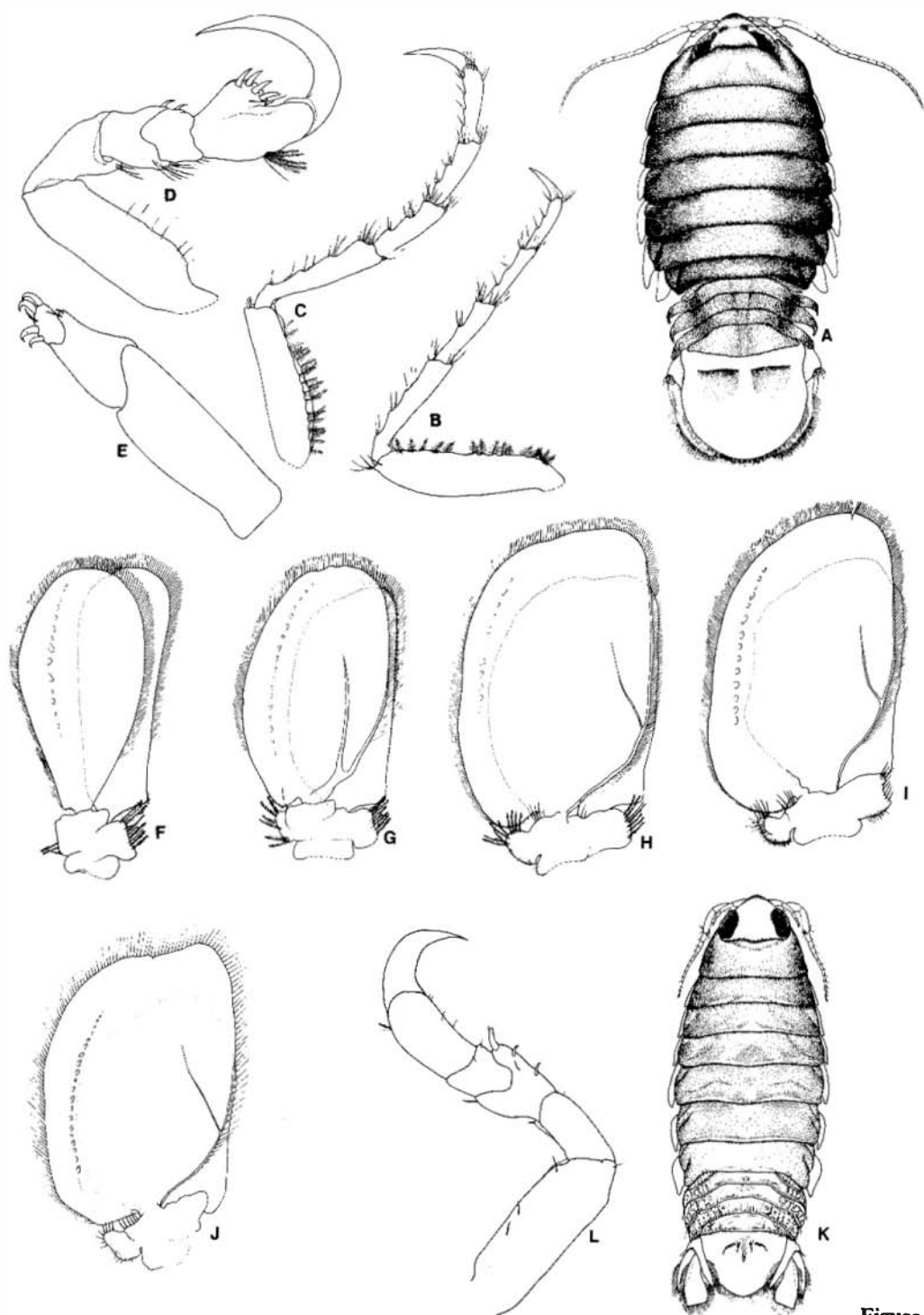


Figura 14

*Rocinela murilloi*: A, dorsal view (from the type); B, pereopod VII; C, pereopod IV; D, pereopod I; E, maxilliped; F, pleopod I; G, pleopod 2; H, pleopod 3; I, pleopod 4; J, pleopod 5. *Rocinela signata*: K, dorsal view; L, pereopod I.

Mexico). It is most often taken free-living on the bottom, and has been collected from sand, rocks and coral habitats, to depths as great as 73 m.

Menzies and Glynn (1968) synonymized the Pacific form (*Rocinela aries* Schioedte and Meinert, 1879) with the Atlantic form, *R. signata*.

**Distribution:** Amphi-American. In west Atlantic from Florida throughout the Gulf coast of the U.S., Mexico, and Central America; West Indies and Caribbean; south to Brazil. In the east Pacific *R. signata* has been recorded from: southern California (rare? Menzies, 1962b); throughout Baja California and the Gulf of California; Socorro Is.; and Panama. Although we have not yet recorded this species from Pacific Costa Rican waters its occurrence is anticipated. Menzies and Glynn (1968) suggested that *R. signata* may be pantropical in distribution, although they provided no evidence in support of that speculation.

*Rocinela murilloi* n. sp.

Fig. 14 a-j

**Diagnosis:** Large, to 50 mm length. Coxae distinct and free on pereonites II-VII, becoming larger posteriorward, those of V-VII extended to or beyond posterior margin of their respective pereonites. Cephalon about twice as wide as long; eyes large, dark, widely separated. Antenna 1 extended barely to pereonite I; antenna 2 extended to pereonite III. Maxillipedal palp 2-articulate; apical article with four, stout, recurved spines and a single slender spine. Pereopod 1 propus with 4-5 large spines; carpus and merus with 1 large spine each; all articles except dactyl with tufts of setae on outside margin. Pereopods IV and VII with numerous slender spines, as figured. Pleonites 1 and 5 manifestly narrower than others; pleonite 5 longer than 1-4. Pleotelson with a pair of submedian pits or indentations, as figured; without distinct pigment patterns. Pleopods 1-5 with row of yellowish maculae on exopods; 2-5 with marginal vein on exopods; 1-2 with plumose marginal setae on both lamellae; 3-5 with plumose marginal setae on exopods only.

**Remarks:** We have recovered only a single collection (10 specimens) of this new *Rocinela*.

They were taken from 1866 m, by beam trawl, from the *Velero IV*; 12-13 May 1973; 2352-0518 hrs; 9°45'N 85°55'24"W; 14 mi. 233°T from Point Guiones (at the mouth of Golfo de Nicoya). We take great pleasure in naming this species after Dr. Manuel M. Murillo (at this writing, Vice President for Research, Universidad de Costa Rica), whose assistance made this study possible.

**Type deposition:** Holotype, AHF No. 737; nongravid female. Paratopotypes, 8 specimens deposited AHF; 1 deposited U.S. National Museum, Washington, D.C.; 1 deposited Universidad de Costa Rica, Marine Invertebrate Museum.

**Distribution:** Known from only the type locality.

#### Family Cymothoidae

Body cirolanidlike, but often twisted to one side or another. All pereopods distinctly prehensile, with dactyls longer than propi. Mandible lacking molar process and lacinia mobilis; incisor blade-like; palp of 3 articles. Maxilliped reduced to small palp of 2 articles. Maxillipeds, maxillae 1, and maxillae 2 with strong, recurved, terminal and subterminal spines. Antennae reduced, peduncle not distinct from flagellum. Bases of posterior pereopods often enlarged into elevated carinae, and grooved to receive ischium-merus. Pleopods and uropods (in adults) without marginal setae. Pleopods often with "accessory gills" (i.e. lamellar plates or digitiform processes).

The Cymothoidae are external parasites on marine and freshwater fishes. They attach either on the epidermis, in the gills, or in the mouth of the host fish. This is a large and taxonomically confused family, with over 42 nominal genera and 250 species. The most recent revisionary/monographic work on the group is Brusca (1981), and that paper should be consulted for detailed information on all species included in the following discussion. All species in the family are probably protandrous hermaphrodites. The juveniles possess typical cirolanoid setation on the pleopods, uropods, and pleotelson, and are active swimmers. Once they have attached to the host fish they become functional males and lose this setation. After a period of time they change sex to

become functional females. Host specificity is strong in some species, but weak in others. Many species are known to be widespread in distribution; not unexpected of parasites of oceanic fishes. For a review of the natural history and evolution of the family, see Brusca (1981).

Although 10 genera have been reported from the east Pacific, one of these (*Braga*) was

recently shown to be an incorrect record (Thun and Brusca, 1980), and another (*Aegathoa*) represents what is now known to be a morphological stage representing juveniles of other genera. We have 4 species of Cymothoidae in our collections from Costa Rica, and consider an additional 5 as highly probable to occur in this region.

#### Key to the Species of Pacific Costa Rican Cymothoidae

1. Cephalon immersed (posteriorly sunk) in pereonite 1; posterior margin of cephalon not trisinate . . . . . 2
- Cephalon not immersed in pereonite 1; posterior margin of cephalon distinctly trisinate . . . . . 7
2. Basal articles of antennae 1 expanded and touching (Fig. 16 a,b) . . . . . *Ceratothoa gaudichaudii*
- Basal articles of antennae not expanded and touching (although they may be nearly touching) . . . . . 3
3. Pleon continuous with lateral margins of pereon, forming a more-or-less continuous and symmetrical body margin; pleonites 1-2 only occasionally somewhat immersed in pereon . . . . . 4
- Pleon slightly or abruptly narrower than pereon, disrupting continuity of body margins; pleon generally deeply immersed in pereon . . . . . 6
4. Body strongly convex dorsally; cephalon subquadrate; pleotelson narrowing abruptly; pereonites II-VI of female with anterolateral bosses (Fig. 16 i-k) . . . . . *Lironeca convexa*
- Body not strongly convex dorsally (excepting *Idusa carinata* – below); cephalon not subquadrate; pleotelson not narrowing abruptly; pereonites II-VI of female without anterolateral bosses . . . . . 5
5. Uropods reaching considerably beyond posterior margin of pleotelson; pleopods 1-5 with dendritic, finger-like accessory gills; females without carinae on bases of posterior pereopods (Fig. 16 g-h) . . . . . *Lironeca bowmani*
- Uropods falling short of, or reaching barely beyond posterior margin of pleotelson; pleopods 1-5 without dendritic accessory gills; females with carinae on bases of posterior pereopods (Fig. 16 f-g) . . . . . *Lironeca vulgaris*
6. Body strongly compressed laterally, dorsum strongly hunched; bases of antennae 1 nearly touching; pleon weakly but distinctly narrower than pereon (Fig. 16 d) . . . . . *Idusa carinata*
- Body normally not as above; bases of antennae 1 widely separated; pleon abruptly narrower than pereon (Fig. 16 c) . . . . . *Cymothoa exigua*
7. Cephalon narrows anteriorly to form an acute projection produced ventrally between first antennae; posterolateral angles of pereonites II-VI not produced; coxal plates short, barely reaching or, more commonly, falling short of posterior border of respective segments by considerable distance (Fig. 15 a) . . . . . *Anilocra meridionalis*
- Cephalon not as above, frontal margin without acute projection; posterolateral angles of pereonites II-VI manifestly produced, increasingly so posteriorly; coxal plates long, usually extended to or somewhat beyond medial posterior margin of respective pereonites . . . . . 8
8. Frontal margin of cephalon concave (medially excavate); posterolateral angles of pereonites I-VI rounded, not produced into acute angles (Fig. 15 c) . . . . . *Nerocila excisa*
- Frontal margin of cephalon convex; posterolateral angles of all, or just posterior pereonites produced into acute or subacute angles (Fig. 15 b-d) . . . . . *Nerocila acuminata*

#### Genus *Anilocra* Leach, 1818

**Diagnosis:** Body narrow, somewhat more compressed and dorsally convex than in *Nerocila*. Cephalon usually narrows anteriorly to a triangular apex, folded ventrally between bases of first antennae; downward folding gives anterior margin of cephalon truncate appearance in dorsal aspect. Cephalon with poste-

rior border forming 3 weak lobes, not nearly as prominent as in *Nerocila*; cephalon not at all, or only weakly immersed in pereonite I. Anterior border of pereonite I trisinate, matching posterior border of cephalon. Posterolateral angle of pereonite I usually not produced or prominent; those of II-VI never produced or prominent; those of VII always more-or-less produced. Coxal plates small and compact,



failing to reach posterior margins of their respective pereonites by a considerable distance. Pereopods gradually increasing in length, seventh often manifestly longer than sixth. Pleon not at all, or only slightly immersed in pereonite VII. Pleopods 3-5 often thrown into deep pockets or pleats.

**Remarks:** Specimens of *Anilocra* are rarely encountered in the eastern Pacific. *Anilocra meridionalis* is occasionally collected. The presence of *A. laticauda* H. Milne Edwards, 1840 (= *A. laevis* Miers, 1877) in this region is questionable (see Brusca, 1981). Species in this genus are external parasites on marine fishes.

*Anilocra meridionalis* Richardson, 1914

Fig. 15a

For synonymy see Brusca, 1981.

**Diagnosis:** Cephalon with posterior margin weakly trisinate and weakly immersed in pereonite I. Posterolateral angles of all pereonites evenly rounded, not extended or acute. Pereopods without carinae on bases, although those of posteriormost legs have a shallow groove to receive the ischium-merus. Pleon not at all immersed in pereonite VII. Pleonites decrease gradually in width posteriorly. Pleotelson slightly longer than wide; posterior margin evenly rounded. Pleopods simple, without well developed accessory lamellae; endopod of pleopod 5 strongly pleated. Uropodal rami evenly ovate, subequal in size or exopod barely longer than endopod; rami reaching barely beyond posterior margin of pleotelson.

**Remarks:** While we have not yet recorded this species from Costa Rican waters, it is expected to occur offshore, especially in the Cocos Island region. The host fish(es) of this isopod are not known. Limited data suggest *A. meridionalis* occurs from shallow water to at least 600 meters.

**Distribution:** An offshore species, all published records being from near the islands of Galapagos, Revillagigedos, Clipperton, and Hawaii.

Genus *Nerocila* Leach, 1818

**Diagnosis:** Body generally more depressed than in most other cymothoid genera; dorsal chromatophores usually arranged in 3 longitudinal rows. Cephalon with anterior margin convex, acutely convex or concave; never projected anteriorly as in *Anilocra*. Cephalon with posterior border manifestly trilobate; cephalon not at all, or only weakly immersed in pereonite I.. Anterior border of pereonite I trisinate, matching posterior border of cephalon. Posterolateral angles of pereonites weakly to strongly produced, usually increasingly so posteriorly. Coxal plates well developed and prominent, generally extended almost to or to (but rarely beyond) posterolateral angles of their respective pereonites; coxal plates often do extend beyond medial margin of their respective pereonites. Pleon not at all immersed in pereon; pleonites subequal in length: pleonites 1 and 2 usually with prominent lateral extensions (epimeres). Pleopods typically with small lamellar accessory gills; pleopods 3-5 often thrown into deep pockets or folds. Juveniles and males of most species with pereopodal spines on posteriormost legs; females rarely with pereopodal spines.

**Remarks:** Considerable intraspecific morphological variation exists in most species of *Nerocila*. Of about 40 nominal species in the genus, world-wide, only 5 are known from the New World, and only 2 of these occur in the eastern Pacific (*N. excisa* and *N. acuminata*). As in *Anilocra*, species of *Nerocila* are true ectoparasites, most attaching on or at the base of the host fish's fin, or on the isthmus. Most species tend to show a broad (weak) host fish preference, based more on life history strategies and ecological preferences than on taxonomic specificity, with demersal and/or schooling fishes being preferred hosts.

*Nerocila acuminata*

Schioedte and Meinert, 1881

Fig. 15 b-d

For synonymy see Brusca, 1981.

**Diagnosis:** Length to 25 mm; usually with 3 longitudinal rows of dense chromatophores on

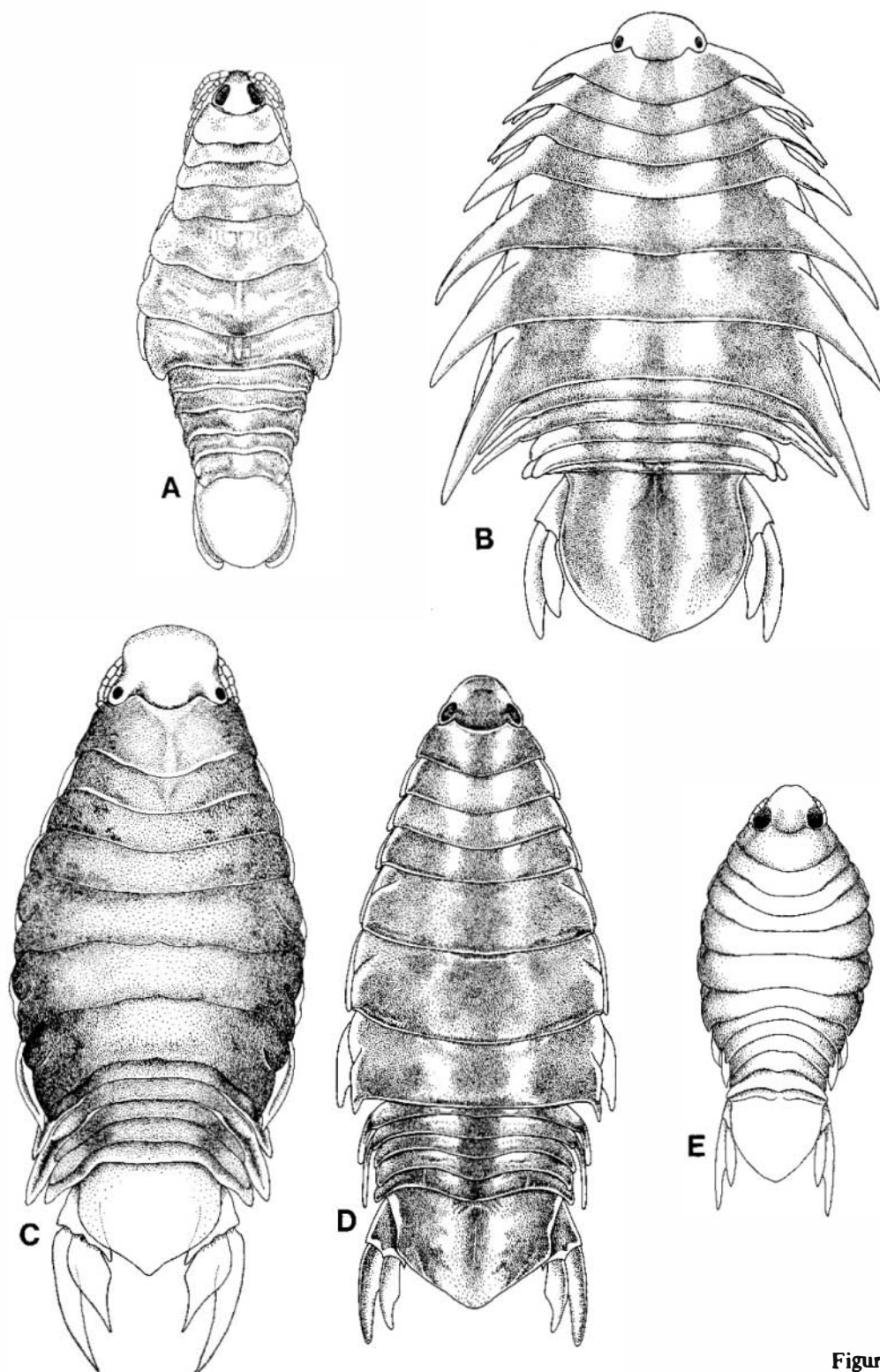


Figura 15

A, *Anilocra meridionalis* (from the type). B, *Nerocila acuminata*, aster form. C, *Nerocila acuminata*, acuminata form, female. D, *Nerocila acuminata*, acuminata form, male. E, *Nerocila excisa* (after Trilles, 1972c).

dorsum. Cephalon with frontal margin evenly rounded in females, subacute in males. Eyes moderately large to small; large females occasionally with eyes so reduced as to be apparently wanting. Posterolateral angles of all, or only posterior pereonites produced, acute or subacute, increasing in length posteriorly, those of VII may be extended up to  $3/4$  length of pleon. Coxal plates usually all visible in dorsal aspect; posterior angles of all, or only posterior coxae produced; subacute or acute. Posterior pereopods with bases flattened and somewhat grooved, without carinae. Pleopods with lamellar accessory gill on lateral margin of basis (usually folded in midline), and on medio-proximal margin of endopod, the latter being considerably folded on pleopods 3-5. Pleopods 4 and 5 with endopod thrown into deep transverse pockets or folds. Pleotelson shield-shaped, posterior margin slightly acuminate. Inner angle of uropodal basis developed into a large spine; exopod lanceolate; endopod subpyriform, shorter than exopod; both uropodal rami extending beyond posterior border of pleotelson.

**Remarks:** Brusca (1978a) provides descriptions and figures for juveniles (aegathoid stages). Brusca (1981) synonymized *N. californica* Schioedte and Meinert, 1881 with *Nerocila acuminata*. He also designated two distinct forms: *N. acuminata*, *acuminata*-form and *N. acuminata*, *aster*-form. In the former, the posterolateral angles of all, or only the posterior pereonites are produced, those of the anterior pereonites always being only weakly produced, rounded or subacute, and never reaching beyond the posterior borders of their respective segments. Similarly, the coxae of the *acuminata*-form rarely reach beyond the posterior borders of their respective segments. In *N. acuminata*, *aster*-form, the posterolateral angles of all the pereonites are strongly produced and acute, and all reach well beyond the medial posterior borders of their respective segments; those of VII typically reach at least to the anterior border of the pleotelson. The *aster*-form also has the coxal plates strongly produced, with acute posterior angles. These greatly extended, sharply pointed pereonites and coxae give the *aster*-form of *N. acuminata* a starlike appearance, hence the name. Morphological intermediates between the two forms occur, but are rare. Only the *acuminata*-form has so far been collected in Costa Rican waters, although the

*aster*-form is expected to also occur here, having been reported from western Mexico, the Galapagos and Tres Marias Islands, Hawaii, and various localities in the Caribbean.

*Nerocila acuminata* is known from at least 40 different host fishes in the eastern Pacific (see Brusca, 1981), evincing its low host specificity. Most records are from species of the families Engraulidae, Atherinidae, Serranidae, Mugilidae and Embiotocidae. Infestation rates are occasionally high in schooling species; to 57% of a catch for some embiotocids and to 90% for some engraulids. *Nerocila acuminata* has been taken from "Pargo" (Lutjanidae; species unknown), in shrimp trawls, from outside the Gulf of Nicoya (off Tárcoles). The following species of fishes, occurring in Pacific Costa Rican waters, are known to serve as hosts to *N. acuminata* elsewhere within its range: anchoveta (*Cetengraulis mysticetus*), broomtail grouper (*Mycteroperca xenarcha*), leatherjacket (*Oligoplites altus*), highfin corbina (*Menticirrhus nasus*), striped mullet (*Mugil cephalus*), sailfish (*Istiophorus platypterus*), striped marlin (*Tetrapturus audax*), oval flounder (*Syacium ovale*), and possibly the Pacific mackerel (*Scomber japonicus*). When taken in bottom trawls, these isopods commonly abandon the host before the trawl reaches the surface, hence caution must be used in determining which was the proper host fish. Tissue erosion at the site of attachment of the parasite, which can be considerable, is evidence of proper host identification.

**Distribution:** The range of *N. acuminata* in the eastern Pacific is from southern California to Peru, including the Gulf of California, Hawaii, and the offshore islands of Las Tres Marias and Galapagos.

*Nerocila excisa* (Richardson, 1901)  
Fig. 15e

For synonymy see Brusca, 1981.

**Diagnosis:** Cephalon with frontal margin distinctly excavate or concave (females occasionally lacking this concavity). Posterolateral angles of pereonites I-VI rounded, never produced into acute angles. Coxal plates of pereonites reaching posterior margin of their respective segment, or nearly so: those of V-VII

with posterior portions free from body margin; posterior angles of all coxae evenly rounded to subacute, never extended sharply beyond posterior borders of respective pereonites. Pereopods without carinae. Uropods extended beyond posterior margin of pleotelson.

**Remarks:** *Nerocila excisa* is principally an Indo-West Pacific species, not known from the mainland coast of America. It has been reported from Cocos Island and from several open ocean stations off Ecuador. Trilles (1972) comments on Richardson's description and provides figures. We have not ourselves collected this species in Costa Rican waters.

This species has been reported from the fin of a dolphinfish (*Coryphaena hippurus*), from the stomach of the same species, and from a soapfish (*Grammistes* sp.). No other host records are known.

**Distribution:** Oceanic Indo-West Pacific and eastern tropical Pacific.

#### Genus *Ceratothoa* Dana, 1853

**Diagnosis:** Cephalon more-or-less sunk in pereonite I; posterior border not trisinate. Basal articles of antennae 1 expanded and touching. Coxal plates compact. Anterior coxal plates never extended beyond posterior borders of their respective pereonites; posterior coxal plates may or may not be extended beyond posterior borders of their segments. Pleon with anterior segments narrower than and sunk in pereon. Some species lacking appendix masculina on second pleopods (of males).

**Remarks:** See Bowman (1978) for a discussion of nomenclatural problems with the genera *Ceratothoa*, *Codonophilus*, and *Glossobius*. We follow Bowman's recommendations, and herein consider *Ceratothoa* to be the senior synonym of both *Meinertia* and *Codonophilus*. There are two species of *Ceratothoa* known from the eastern Pacific, *C. gilberti* Richardson, 1904, and *C. gaudichaudii*. The former is probably endemic to the Gulf of California.

*Ceratothoa gaudichaudii*  
(H. Milne Edwards, 1840)

Fig. 16 a,b

For synonymy see Brusca, 1981.

**Diagnosis:** Cephalon with frontal margin subacute to truncate; antennae short, failing to reach midline of pereonite 1, and often falling short of posterior margin of cephalon. Dorsum of body moderately to strongly convex. Lateral regions of all pereonites weakly swollen above coxae, but never raised into distinct bosses. Posterolateral angles of all pereonites unproduced, smoothly rounded. All coxae compact, rounded, never produced; all coxae fail to reach, or barely reach posterior margins of respective segments. Pereopods with shallow grooves on bases; IV-VII with bases produced into large carinae; merus expanded, increasingly so on more posterior pereopods. Pleonite 1 narrow; 4-5 manifestly wider than 1; 3-5 subequal in width. Posterior margin of pleonite 5 trisinate (in female). Posterior margin of pleotelson evenly rounded. Uropods extended slightly beyond posterior margin of pleotelson; exopod and endopod similar in shape, exopod slightly larger than endopod.

**Remarks:** A wide ranging species, notably absent from the Gulf of California where Brusca (1981) has speculated it is excluded by competition with *C. gilberti*. We have not yet found this species in Costa Rican waters, although it almost surely occurs here as there are abundant records to the north and south.

See Brusca (1981) for a complete list of reported host fishes. Most records are from pelagic schooling fishes, especially members of the families Scombridae, Carangidae and Mugilidae.

**Distribution:** Southern California to Cape Horn, and around to southern Patagonia, South America; common from northern Mexico to northern Chile; rare south of Valparaíso.

#### Genus *Cymothoa* Fabricius, 1787

**Diagnosis:** Cephalon more-or-less immersed in pereonite 1, usually deeply immersed; anterior margin of pereonite I broadly excavate, with anterolateral corners produced to embrace cephalon. Antennae 1 widely separated at base; basal articles not expanded. Anterior coxal plates not reaching posterior borders of respective pereonites; posterior coxal plates nearly reaching, or extended slightly beyond posterior borders of pereonites. Pleon abruptly narrower than, and deeply immersed in, pereon. Pleonites increasing in length and width posteriorly.

**Remarks:** A poorly understood genus, with six species reported from the New World. *Cymothoa exigua* is the only species known from the eastern Pacific.

*Cymothoa exigua*

Schioedte and Meinert, 1884

Fig. 16 c

For synonymy see Brusca, 1981.

**Diagnosis:** Cephalon with posterior border weakly to moderately immersed in pereonite I. Antennae 1 of 7-9 articles; antennae 2 of 7-10 articles. Pereonite I longest; pereonites V-VI widest. All coxae fail to reach, or barely reach, posterior margins of respective segments; posterior angles of II-III (or IV) forming 90° angles; those of IV-VII subacute. Pereopods IV-VII with carinae on bases, increasing in size posteriorly. Pleonites 1-5 with medial elevation; 4-5 widest; 5 longest. All pleopods with lateral accessory lamella on bases, increasing in size posteriorly, as large as endopod on pleopod 5 (in females). Pleotelson wider than long, posterior margin concave in large individuals; straight or slightly convex in smaller individuals. Uropodal rami narrow and elongate, but not extended beyond posterior border of pleotelson.

**Remarks:** *Cymothoa exigua* has been reported from at least 8 different host fishes. It is very common on the bronzestriped grunt, *Orthopristis reddingi* in northern Mexico, and has been reported from several species of snappers (Lutjanidae), croaker and corbina (Sciaenidae). It has been recorded on *Lutjanus maculatus* from Panama. Females always occur in the buccal cavity, and males in the gill chambers (unless "in copula" with the female, in the host's mouth). All records of *C. exigua* are from depths shallower than 60 meters.

**Distribution:** Throughout the Gulf of California, south to Ecuador and the Galapagos Islands; our single Costa Rican record is from the Golfo de Nicoya, between Islas Jesucita and Negros.

Genus *Lironeca* Leach, 1818

**Diagnosis:** Cephalon weakly to deeply immersed in pereonite I; posterior border rarely

trisinuate. Anterior border of pereonite I broadly excavate to receive cephalon. Antennae 1 widely separated at base, basal articles not expanded. Pereopods in males usually with carinae on bases of posterior pairs; in females with or without carinae. Pleonites subequal in width; 1-2 only rarely narrowed or weakly immersed into pereonite VII. Pleopods often highly folded and/or with lamellar or digitiform accessory gills.

**Remarks:** Several papers have appeared in the recent literature on the biology of eastern Pacific *Lironeca* (e.g. Menzies *et al.*, 1955; Brusca, 1978b). In some species, both male and female inhabit the gill chamber, feeding either on the gills or upon the epithelium of the inner surface of the operculum (e.g. *L. puhi* Bowman, and *L. bowmani* Brusca). In others, the male infests the gill chamber whereas the female inhabits the buccal region, generally attaching near the base of the host's tongue. In some species females live in either the mouth or the gill chamber (e.g. *L. vulgaris* Stimpson; *L. ovalis* [Say, 1818]). Five species of *Lironeca* occur in the eastern Pacific, 3 of which are known or expected to occur in Costa Rican waters.

*Lironeca vulgaris* Stimpson, 1857

Fig. 16 e-f

For synonymy see Brusca, 1981.

**Diagnosis:** Cephalon with frontal margin weakly truncate; antennae 1 of 8 articles; antennae 2 of 10-11 articles. Pereonite I longest; IV-V widest. Coxal plates IV-VII or V-VII free distally, with posteriorly directed subacute angles; all extended to or beyond posterior margins of respective pereonites. Pereopods IV-VII with carina on bases, increasing in size posteriorly. Midline of pleon more-or-less elevated, forming a slight median rise. Pleotelson evenly rounded; width approximately 2 times length. Basis of pleopods 1-5 with lateral accessory lamella of variable size; pleopods 1-5 with medioproximal accessory lamella on endopod; pleopod 2 of female with at least a remnant of male appendix masculinum. Exopod and endopod of uropod subequal.

Brusca (1978b, 1981) discussed this species at some length, including its synonymy with *L. panamensis* Schioedte and Meinert, 1884.

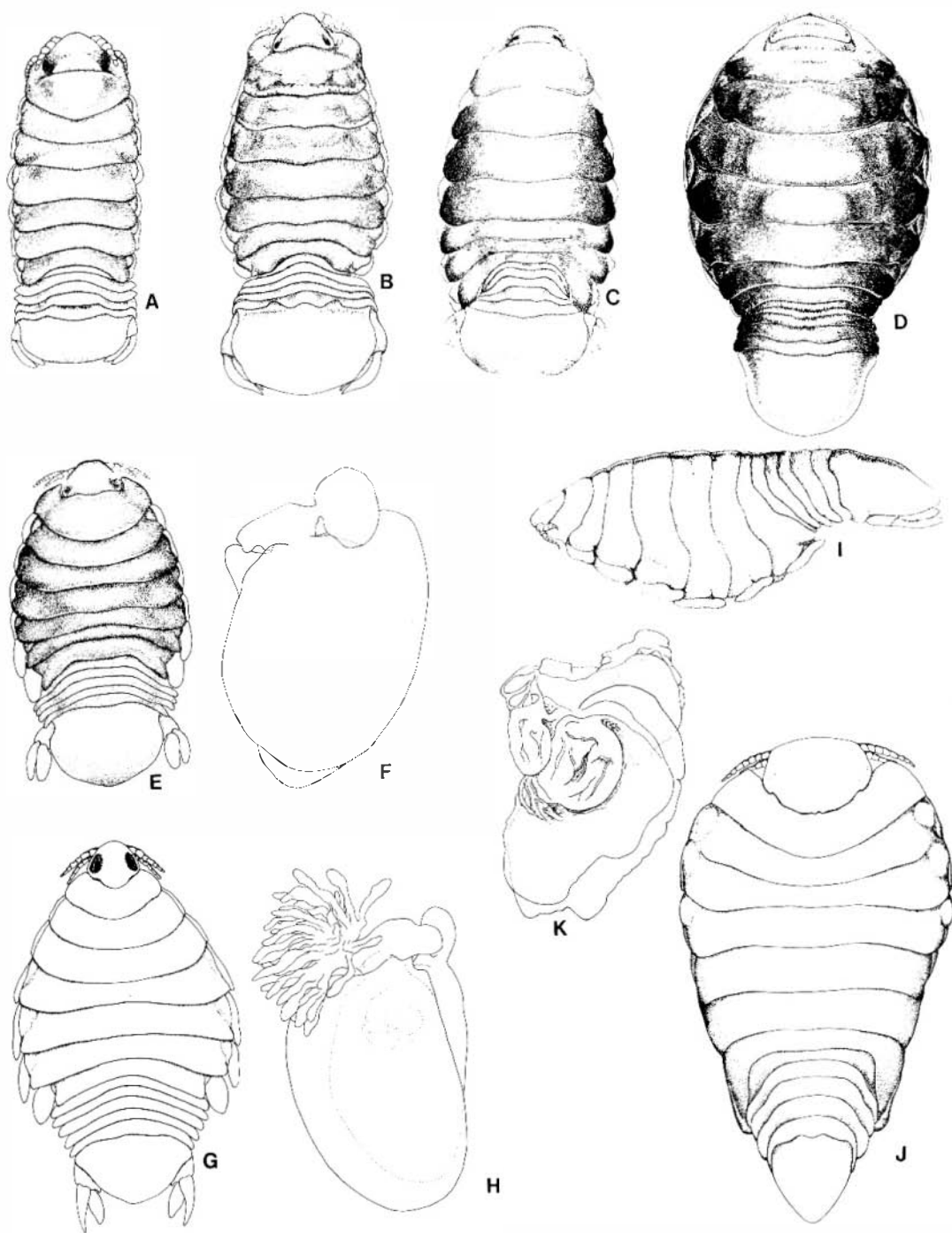


Figura 16

A, *Ceratothoa gaudichaudii*, male. B, *Ceratothoa gaudichaudii*, female. C, *Cymothoa exigua*, female. D, *Idusa carinata*, female. E, *Lironeca vulgaris*, female. F, *Lironeca vulgaris*, pleopod 3. G, *Lironeca bowmani*, female. H, *Lironeca bowmani*, pleopod 3. I, *Lironeca convexa*, lateral view. J, *Lironeca convexa*, dorsal view. K, *Lironeca convexa*, pleopod 3. (all figs. from Brusca, 1981).

**Remarks:** *Lironeca vulgaris* has been reported from 30 species of host fish (Brusca, 1981). While it obviously possesses a low level of host specificity, it does show a strong preference for bottom fishes of the families Scorpaenidae, Bothidae and Synodontidae, and schooling fishes of the family Embiotocidae. It is recovered regularly from surfperch, lingcod, sanddabs and lizard-fish. Although we have not made any positive host identifications for this isopod in Costa Rican waters, the following fishes occurring in this region are known to serve as hosts elsewhere in its range: *Trachurus symmetricus* (jack mackerel), *Serranus aequidens* (a tropical serranid), and *Cetengraulis mysticetus* (anchoveta). Both male and female are usually found in the host's gill chamber, although females occasionally migrate into the buccal region, affixing to the fish's tongue.

**Distribution:** A wide ranging species, distributed from Oregon (U.S.A.) to Colombia, South America, including the Galapagos and Juan Fernández Islands; common from San Francisco, California, southward; from depths of 1-311 meters. Our single Costa Rican record is from the Golfo de Nicoya.

*Lironeca bowmani* Brusca, 1981

Fig. 16 g-h

**Diagnosis:** Cephalon with posterior border moderately to strongly trisinate; weakly inserted into pereonite I. Antennae 1 of 8 articles; antennae 2 of 7-10 articles. Pereonite I longest; V-VI widest in smaller individuals, IV-V widest in larger specimens. Coxae II-III with posterior angles rounded or acute; IV-VII acute; II-III or II-IV extended barely past posterior margin of respective pereonites; V-VII extended well beyond posterior border of respective pereonites. Pereopods (in female) lacking carinae on bases. All pleopods with dendritic accessory gill (arising from endopod on pleopod 1; from basis on pleopods 2-5). Pleotelson shield-shaped, posterior margin subacuminate; width only slightly greater than length. Uropodal endopod and exopod tapering distally, extended beyond posterior border of pleotelson; exopod shorter and broader than endopod.

**Remarks:** *Lironeca bowmani* is strikingly different from all eastern Pacific congeners in

its possession of complex digitate accessory gills on the pleopods. In addition, the uropods are manifestly longer than any other eastern Pacific *Lironeca*, extending well beyond the posterior margin of the pleotelson.

*Lironeca bowmani* has been recovered from three species of host fishes from Mexican waters. Positive host identifications for the southern part of its range have not been made.

**Distribution:** Present records are from throughout the Gulf of California and western Mexico, and from Malpelo Island (Colombia). The absence of records between central Mexico and Panama is most likely due to inadequate sampling. Existing collections are from shallow water to 80 meters.

*Lironeca convexa* Richardson, 1905

Fig. 16 i-k

For synonymy see Brusca, 1981.

**Diagnosis:** Cephalon subquadrate; posterior border weakly trisinate and deeply immersed into pereonite I; frontal margin broad, weakly convex. Antennae 1 of 7-8 articles; antennae 2 of 8-11 articles. Pereon strongly convex dorsally. Pereonite I longest, anterior margin weakly crenulate; anterolateral angles broadly rounded, produced forward to border posterior 2/3 of cephalon. Pereonites IV-V widest. Pereonites II-IV with anterolateral bosses. Coxae of pereonites II-VII occupy entire lateral margins of respective pereonites, VII often extended barely beyond posterior border of its somite; posterior angles of coxae II-IV abruptly rounded, those of V-VI broadly rounded, VII rounded or subacute. Females with carinae lacking on bases of pereopods I-VI, and weakly developed on VII; males with distinct carinae on bases of pereopods IV-VII. Pleonites decreasing gradually in width posteriorly. Pleotelson tapers strongly posteriorly, apex acutely rounded; maximum width subequal to length. Pleopods 1-5 with lamellar accessory gill on bases; endopods with medioproximal accessory lamella, large and folded on 3-5; exopods with lateral accessory lamella. Uropods large, extended to or past posterior margin of pleotelson; endopod wider, but shorter than exopod.

**Remarks:** This species is easily distinguished from its eastern Pacific congeners by the presence of the anterolateral dorsal bosses on pereonites II-IV, and the strong, dorsally-convex body form.

Most host records are from the Pacific bumper, *Chloroscombrus orqueta* (Carangidae), which ranges from southern California to Perú. Additional host records include pompanos (*Trachinotus* spp.) and an unidentified species of *Serranus*. See Menzies *et al.* (1955) and Brusca (1981) for further data. Females are invariably found in the host's buccal cavity, males in the gill chamber.

**Distribution:** Southern California to the Gulf of Guayaquil, Ecuador; uncommon north of Nayarit, Mexico. Although we have not collected this species in Costa Rican waters, its occurrence here is anticipated; we have records from both El Salvador and Panama.

Genus *Idusa* Schioedte and Meinert, 1883

**Diagnosis:** Body narrow, laterally compressed and dorsally convex. Cephalon immersed in pereonite I; anterior border of pereonite I broadly excavated to receive cephalon. Basal articles of antennae 1 nearly touching at base, but not expanded as in *Ceratothoa*. Posterolateral angles of pereonites not acute or extended. Coxal plates small and compact. Pleon somewhat narrower than, and somewhat immersed in pereon.

**Remarks:** *Idusa* is a small genus, 6 species having been described from the east and west Pacific. Only one species is known from the New World.

*Idusa carinata* Richardson, 1904

Fig. 16 d

For synonymy see Brusca, 1981

**Diagnosis:** Anterior margin of cephalon medially produced and acute. Antennae 1 of 5-7 articles; antennae 2 of 7-9 articles. Pereonite I longest, anterolateral angles acute, produced to border eyes. Pereonites IV-V widest. Coxal plates not visible in dorsal aspect due to lateral compression of body; in lateral view II-VI extended 2/3-3/4 the distance to the posterior

borders of their respective pereonites; VII extended to posterior margin of its pereonite; I usually with a deep suture line, indicating incomplete fusion with its somite. All pereopods with carinae on bases, increasing in size posteriorly, those of posterior legs strongly grooved to receive ischium-merus-carpus. Pleonites increasing gradually in length and width posteriorly. Pleopods 3-5 with small medio-proximal extension on endopod. Posterior margin of pleotelson evenly rounded; pleotelson often strongly "folded" or compressed laterally. Uropodal endopod and exopod minute, substyliform, subequal in length to basis.

**Remarks:** A rare species, so far known from only 4 collections; 2 from the Gulf of Panamá and 2 from Guayaquil, Ecuador. Its discovery in Costa Rican waters is anticipated.

The only host data recorded for *Idusa carinata* is that accompanying the original type specimens, in which Richardson stated, "always found in mouth of *Mugil hospes*", a shallow water mullet (Mugilidae).

**Distribution:** So far reported from only Ecuador and Panama.

## Family Serolidae

Body strongly depressed and usually broad. Antennae 1 with 4 peduncular articles; antennae 2 with 5. Mandible and maxilliped with palp; maxillipedal palp of 2-4 articles. Pereonite I fused medially with cephalon. Tergum of pereonite VII usually absent, or if present incomplete, making this segment appear missing in the dorsal aspect. Pereopod I of both sexes, and II of adult males, subchelate, with dactyl folding back upon highly inflated propus. Coxal plates of posterior pereonites often not visible in dorsal aspect. Pleopods 4-5 large, indurated and operculiform; pleopods 1-3 small, natatory. Pleonites 4-6 fused with telson, forming a large terminal pleotelson. Uropods small, not arching over pleon; peduncle and endopod coalesced in some species, in which case the exopod may be greatly reduced.

The family Serolidae is principally cold-water in distribution, nearly all of the described species restricted to the Southern Hemisphere (see Sheppard, 1933 and Kussakin, 1973).



Several species are known to penetrate subtropical waters in the west Atlantic (*Serolis mgrayi* Menzies and Frankenberg, and *S. vema* Menzies in the northern hemisphere; several species in the southern hemisphere), and in the eastern Pacific (*S. carinata* Lockington). There exists only two described species in this family from truly tropical waters, *S. yongei* Hale (Great Barrier Reef, Australia) and *S. tropica* Glynn (Central America). Serolids range in depth from the intertidal to the abyss, although most species are shallow-water (0-100m). Deep sea species are generally blind or have degenerate eyes. Serolids are carnivorous or omnivorous, epibenthic, highly motile animals capable of varying degrees of shallow burrowing.

Although there are several genera in the family, *Serolis* is the largest and best known, and is the only genus reported from North American waters. Considerable work has been published on the natural history of the Brazilian species of this genus by Moreira (1971; 1973a; 1973b; 1974a; 1974b; 1974c; 1976a; 1976b; 1977a; 1977b) and Bastida and Torti (1967). Many species appear to be predators and/or scavengers, and most lead a benthic life-style burrowing just beneath the surface of fine sediments and sands. Several species have been reported from intertidal habitats.

#### Genus *Serolis* Leach, 1818

**Diagnosis:** With the characters of the family.

*Serolis tropica* Glynn, 1976

Fig. 17 a

**Diagnosis:** Peduncular articles of antennae stout; articles 2-3 of antennae 2 form right angle to one another (resembling antennal articles 1 and 2 of *Eurydice*). Pereon without mid-dorsal spines; posterolateral angles of pereonites rounded, not acute. Coxal plates of pereonite VI extend nearly to midline of pleotelson. Suture between pereon and pleonite 1 complete. Pleotelson with 3 dorsal carinae; mid-carina extremely thin, lateral carinae weakly formed; lateral notch of pleotelson shallow, not forming distinct tooth. Uropods biramous; posterolateral angle of peduncle obtuse.

**Remarks:** An easily recognized species, and one of only two *Serolis* known from the entire

eastern Pacific. The other, *S. carinata*, ranges from southern California to the Gulf of California, and is easily distinguished from *S. tropica* by the presence of a row of distinct mid-dorsal spines on the cephalon and pereon. *Serolis tropica* has not been reported since its original description and although we have not yet collected it in Costa Rica its presence there is anticipated.

Glynn (1976) reported *S. tropica* from the low intertidal region near the Pacific entrance to the Panama Canal (Bay of Panama). All specimens were collected from sand and shell bottom substrates.

**Distribution:** So far reported only from the type locality, the Bay of Panamá.

#### Family Limnoriidae

Small (2-4 mm total length), wood or alga boring forms. Eyes lateral. Antennae separated along midline, not contiguous at base; both pairs of antennae nearly in transverse line, neither markedly more anterior than other; obvious scale present on first antenna. Mandible lacking molar process and with reduced lacinia. Posterior part of cephalon slips under anterior margin of first pereonite. Penes consist of a pair of elongate plates that articulate with body. Coxal plates present on pereonites II to VII. Uropods lateral, either tubular or claw-like, not expanded and flattened. Maxillipedal palp of 5 articles; mandible usually with a rasp and file arrangement. Pleon consisting of five distinct somites plus a large semicircular pleotelson.

In his excellent monograph, Menzies (1957) revised the family Limnoriidae (the "gribbles" as they are commonly called) dividing the previously monogeneric family into two genera: *Limnoria* Leach, 1813; and *Paralimnoria* Menzies, 1957. The former genus is further divided into two subgenera. *Limnoria* containing only wood boring species and *Phycolimnoria* containing only algal boring species. To date, only the genus *Limnoria* has been reported from the west coast of North America.

The Limnoriidae are by far the most economically important isopods, accounting for millions of dollars in damage to wooden marine structures annually. Characteristically wood boring *Limnoria* make a shallow burrow in the outer few inches of the wood. Excavation of a

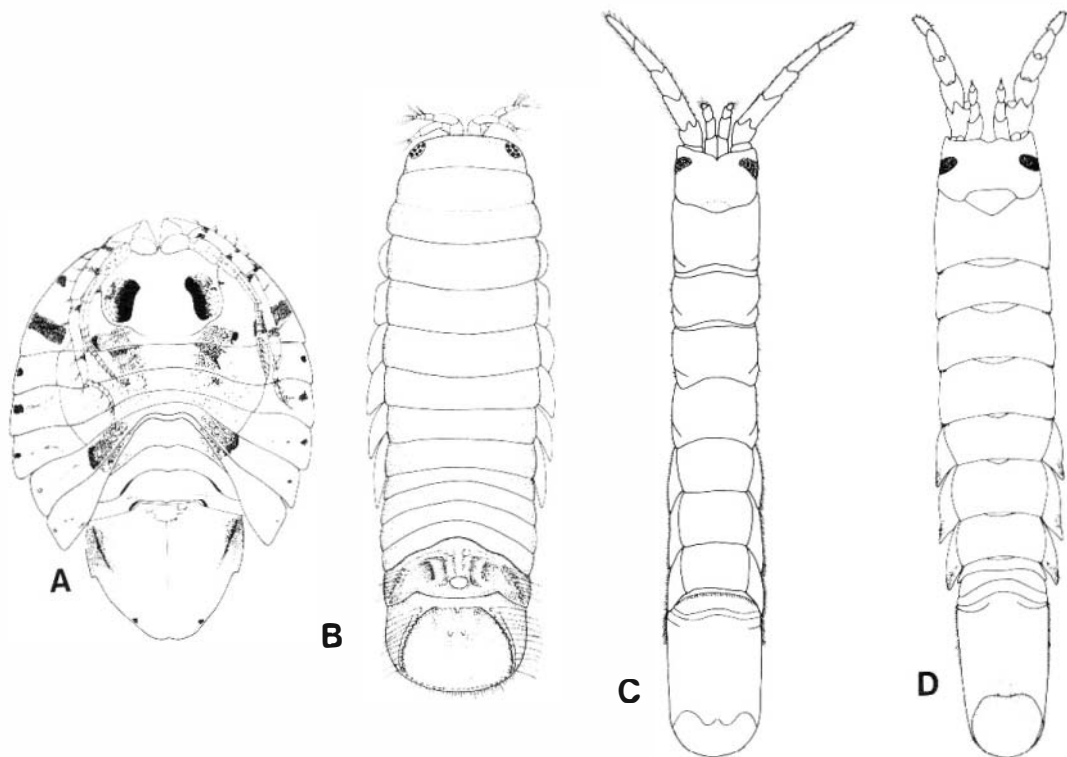


Figura 17

A. *Serolis tropica* (from Glynn, 1976). B. *Limnoria tripunctata* (after Menzies, 1957, and Menzies and Glynn, 1968). C. *Cleantioides occidentalis* (from Brusca and (1979a). D. *Cleantioides planicauda* (from a specimen collected off Oaxaca, Mexico).

new burrow is started within a few hours of the isopod settling on a piece of wood. When it has constructed the burrow deep enough to shelter two adults, it is joined by a second isopod, usually of the opposite sex. Copulation is believed to take place within the burrow. As young animals are released from the brood pouch, they in turn begin excavating side burrows from their parent's burrow within a few hours of being released. Even at moderate population densities, such burrowing creates an outer layer of very fragile wood which is easily eroded by wave action, resulting in the "hour glass" shape characteristic of *Limnoria* infested pilings. The highest concentration of animals is typically found within the intertidal zone.

It was once thought that members of this family burrowed for shelter, but now it is known that they also ingest the wood as a food source (or algae, in the case of *Phycolimmoria*). Unlike some terrestrial insects, such as termites, *Limnoria* produces its own cellulase and does not harbor any microbial symbionts in the gut

(Ray and Julian, 1952; Ray and Stuntz, 1959; Ray, 1959a; 1959b; 1959c; Fahrenback, 1959). Boyle and Mitchell (1978) showed that *L. lignorum* and *L. tripunctata* guts were devoid of all microorganisms, including bacteria, suggesting that some interesting antibiotic compounds may be produced by these isopods.

Algae burrowing species infest the holdfasts of brown algae belonging to the order Laminariales (the "kelps"). Unlike the wood boring species their burrows are difficult to detect, and are best seen by slicing thin sections from the holdfast. Also unlike wood boring species, *Phycolimmoria* lacks the characteristic highly branched burrow. If present, generally a single burrow will be exposed running down one or more of the rhizoids. Periodically, both algae and wood boring species excavate "air" holes to the exterior which insure the circulation of oxygenated water within the burrow.

Seasonal migration has been demonstrated for *L. (L.) lignorum* at Friday Harbor, Washington by Johnson (1935) and Johnson and Miller

(1935). Johnson and Menzies (1956) showed that seasonal migration of *L. (L.) tripunctata* at San Diego Bay, California is probably due to a combination of reaching sexual maturity and population pressure due to overcrowding. The migration phenomenon is strongly influenced by peak water temperature, since increased temperatures accelerate the rate of growth, attainment of sexual maturity, egg production, and incubation period. Menzies (1961) demonstrated that *L. (L.) tripunctata* probably also undergoes a diurnal migration. Kofoed and Miller (1929) studied the salinity tolerances of *Limnoria*. In general, prolonged salinities less than 15 percent are lethal to these isopods (Menzies, 1957). Menzies (1954) studied the reproductive biology of the family in detail. A brief account of the parasites of *Limnoria* is given in Kofoed and Miller (1927). Several workers have dealt with symbiotic protozoans of *Limnoria* (Kofoed and Miller, 1927; Mohr and LeVeque, 1948; Mohr, 1959; and Mohr *et al.*, 1963) from the eastern Pacific Ocean. The most common epizotic protozoans on California *Limnoria* are the folliculinid, *Mirofolliculina limnoriae*, and members of the family Chonotrichidae. The former species is readily recognizable as large dark spots on the dorsal surface of the pleotelson and adjacent segments. Reish (1954) reported five species of polychaetes and a turbellarian to be predators on *Limnoria*.

*Limnoria* Leach, 1813

**Diagnosis:** Flagellum of first antenna of 4 articles. Flagellum of second antenna of 3-5 articles. Mandibular incisor with or without "rasp and file"; lacinoid seta of right mandible always flattened, never tubular, and with apex of variable structure. Exopod of uropod much shorter than endopod, and provided with an apical claw; endopod elongate, apex blunt, lacking claw. Fifth pair of pleopods lack marginal setae.

**Remarks:** *Limnoria* can most readily be distinguished from *Paralimnoria* by the characteristics of the uropods. In the latter species, both branches are similar, exopod and endopod each elongate and with an apical claw. Other differences in *Paralimnoria* include: flagellum of the first antenna of five articles; lacinoid seta of right mandible tubular; and, fifth pair of pleopods with marginal setae.

We have not collected any Limnoriidae in Pacific Costa Rican waters, nor have any been reported in the literature. However, *Limnoria tripunctata* is suspected to occur here, as it is the most widely distributed limnoriid in North and Central America, occurring on both coasts of the Americas in waters ranging from at least 15 °C to 30 °C.

*Limnoria (Limnoria) tripunctata* Menzies, 1951  
Figs. 17b, 18

Synonymy (partial), subsequent to Menzies, 1957: Johnson and Menzies, 1956: 54; Kampf, 1957: 359; Menzies and Becker, 1957: 85; Menzies, 1958: 267; 1959: 10; 1961: 170; 1968: 802; Bourdillon, 1958: 437; Menzies and Beckman, 1958: 172; Becher and Kampf, 1958: 1; Kohlmeyer *et al.*, 1959: 457; Lane, 1959: 34; Ray, 1959c: 46; Becker, 1959: 62; Mohr, 1959: 84; Menzies and Robinson, 1960: 132; Beckman and Menzies, 1960: 9; Eltringham and Hockley, 1961: 466; Eltringham, 1964: 675; 1965: 145; Menzies *et al.*, 1963: 99; Jones, 1963: 589; Anderson and Reish, 1967: 56; Menzies and Glynn, 1968: 23; Naylor, 1972: 23; Bastida and Torti, 1972: 143; Sleeter and Coull, 1973: 97; Miller, 1975: 296, 307; Carlton, 1975: 18; Sleeter *et al.*, 1978: 329.

**Diagnosis:** Flagellum of second antenna of 5 articles. Epipod of maxilliped triangulate; 2.5 times as long as wide; just reaching the articulation of the palp-endopod. Mandibular palp of 3 articles. Dorsal surface of pleon with 2 anteriorly located, medial, elevated nodes and a single posteriorly elevated area; central part depressed. Pleotelson medially with one anteriorly located tubercle followed by a pair of tubercles, each of which is followed by a longitudinal carina. Dorsal surface of posterior margin of pleotelson tuberculate, spike-like bristles lacking; lateral crests conspicuously tuberculate. Lacinoid seta of right mandible abruptly curved distally, bearing 2 prominent, flattened, apically spinose projections.

**Remarks:** The three pleotelson tubercles of *L. (L.) tripunctata* are similar to those of *L. (L.) japonica* Richardson, 1909, but the latter species is distinguished as follows: pleonite 5 with two medially located tubercles, the anterior tubercle separated from the posterior one

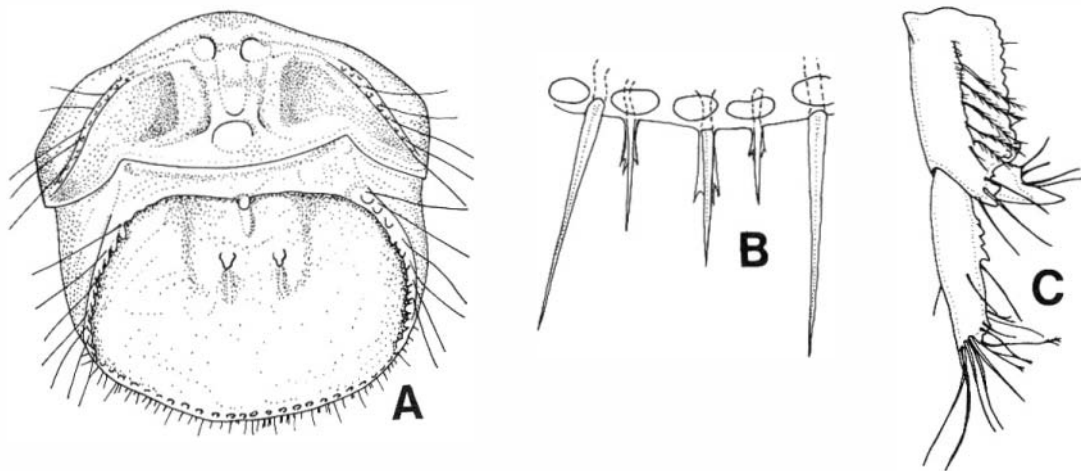


Figura 18

*Limnoria tripunctata* (after Menzies, 1957): a, pleotelson. b, posterior edge of pleotelson. c, uropod.

by a prominent sulcus; flagellum of second antenna with 4, not 5 articles; and, the pleotelsonal margin lacks the tuberculations characteristic of *L. (L.) tripunctata*.

Esakova (1965) synonymized *L. tripunctata* with the much older Russian species *L. tuberculata* Sovinsky, 1884. Although we have not had an opportunity to examine the latter species, Esakova's (1965) figures (1a and 2) suggest that these species may be distinct. The most noticeable difference is a row of small tubercles (or perhaps large granules) posterior to the 2 posterior tubercles on the pleotelson. It should be further noted that these tubercles occur only on the posterior half of the pleotelson, while in *L. tripunctata* there is a very low, nearly indistinguishable ridge directly behind the 2 posteriormost tubercles. These ridges do not extend much past the midline of the pleotelson. Other differences, such as the general shape of the pleon and the posterior fringe of setae on the pleotelson also suggest that *L. tripunctata* is a distinct species. Fresh material of these species should be carefully compared before this proposed synonymy is accepted.

Of all the *Limnoria* species, this is perhaps the most widely distributed. It may also be the most economically important species in the family, as the attack of wooden structures by *L. tripunctata* is not prevented by treatment with creosote. In California, it is not unusual to find this species co-occurring in the same piece of wood with *L. (L.) quadripunctata*. In San

Francisco and Los Angeles-Long Beach harbors, the latter species is apparently restricted to the colder water near the harbor entrances, while *L. (L.) tripunctata* penetrates the warmer regions of the back bays (Menzies, 1958). The period following the discovery of gold in California in 1849 has been proposed by Carlton (1975) as a possible date of introduction into California. During the Gold Rush period, numerous wooden sailing craft left Atlantic ports for the trip around Cape Horn, only to be abandoned in San Francisco Bay.

**Distribution:** A circum-tropical/warm-temperate species. In the eastern Pacific *L. tripunctata* ranges from British Columbia, Canada (about 51°N) south to at least Panama and Ecuador. Its principal distribution is in warmer waters and north of central California it is generally restricted to the warm, less saline regions of bays and estuaries, while the less eurytopic species *L. lignorum* inhabits the outer bay regions and outer coasts. An alternative to the Atlantic-Pacific introduction hypothesis suggested by Carlton is the possibility that this species remains as a remnant of the pre-Pliocene transisthmian fauna (the "Tertiary Caribbean Province" of Woodring, 1966).

#### SUBORDER VALVIFERA

The suborder Valvifera is perhaps the most distinct of all isopod taxa of this categorical

rank standing apart from all other isopod suborders in several regards, most notably in the morphology of the pereopodal coxae, uropods and penes. Only in the Valvifera are the uropods modified to form opercular coverings for the pleopods; a remarkable and complex anatomical adaptation. Also, only in the Valvifera do the pereopodal coxae expand ventrally to form "ventral coxal plates" (as well as dorsolaterally to form the typical "dorsal coxal plates"). The Valvifera also have moved the opening of the vas deferens and the penes to the pleon, an arrangement found in only one other isopod taxon, the Oniscoidea. In the Valvifera the penes are situated on pleonite I or on the articulation between pleonite I and pereonite VII. The suborder is currently composed of 6 families. The family Idoteidae contains 5 subfamilies, only one of which is probably represented on Pacific Costa Rican shores (the Idoteinae).

The idoteid subfamily Idoteinae contains 22 nominal genera (Brusca, 1984). The majority of the species are shallow-water, most being intertidal or shallow-subtidal forms. Very few species are restricted to depths greater than 30 m, although a number of the shallow-water taxa are known to range occasionally to these depths or undergo submersion in the low latitude portion of their range. The Pacific North American idoteid fauna is well known,

and is reviewed in Menzies (1950), Menzies and Miller (1972), Brusca and Wallerstein (1977, 1979a, b), Wallerstein and Brusca (1982) and Brusca (1984).

### Family Idoteidae

Valviferan isopods with the body generally somewhat depressed; ovate, oblong or elongate. First pair of antennae usually shorter than second pair, and with flagellum reduced to 1-4 minute articles. Flagellum of second antennae multiarticulate, reduced to a few vestigial articles, or reduced to a single large clavate article. Mouth parts well developed, of the chewing and biting type; mandibles without palp; maxillipedal palp of 3-5 articles. Pereopods ambulatory, anteriormost ones occasionally approaching subchelate form. Pleonites tend towards fusion; pleon of 4 or fewer free pleonites, plus the pleotelson; pleonites entirely fused in some genera. Uropods uniramous or biramous. Penes fused basally, or rarely separated at base.

Idoteids are common in temperate littoral habitats, but rare in tropical latitudes. Only one species has been reported from Pacific Costa Rica (*Cleantioides occidentalis*), although a second is expected to occur here, perhaps with some rarity (*Cleantioides planicauda*).

### Key to the Species of Pacific Costa Rican Idoteidae

1. Coxal plates visible in dorsal aspect on pereonites II-VII; maxillipedal palp of 4 articles . . . . *C. occidentalis*
- Coxal plates visible in dorsal aspect on pereonites V-VII only; maxillipedal palp of 5 articles . . . . *C. planicauda*

### Genus *Cleantioides* Kensley and Kaufman, 1978

**Diagnosis:** Body parallel-sided; 5-6 times longer than broad. Flagellum of antenna two of a single clavate article. Maxillipedal palp of 4 or 5 articles. Pereopods IV greatly reduced, nonambulatory. Pleon composed of 3 complete and 1 incomplete segments (the latter indicated by lateral "incisions" or "suture lines"), plus pleotelson. Uropods uniramous.

**Remarks:** Considerable confusion exists regarding the status of the genera *Cleantioides*,

*Cleantis*, and *Zenobiana* (reviewed in Tattersall, 1921; Kensley and Kaufman, 1978; and Brusca and Wallerstein, 1979a). Based on the diagnosis of this genus established by Brusca (1984), *Cleantioides* appears to contain only two valid species, both of which are discussed below.

### *Cleantioides occidentalis* (Richardson, 1899) Fig. 17c

For synonymy see Brusca and Wallerstein, 1979a.

**Diagnosis:** Body nearly 6 times longer than wide. Supra-antennal line with a small median

emargination; apex of frontal process broadly rounded; frontal lamina 1 produced medially; frontal lamina 2 truncate. Maxillipedal palp of 4 articles; endite with 2-4 coupling hooks. Lateral margins of body with dense tufts of plumose setae. Coxal plates visible in dorsal aspect on pereonites II-VII. Pleotelson with a pair of dorsal humps; appendix masculinum of male arises medially on endopod of pleopod 2.

**Remarks:** We have seen only one collection of this species from Costa Rican waters (Golfo Dulce; 20-44 m; coarse sand substrate; March, 1939; *Velero III*). Numerous additional specimens have been examined from throughout western Mexico, Guatemala, Panama, Ecuador and the Galapagos Islands.

*C. occidentalis* is typically found in intertidal and shallow subtidal waters, on sand and muddy-sand substrates. It has been reported from depths as great as 50 m, and in salinities ranging from that of the open sea to approximately 26 ppt.

**Distribution:** Northern Gulf of California, Mexico, south to Ecuador, including the Galapagos Islands.

*Cleantioides planicauda* Richardson, 1899

Fig. 17d

Synonymy subsequent to Richardson, 1905: *Cleantis planicauda*. Menzies 1962a (in error, see Brusca and Wallerstein, 1979a); Menzies and Frankenberg, 1966: 23; Brusca and Wallerstein, 1979a: 90, 1979b: 266. *Cleantioides planicauda*. Kensley and Kaufman, 1978: 661 (Brusca, 1984)

**Diagnosis:** Body about 5.4-5.6 times longer than wide. Supraantennal line with a small median emargination; apex of frontal process subacute; frontal lamina 1 acutely rounded; frontal lamina 2 truncate. Maxillipedal palp of 5 articles; endite with 3 coupling hooks. Lateral margins of pleotelson with tufts of plumose setae. Coxal plates visible in dorsal aspect on pereonites V-VII only. Pleotelson with distal portion of dorsal surface strongly excavate.

**Remarks and Distribution:** An ampho-American species, known from throughout the Caribbean region (Puerto Rico to Florida) and north to Georgia. In the eastern Pacific it has so

far been reported from only a single locality, off southern Mexico (Brusca and Wallerstein, 1979a; 1979b). Authorship of this species is usually shown as, "*C. planicauda* Benedict in Richardson, 1899", acknowledging that Richardson's original description was taken from a manuscript by James E. Benedict. However, Benedict never published the manuscript (or if he did he omitted this species), hence the valid authorship belongs to Richardson.

## SUBORDER ANTHURIDEA

Anthurids are quickly recognized by their long, narrow, cylindrical body form (length 6-15 times width). They are diagnosed as follows: Antennae usually short, with few flagellar articles; antennae 1 always with peduncles of 3 articles; antennae 2 always with peduncles of 5 articles. Maxilliped with small endite but no coupling hooks; palp of 0-5 articles, apex pointed or rounded. Mandible with or without a palp; without lacinia mobilis, although a small lobe may be present that is said to be the remainder of the setiferous lobe that, in other peracarids, sits between the lacinia and molar process; this lobe has been referred to as the "lamina dentata" (Wägele, 1981b). Maxillae 1 and 2 usually uniramous. Pereonites mostly longer than wide, in contrast to most isopods in which the reverse is the case. Distinct coxal plates usually not evident. Anterior pereopods often tend towards subchelate form, particularly first pair. Pleon relatively short, consisting of 5 pleonites plus the pleotelson, or 6 pleonites plus the telson. Oftentimes some or all pleonites may fuse, although segmentation is generally still evident by virtue of free lateral margins, lateral grooves or suture lines, or pigmentation pattern. Uropods distinct, attaching laterally but with exopods curving dorsally to arch over pleotelson; statocysts often present in pleotelson.

The body somites of anthurids often possess minute dorsal pores, or well-developed ridges and grooves. Sexual dimorphism is usually distinct in the structure of the first antennae (flagellum often elongate and brush-like in males). Many species are known to be protogynic sequential hermaphrodites.

Norman and Stebbing (1886), and later Barnard (1925, in a detailed and highly praised

study of the Anthuridca), divided this suborder into two groups based on mouth part morphology and other characters. Menzies and Glynn (1968) gave these groups formal nomenclatural status in assigning them familial recognition. A third family, the Hyssuridae, was recently created for those presumably primitive genera lacking telsonic statocysts and possessing long free pleonites (Wägele, 1981a; 1981b; 1981c). These three families are characterized below.

The Hyssuridae have a body about 15 times longer than wide. The adults are small, mostly 3-8 mm long, although some reach 10 mm in length. The pleonites are elongate and unfused and none of the pleopods are operculate. The pleotelson lacks statocysts. About 10 genera of Hyssurids are recognized in the world.

The Anthuridae are not as slender as the Hyssuridae, always have a pair of telsonic statocysts, and have the first pleopod larger than all others, with the exopod forming an operculum covering the other pleopods. The maxillipedal palp consists of 4 or fewer articles and is as broad as the basipodite. As in the Hyssuridae, the mouth parts are "normal" (biting); the apex of the mandibular palp is rounded and the mandibular incisor is usually toothed. About 35 genera are recognized in the world.

The Paranthuridae bear a single telsonic statocyst, or have secondarily lost it. The mandibular palp is composed of 1-3 articles. Paranthurid mouthparts are pointed and modified for "piercing and sucking"; the mandibular incisor is pointed and lacks teeth; maxillae 1 are long, pointed, barbed stylets; the maxilliped is elongate and tapering, with a reduced palp. There have been about 12 genera assigned to this family (see Poore, 1980, for an excellent review of the family and a key to the genera).

Anthurids, while not being represented by as many species as most other isopod suborders, are an abundant and important component of the offshore soft-sediment marine environment. Most are small, less than 15 mm in length, and live in sediment burrows of either their own construction or of other animals. They also occur commonly in algal mats on hard substrates in both littoral and sublittoral habitats. Although the majority of species are marine, a few freshwater forms are also known. A total of about 125 species have been described.

Anthurids are rare in the New World tropics, and until now only 5 species had been reported from the tropical eastern Pacific, none of which were actually known to occur south of the subtropical Gulf of California (Schultz, 1977; Nunomura, 1978; Brusca, 1980): *Califanthura squamosissima* (Menzies), *Paranthura elegans* Menzies, *Mesanthura occidentalis* Menzies and Barnard, *Cortezura penascoensis* Schultz, and *Paranthura californiae* Nunomura. We have collected a single species of Anthruidea from Pacific Costa Rican shores, *Cyathura guaroensis* n.sp. It is the first anthurid reported from the Panamic Province.

Family Anthuridae Leach, 1814

Genus *Cyathura* Norman and Stebbing, 1886

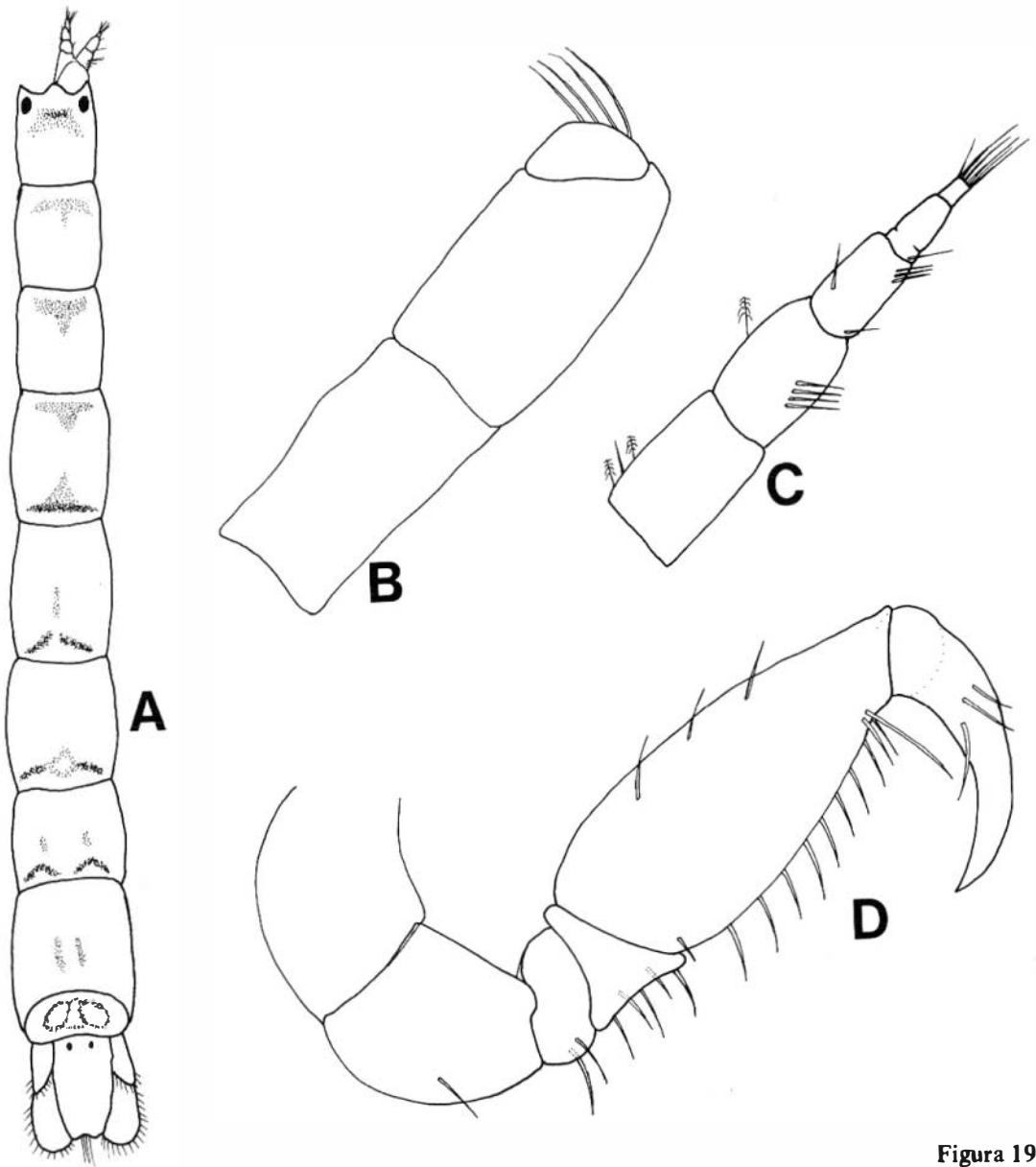
**Diagnosis:** Mouth parts for chewing (*i.e.* apex of maxilliped rounded); maxilliped of 4 articles (3 free). Eyes usually present. Pereon often with dorsolateral keels and pits. Carpus of pereopods IV-VII underriding propus. Pleonal sutures indistinct dorsally. Pleopod 1 not indurate. Pleotelson thin and smooth.

**Remarks:** This genus contains more species than any other New World anthurid taxon. Many *Cyathura* are blind hypogean interstitial species. Of the 8 species now known from the New World, only two occur in the Pacific (*C. munda* and *C. guaroensis* n.sp.). A common Atlantic species, *C. polita* (Stimpson) has been the subject of intensive study by W.D. Burbanck and his colleagues since 1959 (for a review of the ecology of *C. polita*, including a list of references, see Burbanck and Burbanck, 1979).

*Cyathura guaroensis* n. sp.

Fig. 19

**Diagnosis:** Moderate in size, to 4 mm length. Rostral projection equalling forward extent of anterolateral angles of cephalon. Eyes small, ornatidia not discernible. Uropodal exopods very short; endopods long, extended beyond posterior margin of telson; both uropodal rami with setose margins. Telson with apical concavity bearing 4 long setae; paired statocysts present anteriorly. Maxilliped with 3 free articles, the distalmost bearing 4 long setae. Pereopod 1 propus without large tooth on

**Figura 19**

*Cyathura guaroensis*: a, dorsal view. b, maxilliped. c, antenna 1. d, pereopod 1. (all figs. from the holotype).

inferior margin, and with a row of 9 marginal setae along inferior margin. Antenna one with peduncle of 3 articles; flagellum of 2 articles, the second bearing long apical setae. Pereonites smooth, without dorsal pits or ridges; with distinct and typical chromatophore patterns; dorsal chromatophore bands situated anteriorly on pereonites I-III, posteriorly on pereonites III-VII. Posterior margin of pleonite 6 concave, but without dorsal medial cleft.

**Remarks:** *Cyathura guaroensis* closely resembles *C. munda* Menzies, known from central California to the Mexican border. It can be distinguished by the following characters: dorsal pigment pattern; setal pattern and lack of a tooth on the inferior margin of the propus of the first pereonite; and possession of large uropodal endopods, extended beyond the posterior margin of the pleotelson. *Cyathura guaroensis* can be distinguished from its tropical west



Atlantic congeners by its concave pleotelson margin. We have named this species after the regional liquor of Costa Rica, "Guaro"; *salud!*

**Type Deposition:** Holotype, AHF No. 8012, Allan Hancock Foundation, University of Southern California: Costa Rica, Guanacaste Prov., Playas del Coco; rocky points of town; 27 April 1980; Coll. R.C. Brusca and A.M. Mackey. Paratypes, 7 specimens: 6 from same locality as holotype; 1 specimen from Puntarenas Prov., Playa Tárcoles; outside mouth of Golfo de Nicoya, ca. 9°45'N, 84°50'W (scattered rocks on dark sand; intertidal; H<sub>2</sub>O temp. 29°C; 22 Feb. 1980; Coll. R.C. Brusca and A.M. Mackey).

**Distribution:** Known only from Costa Rica, from the two localities described above.

### SUBORDER ASELLOTA

Body fragile, usually not heavily sclerotized. Mouthparts normal, not exceptionally modified. Coxal plates, if present, small, often indistinct in dorsal aspect. Pereopod I generally subchelate, sometimes sexually dimorphic. Pleon composed of pleotelson plus up to 3 free pleonites. Pleopods not adapted for swimming, respiratory in nature. First pair of pleopods usually modified into a thin opercular plate protecting posterior pleopods, variously modified in male. Female with 4 pairs of pleopods (first pair absent); male with 5 pairs. Uropods biramous, terminal. Never parasitic. Intertidal, near shore, and deep sea species; small, usually less than 6 mm in length.

The Asellota is a difficult suborder to characterize because of the great diversity of genera and the many different body plans represented. The higher classification of the asellotes is in considerable disorder, thus the above diagnosis should be regarded as preliminary until more comprehensive revisions of the asellote families have been undertaken. Some genera contain species that are slender and extremely elongate, others are very broad and depressed, some have only the middle pereonites slender, and still others show considerable fusion in both the pereon and pleon.

Asellote isopods are in general very small and fragile animals. Shallow-water forms (e.g. *Munna*) might reach a size of 2-3 mm as adults,

but some deep-sea members of this same genus attain sizes greater than 1 cm. In general, the cuticle of most species in this taxon is not as heavily calcified as in other isopod suborders; the exception being some deep-sea genera, which are heavily calcified (e.g. *Storothyngura*). Most Asellota are very poor swimmers, but some deep-sea Paraselloidea have evolved flat paddle-shaped pereopods V-VII, and large muscular pereonites (e.g. *Munnopsis*, *Storothyngura*, *Eurycope*). In general, asellotes are detritus feeders although some species undoubtedly prey upon smaller macroscopic animals (protozoans, rotifers, nematodes, etc.). Little is known regarding the ecology of most asellotes.

The importance of pleopod morphology in the classification of the Asellota has been demonstrated many times (Hansen, 1904-05; 1916; Racovitza, 1920; Menzies, 1960; Wolff, 1962; Amar, 1957; Hessler, *et al.*, 1979; Wilson and Hessler, 1980). However, no one has attempted a comprehensive revision of the families and genera in order to arrive at a single functional classification. Four superfamilies (tribes of some authors) are now generally recognized: Aselloidea, Stenetrioidea, Parastenetroidea, and Paraselloidea. The first of these, Aselloidea, is composed of exclusively fresh water genera (e.g. *Asellus*, *Caecidotea*, *Mancasellus*, *Stenasellus*). The Aselloidea are characterized by the male first and second pleopods, and the female second pleopod (the first being lost in the Asellota) being much smaller than the third pleopod. These pleopods have not undergone any fusion.

The superfamily Stenetrioidea, like the Aselloidea, are perhaps among the most primitive members of the suborder. Stenetrioidea is represented by a single wide spread genus (*Stenetrium*), which attains its highest diversity in the shallow waters of the subtropics. Only a few abyssal representatives are known. Although this genus has not been reported from the eastern Pacific Ocean, Menzies and Glynn (1968) reported 3 species from Puerto Rico. Thus, the discovery of this superfamily on the Pacific shores of Central America would not be particularly surprising. The Stenetrioidea are characterized by having the first 2 male pleopods and the female second pleopod much smaller than the operculate third pleopod, as in the Aselloidea. They differ from the Aselloidea in that the basal joint of the male first pleopod

is fused and the female second pleopod forms a small, pear-shaped operculum.

The Parastentrioidea (= Gnathostenetroidoidea) are represented by a single species *Gnathostenetroides laodicense* Amar, 1957, from the Mediterranean Sea. This species is distinguished by having the first 2 male pleopods and the female second pleopod large, forming an operculum which totally covers pleopods 3 to 5. The basal joint of the male first pleopod is short and totally fused. The rami are separated, large, and entirely cover the succeeding pleopods. The female operculum has a broad median incision terminally.

The remaining superfamily, Paraselloidea, makes up the bulk of the Asellota genera and species. The diversity of shallow-water genera is perhaps highest in the Southern Hemisphere, but the superfamily is also well represented in the Northern Hemisphere. Perhaps the greatest diversity of Paraselloidea is attained in the deep-sea, from which at least some major shallow water lineages are believed to have originated (Hessler *et al.*, 1979). Kussaken (1973), however, contends that the tropical shallow-water fauna is the most ancient, while the deep-sea fauna is the youngest. The Paraselloidea are considered to be evolutionarily the most advanced Asellota, and like the intermediate Parastentrioidea they are characterized by the first 2 male pleopods (and the female second pleopod) being large, forming an operculum which totally covers the remaining pleopods. However, they differ in that the basal article of the male first pleopod is elongate, coupled (sometimes fused) with each other along the midline, and covering only the interior margins of pleopod 2. The female operculum only occasionally has a median incision terminally.

Although we have not collected any asellotes from Pacific Costa Rica, we include diagnoses and comments on four genera of Paraselloidea which are known from other areas in Central America, in the four most widespread families in the New World. The deep-sea and shelf environment off Pacific Costa Rica is virtually unexplored. However, when samples become available many new species will undoubtedly be discovered.

#### Family Munnidae

Body subpyriform. Cephalon comparatively large; eyes generally present (absent in deep-sea

species), and on short lateral projections (peduncles). Antenna 1 short, of about 7 articles. Antenna 2 may be longer or shorter than body, with 4 proximal, subequal articles projecting anteriorly and dorsally; flagellum with variable number of articles; antennal scale sometimes present. Mandibular palp longer or shorter than body of mandible; rarely absent; distal articles armed with 2 or more curved comb setae and numerous cuticular combs. Pereopod I prehensile; remaining pereopods ambulatory. Pleopod 1 of male truncate distally; penes enter pleopodal sperm duct externally. Uropods minute; biramous or uniramous; peduncle absent. Anus terminal, not covered by opercular pleopods (after Wilson, 1980).

The Munnidae are a small heterogenous group of isopods, most being found in shallow subtidal regions around the world. Diversity seems to be highest in the cold temperate and boreal regions of the Northern Hemisphere, with a few species known from the deep sea.

In the past, numerous genera were placed in this "catchall" family of small, spider-like (due to their small body and unusually long legs) isopods. Wilson (1980), however revised the classification of the family, reducing it to 4 genera (*Munna*, *Astranus*, *Echinomunna* and *Zoromunna*).

#### Genus *Munna* Krøyer, 1839

Fig. 20a

**Diagnosis:** Body smooth, lacking spines except on coxal plates; coxal plates visible in dorsal view on pereonites II-VII. Eyes, when present, on short immovable stalks; preocular lobes generally present. Molar process of mandible strong and subcylindrical, the distal end truncate.

**Remarks:** The genus *Munna* is a large cosmopolitan taxon, which probably represents a complex of several genera (Wilson, 1980). As it is presently conceived, it attains, its greatest diversity in cold, high latitude, shallow water (less than 200 meters) in the Northern Hemisphere. However, the genus is well represented in the abyssal region of the world oceans. *Munna* are among the smallest isopods, only the Microcerberidea being smaller. Most species are less than 2 mm in body length, although some deep sea species reach sizes of 10-15 mm.

Menzies (1962a) divided the genus *Munna* into 3 subgenera (*Munna*, *Uromunna*, and *Neomunna*) on the basis of cross-sectional shape of the uropodal rami, and the presence of hooked spines at its apex. This system has been followed by most workers. However, the uropods are very small and difficult to see clearly, even with the best of microscopes. Schultz (1979) erected a fourth subgenus, *Pangamunna*, for a single marine and brackish-water species which lacks a mandibular palp (*Munna reynoldsi*).

Although no species of *Munna* have been reported from Pacific Costa Rican waters, we have herein included a generic diagnosis in anticipation of such a discovery. *Munna* (*Pangamunna*) *reynoldsi*, a west Atlantic species, has been recently recorded from brackish waters of the Panama Canal, both the Atlantic and Pacific sides (Schultz, 1979), and one of us (E.I.) has a collection of unidentified *Munna* from the open coast of Pacific Panama (Fig. 20a).

#### Family Ianiridae

Antennae 1 short; antennae 2 usually longer than width of cephalon, with a distinct scale. Eyes, when present, subdorsal. Maxillipedal palp with first 3 articles expanded, over half as wide as endite and much wider than distal 2 articles. Mandibular molar process well-developed, strong, expanded and apically truncate. Pereopods not modified for swimming; dactyls of pereopod I with two "claws" (biungulate); pereopods II-VII with 3 claws (triungulate). Coxal plates visible in dorsal view on most pereonites. Pleon composed of 2 somites; first narrow and inconspicuous; second large and shield-shaped. Uropods subterminal or terminal, with peduncle generally biramous.

A cosmopolitan family containing at least 35 genera and over 135 species. For some time this family has served as a "catchall" taxon for any group which approximated its characteristics. The result is a large number of genera and species which appear to have very little in common with one another. The family, as currently defined, contains numerous intertidal, shallow-subtidal, and deep-sea species.

Genus *Ianiropsis* G.O. Sars, 1897-99

Fig. 20b

**Diagnosis:** Cephalon, pereon, and pleon lacking projecting lappets. Cephalon lacking long

rostrum. Coxal plates visible in dorsal view on pereonites II-VII. Uropods biramous. Maxillipedal palp with first 3 articles about as wide as endite. Male first pleopods expanded laterally at apex; second pleopods conceal third pleopods in ventral view; exopod of pleopod 3 narrower than endopod. Propodus of pereopod I without serrations near its origin (after Menzies, 1962a).

**Remarks:** A complex and poorly understood genus composed of numerous species, all very similar to one another. Some have spinelike serrations on the lateraledges of the pleotelson, while in others those borders are smooth. In certain species the general shape and relative lengths of the uropods are distinctive. The most reliable diagnostic features seem to be present on the male first pleopod, particularly at the lateral apex (e.g. apex entire, bifurcate, directed laterally, directed abruptly posteriorly, etc.; Menzies, 1962a). No species of *Ianiropsis* have yet been reported from Pacific Costa Rican waters. However, we have seen specimens from this genus from both the Gulf of California and Pacific Panama. Menzies (1962a) reported 3 species from coastal Chile, including the Californian *Ianiropsis tridens* Menzies, 1952 (fig. 20b). The discovery of this or other species of *Ianiropsis* from Pacific Costa Rican waters is anticipated, and for this reason we have included a diagnosis of the genus.

#### Family Jaeropsidae

Fig. 20c

Mandible with molar process reduced, elongated, and lacking a grinding edge. Maxillipedal palp with articles narrow and similar, all less than one-half width of endite. Pereonites equal in width, wider than long. Pereopods with at least 2 claws (biungulate), all similar in general structure and none adapted for swimming. Uropods with peduncles (from Menzies, 1962a).

A monogeneric family (*Jaeropsis* Koehler, 1885) known from all oceans of the world (except the Arctic Ocean); most species are known from the Antarctic region. Although no records of this family or genus yet exist for Pacific Costa Rican shores, one of us (E.I.) has examined specimens of an unidentified species from the intertidal region of the Bay of Panama (Fig. 20c), and hence its occurrence in Costa Rican waters is anticipated.

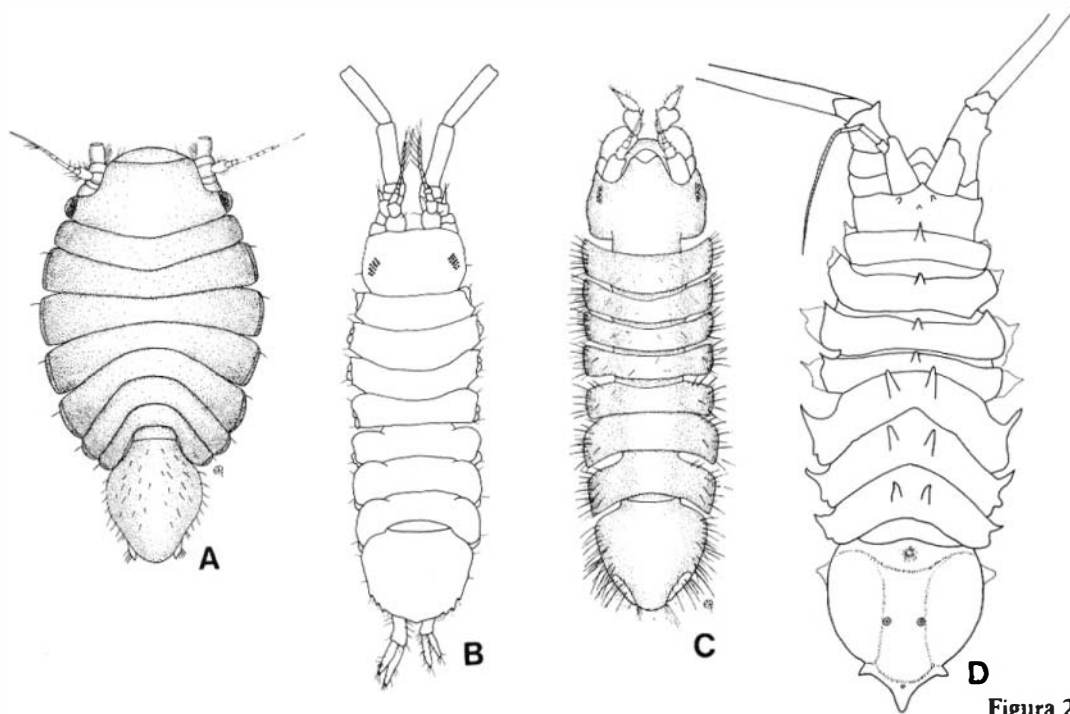


Figura 20

a, *Munna* sp., female, an unidentified specimen from Bahía Panama, Panama. b, *Ianiropsis tridens* Menzies, 1952; presently known from California and northern Chile (after Menzies, 1962). c, *Jaeropsis* sp., an unidentified specimen from Bahía Panama, Panama. d, *Storthyngura pulchra* (after Markham, 1978).

### Family Eurycopidae

#### Fig. 20

Pleopods 1 of male fused along midline, consisting of an elongate peduncle, lacking rami. Pleopods 2 of male coupled loosely with first pair. Pleopods 1 of female wanting; second pleopods fused along midline to form a large operculum covering the remaining pleopods. Pleon of 1 or 2 free somites. Pereopods V-VII natatory, paddlelike.

The Eurycopidae is a very large and important family, containing many species that still await names and descriptions. R. Hessler and G. Wilson of Scripps Institution of Oceanography are actively investigating the systematics, biology and evolution of this group. The Eurycopinae was revised at the subfamilial level by Wolff (1962), but the generic distributions are still not well understood. The current classification recognizes 4 subfamilies: Eurycopinae, Acanthocopinae, Bathypsarinae, and Syneurycopinae. The Eurycopinae contains 7 genera: *Eurycope*, *Munnicope*, *Betamorpha*, *Lipomera*, *Munneurycope*, *Munnopsurus*, and

*Storthyngura*. Although only the latter has been reported from the tropical eastern Pacific, others are expected to occur there. The type genus, *Eurycope*, has been recently revised (Wilson and Hessler, 1981).

#### Genus *Storthyngura* Vanhoffen, 1914

##### Fig. 20d

**Diagnosis:** Dorsum of body spinose. Last 3 pereonites immovable, but usually with indications of separation. Pleon with lateral spinelike projections. Uropods biramous.

**Remarks:** The genus *Storthyngura* contains about 40 described species. All are deepwater forms. This large and poorly understood group is in need of critical reexamination in light of its relationships to other genera of Eurycopinae. Its phylogenetic relationships were discussed by George and Menzies (1968).

A single species of *Storthyngura*, *S. pulchra* (Hansen, 1897) has been reported from deep-water environments off Panama and the Galapagos (Hansen, 1897, as *Eurycope pulchra*), off

Costa Rica and Panama (Wolff, 1956), and more recently off the coasts of Oregon and Washington (Markham, 1978; Fig. 20d). *S. pulchra* may eventually prove to be conspecific with *S. caribbea* (Benedict) of the Caribbean Sea, and *S. kermadecensis* Wolff from the Kermadec Trench (Markham, 1978). *S. pulchra* is one of the most widespread species of the genus, its known north-south range extending from 2°34'N to 48°30'N. The depth range is 2487-3570 m. This species is easily recognized from any other asellotes known from the tropical eastern Pacific by its unique second antennae; the flagellum is composed of only 3 articles but the first two are each as long as the entire body.

#### SUBORDER GNATHIIDEA

Small distinct isopods, lacking pereopods on the last pereonite and possessing a characteristic triangular or T-shaped pleotelson. The pleon is abruptly narrower than the pereon. Males, females and juveniles are very different in form from one another (many were originally described in different genera). The last pereonite is greatly reduced and best seen in males, where it is narrow and subequal to the pleonites. Pleonites distinct, much narrower than pereon. Males have greatly enlarged mandibles, reminiscent of certain ant or termite castes; the enlarged mandibles are for show and probably play no role in feeding or defense. Females lack mandibles altogether. The second thoracomere is entirely fused with the cephalon in males, its legs (thoracopods) thus forming a second pair of maxillipeds, the pylopods (= gnathopods), which cover the large buccal field. In females, the second thoracomere is only partially incorporated into the cephalon but the second thoracopods still form pylopods. Gnathiids thus have only 6 pereonites and 5 pair of pereopods. The only other isopods to fuse the first pereonite to the cephalon are certain Epicaridea and the New Guinea mangrove-boring cirolanid, *Ceratolana papuae* Bowman, 1977. Male gnathiids have a broad, flattened cephalon, often with various tubercles or bosses; females have a small, narrowed cephalon that lacks developed mandibles and maxillae. Juveniles ("pranzia") have small mandibles that protrude forward from the front of the cephalon.

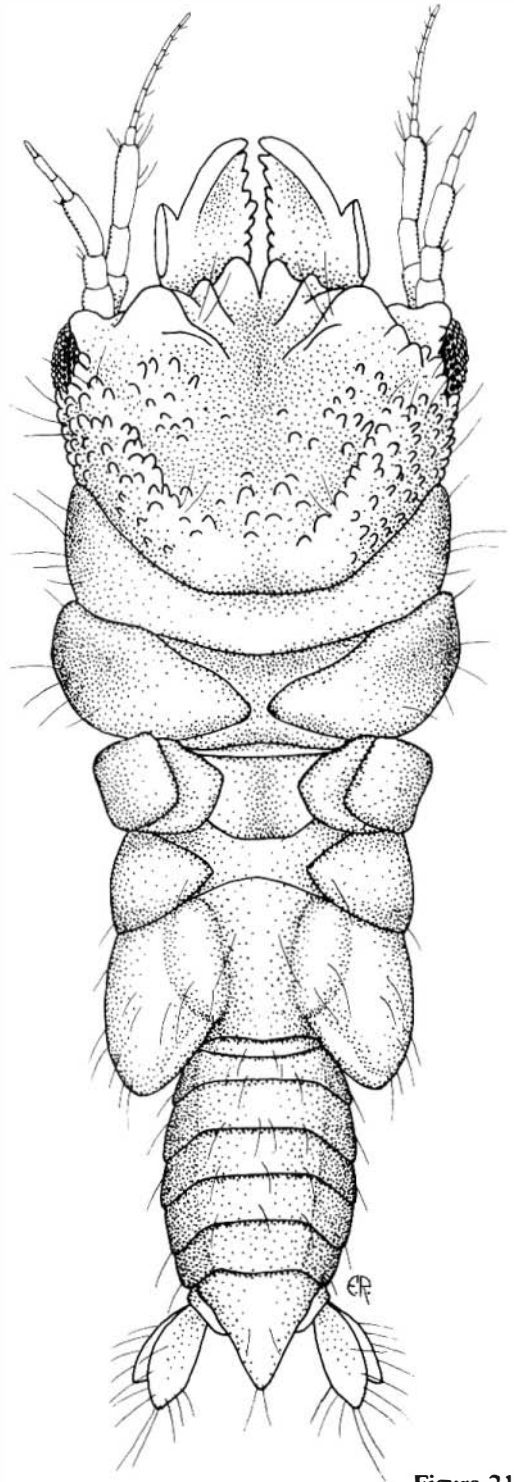


Figura 21

*Gnathia* sp. An unidentified male gnathiid from the rocky intertidal of Playas Coco.

Females have a large rotund pereon in which pereonites III-V are partly or entirely fused. The maxillae of males are rudimentary. The eyes in some species are on short "stalks". Females incubate the eggs internally. The uropods are biramous and attached laterally to form a "tail fan" in conjunction with the pleotelson.

Gnathiids are found from the intertidal zone to the deep sea and are often numerous in soft-bottom benthic samples. Adults are benthic but the juvenile stages ("pranzias") are temporary parasites on fishes, although they are often collected "free-living" in benthic samples. Pranzia are efficient swimmers but adults apparently have only limited swimming capabilities. Adults are suspected of being non-feeding. Females and juveniles cannot usually be identified to species and the taxonomy of the suborder is based on males. There are about 110 described species; all are marine. The best study on the Gnathiidae is still probably Monod's (1926) monograph on the group (also see Holdich and Harrison, 1980). We have recovered only a single specimen from Costa Rican shores, but with appropriate collecting techniques numerous species should be found in this region.

#### Genus *Gnathia* Leach, 1814

##### Fig. 21

**Diagnosis:** Male pylopod 2 or 3-articulated. First article operculate, large, with outer (straight) margin much longer than that of second articles. Third article, if present, much smaller than second article.

**Remarks:** A single male specimen of this genus was collected in the intertidal region of Playa del Coco, amongst rocks and fine sand at Punta Centinela.

#### LITERATURE CITED

- Alheit, J., & E. Naylor. 1976. Behavioural basis of intertidal zonation in *Eurydice pulchra* Leach. J. Exp. Mar. Biol. Ecol., 23: 135-144.
- Amar, R. 1957. *Gnathostenetroides laodicense* nov. gen. n. sp. type nouveau d' Asellota et classification des Isopodes Asellotes. Bull. Inst. Oceanogr., 1100: 1-10. (Marseille).
- Anderson, J. W., & D. J. Reish. 1967. The effects of varied dissolved oxygen concentration and temperature on the wood-boring isopod genus *Limnoria*. Mar. Biol., 1: 56-59.
- Andersson, A., E. Hallberg, & S. B. Johnson. 1978. The fine structure of the compound eye of *Tanaid cavolinii* Milne-Edwards (Crustacea: Tanaidacea). Acta Zool. (Stockholm), 59: 49-55.
- Bakus, G. J. 1968. Zonation in marine gastropods of Costa Rica and species diversity. The Veliger, 10: 207-211.
- Bakus, G. J. 1969. Energetics and feeding in shallow marine waters, p. 275-369. In W. J. L. Felts, & R. J. Harrison (eds.). Internat. Rev. Gen. and Exper. Zool. Academic Press, New York.
- Barnard, K. H. 1925. A revision of the family Anthuridae (Crustacea, Isopoda), with remarks on certain morphological peculiarities. J. Linn. Soc. (Zool.), 36: 109-160.
- Bastida, R., & M. R. Torti. 1967. Una nueva especie de Isopoda Scrolidae para las costas de la Provincia de Buenos Aires (Argentina). Bol. Mus. Nat. D'Hist. Natur., 39: 573-582.
- Bastida, R., & M. R. Torti. 1972. Organismos perforantes de las costas Argentinas. II. La presencia de *Limnoria (Limnoria) tripunctata* Menzies, 1961 (Isopoda, Limnoriidae) en el Puerto de Mar del Plata. Physis, 31: 143-153.
- Becker, G. 1959. Biological investigations on marine borers in Berlin-Dahlem, p. 62-83. In D. L. Ray (ed.). Marine Boring and Fouling Organisms, Univ. Washington Press.
- Becker, G., & W. D. Kampf. 1958. Funde der holzzerstörenden isopoden-gattung *Limnoria* an der Festlandküste Indiens und Neubeschreibung von *Limnoria indica*. Z. Anz. Zool., 45: 1-9.
- Beckman, C., & R. J. Menzies. 1960. The relationship of reproductive temperature and the geographical range of the marine wood-borer *Limnoria tripunctata*. Biol. Bull., 118: 9-16.
- Bennett, E. B. 1963. An oceanographic atlas of the eastern tropical Pacific Ocean, based on data from EASTROPIC expedition, Oct.-Dec. 1955. Bull. Inter-Amer. Trop. Tuna Comm., 8: 33-165.
- Bertness, M. D. 1980. Shell preferences and utilization patterns in littoral hermit crabs of the Bay of Panama. J. Exp. Mar. Ecol., 48: 1-16.
- Bertness, M. D. 1981a. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda: Anomura). Crustaceana, 40: 197-205.
- Bertness, M. D. 1981b. Interference, exploitation and sexual components of competition in a tropical hermit crab assemblage. J. Exp. Mar. Biol. Ecol., 49: 189-202.

- Bertness, M. D. 1981c. Pattern and plasticity in tropical hermit crab growth and reproduction. *Amer. Nat.*, 117: 754-773.
- Bertness, M. D. 1981d. Conflicting advantages in resource utilization: the hermit crab housing dilemma. *Amer. Nat.*, 118: 432-437.
- Bertness, M. D. 1981e. Seasonality in tropical hermit crab reproduction in the Bay of Panama. *Biotropica*, 13: 292-300.
- Bertness, M. D. 1981f. Competitive dynamics of a tropical hermit crab assemblage. *Ecology*, 62: 751-761.
- Bertness, M. D. 1981g. Predation, physical stress and the organization of a tropical rocky intertidal hermit crab community. *Ecology*, 62: 411-425.
- Bertness, M. D. 1982. Shell utilization, predation pressure and thermal stress in Panamanian hermit crabs: an interoceanic comparison. *J. Exp. Mar. Biol. Ecol.*, 64: 159-187.
- Bertness, M. D., & C. Cunningham. 1981. Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Mar. Biol. Ecol.*, 50: 213-230.
- Bertness, M. D., S. D. Garrity, & S. C. Levings. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution*, 35: 996-1007.
- Bird, P. M. 1981. The occurrence of *Cirolana borealis* (Isopoda) in the hearts of sharks from Atlantic coastal waters of Florida. *Fish. Bull.*, 79: 376-383.
- Birstein, I. A. 1973. Deep water isopods (Crustacea: Isopoda) of the north-western part of the Pacific Ocean. [translated from the Russian & published by the Indian National Scientific Documentation Centre, New Delhi.] 316 p.
- Blackburn, M. 1966. Biological oceanography of the eastern tropical Pacific: summary of existing information. U.S. Fish Wildl. Serv. SSRF-540: 1-18.
- Blackburn, M. 1968. Micronekton of eastern tropical Pacific Ocean: family composition, distribution, abundance and relations to tuna. U.S. Fish. Bull., 67: 71-115.
- Blackburn, M., R. M. Laurs, R. W. Owen, & B. Zeitzschel. 1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. *Mar. Biol.*, 7: 14-31.
- Boone, P. L. 1918. Descriptions of ten new isopods. *Proc. U.S. Natl. Mus.*, 54: 591-604.
- Bott, R. 1954. Ein neuer littoraler isopod aus Peru. *Senckenberg. Biol.*, 35: 107-108.
- Bourdillon, A. 1958. La dissémination des Crustacés xylophage *Limnoria tripunctata* Menzies et *Chelura terebrans* Philippi. *Ann. Biol.*, 34: 437-463.
- Bowman, T. E. 1971. *Excirolana kumari*, a new tubicolous isopod from Malaysia. *Crustaceana*, 20: 70-77.
- Bowman, T. E. 1977. Isopod crustaceans (except Anthuridae) collected on the Presidential cruise of 1938. *Proc. Biol. Soc. Wash.*, 89: 653-666.
- Bowman, T. E. 1978. Nomenclatural problems in the cymothoid isopod genera *Ceratothoa*, *Codonophilus*, *Glossobius* and *Meinertia* - their solution by applying the law of priority. *Crustaceana*, 34: 217-219.
- Bowman, T. E., & H. Kuhne. 1974. *Cymodetta gambosa*, a new sphaeromatid isopod (Crustacea) from Australia, with notes on its mating behavior. *Rec. Australian Mus.*, 29: 235-244.
- Boyle, P. J., & R. Mitchell. 1978. Absence of microorganisms in crustacean digestive tracts. *Science*, 200: 1157-1159.
- Broenkow, W. W. 1965. Nutrient distribution in the Costa Rica Dome in the eastern tropical Pacific Ocean. *Limnol. Oceanogr.*, 10: 40-52.
- Bruce, N. L. 1981. Cirolanidae (Crustacea: Isopoda) of Australia: Diagnoses of *Cirolana* Leach, *Metacirolana* Nierstrasz, *Neocirolana* Hale, *Anopsilana* Paulian & DeBouteville, and three new genera *Naratolana*, *Politolana*, and *Cartetolana*. *Aust. J. Mar. Freshw. Res.*, 32: 945-966.
- Bruce, N. L., & T. E. Bowman. 1982. The status of *Cirolana parva* Hansen, 1890 (Crustacea: Isopoda: Cirolanidae) with notes on its distribution. *Proc. Biol. Soc. Wash.*, 95: 325-333.
- Bruce, N. L., R. C. Brusca, & P. Delaney. 1982. The status of the isopod families Corallanidae Hansen, 1890, and Excorallanidae Stebbing, 1904 (Hlabellifera). *J. Crustacean Biol.*, 2: 464-468.
- Bruce, N. L., & D. A. Jones. 1981. The systematics and ecology of some cirolanid isopods from southern Japan. *J. Nat. Hist.*, 15: 67-85.
- Brusca, C. J., R. C. Brusca. 1978. A Naturalist's Seashore Guide. Common Marine Life of the Northern California Coast and Adjacent Shores. Mad River Press, Eureka, Ca. 205 pp.
- Brusca, R. C. 1977. Range extensions and new host records of cymothoid isopods (Isopoda: Cymothoidae), in the east Pacific. *Bull. So. Calif. Acad. Sci.*, 76: 128-131.
- Brusca, R. C. 1978a. Studies on the cymothoid fish symbionts of the eastern Pacific (Isopoda: Cymothoidae). I. Biology of *Nerocila californica*. *Crustaceana*, 34: 141-154.

- Brusca, R. C. 1978b. Studies on the cymothoid fish symbionts of the eastern Pacific (Crustacea: Isopoda: Cymothoidae). II. Biology and systematics of *Lironexa vulgaris*. Occ. Paps. Allan Hancock Fdn. (n.s.), 2: 1-19.
- Brusca, R. C. 1980. Common Intertidal Invertebrates of the Gulf of California. 2d. Univ. Arizona Press, Tucson. 513 p.
- Brusca, R. C. 1981. A monograph on the Isopoda Cymothoidae (Crustacea) of the Eastern Pacific. Zool. J., Linn. Soc., 73: 117-199.
- Brusca, R. C. 1983a. A monograph on the isopod family Aegidae in the tropical eastern Pacific. I. The genus *Aega*. Monogr., Allan Hancock Fdn., 12: 1-39.
- Brusca, R. C. 1983b. Two new idoteid isopods from Baja California and the Gulf of California (Mexico) and an analysis of the evolutionary history of the genus *Colidotea* (Crustacea: Isopoda: Idoteidae). Trans. San Diego Nat. Hist. Soc., 20: 69-79.
- Brusca, R. C. 1984. Phylogeny, evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Calvifera). Trans. San Diego Nat. Hist. Soc., 20: 99-134.
- Brusca, R. C. 1984. Shallow-water marine ecology in the Gulf of California. In R. Schwatlose, A. Ayala-Castanares (eds.). The Gulf of California: Origin, Evolution, Waters, Marine Life and Natural Resources. Univ. Nac. Autonoma Mexico, D.F.
- Brusca, R.C., & M. Gilligan. 1983 Tongue replacement in a fish by a parasitic isopod. Copeia, 3: 813-816.
- Brusca, R. C., & M. Ninos. 1978. The status of *Cirolana californiensis* Schultz, and *C. deminuta* Menzies and George, with a key to the California species of *Cirolana* (Isopoda: Cirolanidae). Proc. Biol. Soc. Wash., 91: 379-385.
- Brusca, R. C., & B. R. Wallerstein. 1977. The marine isopod crustaceans of the Gulf of California. I. Family Idoteidae. Amer. Mus. Novit., No. 2634: 1-17.
- Brusca, R. C., & B. R. Wallerstein. 1979a. The marine isopod crustaceans of the Gulf of California. II. Idoteidae. New genus, new species, new records and comments on the morphology, taxonomy and evolution within the family. Proc. Biol. Soc. Wash., 92: 253-271.
- Brusca, R. C., & B. R. Wallerstein. 1979b. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow-water zoogeography for the region. Bull. Biol. Soc. Wash., 3: 67-105.
- Burbanck, W. D., & M. P. Burbank. 1979. *Cyathura* (Arthropoda: Crustacea: Isopoda: Anthuridae), p. 293-343. In C. W. Hart, Jr., S. L. H. Fuller (eds.). Pollution Ecology of Estuarine Invertebrates. Academic Press, New York.
- Buss, L. W., E. W. Iverson. 1981. A new genus and species of Sphaeromatidae (Crustacea: Isopoda) with experiments and observations on its reproductive biology, interspecific interactions and color polymorphisms. Postilla, 184: 1-23.
- Carlton, J. T. 1975. Introduced intertidal invertebrates, p. 17-25. In R. I. Smith, J. T. Carlton (eds.). Light's Manual: Intertidal Invertebrates of the Central California Coast, 3d ed., Univ. Calif. Press.
- Carlton, J. T., E. W. Iverson. 1981. Biogeography and natural history of *Sphaeroma walkeri* Stebbing and its introduction to San Diego Bay, California. J. Nat. Hist., 15: 31-48.
- Carvacho, A., & C. Yanez. 1971. *Excorallana meridionalis* n. sp. primer Excorallaninae para la costa del Pacifico sud oriental (Isopoda, Cirolanidae). Rev. Biol. Mar., 14: 129-134.
- Castaing, A., J.A. Jimenez, & C.R. Villalobos. 1980. Observaciones sobre la ecología de manglares de la Costa Pacífica de Costa Rica y su relación con la distribución del molusco *Geloina inflata* (Phillipi) (Pelecypoda: Corbiculidae). Rev. Biol. Trop., 28: 323-339.
- Coventry, G. A. 1944. Results of the 5th George Vanderbilt Expedition (1941). Crustacea. Monogr. Acad. Nat. Sci. Phil., 6: 531-544.
- Croizat, L., G. Nelson, & D. E. Rosen. 1974. Centers of origin and related concepts. Syst. Zool., 23: 265-287.
- Dahl, E. 1953. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos, 4: 1-27.
- Dahl, E., & R. R. Hessler. 1982. The crustacean Iacinia mobilis: a reconsideration of its origin, function and phylogenetic implications. Zool. J. Linn. Soc., 84: 133-146.
- Dana, J. D. 1853. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. Vol. XIII. Crustacea. Part II: 692-1618. (dated 1852, but published 1853).
- Delaney, P. M. 1984. Isopods of the genus *Excorallana* Stebbing, 1904, in the Gulf of California, Mexico, with descriptions of two new species and a key to the known species (Crustacea, Isopoda, Corallanidae). Bull. Mar. Sci., 34: 1-20.
- Dexter, D. M. 1972. Comparison of the community structures in a Pacific and Atlantic Panamanian beach. Bull. Mar. Sci., 22: 449-462.



- Dexter, D. M. 1974. Sandy beach fauna of the Pacific and Atlantic coasts of Costa Rica and Colombia. *Rev. Biol. Trop.*, 22: 51-66.
- Dexter, D. M. 1976. The sandy-beach fauna of Mexico. *Sthwest. Nat.*, 20: 479-485.
- Dexter, D. M. 1977. Natural history of the Pan-American sand beach isopod *Excirolana braziliensis* (Crustacea: Malacostraca). *J. Zool., London*, 183: 103-109.
- Dexter, D. M. 1979. Community structure and seasonal variation in intertidal Panamanian sandy beaches. *Estuar. Coast. Mar. Sci.*, 9: 543-558.
- Eleftheriou, A., D. A. Jones. 1976. The genus *Eurydice* on the west coast of India. *J. Zool.*, 178: 385-394.
- Elofsson, R., E. Hallberg. 1977. Compound eyes of some deep-sea and fjord mysid crustaceans. *Acta Zool. (Stockholm)*, 58: 169-177.
- Eltringham, S. K. 1964. Blood concentrations of *Limnoria* (Isopoda) in relation to salinity. *J. Mar. Biol. Assoc. U.K.*, 44: 675-683.
- Eltringham, S. K. 1965. Respiration of *Limnoria* (Isopoda) in relation to salinity. *J. Mar. Biol. Assoc. U.K.*, 45: 145-152.
- Eltringham, S. K., & A. R. Hockley. 1961. Migration and reproduction of the wood-boring isopod, *Limnoria* in Southampton Water. *Limnol. Oceanogr.*, 6: 466-482.
- Esakova, C. E. 1965. Taxonomic position of *Limnoria* (Crustacea, Isopoda) dwelling off shore the Soviet Black Sea [sic]. 300 *логический журнал*, 44: 592-599.
- Estevez, E.D. 1978. Ecology of *Sphaeroma terebrans* Bate, a wood boring isopod, in a Florida mangrove forest. Ph.D. Thesis, Univ. So. Florida. 154 pp.
- Estevez, E.D., & J.L. Simon. 1974. Systematics and ecology of *Sphaeroma* in the mangrove habitats of Florida, p. 286-304. In G. Walsh, S. Snedaker, H. Teas (eds.). *Proc. Internat. Symp., Biology and management of mangroves*. Inst. Food Agr. Sci., Univ. Florida. 846 pp.
- Fahrenbach, W. H. 1959. Studies on the histology and cytology of midgut diverticula of *Limnoria lignorum*, p. 96-102. In D. L. Ray (ed.). *Marine Boring and Fouling Organisms*, Univ. Washington Press.
- Fee, A. R. 1926. The Isopoda of Departure Bay and vicinity, with descriptions of new species, variations and color notes. *Canad. Biol. Fish. (n.s.)* 3: 13-46.
- Fincham, A. A. 1974. Rhythmic swimming of the isopod *Exosphaeroma obtusum* (Dana). *N. Z. J. Mar. Freshw. Res.*, 8: 655-662.
- Fischer, R. 1979. Biologische erosión von basalten der Pazifikküste Costa Ricas. *Nachr. Dt. Geol. Ges.*, 21: 13. (Hannover).
- Fischer, R. 1980. Biocrosion durch gelege von *Nerita funiculata* und *Nerita scabricosta* (Gastropoda). *N. Jb. Geol. Paläont., Mh.*, 1980: 287-292.
- Fischer, R. 1981a. La biocrosión de la costa Pacífica de Costa Rica. *Anais 2. Congr. Latinoamer. Paleontol.*, Porto Alegre: 907-918.
- Fischer, R. 1981b. Bioerosion of basalt of the Pacific coast of Costa Rica. *Senckenbergiana Marit.*, 13: 1-41.
- Fisch, S. 1970. The biology of *Eurydice pulchra* (Crustacea: Isopoda). *J. Mar. Biol. Assoc., U.K.*, 50: 753-768.
- Fish, J. D., & S. Fish. 1972. The swimming rhythm of *Eurydice pulchra* Leach and a possible explanation of intertidal migration. *J. Exp. Mar. Biol. Ecol.*, 8: 195-200.
- Forsbergh, E. D. 1963. Some relationships of meteorological, hydrographic and biological variables in the Gulf of Panama. *Bull. Inter-Amer. Trop. Tuna Comm.*, 7: 1-109.
- Forsbergh, E. D. 1969. On the climatology, oceanography and fisheries of the Panama Bight. *Bull. Inter-Amer. Trop. Tuna Comm.*, 14: 49-385.
- Forsbergh, E. D., & J. Joseph. 1964. Biological production in the eastern Pacific Ocean. *Bull. Inter-Amer. Trop. Tuna Comm.*, 8: 478-527.
- Gaines, S. D., & J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. 11. Biogeography. *Ann. Rev. Ecol. Syst.*, 13: 111-138.
- Gaud, D. T., & J. B. Buchanan. 1956. The fauna of sandy beaches in the Gold Coast. *Oikos*, 7: 293-301.
- George, R. Y., & R. J. Menzies. 1968. Distribution and probable origin of the species in the deep sea isopod genus *Storothyngura*. *Crustaceana*, 15: 171-187.
- Gierloff-Emden, H. G. 1976. La Costa de El Salvador. *Monografía Morfológica-Oceanográfica*. Ministerio de Educación, San Salvador, El Salvador. 285 pp.
- Glynn, P. W. 1968. A new genus and two new species of sphaeromatid isopods from the high intertidal at Naos Island, Panama. *Proc. Biol. Soc. Wash.*, 81: 587-604.
- Glynn, P. W. 1970. Growth of algal epiphytes on a tropical marine isopod. *J. Exper. Mar. Biol. Ecol.*, 5: 88-93.
- Glynn, P. W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama. *Bull. Biol. Soc. Wash.*, 2: 13-30.

- Glynn, P. W. 1974a. Rolling stones among the Scleractinia: mobile coralloliths in the Gulf of Panama. Proc. Second Internat. Coral Reef Symp., 2: 183-198 (Brisbane).
- Glynn, P. W. 1974b. The impact of *Acanthaster* on corals and coral reefs in the eastern Pacific. Environ. Conserv., 1: 295-304.
- Glynn, P. W. 1976a. Some physical and biological determinants of coral community structure in the eastern Pacific. Ecol. Monogr., 46: 431-456.
- Glynn, P. W. 1976b. A new shallow-water serolid (Isopoda: Flabellifera) from the Pacific coast of Panama. J. Nat. Hist., 10: 7-16.
- Glynn, P. W. 1977a. Interactions between *Acanthaster* and *Hymenocera* in the field and laboratory. Proc. Third Internat. Coral Reef Symp., 3: 209-215 (Univ. Miami, Miami).
- Glynn, P. W. 1977b. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. J. Mar. Res., 35: 567-585.
- Glynn, P. W. 1980. Defense by symbiotic Crustacea of host corals elicited by chemical cues from predator. Oecologia (Berl.), 47: 287-290.
- Glynn, P. W. 1982. Coral communities and their modifications relative to past and prospective Central American seaways. Adv. Mar. Biol., 19: 91-132.
- Glynn, P. W., D. M. Dexter, & T. E. Bowman, 1975. *Excirrolana braziliensis*, a Pan-American sand beach isopod: taxonomic status, zonation and distribution. J. Zool., London, 175: 509-521.
- Glynn, P. W., & C. S. Glynn. 1974. On the systematics of *Ancinus* (Isopoda: Sphaeromatidae), with the description of a new species from the tropical eastern Pacific. Pac. Sci., 28: 401-422.
- Glynn, P. W., & I. G. Macintyre. 1977. Growth rate and age of coral reefs on the Pacific coast of Panama. Proc. Third Internat. Coral Reef Symp., 3: 251-259 (Univ. Miami, Miami).
- Glynn, P. W., & R. H. Stewart. 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. Limnol. Oceanogr., 18: 367-379.
- Glynn, P. W., R. H. Stewart, & J. E. McCosker. 1972. Pacific coral reefs of Panama: structure, distribution and predators. Geol. Rundschau, 61: 483-519.
- Glynn, P. W., G. M. Wellington, & C. Birkeland. 1978. Coral reef growth in the Galapagos: limitation by sea urchins. Science, 203: 47-49.
- Hallberg, E. 1977. The fine structure of the compound eyes of the mysids (Crustacea: Mysidacea). Cell Tiss. Res., 184: 45-65.
- Hallberg, E., & M. Andersson. 1978. The adaptive pigment migrations in the compound eye of *Neomysis integer*. Ms.
- Hansen, H. J. 1890. Cirolanidae et familiae nonnullae propincae, Musei Hauniensis. Vidensk. Selsk. Skr. (6)5(3): 237-426.
- Hansen, H. J. 1897. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer "Albatross", during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding. Bull. Mus. Comp. Zool., Harvard, 31: 95-129.
- Hansen, H. J. 1904-05. On the morphology and classification of the *Asellota* group of crustaceans with the descriptions of the genus *Stenetrium* Haswell and its species. Proc. Zool. Soc. London, 2: 302-331.
- Hansen, H. J. 1916. The Danish Ingolf-Expedition. Crustacea, Malacostraca. 3. Copenhagen. 262 p.
- Harrison, K., & D. M. Holdich. 1982. Revision of the genera *Dynamenella*, *Ischyromene*, *Dynamenopsis* and *Cymodecella* (Crustacea: Isopoda), including a new genus and five new species of eubranchiata sphaeromatids from Queensland waters. J. Crustacean Biol., 2: 84-119.
- Hastings, M. H. 1981. Semi-lunar variations of endogenous circa-tidal rhythms of activity and respiration in the isopod *Eurydice pulchra*. Mar. Ecol. Prog. Ser., 4: 85-90.
- Hatch, M. H. 1947. The Chelifera and Isopoda of Washington and adjacent regions. Univ. Wash. Publ. Biology, 10: 155-247.
- Hessler, R. R., G. D. Wilson, & D. Thistle. 1979. The deep-sea isopods: A biogeographic and phylogenetic overview. Sarsia, 64: 67-75.
- Hickey, B. M. 1979. The California Current system - hypotheses and facts. Progr. Oceanogr., 8: 191-297.
- Hofmann, E. E., A. J. Busalacchi, & J. J. O'Brien. 1981. Wind generation of the Costa Rica Dome. Science, 214: 552-554.
- Holdich, D. M. 1968a. The biology of *Dynamene bidentata* (Adams) and some related sphaeromatid isopods. Ph. D. thesis, Univ. Wales.
- Holdich, D. M. 1968b. Reproduction, growth and bionomics of *Dynamene bidentata* (Crustacea: Isopoda). Proc. Zool. Soc. London, 156: 137-153.
- Holdich, D. M. 1969. Polychromatism in the genus *Dynamene* (Crustacea, Isopoda). Publ. Sta. Zool. Napoli, 37: 18-27.

- Holdich, D. M. 1970. The distribution and habitat preferences of the Afro-European species of *Dynamene* (Crustacea: Isopoda). J. Nat. Hist., 4: 419-438.
- Holdich, D. M. 1971. Changes in physiology, structure and histochemistry occurring during the life-history of the sexually dimorphic isopod *Dynamene bidentata* (Crustacea: Peracarida). Mar. Biol., 8: 35-47.
- Holdich, D. M. and K. Harrison. 1980. The crustacean isopod genus *Gnathia* Leach from Queensland waters with descriptions of 9 new species. Aust. J. Mar. Freshw. Res., 31: 215-240.
- Holdich, D. M., & N. A. Ratcliffe. 1970. A light and electron microscope study of the hindgut of the herbivorous isopod *Dynamene bidentata* (Crustacea: Isopoda). Z. Zellforsch., 111: 209-227.
- Holmes, R. W., M. B. Schoefer, & B. M. Shimada. 1957. Primary production, chlorophyll and zooplankton volumes in the tropical eastern Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm., 2: 129-169.
- Iverson, J. W. 1982. Revision of the isopod family Sphacromatidae (Crustacea: Isopoda: Flabellifera). I. Subfamily names with diagnoses and key. J. Crustacean Biol., 2: 248-254.
- Ives, J. E. 1891. Crustacea from the northern coast of Yucatan, the harbor of Vera Cruz, the west coast of Florida, and the Bermuda Islands. Proc. Acad. Nat. Sci., Phila., 43: 176-200.
- Jackson, H. G. 1926. The morphology of the isopod head. Part I. The head of *Ligia oceanica*. Proc. Zool. Soc. London, 1926: 885-911.
- Jackson, H. G. 1928. The morphology of the isopod head. Part II. The terrestrial isopods. Proc. Zool. Soc. London, 1928: 561-595.
- Johnson, J. H. 1961. Sea surface temperature monthly average and anomaly charts, northeastern Pacific Ocean, 1947-1958. U.S. Fish Wildlife Serv., Spec. Sci. Rpt. (Fish.), No. 385, 56 p.
- Johnson M. W. 1935. Seasonal migrations of the woodborer *Limnoria lignorum* (Rathke) at Friday Harbor, Washington. Biol. Bull., 69: 427-438.
- Johnson, M. W., & R. J. Menzies. 1956. The migratory habits of the marine gribble *Limnoria tripunctata* Menzies in San Diego Harbor, Calif. Biol. Bull., 110: 54-68.
- Johnson, M. W., & R. C. Miller. 1935. The seasonal settlement of shipworms, barnacles and other wharf-pile organisms at Friday Harbor, Washington. Biol. Bull., 69: 427-438.
- Johnson, W. S. 1976a. Population energetics of the intertidal isopod *Cirolana harfordi*. Mar. Biol., 36: 351-357.
- Johnson, W. S. 1976b. Biology and population dynamics of the intertidal isopod *Cirolana harfordi*. Mar. Biol., 36: 343-350.
- Jones, D. A. 1968. The functional morphology of the digestive system in the carnivorous intertidal isopod *Eurydice*. J. Zool., 156: 363-376.
- Jones, D. A. 1970a. Factors affecting the distribution of the intertidal isopods *Eurydice pulchra* Leach and *Eurydice affinis* Hansen in Britain. J. Anim. Ecol., 39: 455-472.
- Jones, D. A. 1970b. Population densities and breeding of *Eurydice pulchra* Leach and *Eurydice affinis* Hansen in Britain. J. Mar. Biol. Assoc., U.K., 50: 635-655.
- Jones, D. A. 1974. The systematics and ecology of some sand beach isopods (family Cirolanidae) from the coast of Saudi Arabia. Crustaceana, 26: 202-211.
- Jones, D. A. 1976. The systematics and ecology of some isopods of the genus *Cirolana* (Cirolanidae) from the Indian Ocean region. J. Zool., 178: 209-222.
- Jones, D. A., & J. D. Icely. 1981. *Excirrolana bowmani*, a new mangrove-boring isopod from Kenya (Isopoda, Cirolanidae). Crustaceana, 40: 266-271.
- Jones, D. A., & E. Naylor. 1970. The swimming rhythm of the sand beach isopod *Eurydice pulchra*. J. Exper. Mar. Biol. Ecol., 4: 188-199.
- Jones, L. T. 1963. The geographical and vertical distribution of British *Limnoria* (Crustacea: Isopoda). J. Mar. Biol. Assoc. U.K., 43: 589-603.
- Kampf, W. D. 1957. Über die wirkung von umwelt-faktoren auf die holzböhrassel *Limnoria tripunctata* Menzies (Isopoda). Zeitschr. f. Angewandte Zool., 44 (Drittes Heft): 359-375.
- Kensley, B., & H. W. Kaufman. 1978. *Cleantioides*, a new idoteid genus from Baja California and Panama. Proc. Biol. Soc. Wash., 91: 658-665.
- Kerambrum, P. 1970a. Remplacement de *Sphaeroma serratum* par *S. hookeri* dans l'Étang de Berre par suite de sa dessalure. Mar. Biol., 6: 128-134.
- Kerambrum, P. 1970b. Changement du rapport C/N au cours du développement chez *Sphaeroma serratum* (Crustace Isopode). C.R. Hebd. Seanc. Acad. Sci., Paris, 270D: 635-637.
- Kerambrum, P. 1971. Le matériel minéral de *Sphaeroma hookeri* (Isopoda: Flabellifera). Croissance comparée de la teneur en cendres dans différentes populations. Mar. Biol., 11: 330-336.
- Kerambrum, P. 1972. Dimorphisme Sexuel biochimique de *Sphaeroma hookeri* (Isopoda: Flabellifera) relatif à sa teneur en carbone, azote et hydrogène. Mar. Biol., 13: 34-42.

- Kerambrum, P. 1974. Sur la composition chimique élémentaire de *Sphaeroma hookeri* Leach (Crustacea: Isopoda: Flabellifera). Rapp. Comm. Int. Mer Médit., 22(6): 41.
- Kerambrum, P. 1975a. Evolution de la composition chimique élémentaire relative de *Sphaeroma hookeri* (Isopode: Flabellifere) au cours du cycle d'intermue. Vie Milieu, 25, ser. A: 235-249.
- Kerambrum, P. 1975b. Variabilité biochimique et génétique de *Sphaeroma ghigii*, *S. hookeri*, et *S. serratum*. 3: 95-100.
- Kerambrum, P. 1975c. Variabilité biochimique et génétique de *Sphaeroma ghigii*, *S. hookeri* et *S. serratum*. Variations intraspécifiques. Biochem. Syst. & Ecol., 3: 101-109.
- Klapow, L. A. 1970. Ovoviparity in the genus *Exciorolana* (Crustacea: Isopoda). J. Zool., 162: 359-369.
- Klapow, L. A. 1971. The ecology and behavior of a sandbeach isopod, *Exciorolana chiltoni*: distribution, abundance, reproduction and swimming activity. Ph.D. Thesis, Univ. Calif. San Diego. 215 p.
- Klapow, L. A. 1972a. Fortnightly molting and reproductive cycles in the sand-beach isopod, *Exciorolana chiltoni*. Biol. Bull., 143: 568-591.
- Klapow, L. A. 1972b. Natural and artificial rephasing of a tidal rhythm. J. Comp. Physiol., 79: 233-258.
- Kofoed, C. A., & R. C. Miller. 1927. *Limnoria* and its allies: the crustacean borers, p. 306-349. In C. L. Hill, & C. A. Kofoed, Marine Borers and their Relation to Marine Construction on the Pacific Coast, being the final Report of the San Francisco Bay Marine Piling Committee. Univ. Calif. Press. Berkeley.
- Kohlmeyer, J., G. Becker, & W. D. Kampf. 1959. Versuche zur Kenntnis der Ernährung der Holzbohrassel *Limnoria tripunctata* und ihre Beziehung zu holzerstörenden Pilzen. Z. Anz. Zool., 46: 457-489.
- Kussaking, O. G. 1973. Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep-sea fauna origin. Mar. Biol., 23: 19-34.
- Lane, C. E. 1959. The general histology and nutrition of *Limnoria*, p. 34-45. In D. L. Ray (ed.). Marine Boring and Fouling Organisms. Univ. Washington Press.
- Leboeuf, R. D., & N. R. Howe. 1981. Melanophores and their role in color change and the ecology of the marine isopod, *Sphaeroma quadridentatum* Say. Crustaceana, 40: 225-234.
- Lemos de Castro, A. 1960. Quatro espécies novas, Brasileiras, de *Exciorolana* Stebbing. 1904. Sep. Arq. Mus. Nac., 50: 61-78.
- Lemos de Castro, A. 1964. Redescricao de *Exciorolana quadricornis* (Hansen) E chave de classificação para as espécies do genero. Oceanogr. Biol., No. 6, Contrb. Avulsas Inst. Oceanogr., 7 p.
- Lemos de Castro, A. 1969. Sobre as espécies de *Exciorolana* Richardson do litoral Atlantico das Americas (Isopoda: Cirolanidae). Bol. Mus. Nac., (n.s.) 271: 1-21.
- Lessios, H. A. 1981. Reproductive periodicity of the echinoids *Diadema* and *Echinometra* on the two coasts of Panama. J. Exp. Mar. Biol. Ecol., 50: 47-61.
- Loyola e Silva, J. 1971. Sobre os gêneros *Ancinus* Milne Edwards, 1840, e *Bathycopea* Tattersall, 1909, da coleção U.S. Nat. Mus. (Isopoda, Crustacea). Arq. Mus. Nac., 54: 209-233.
- Lubchenco, J., & S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst., 12: 405-437.
- Markham, J. C. 1978. Northward extension of the range of the eastern Pacific deep-water asclote isopod *Storhyngura pulchra* (Hansen, 1897). Crustaceana, 35: 64-70.
- McCormick, L. 1969. General features of Crustacea, p. R57-R128. In R. C. Moore, & C. Leichert (eds.). Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Geol. Soc. Amer. and Univ. Kansas.
- Menge, B. A., & J. Lubchenco. 1981. Community organization in temperate and tropical intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecol. Monogr., 51: 429-450.
- Menzies, R. J. 1950. The taxonomy, ecology and distribution of northern California isopods of the genus *Idothea* with the description of a new species. Wasmann J. Biol., 8: 155-195.
- Menzies, R. J. 1954. The comparative biology of reproduction in the wood-boring isopod crustacean *Limnoria*. Bull. Mus. Comp. Zool., 112: 362-388.
- Menzies, R. J. 1957. The marine borer family Limnoriidae (Crustacea: Isopoda), Part I: Northern and Central America: systematics, distribution and ecology. Bull. Mar. Sci. Gulf Carib., 7: 101-200.
- Menzies, R. J. 1958. The distribution of wood-boring *Limnoria* in California. Proc. Calif. Acad. Sci., 29: 267-272.
- Menzies, R. J. 1959. The identification and distribution of the species of *Limnoria*, p. 10-33. In D. L. Ray (ed.). Marine Boring and Fouling Organisms, Univ. Washington Press.

- Menzies, R. J. 1960. Isopoda. McGraw-Hill Encyclopedia of Science and Technology, 1960: 283-284.
- Menzies, R. J. 1961. Suggestion of night-time migration by the wood-borer *Limnoria*. *Oikos*, 12: 170-172.
- Menzies, R. J. 1962a. The zoogeography, ecology, and systematics of the Chilean marine isopods. Rpts. Lund Univ. Chile Exped. 1948-49. 42: 1-162.
- Menzies, R. J. 1962b. The marine isopod fauna of Bahía San Quintín, Baja California, Mexico. *Pacific Nat.*, 3: 337-348.
- Menzies, R. J. 1968. Transport of marine life between oceans through the Panama Canal. *Nature*, 220: 802-803.
- Menzies, R. J., & J. L. Barnard. 1959. Marine Isopoda on the coastal shelf bottoms of southern California: Systematics and ecology. *Pacific Nat.*, 1: 3-35.
- Menzies, R. J., & G. Becker. 1957. Holzzerstorende *Limnoria* *arten* (Crustacea, Isopoda) aus dem mitelmeer mit neubeschreibung von *L. carinata*. *Z. Ange. Zool.*, 44 (Erstes Heft): 85-92.
- Menzies, R. J., & C. Beckman. 1958. Occurrence of *Limnoria tripunctata* at the Cape Cod Peninsula. *Ecology*, 39: 172-176.
- Menzies, R. J., T. E. Bowman, & F. G. Alverson. 1955. Studies on the biology of the fish parasite *Lironexa convexa* Richardson (Crustacea, Isopoda; Cymothoidae). *Wasmann J. Biol.*, 13: 277-295.
- Menzies, R. J., & D. Frankenberg. 1966. Handbook on the Common Marine Isopod Crustacea of Georgia. Univ. Georgia Press, Athens. 93 p.
- Menzies, R. J., & R. Y. George. 1972. Isopoda Crustacea of the Peru-Chile Trench. *Anton Bruun Rpt.* No. 9: 1-124.
- Menzies, R. J., & P. W. Glynn. 1968. The common marine isopod Crustacea of Puerto Rico. Studies on the fauna of Curaçao and other Caribbean Islands, Vol. 27. The Hague, Martinus Nijhoff. 133 p.
- Menzies, R. J., & M. A. Miller. 1972. Systematics and zoogeography of the genus *Synidotea* (Crustacea: Isopoda) with an account of Californian species. *Smithson. Contrb. Zool.*, 102: 1-33.
- Menzies, R. J., J. L. Mohr, & C. M. Wakeman. 1963. The seasonal settlement of wood-borers in Los Angeles-Long Beach Harbors. *Wasmann J. Biol.*, 21: 97-120.
- Menzies, R. J., & D. J. Robinson. 1960. Informe sobre los isópodos taladradores marinos colectados en el oriente de Venezuela. *Mem. Soc. Cien. Nat., La Salle*, 20: 132-137.
- Miller, M. A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In* R. I. Smith, & J. T. Carlton, (eds.). *Light's Manual: Intertidal Invertebrates of the Central California Coast*, 3d ed. Univ. Calif. Press, Berkeley.
- Mohr, J. L. 1959. On the protozoan associates of *Limnoria*, p. 84-95. *In* D. L. Ray (ed.). *Marine Boring and Fouling Organisms*, Univ. Washington Press.
- Mohr, J. L., H. Matsudo, & Y.-M. Leung. 1970. The ciliate taxon *Chonotricha*. *Oceanogr. Mar. Biol., Ann. Rev.*, 8: 415-456.
- Monod, T. 1926. Les Gnathiidae, essai monographique (morphologie, biologie, systématique). *Mem. Soc. Sci. Nat. Maroc*, 13: 1-668.
- Monod, T. 1969. Sur trois Crustacés Isopodes marins de la région Guyane-Amazone. *Cah. O.R.S.T.O.M., sér. Océanogr.*, 7, 3: 47-68.
- Moreira, P. S. 1971. Species of *Serolis* (Isopoda, Flabellifera) from southern Brazil. *Bol. Inst. Oceanogr., São Paulo*, 20: 84-144.
- Moreira, P. S. 1973a. Biología de *Serolis completa* (Crustacea, Isopoda, Flabellifera). I. Estadios de desenvolvimento. *Bol. Inst. Oceanogr., São Paulo*, 22: 93-108.
- Moreira, P. S. 1973b. The biology of species of *Serolis* (Crustacea, Isopoda, Flabellifera): Reproductive behavior of *Serolis polaris* Richardson, 1911. *Bol. Inst. Oceanogr., São Paulo*, 22: 109-122.
- Moreira, P. S. 1974a. Cryptic protective coloration in *Serolis laevis* and *Serolis polaris* (Isopoda, Flabellifera). *Crustaceana*, 27: 1-4.
- Moreira, P. S. 1974b. New records of species of *Serolis* (Crustacea, Isopoda, Flabellifera) from southern Brazil. *Bol. Inst. Oceanogr., São Paulo*, 23: 103-119.
- Moreira, P. S. 1974c. New records and a new species of *Serolis* (Crustacea, Isopoda, Flabellifera) from southern Brazil. *Bol. Inst. Oceanogr., São Paulo*, 23: 121-153.
- Moreira, P. S. 1976a. Crustacea Isopoda collected during the OC/S "Almirante Saldanha" cruises in southern South America. I. Species of *Serolis* (Flabellifera, Serolidae). *Bol. Inst. Oceanogr., São Paulo*, 25: 113-130.
- Moreira, P. S. 1976b. A remarkable new species of *Serolis* (Crustacea, Isopoda, Flabellifera) from the continental shelf of southern Brazil. *Bull. Mar. Sci.*, 26: 216-224.
- Moreira, P. S. 1977a. Crustacea Isopoda collected during the OC/S "Almirante Saldanha" cruises in southern South America. II. Additions to the species of *Serolis* (Flabellifera, Serolidae). *Bol. Inst. Oceanogr., São Paulo*, 26: 257-271.

- Moreira, P. S. 1977b. New bathyl species of *Serolis* (Isopoda, Flabellifera) from the western south Atlantic Ocean. *Crustaceana*, 33: 133-148.
- Naylor, E. 1972. British Marine Isopods. Synopses of British Fauna (n.s.). The Linn. Soc. No. 3. Academic Press. 86 p.
- Norman, A. M., & T. R.R. Stebbing. 1886. On the Isopoda of the "Lightning", "Porcupine", and "Valorous" expeditions. *Trans. Zool. Soc. London*, 12: 77-141.
- Nunomura, N. 1978. Tanaidaceans and anthuridean isopods collected on the Presidential Cruise of 1938. *Proc. Biol. Soc. Wash.*, 91: 936-952.
- Owen, R. W., & B. Zeitzschel. 1970. Phytoplankton production: seasonal change in the oceanic eastern tropical Pacific. *Mar. Biol.*, 7: 32-36.
- Paine, R. T. 1966. Food web complexity and species diversity. *Amer. Nat.*, 100: 65-75.
- Patzert, W. C. 1978. El Niño watch atlas. Univ. Calif., Scripps Inst. Oceanogr., Ref. Ser. No. 78-7. unpaginated.
- Pennak, R. W. 1958. A new micro-isopod from a Mexican marine beach. *Trans. Amer. Micros. Soc.*, 127: 298-303.
- Peterson, C. L. 1960. The physical oceanography of the Gulf of Nicoya, Costa Rica, a tropical estuary. *Bull. Inter-Amer. Trop. Tuna Comm.*, 4: 138-216.
- Pillai, N. K. 1955. Wood-boring Crustacea of Travancore. I. Sphaeromatidae. *Trivandrum (Bull. Cent. Res. Inst., Univ. Travancore), Ser. C., Natural Sci.*, 4: 127-139.
- Poore, G. C. B. 1980. A revision of the genera of the Paranthuridae (Crustacea: Isopoda: Anthuridea) with a catalogue of species. *Zool. J. Linn. Soc.*, 68: 53-67.
- Racovitza, E. G. 1920. Notes sur les Isopodes—6. *Asellus communis* Say. 7. Les plcopodes I et II des Ascllides; morphologie et development. *Arch. Zool. Exper. Gen.*, 58A: 79-115.
- Ray, D. L. 1959a. Nutritional physiology of *Limnoria*, p. 46-61. *In* D. L. Ray (ed.). *Marine Boring and Fouling Organisms*, Univ. Washington Press.
- Ray, D. L. 1959b. Marine fungi and wood borer attack. *Proc. Amer. Wood Preserv. Assoc.*, 54: 1-7.
- Ray, D. L. 1959c. Some properties of cellulase from *Limnoria*, p. 372-396. *In* D. L. Ray (ed.). *Marine Boring and Fouling Organisms*, Univ. Washington Press.
- Ray, D. L., & J. R. Julian. 1952. Occurrence of cellulase in *Limnoria*. *Nature*, 169: 32.
- Ray, D. L., & D. E. Stuntz. 1959. Possible relation between marine fungi and *Limnoria* attack on submerged wood. *Science*, 129: 93-94.
- Rehm, A. & H. J. Humm. 1973. *Sphaeroma terebrans*: A threat to the mangroves of southwestern Florida. *Science*, 182: 173-174.
- Reid, J. L., Jr. 1960. Oceanography of the north-eastern Pacific Ocean during the last ten years. *Calif. Coop. Oceanic Fish. Invest. Rep.* 7: 77-90.
- Reish, D. J., T. J. Kawling, & T. C. Schreiber. 1975. Annotated checklist of the marine invertebrates of Anaheim Bay p. 41-51. *In* E. D. Lane and C. W. Hill (eds.). *The marine resources of Anaheim Bay*. *Calif. State Fish Game, Bull.*, 165: 41-51.
- Renner, J. A. 1963. Sea surface temperature monthly average and anomaly charts, eastern tropical Pacific Ocean, 1947-1958. *U.S. Fish Wildlife Serv., Spec. Sci. Rpt. (Fish.)*, No. 442, 57 p.
- Richardson, H. R. 1901. Key to the isopods of the Atlantic coast of North America, with descriptions of new and little known species. *Proc. U.S. Natl. Mus.*, 23: 493-579.
- Richardson, H. R. 1905. A monograph on the isopods of North America. *Bull. U.S. Natl. Mus.* 54: 1-727.
- Richardson, H. R. 1910a. Terrestrial isopods collected in Costa Rica by J. F. Tristan with descriptions of a new genus and species. *Proc. U.S. Natl. Mus.*, 39: 93-95.
- Richardson, H. R. 1910b. Description of a new terrestrial isopod from Guatemala. *Proc. U.S. Natl. Mus.*, 37: 495-497.
- Richardson, H. R. 1912. Marine and terrestrial isopods from Jamaica. *Proc. U.S. Natl. Mus.*, 42: 187-194.
- Richardson, H. R. 1913. Terrestrial isopods collected in Costa Rica by Mr. Picado, with the description of a new genus and species. *Proc. U.S. Natl. Mus.*, 44: 337-340.
- Richardson, H. R. 1914. Reports on the scientific results of the expedition to the tropical Pacific in charge of Alexander Agassiz, on the U.S. Fish Commission Steamer "Albatross", from August, 1899, to March, 1900, Commander Jefferson F. Moser, U.S.N., commanding, XVIII. (and) Reports on the scientific results of the expedition to the eastern tropical Pacific in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross", from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., commanding. *Bull. Mus. Comp. Zool., Harvard*, 58(8): 361-371.
- Rotramel, G. L. 1975. Filter feeding by the marine boring isopod *Sphaeroma quoyanum* H. Milne Edwards, 1840 (Isopoda, Sphaeromatidae). *Crustaceana*, 28: 7-10.

- Salvat, B. 1966. *Eurydice pulchra* (Leach, 1915), *E. affinis* (Hansen, 1905) (Isopodes, Cirolanidae), taxonomie, ethologie, ecologie, repartition vertical, et cycle reproducteur. Act. Soc. Linn. Bordeaux, 103(A): 1-77.
- Saur, J. F. T., & D. D. Stewart. 1967. Expendable bathythermograph data on subsurface thermal structure in the eastern Pacific Ocean. U.S. Fish Wildlife Serv., Spec. Sci. Rpt. (Fish.), No. 548.
- Schaefer, M. B., Y. M. M. Bishop, & G. V. Howard. 1958. Some aspects of upwelling in the Gulf of Panama. Bull. Inter-Amer. Trop. Tuna Comm., 3: 77-130.
- Schultz, G. A. 1966. Submarine canyons of southern California. Part 4. Systematics: Isopoda. Allan Hancock Pacif. Expeds., 27: 1-56.
- Schultz, G. A. 1969. Anomalous specimens of *Philoscia pruinos* (Richardson, 1913) from Costa Rica. Rev. Biol. Trop., 16: 129-143.
- Schultz, G. A. 1973. *Ancinus* H. Milne Edwards in the New World (Isopoda: Flabellifera). Crustaceana, 25: 267-275.
- Schultz, G. A. 1974. The status of the terrestrial isopod crustaceans *Philoscia muscorum*, *P. vittata*, *P. robusta* and *P. miamiensis* in the New World (Oniscoidea, Philosciidae). Crustaceana, 27: 147-153.
- Schultz, G. A. 1977. Anthurids from the west coast of North America, including a new species and three new genera (Crustacea, Isopoda). Proc. Biol. Soc. Wash., 90: 839-848.
- Schultz, G. A. 1979. Louisiana and Panama Canal locations and ecology of *Munna* (*Pangamunna* nov. subgen.) *reynoldsi* Frankenberg and Menzies (Isopoda: Asellota). Proc. Biol. Soc. Wash., 92: 577-579.
- Schuster, O. 1954. Zwei neue Crustaceen von der Pazifischen kuste mittle-Amerikas (Amphipoda und Isopoda). Senckenberg. Biol., 35: 103-105.
- Sheppard, E. M. 1933. Isopoda Crustacea. Part I. The family Serolidae. Discovery Rpts., No. 7: 253-362.
- Sheppard, E. M. 1957. Isopod Crustacea. Part II. The suborder Valvifera, Families Idotheidae, Pseudidotheidae and Xenarcturidae, Fam. N. with a supplement to Isopoda Crustacea Part I. the family Serolidae. Discovery Rpts., No. 29: 141-198.
- Simberloff, D., B. J. Brown, & S. Lowrie. 1978. Isopod and insect root borers may benefit Florida mangroves. Science, 201: 630-632.
- Sleeter, T. D., P. J. Boyle, A. M. Cundell, & R. Mitchell. 1978. Relationships between marine microorganisms and the wood-boring isopod *Limnoria tripunctata*. Mar. Biol., 45: 329-336.
- Sleeter, T. D., B. C. Coull. 1973. Invertebrates associated with the marine wood boring isopod *Limnoria tripunctata*. Oecologia, 13: 97-102.
- Soika, G. A. 1955. Ethologie, ecologie, systématique et biogeographie des *Eurydice* s. str. Vie Milieu, 6: 1-17.
- Spight, T. M. 1976. Censuses of rocky shore prosobranchs from Washington and Costa Rica. Veliger, 18: 309-317.
- Spight, T. M. 1977. Diversity of shallow-water gastropod communities on temperate and tropical beaches. Amer. Nat., 3: 1077-1097.
- Stebbing, T. R.R. 1904a. Gregarious Crustacea from Ceylon. Spolia Zeylanica, 2: 1-29.
- Stebbing, T. R.R. 1904b. Marine crustaceans. XII. Isopoda, with description of a new genus, p. 699-721. In J. S. Gardiner, (ed.). Fauna and geography of the Maldive and Laccadive Archipelagos, 2.
- Sverdrup, H. U. 1947. Wind-driven currents in a baroclinic ocean, with application to the equatorial currents of the eastern Pacific. Proc. Natl. Acad. Sci., 33: 318-326.
- Tattersall, W. M. 1921. Mysidacea, Tanaidacea and Isopoda. p. 405-432. In N. Annandale (ed.). Zoological results of a tour in the Far East. Mem. Asiatic Soc. Bengal, 6.
- Thielemann, M. 1910. Beiträge zur kenntnis der Isopodenfauna Ostasiens. Inaugural-Dissertation, Aus dem Zoologischen Institut der Univ. Leipzig, Munchen. 109 p.
- Thomas, W. H. 1977. Nutrient-phytoplankton interrelationships in the eastern tropical Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm., 17: 173-212.
- Thun, M., & R. C. Brusca. 1980. On the status of the eastern Pacific cymothoid fish parasite *Braga occidentalis* Boone, and its synonymy with *B. patagonica* Schioedte and Meinert (Crustacea: Isopoda: Cymothoidae). Bull. So. Calif. Acad. Sci., 79: 130-132.
- Trilles, J. P. 1972. Sur quatre isopodes cymothoides du Pacifique (Nouvelle Calédonie). Cah. O.R.S.T.O.M., Ser, Oceanogr., 10: 3-17.
- U.S. Dept. Comm. 1952 (Rev. Ed.). Surface water temperatures at tide stations. Pacific coast of North and South America and Pacific Ocean islands. Spec. Publ., No. 280 (formerly No. TW-2), edited by U.S. Coast and Geodetic Survey, Wash., D.C.
- VanName, W.G. 1925. The isopods of Kartabo, Bartica District, British Guiana. Zoologica, 6: 461-503.

- VanName, W. G. 1926. Forest isopods from Barro Colorado Island, Panama Canal Zone. Amer. Mus. Novit., No. 206. 15 p.
- Villalobos, C. R. 1979a. Variations in population structure in the genus *Tetracrita* (Crustacea: Cirripedia) between temperate and tropical populations. I. Fecundity, recruitment, mortality and growth in *Tetracrita rubescens*. Rev. Biol. Trop., 27: 279-291.
- Villalobos, C. R. 1979b. Variations in population structure in the genus *Tetracrita* (Crustacea: Cirripedia) between temperate and tropical populations. II. The age structure of *Tetracrita rubescens*. Rev. Biol. Trop., 27: 293-300.
- Villalobos, C. R. 1980a. Variations in population structure in the genus *Tetracrita* (Crustacea: Cirripedia) between temperate and tropical populations. III. *Tetracrita stalactifera* in Costa Rica. Rev. Biol. Trop., 28: 193-201.
- Villalobos, C. R. 1980b. Variations in population structure in the genus *Tetracrita* (Crustacea: Cirripedia) between temperate and tropical populations. IV. The age structure of *Tetracrita stalactifera* and concluding remarks. Rev. Biol. Trop., 28: 353-359.
- Villalobos, C. R. 1982. Animales y plantas comunes de las costas de Costa Rica. Editorial Universidad Estatal a Distancia. San José, Costa Rica. 147.
- Wägele, J. W. 1981a. Zur phylogenie der Anthuridea (Crustacea, Isopoda). Mit beiträgen zur lebensweise, morphologie, anatomie und taxonomie. Zoologica, 132: 1-127.
- Wägele, J. W. 1981b. Study of the Hyssuridae (Crustacea: Isopoda: Anthuridea) from the Mediterranean and the Red Sea. Israel J. Zool., 30: 47-87.
- Wägele, J. W. 1981c. Study of the Anthuridae (Crustacea: Isopoda: Anthuridea) from the Mediterranean and the Red Sea. Israel J. Zool., 30: 113-159.
- Wallerstein, B. W., & R. C. Brusca. 1982. Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow-water idoteid isopods (Crustacea: Isopoda: Idoteidae). J. Biogeogr., 9: 135-150.
- Wilson, G. 1980. New insights into the colonization of the deep sea: systematics and zoogeography of the Munnidae and the Pleurogoniidae comb. nov. (Isopoda: Janiroidea). J. Nat. Hist., 14: 215-236.
- Wilson, G. D., & R. R. Hessler. 1980. Taxonomic characters in the morphology of the genus *Eurycope* (Isopoda: Asellota), with a redescription of *Eurycope cornuta* (G. O. Sars, 1864). Cashiers Biol. Mar., 21: 241-263.
- Wilson, G. D., & R. R. Hessler. 1981. A revision of the genus *Eurycope* (Isopoda, Asellota) with descriptions of three new genera. J. Crustacean Biol., 1: 401-423.
- Wolff, T. 1956. Isopoda from depths exceeding 6000 meters. Galathea Rpt., 2: 85-157.
- Wolff, T. 1962. The systematics and biology of the bathyl and abyssal Isopoda Asellota. Galathea Rpt., 6: 7-320.
- Woodring, W. P. 1966. The Panama land bridge as a sea barrier. Proc. Amer. Phil. Soc., 110: 425-433.
- Wooster, W. S., & J. L. Reid, Jr. 1963. Eastern boundary currents, p. 253-280. In J. Hill (d.), The Sea, vol. 2. Interscience Publ., New York.
- Wyrtki, K. 1964. Upwelling in the Costa Rica Dome. U.S. Fish. Bull., 63: 355-372.
- Wyrtki, K. 1965a. Surface currents of the eastern tropical Pacific Ocean. Bull. Inter-Amer. Trop. Tuna Comm., 9: 269-304.
- Wyrtki, K. 1965b. Summary of the physical oceanography of the east Pacific Ocean. Univ. Calif. IMR 65-10.
- Wyrtki, K. 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Ann. Rev., 4: 33-68.



## ERRATA

Brusca, R. C., & E.W. Iverson: A Guide to the Marine Isopod Crustacea of Pacific Costa Rica. Rev. Biol. Trop., 33 (Supl. 1), 1985.

### Should be

page 6, rgt column, 27 lines from top	maxillipeds
page 6, rgt column, last word	or
page 7, rgt column, 14 lines from top	Cymothoidae
page 8, left column, 7 lines from bottom	They viewed the maxillules to be...
page 8, left column, 16 lines from bottom	thoracomere
page 8, left column, last line	Anthuridae
page 22, rgt column, 4 lines from bottom	pleotelson
page 27, figure legend, third line	enlarged
page 33, rgt column, 2 lines from top	...yearly production.
page 34, footnote	( <i>E. kincaidi</i> ...
page 55, figure legend	Brusca & Wallerstein, 1979a
page 59, left column, 15 lines from bottom	Brusca, 1984: 110
page 66, 4 lines from top	<i>pulchra</i>
Headings on odd pages should read: <i>BRUSCA &amp; IVERSON</i> : A Guide to the Marine Isopod Crustacea of Pacific Costa Rica.	