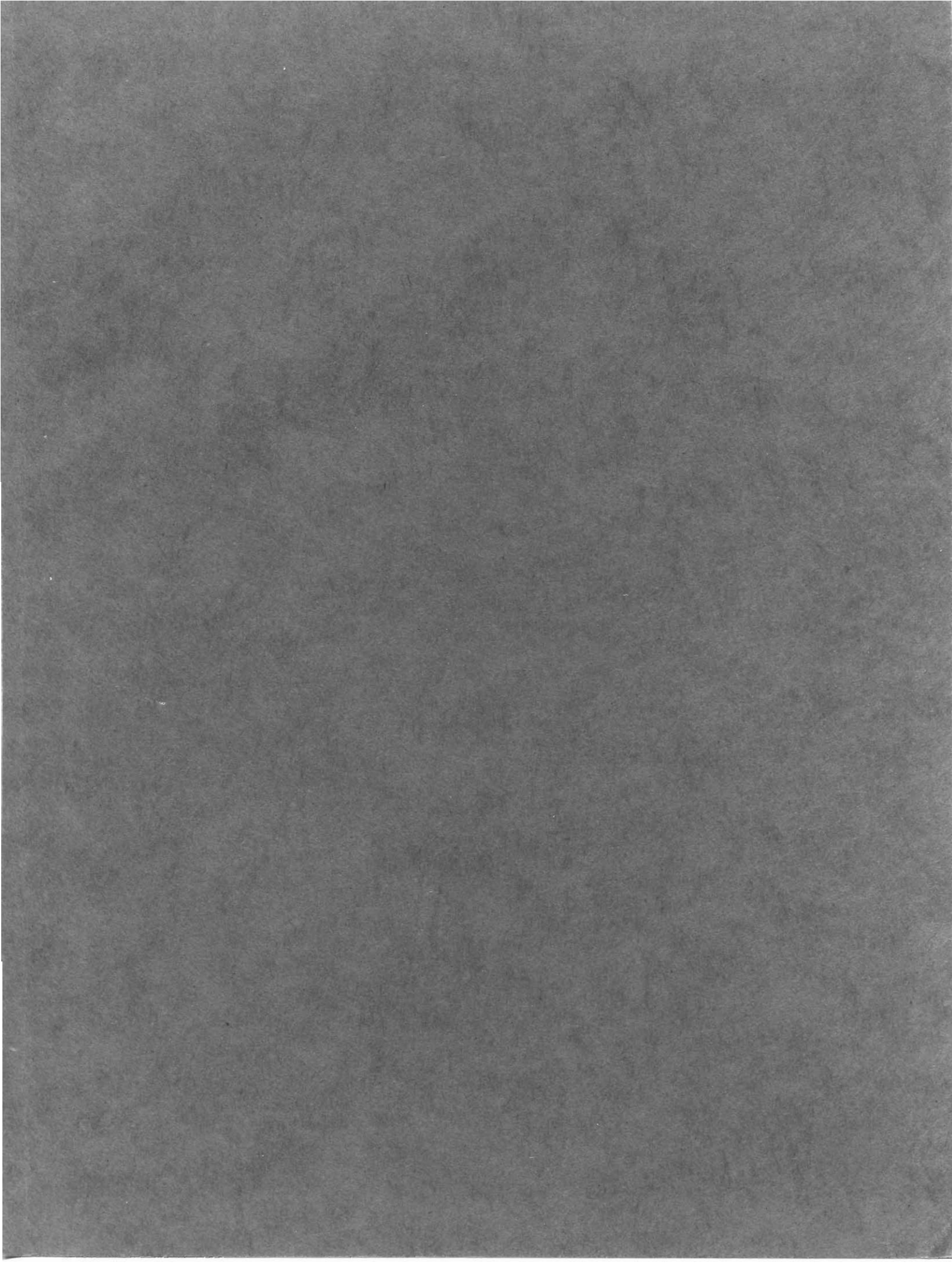
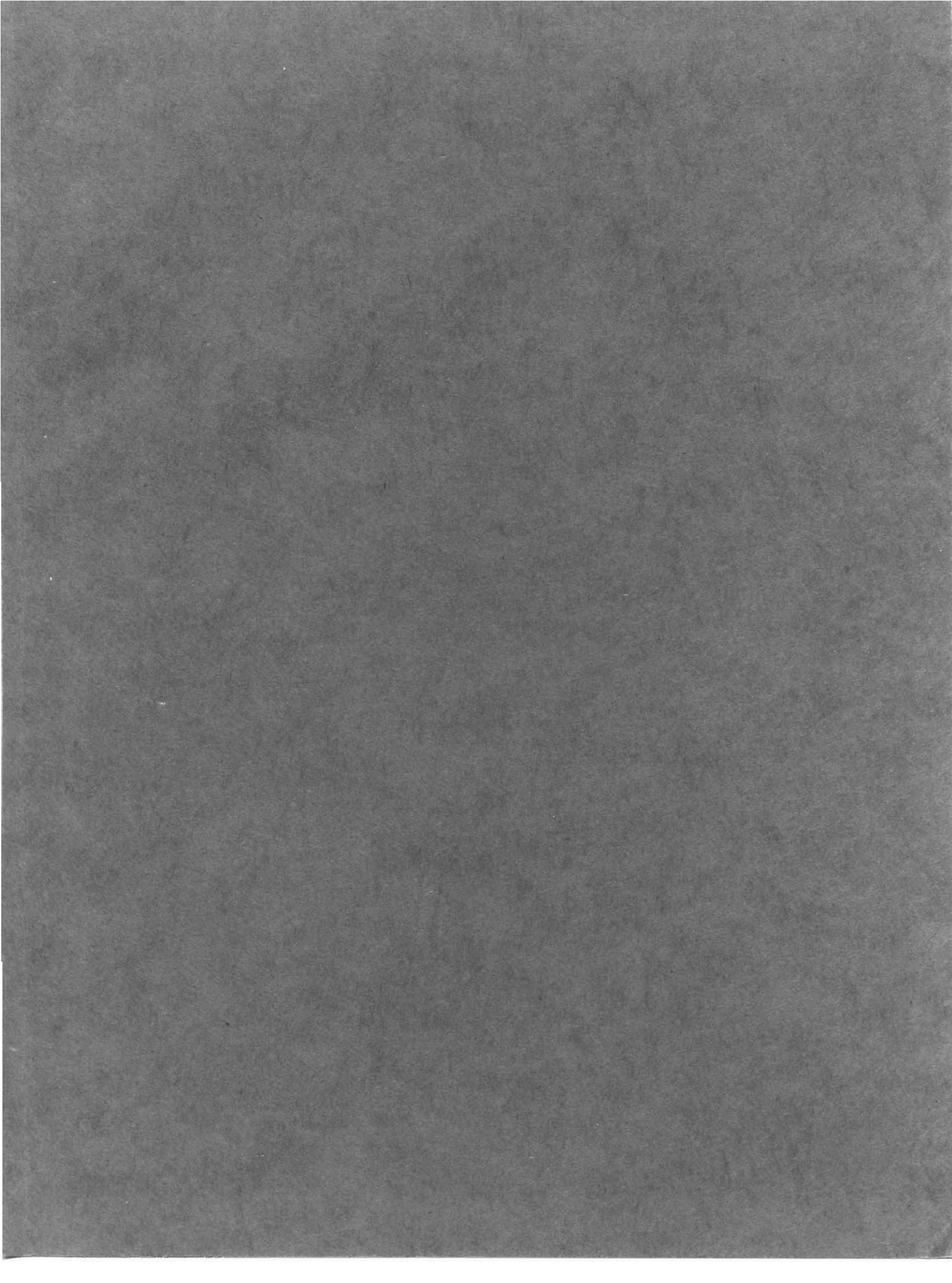


COMPARATIVE MORPHOLOGY
OF RECENT
CRUSTACEA



PATSY A. McLAUGHLIN

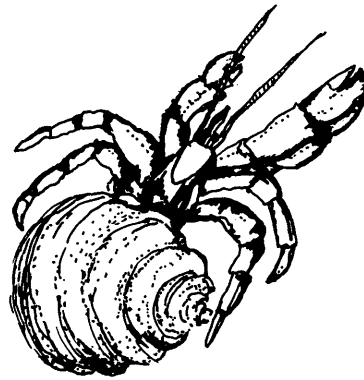




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*Dedicated to
Professor Dr. Lipke B. Holthuis
and the memory of
Dr. Waldo L. Schmitt (1887 – 1977)*

Two outstanding carcinologists

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PREFACE

Since Calman's monograph on crustacean morphology was published shortly after the turn of the century, our knowledge of crustacean biology has increased manifold. Recent interest in the roles played by crustaceans in the environment has taken investigations of this highly diverse group of invertebrates out of the exclusive realms of basic science and fisheries and made them topics of applied research as well. As a result, the literature pertaining to crustaceans is not only prolific, but also widely scattered and often highly specialized and technical.

This book summarizes much of the more recently acquired basic data and the current interpretations of existing information. Its format has been developed with two purposes in mind. The first is the presentation of the material in the form of a text in crustacean biology, complete with step-by-step directions for the study of specific groups. The second is to provide a concise reference to the major morphological and anatomical characters of the higher crustacean taxa for both specialists and nonspecialists.

Many evolutionary and phylogenetic carcinological questions have not yet been resolved. Consequently not all carcinologists will agree with the classification and terminology employed in this text. With regard to the classification, I have adopted a conservative approach, preferring to await further evidence before taking the major step of recognizing the Crustacea as a distinct phylum. With regard to terminology, although I recognize and appreciate the usefulness of specialized terms in particular situations, I believe that the use of uniform terms for homologous structures reduces confusion and makes the subject matter more comprehensible to the general reader.

The field of carcinology is a vast and exciting one in which our present level of scientific knowledge is still relatively limited. I hope that this book provides a basic knowledge of the Crustacea upon which future carcinologists will build.

October 1979

Patsy A. McLaughlin

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P.A.M.

COMPARATIVE MORPHOLOGY
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CRUSTACEA

INTRODUCTION

The superclass Crustacea is one of the largest, most diverse, and most successful groups of invertebrates. The commercial importance of numerous species of shrimps, crabs, and lobsters has long been recognized. Limnologists have been aware of the contributions made by the numerous small crustacean groups to lake and stream ecosystems. Similarly, fishery biologists have learned that the variety of planktonic crustaceans play a significant role in the food chains of fishes. More recently, benthic biologists and ecologists have discovered that a broad spectrum of benthic crustaceans serve vital roles in trophic levels and energy cycles within communities.

The literature on some of the taxa, such as the copepods and decapods, is extremely extensive, highly technical and specialized, and not readily adapted for general usage. In contrast, literature on some of the less familiar or lesser known groups is extremely meager. A few historic monographs have dealt with the morphology of the superclass; for example, H. Milne Edwards (1834–1840), Stebbing (1893), Calman (1909). More recently Moore (1969), in a synopsis of the Crustacea, has reviewed both fossil and Recent taxa; the morphology is complete in many groups, but in others is much less extensive. The second edition of Kaestner's (1969) volume on the Crustacea, translated by Levi and Levi (Kaestner 1970), is a more even treatment of the major taxa; however, although the newer taxa, such as the Cephalocarida and Mystacocarida, are included, the morphological sections add little to the information presented by earliest carcinologists, and most of the illustrations have been taken directly from these earlier publications.

The current emphasis on environmental assessment of human activities has placed an increasing burden on the biologist to identify and evaluate the faunal and floral segments of the environment properly. As a practicing carcinologist and systematist and one frequently engaged in environmental assessment projects, I have become acutely aware of the need for a single reference that would present the basic data of the various major crustacean taxa in a concise and systematic manner. This need, accompanied by the attempt to teach a course in crustacean biology, has convinced me that such a reference work would have great practical application if expanded to a laboratory teaching manual as well. Thus this book has evolved. While one of its purposes is to bring to students of crustacean biology a series of exercises that will permit them to familiarize themselves with the basic

morphology of the diverse groups, another is to provide an easy reference to major structures for specialists.

Every attempt has been made to combine a uniform description of morphological structures with the specialized interpretations of carcinologists working with the various taxa. This has not always been possible, and when a choice has been required, it has been made with a preference to the basic morphological patterns. For instance, in copepods and several other major taxa, specialists have tended to disregard thoracic somites that have been incorporated into the cephalon through fusion. Where 2 thoracic somites are fused to the cephalon, the adjacent somite is morphologically the 3rd thoracic somite; however, many specialists would call it the 1st. Each of the thoracic somites (thoracomeres) basically is provided with a pair of appendages, referred to herein as *thoracopods*. In the more primitive crustacean classes there is little or no difficulty in referring to all thoracic appendages as thoracopods. However, in the Malacostraca they are most frequently referred to as pereopods and are numbered according to their relation to the cephalon and its fused thoracic somites (i.e., 1–3). If, for example, the taxon is characterized as having 8 thoracomeres with thoracopods, but the 1st thoracomere is fused to the cephalon and its pair of appendages modified as maxillipeds, the successive 7 pairs of appendages would be referred to as pereopods 1–7. In this text the term *pereopod* has been used primarily for the Eucarida. When the first 3 pairs of thoracic appendages are modified as maxillipeds, the remaining 5 pairs are referred to as pereopods. Another discrepancy in terminology may be found in the designation of cephalic appendages. In several of the major taxa, the cephalic appendages posterior to the mandibles are called either the *maxillulae* and *maxillae* or the *1st* and *2nd maxillae*. The former usage has been adopted throughout, even when it is not customarily used by practicing specialists. Similarly the terms *antennules* and *antennae* are used in preference to *1st* and *2nd antennae*.

In this text, the basic morphology of each major subdivision has been reviewed, in most instances through personal observations, examinations, and dissections. The data have been compiled and presented in systematic tabular form and in general descriptions and instructions for study. Most instructions deliberately have been generalized to permit their adaptation to a variety of representatives of the group. In some instances the illustrations of the external morphology represent specific

animals, and in others a composite form has been drawn. Most major morphological structures have been illustrated as well as described. In addition, the major organ systems for at least one generalized representative of the more common or larger taxa have been described and diagrammatically illustrated. A cursory review of the larval stages of the various crustacean groups has been

presented to give the reader a brief synopsis of the great diversity in larval forms occurring in the superclass.

References to some of the more classical and recent literature have been compiled for each of the principal subdivisions within the superclass. A review of the more general crustacean literature concludes the text; a glossary of technical terms is appended.

BASIC CHARACTERS OF THE SUPERCLASS CRUSTACEA

1. *Exoskeleton*: Of chitin; often thin, almost membranous and transparent, or thick, impregnated with calcium carbonate.
2. *Somite*: Mesoblastic division of body with exoskeleton usually differentiated into dorsal tergite and ventral sternite and with pair of appendages. Major divisions of body include cephalon with 5 usually fused somites and presegmental region (acron) bearing eyes; thorax with variable number of somites in primitive taxa, generally 8 in higher taxa, some or all sometimes partially or entirely fused with cephalon (cephalothorax); abdomen with variable number in primitive taxa, 6 or rarely 7 in higher taxa, excluding telson.
3. *Carapace*: Reduplication of integument of posterior dorsal border of head extending posteriorly over body and/or anteriorly over cephalon, sometimes fused with tergite(s) of one or more thoracic somites, or more extensively enclosing part or all of body (uni- or bivalved).
4. *Cephalic appendages*: Paired antennules (1st antennae); antennae (2nd antennae); mandibles; maxillulae (1st maxillae); maxillae (2nd maxillae). Cephalon sometimes bearing one or more of following additional structures: (1) rostrum; (2) nauplius or compound eyes; (3) labrum and labium; (4) epistome; (5) paired maxillipeds (modified thoracic appendages on somites usually fused with cephalon).
5. *Thoracic appendages*: Paired thoracopods, typically biramous, with outer exopod and inner endopod arising from common basal protopod, sometimes also with inner lobes (endites) or outer lobes (exites) or branchial structures (epipods). Protopod with coxa and basis, rarely also with precoxa; exopod sometimes reduced, endopod frequently segmented. See Figure 1.
6. *Abdominal appendages*: Paired biramous appendages unique to Malacostraca; first 5 pairs referred to as pleopods, 6th pair as uropods; 1 or 2 pairs often modified as gonopods or copulatory structures, particularly in males; occasionally secondarily reduced or absent.

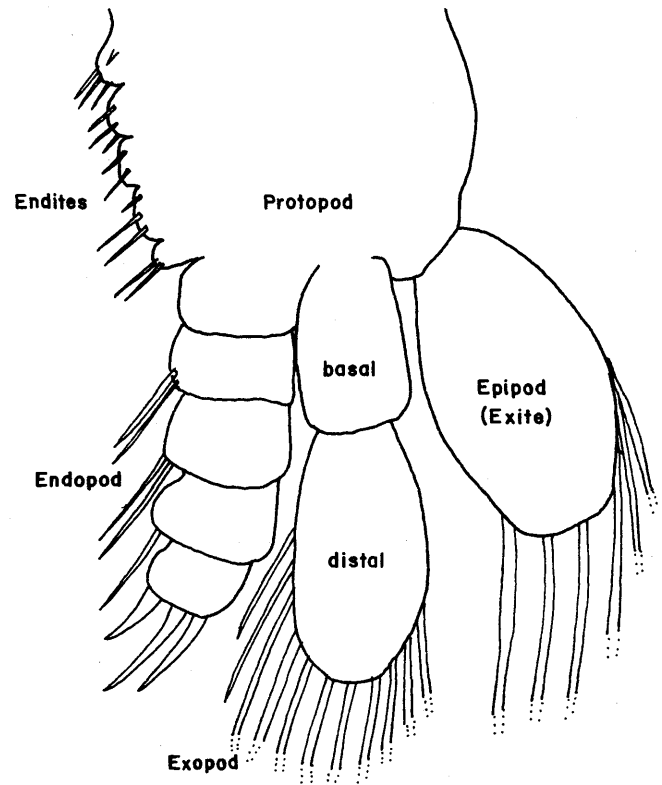


Figure 1 Diagrammatic basic crustacean appendage (thoracopod).

7. *Telson*: Terminal lobe of body, with or without appendages (caudal rami, or taken collectively, a caudal furca) in some of the more primitive taxa*; appendages absent in most of the Malacostraca. Telson not considered a true somite.

*Bowman (1971) has proposed that the "classical" interpretation of a telson is incorrect in that it does not take into consideration the fact that two presumably nonhomologous conditions exist within such a definition, that is, (1) a telson with caudal rami and a terminal anus; and (2) a telson without caudal rami and with a ventrally opening anus. Schminke (1976) has provided evidence purported to refute Bowman's proposal. In this author's opinion, the question of the true nature of the telson remains unresolved. In the text the classical definition of a telson, with or without caudal rami, has been used; however, in those taxa where Bowman disagrees, his interpretation is also indicated.

CLASSIFICATION OF THE CRUSTACEA

Superclass Crustacea

Class Cephalocarida

Class Branchiopoda

Subclass Calmanostraca

Order Notostraca

Order Kazacharthra*

Subclass Sarsostraca

Order Anostraca

Order Lipostraca*

Order Enantiopoda*

Subclass Diplostraca

Order Conchostraca

Order Cladocera

Class Ostracoda

Subclass Archaeocopa*

Subclass Leperditicopa*

Subclass Palaeocopa*

Subclass Podocopa

Subclass Myodocopa

Class Mystacocarida

Class Copepoda

Order Calanoida

Order Harpacticoida

Order Cyclopoida

Order Misophrioida

Order Notodelphyoida

Order Monstrilloida

Order Siphonostomatoida

Order Poecilostomatoida

Class Branchiura

Class Cirripedia

Order Acrothoracica

Order Thoracica

Order Ascothoracica

Order Rhizocephala

Class Malacostraca

Subclass Phyllocarida

Order Leptostraca

Order Canadaspidida*

Order Hymenostraca*

Order Hoplostraca*

Order Archaeostraca*

Subclass Hoplocarida

Order Stomatopoda

Order Aeschronectida*

Order Palaeostomatopoda*

Subclass Eumalacostraca

Superorder Syncarida

Order Anaspidacea

Order Palaeocaridacea*

Order Stygocaridacea

Order Bathynellacea

Superorder Peracarida

Order Mysidacea

Order Thermosbaenacea

Order Spelaeogriphacea

Order Cumacea

Order Tanaidacea

Order Isopoda

Order Amphipoda

Superorder Eucarida

Order Euphausiacea

Order Amphionidacea

Order Decapoda

*Known only from the fossil record.

CLASS CEPHALOCARIDA Sanders, 1955

Recent species	Nine, in four genera: <i>Hutchinsoniella</i> , <i>Lightiella</i> , <i>Sandersiella</i> , and <i>Chiltoniella</i> .
Size range	2.0–3.6 mm, excluding caudal rami.
Carapace	Absent; cephalic shield present.
Eyes	Absent.
Antennules	Uniramous; used in locomotion.
Antennae	Biramous, large, and powerful; used in locomotion and food gathering.
Mandibles	Without palp.
Maxillulae	Biramous; gnathobase present.
Maxillae	Biramous; protopod with several endites (gnathobase), endopod, exopod, and pseudepipod.
Maxillipeds	None.
Thoracic appendages	Seven or 8 pairs of biramous thoracopods, generally similar in structure; 8th occasionally without endopod and gnathobase.
Abdominal appendages	None.
Telson	With caudal rami.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5; thorax with 8; abdomen with 11, excluding telson.
Sexual characters	Common genital opening on posterior surface of protopod of each 6th thoracopod (<i>Hutchinsoniella</i>).
Sexes	Hermaphroditic.
Larval development	Anamorphic; single or pair of embryos during each breeding season; hatch as metanauplii.
Fossil record	Recent.
Feeding types	Nonselective deposit feeders.
Habitat	Species usually occur in areas where surface sediments are covered by layer of flocculent material; however, specimens recently have been collected from bare sand. <i>Lightiella incisa</i> and <i>L. floridana</i> usually are associated with <i>Thalassia</i> beds; other species occur in soft, often highly organic mud or muddy sand, from intertidal depths to approximately 1560 m. <i>Chiltoniella elongata</i> has been collected from soft mud having a slight odor of hydrogen sulfide.
Distribution	East coast of North and South America, Gulf of Mexico, and Caribbean; San Francisco Bay, California; West Africa; Peru; New Zealand; New Caledonia; Japan.

The instructions for the study of cephalocaridan morphology are based primarily on specimens of *Lightiella*; however, pertinent differences between this genus and the other three in the class will be pointed out. The paucity of study material, as well as the small size of cephalocarids, makes individual student dissections in

the classroom virtually impossible. Therefore, the instructions given are for studying whole-mounted specimens and slide preparations of mouthparts and appendages. Observe the general body plan from both dorsal and ventral views before examining the individual appendages (see Figure 2).

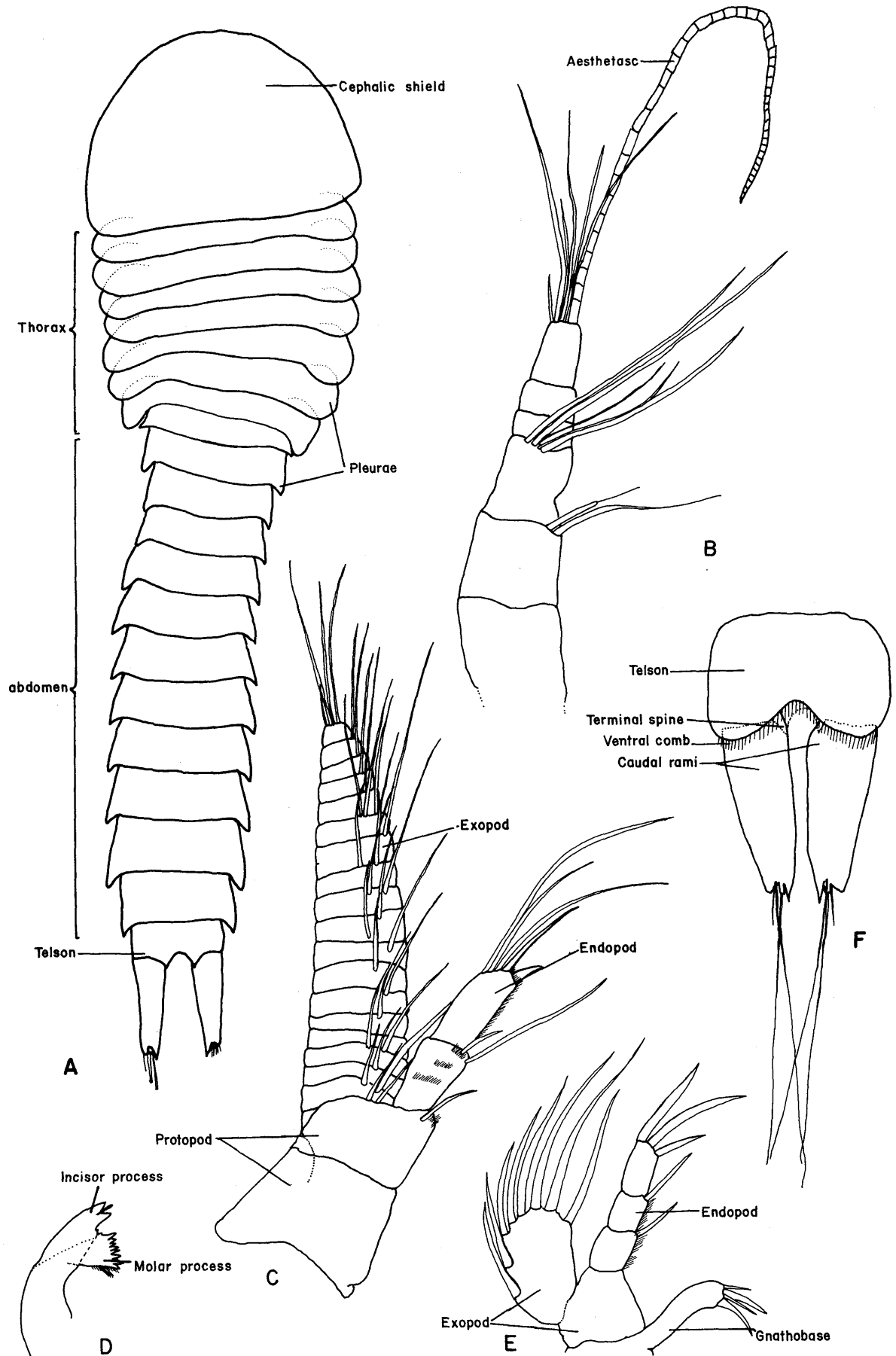


Figure 2 Cephalocarida: A. Whole animal (dorsal view); B. Antennule; C. Antenna; D. Mandible; E. Maxillule; F. Telson and caudal rami (ventral view) [from McLaughlin, 1976].

In dorsal view, an unsegmented cephalic shield formed by the fusion of the cephalic tergites partially overlaps the 1st thoracic somite. Each of the 8 thoracic somites is expanded laterally by pleurae that may be acute or rounded; the pleurae of the 8th somite are reduced much more in *Lightiella* than in the other genera. The 11 abdominal somites also bear lateral pleurae, again less well developed in species of *Lightiella*. The abdomen terminates in a telson and short (*Lightiella*) or long (other genera) caudal rami with terminal setae. [Bowman (1971) refers to the telson as an anal somite and the caudal rami as uropods.]

In ventral view, the antennules and very prominent biramous antennae are located on the inner surface of the cephalic shield anteriorly. In the midline, the bulbous labrum virtually obscures the mandibles and maxillulae. The maxillae, which lie in close approximation to the 1st thoracopods, are differentiated from them by their anterior position and typically fewer spines and setae. Note that there are only 7 pairs of thoracopods in *Lightiella*, and that the 7th pair has a reduced number of setae and endites. Eight pairs of thoracopods are present in the other three genera. In *Sandersiella* the 6th pair is somewhat modified, presumably for reproductive purposes; the 8th pair in *Chiltoniella* lacks endopods. Observe that the telson bears a comb and a pair of postero-medial spines dorsally (spines lacking in *Lightiella serendipita* Jones). In *Hutchinsoniella*, *Sandersiella*, and *Chiltoniella*, the penultimate abdominal somite as well as the telson carries a comb of bristles or setae.

Examine slide preparations of the cephalic and thoracic appendages. The uniramous antennule is 6-segmented and terminates in a sensory seta (aesthetasc), usually of considerable length. The biramous antenna consists of a 2-segmented protopod, 2-segmented endopod, and multisegmented exopod. The 2nd segment of the protopod has a naked (*Chiltoniella*) or setose (*Hutchinsoniella*) knob that is absent in the other two genera. The mandible lacks a palp and usually consists of incisor and molar processes, variously armed. The maxillule (1st maxilla) is biramous and has a well-developed gnathobase. The maxilla (2nd maxilla) and the thoracopods each consist of a protopod bearing a series of endites (usually 4–6), a 5- or 6-segmented endopod, a 2-segmented exopod, and a pseudopod* (see Figure 3). The posteriormost thoracopods frequently have a reduced number of endites and often a 4-segmented endopod.

Stages in cephalocarid larval development have been reported only for *Hutchinsoniella macracantha* Sanders, *Lightiella incisa* Gooding, and *L. serendipita* Jones. *Lightiella* species hatch with more trunk somites than does *Hutchinsoniella*. There is pronounced anamorphic

development of limbs and somites, and the transition from the metanaupliar to juvenile series occurs at the same functional level in all three taxa. The larval limbs are of the same morphology, particularly the cephalic appendages.

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*An epipod, but because of its more distal point of origin on the protopod, typically referred to as a pseudopod.

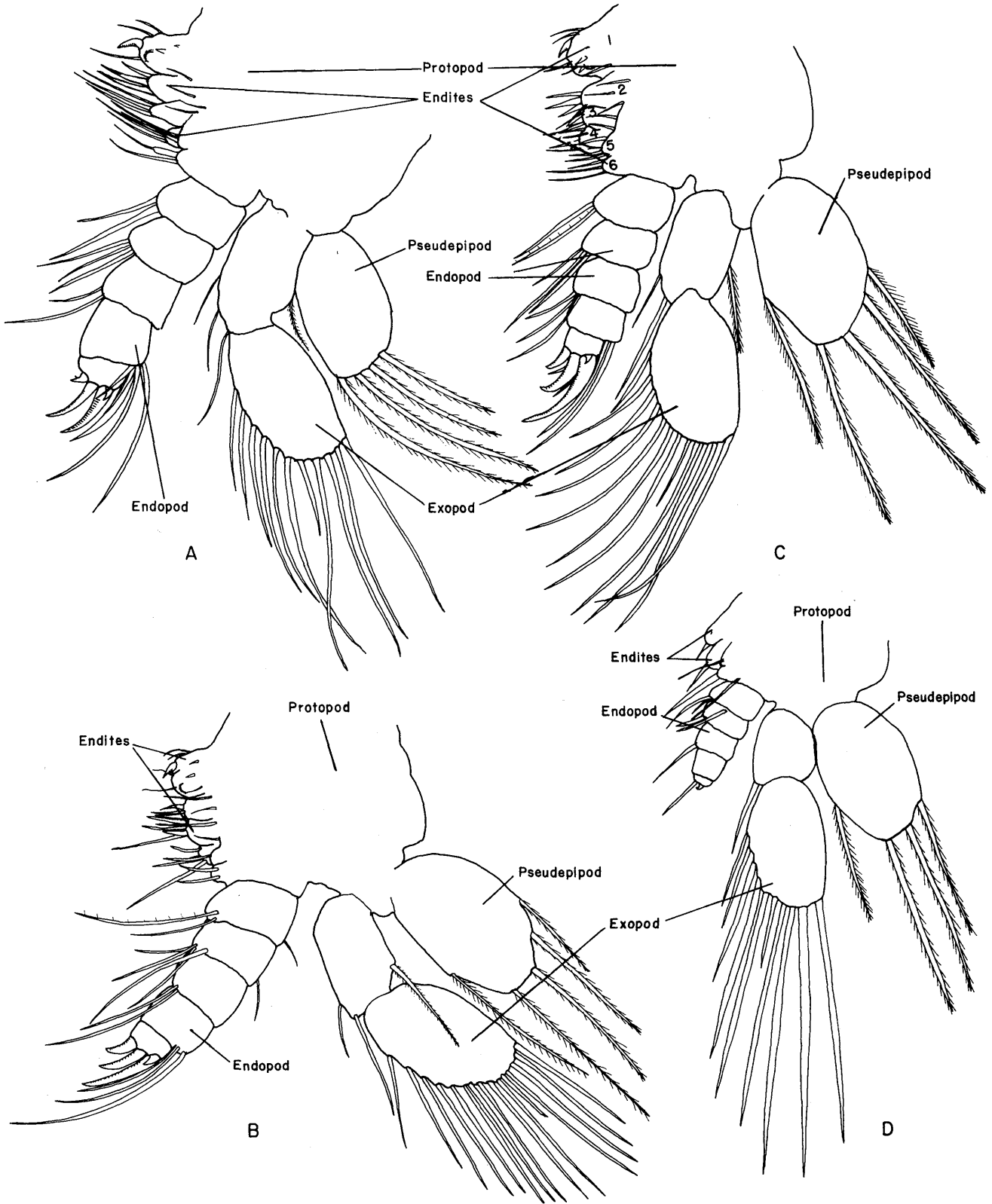


Figure 3 Cephalocarida: A. Maxilla; B. 1st thoracopod; C. 3rd thoracopod; D. 7th thoracopod [from McLaughlin, 1976].

Wakabara, Y., 1970. *Hutchinsoniella macracantha* Sanders, 1955 (Cephalocarida) from Brazil. *Crustaceana*, 19: 102-103.

Wakabara, Y., and S. M. Mizoguchi, 1976. Record of *Sanderiella bathyalis* Hessler and Sanders, 1973 (Cephalocarida) from Brazil. *Crustaceana*, 30: 220-221.

CLASS BRANCHIOPODA Latreille, 1817

The Branchiopoda includes the three subclasses Calmanostraca Tasch, 1969, Sarsostraca Tasch, 1969, and Diplostraca Gerstaecker, 1866. The Calmanostraca and Sarsostraca are represented by the Recent orders Notostraca and Anostraca respectively. The Diplostraca includes the orders Conchostraca and Cladocera. The major characters of the class, although quite variable, do distinguish it from the other crustacean classes. These characters include: (1) The presence, usually, of a carapace, in the form of a dorsal shield or bivalve shell (except in Anostraca). (2) Trunk with variable number of

somites; posterior region without appendages and usually terminating in paired caudal rami.* (3) Antennules usually unsegmented. (4) Mandibles usually without palp. (5) Maxillae usually reduced, vestigial, or absent; without maxillipeds. (6) Thoracopods usually of uniform shape, generally foliaceous. (7) Eyes usually present, paired. The four orders are described and discussed individually.

*Bowman (1971) does not always agree with this interpretation.

ORDER NOTOSTRACA Sars, 1867

Recent species	Nine to twelve, in two genera, <i>Triops</i> (= <i>Apus</i>) and <i>Lepidurus</i> .
Size range	10–40 mm.
Carapace	Present, in form of dorsal shield, with cervical groove.
Eyes	Paired, sessile, compound, and nauplius eye.
Antennules	Uniramous, slender; sometimes obscurely segmented.
Antennae	Reduced, vestigial, or absent.
Mandibles	Without palp.
Maxillulae	Uniramous, small, simple; usually with spines on inner margin.
Maxillae	Varying from well developed (<i>Lepidurus</i> spp.) to reduced or absent (<i>Triops</i> spp.).
Maxillipeds	None.
Thoracic appendages	Eleven pairs of phyllopodlike thoracopods.
Abdominal appendages	Highly variable in number, often nearly twice number of body "rings."
Telson	Heavily chitinized; with segmented caudal rami; frequently with supra-anal plate.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5 somites; thorax with 11 "rings"; abdomen with variable number of "rings"; sometimes with half rings and spirals. Body rings are not homologous with somites of other crustaceans; each ring may bear more than 1 pair of appendages.
Sexual characters	Gonopores on 11th thoracic "ring"; mature female with ovisac; no marked sexual dimorphism.
Sexes	Separate or functional hermaphrodites.
Larval development	Primarily anamorphic; hatch as metanauplii.
Fossil record	Upper Carboniferous.

Feeding types	Primarily detritus feeders; sometimes bodies of dead or living larger animals, e.g., oligochaetes, mollusks, tadpoles, and frog eggs, actively gnawed.
Habitat	Temporary fresh, brackish, or saline ponds; shallow lakes, peat bogs, and moors. Desiccation required in some species to activate hatching mechanisms with return of hydration.
Distribution	Generally worldwide; in the United States not known east of Mississippi River.

The instructions for observations and dissections of notostracan specimens are based on species of *Lepidurus*; the relatively few major morphological differences between *Triops* and this genus will be pointed out. Begin your examination by observing the structures on the dorsal surface of the intact animal (see Figure 4). The head and most of the body rings of the thorax are covered by a broad, somewhat horseshoe-shaped dorsal shield or carapace. Anteriorly, in the midline, the pair of closely set, sessile compound eyes are immediately apparent beneath a capsulelike swelling of the shield. Anterior to, and slightly beneath, the compound eyes is a small simple nauplius or median eye. Directly posterior to the compound eyes, in the midline, observe the nuchal or dorsal organ (circular in *Lepidurus* and somewhat triangular in *Triops*). This structure, whose function is unknown, apparently is not homologous with the nuchal or "neck" organ of anostracans. Posterior to the dorsal organ are 2 transverse grooves: the anterior mandibular and the posterior cervical; the latter delineates the head from the thorax. A low median keel extends posteriorly from the cervical groove. Laterally, on either side of the keel, the maxillary glands can be distinguished between the layers of the carapace. Distinguish the abdomen and observe the number of abdominal body rings visible in dorsal view and the few to numerous small spines on each ring. Are any half rings or spiral rings present? The telson may or may not extend between the pair of caudal rami as a supra-anal plate. In species of *Lepidurus* this plate is well developed; it is absent from all but one species of *Triops*, and in this species it is only rudimentary. The caudal rami are segmented and often armed with minute spinules and moderately long setae. [Bowman (1971) considers that *Lepidurus* species have a telson and that most species of *Triops* have an anal somite.]

Examine the animal in ventral view. The broad, flattened, underturned anterior portion of the dorsal shield, often referred to as the subfrontal plate, medially approximates the basal portion of the very prominent labrum. Below the subfrontal plate and laterad of the labrum, identify the rather small antennules and even smaller antennae. In some species the antennae may be vestigial or entirely wanting. Observe the relationship of the mouthparts to the labrum, phyllopods, and food groove.

The first thoracic appendages are greatly modified; the subsequent phyllopods generally are all similar in structure but are progressively reduced in size. Count the number of thoracic and abdominal appendages. How does this number compare with the number of body rings? Remove and examine a 1st thoracic appendage and one of the more typical thoracic phyllopods. An example of the latter has been illustrated and labeled in Figure 4D. The 6th endite has been called an endopod by Linder (1952). Identify the corresponding structures on the 1st thoracopod. Examine the 11th pair of thoracopods. In mature females ovisacs are attached to this pair of appendages. The presence of ovisacs is the only reliable external means of sex determination in the notostracans.

Before removing the mouthparts from one side of the animal, examine the maxilla carefully to find the duct leading to it from the maxillary gland. You should also be able to identify the external opening of the gland on the maxilla. Having identified these structures, remove, examine, and sketch the maxilla and other mouthparts. In some species of *Triops* the maxillae are reduced to small lobelike structures that receive the duct from the maxillary gland. The maxillulae are small, simple, single-lobed structures. Lying between the maxillulae and the mandibles are another pair of lobelike structures that variously have been interpreted as additional lobes of the maxillulae or paragnaths. Most recent evidence suggests that the latter interpretation is correct. The massive mandibles have broadly toothed triturating surfaces.

Notostracan larvae typically hatch as metanauplii, with the first 3 pairs of appendages (antennules, antennae, and mandibles) well developed and some segmentation apparent. Segments and appendages are added progressively through a series of instars.

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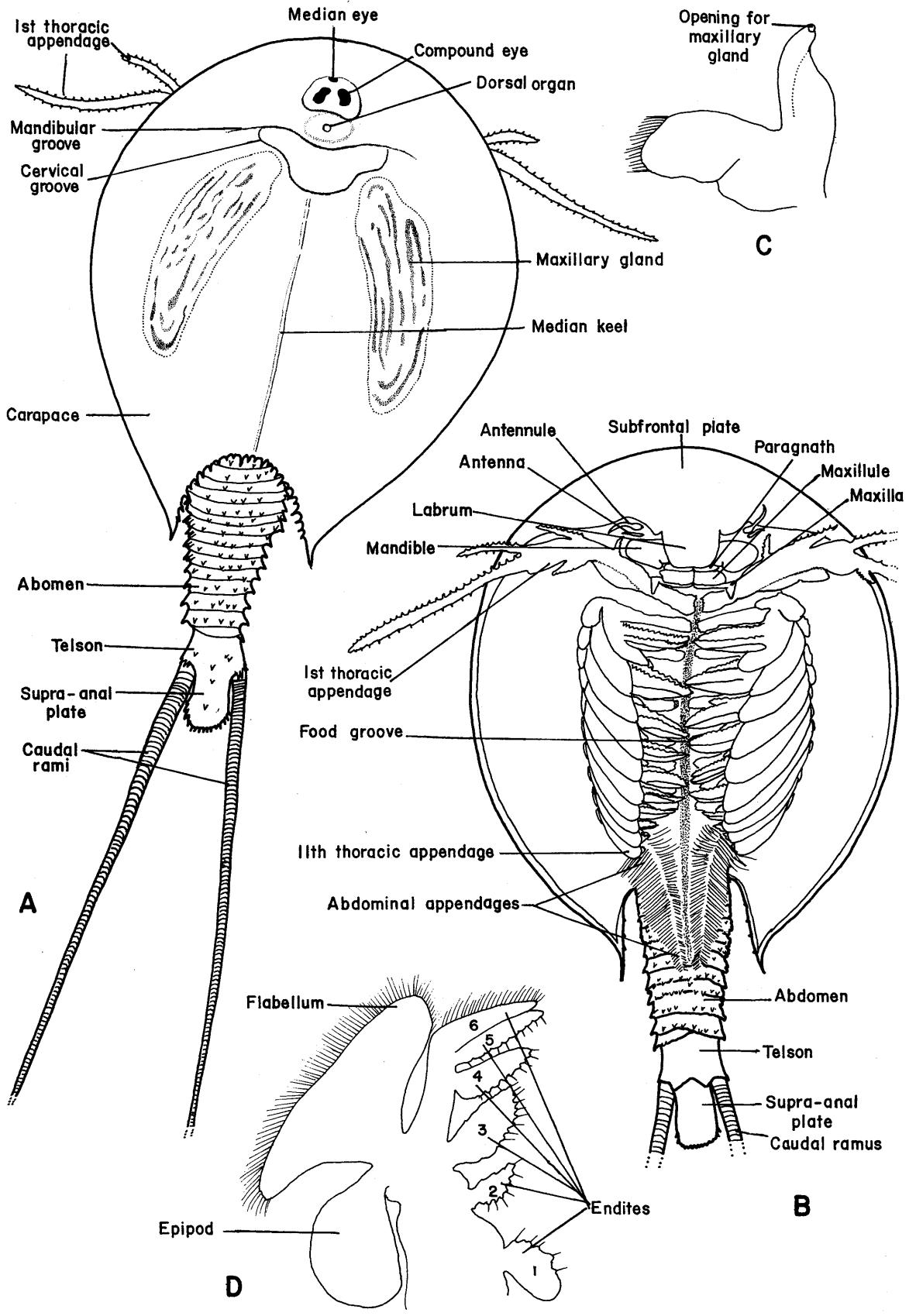


Figure 4 Notostraca: A. Whole animal (dorsal view); B. Whole animal (ventral view); C. Maxilla; D. Typical thoracopod.

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ORDER ANOSTRACA Sars, 1867

- Recent species Approximately 175, in seven families.
- Size range Up to 1 cm in length.
- Carapace Absent.
- Eyes Paired, stalked compound; median nauplius eye often present.
- Antennules Uniramous; short, thin, frequently unsegmented.
- Antennae Uniramous; usually reduced in females; stout and usually 2-segmented, often with accessory appendages in males; basal segments sometimes coalesced forming clypeus or frontal plate.
- Mandibles Without palp, except in *Polyartemia*.
- Maxillulae Uniramous; usually small, simple.
- Maxillae Usually reduced or vestigial.
- Maxillipeds None.
- Thoracic appendages Usually 11, occasionally 17–19, pairs of phyllopod-type, biramous thoracopods; generally similar in structure; posterior pair(s) sometimes reduced.
- Abdominal appendages None.
- Telson With long, setose caudal rami.
- Tagmata Head, thorax, and abdomen.
- Somites Head with 5; thorax with 11–19; abdomen with 8, excluding telson.
- Sexual characters Gonopores of both sexes on coalesced 1st and 2nd abdominal somites; females with ovisac produced, males with paired penes. Antennae of males usually well developed and modified for clasping females during copulation.
- Sexes Separate; however, parthenogenesis may occur.
- Larval development Primarily anamorphic; hatch as metanauplii, or nauplii.
- Fossil record Lower Devonian.
- Feeding types Filter feeders, primarily on plankton, occasionally predatory.
- Habitat Small, temporary, alkaline or freshwater pools; occasionally also in very saline lakes.
- Distribution Worldwide.

The instructions for the study of anostracan morphology are based on a species composite. Not all characters discussed necessarily will be found in a single taxon. Anostracans in general exhibit marked sexual dimorphism, so be sure to examine specimens of both sexes. Observe the overall body structure and segmentation before beginning the dissection (see Figure 5).

The long, clearly segmented body is divided into a head, thorax (bearing phyllopod thoracopods), and abdomen. The first 2 abdominal somites are coalesced and bear reproductive appendages. The abdomen terminates in a telson bearing a pair of caudal rami. [Once again, Bowman (1971) considers that the anostracan body terminates in an anal somite and that its appendages are uropods.]

The head, which is slightly swollen, is clearly distinguishable from the thorax. Laterally the head bears a pair of prominent, stalked compound eyes; medially and distally a small sessile nauplius eye frequently can be observed. Middorsally a nuchal ("neck") organ, presumably a sensory structure, usually is apparent through the integument. The segmentation of the head is indicated primarily by its appendages; however, the presence of a mandibular groove gives the superficial appearance of segmentation. The 1st pair of cephalic appendages, the antennules, are uniramous, thin, generally unsegmented (although frequently there may be a superficial suggestion of segmentation), and often bear terminal setae. The 2nd pair of appendages, the uniramous antennae, usually are reduced, often significantly so, in females. In males they exhibit considerable diversity in form but with few exceptions (*Polyartemiidae*) consist of 2 segments. The basal segments are short, cylindrical, and frequently have sensory hairs and outgrowths, the antennal appendages. In some taxa the basal segments fuse medially to form a platelike structure, the frontal appendage or clypeus. In addition to the prominent, posteriorly directed labrum that covers the mouth ventrally, the mouthparts include a pair of massive mandibles, a pair of moderately small and simple maxillulae, and a pair of even more reduced maxillae. Only the mandibles can be observed easily without dissection.

The thorax consists of 11 somites except in species of *Polyartemia* (19) and *Polyartemiella* (17). Each somite carries a pair of phyllopod appendages; however, in the female of a few species, the posteriormost pairs are reduced or absent. The somites are concave ventrally between the bases of the thoracopods, forming a longitudinal food groove.

The abdomen consists of 8 somites, excluding the telson; however, in a few taxa the division between the 8th somite and the telson is indistinct. The 2 anterior abdominal somites, which are partially or completely coalesced, bear reproductive appendages: in the male a pair of penes; in the female a single ovisac. The successive pre-telsonic somites lack appendages. The unsegmented

caudal rami frequently are fringed with long plumose setae. In a few species the telson is expanded to form a structure reminiscent of the supra-anal plate present in some notostracans.

Having observed the general morphology of both males and females, remove, examine, and sketch one or more of each type of appendage. The antennules, located in close proximity to the stalked eyes, are removed most easily from the dorsal side. Suction discs, hooks, and other modifications for grasping the females may be observed on the antennae of males. Examine these appendages carefully, also noting any frontal appendages, sensory setae, or other copulatory adaptations. Is a clypeus present? With the antenna removed from one side, the large, bulbous labrum can be observed. It need not be removed but may have to be pulled anteriorly to facilitate dissection of the other mouthparts. To either side of the labrum, and partially covered by it, are the prominent mandibles. With the exception of *Polyartemia*, the mandibles are without palps. Remove one of the mandibles and examine the triturating surface. Although anostracans in general are reported to lack paragnaths, the structures between the mandibles and maxillulae described by Lynch (1937) for *Branchinecta gigas* Lynch might well be interpreted as paragnaths. Similar structures are present in several other taxa as well, and apparently do not represent endites of the maxillulae. The latter appendages are relatively simple in form and usually bear a series of filtering spines or setae. The maxillae are either vestigial or reduced to a small simple lobe situated near the base of each 1st phyllopod.

Remove several of the phyllopods and identify the various elements. Are there structural differences between anterior and posterior pairs? How do anostracan thoracopods compare with the thoracopods of cephalocarids?

Examine the coalesced 1st and 2nd abdominal somites and the associated appendages in both sexes. The paired oviducts of the female are united and expanded to form the unpaired ovisac. The penes are eversible, thus they may appear broken or damaged. When fully extended, each apical segment usually is elongate, cylindrical, and frequently armed with serrations, denticulations, or spines. From each penis the looped vas deferens usually can be traced to the basal segment of the appendage. Characters afforded by the male, such as antennae, penes, and seminal vesicles, are some of the primary characters used in identification of taxa.

Using cleared specimens, examine the major internal organ systems (see Figure 6). Dorsally throughout the length of the body is the heart, with 14–18 pairs of segmental ostia. Blood enters the heart through the ostia from the underlying pericardial sinus and flows anteriorly. There are no arteries in anostracans; blood exits from the heart into the hemocoel through an anterior cardiac opening. The pericardial sinus is separated from

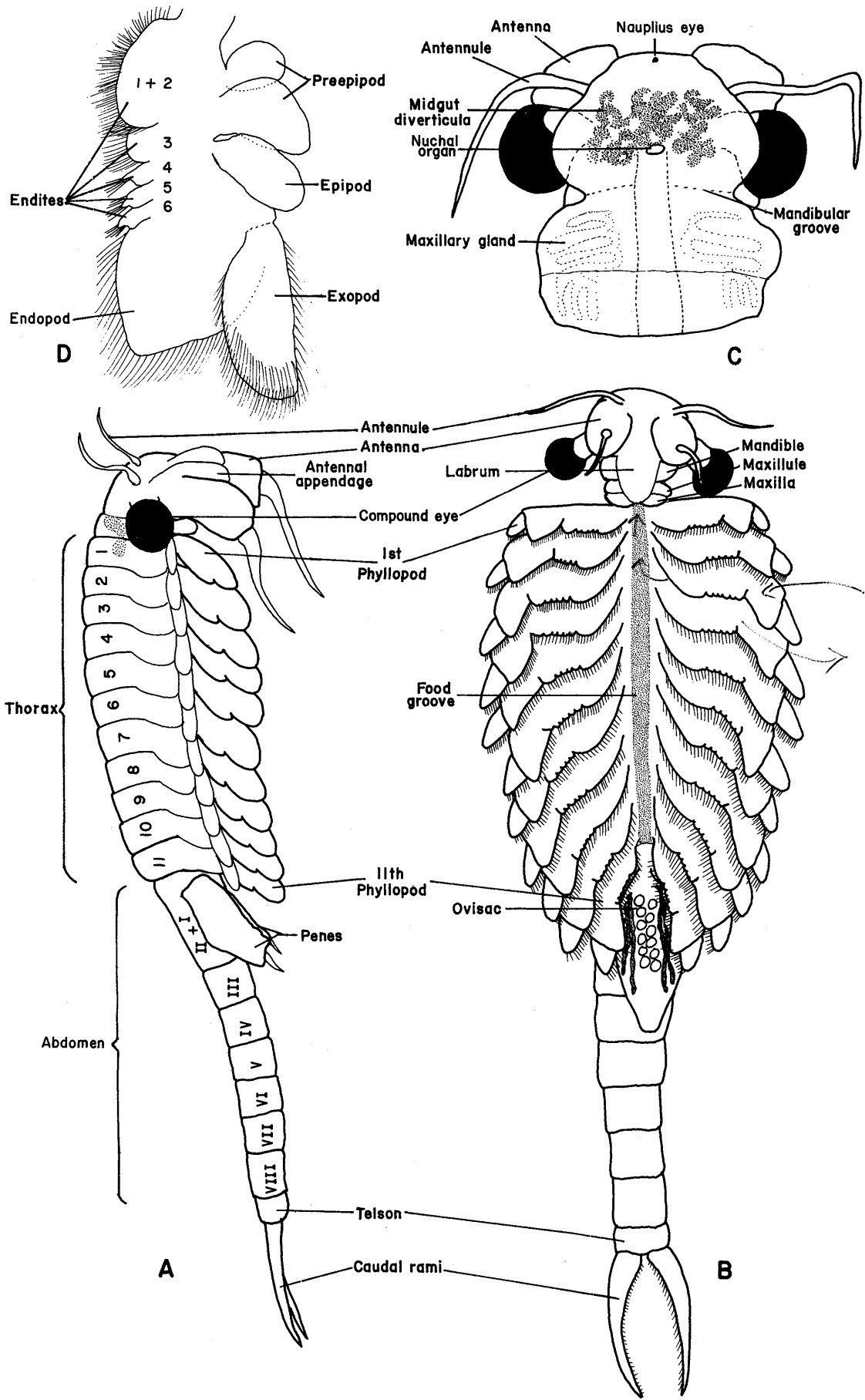


Figure 5 Anostraca: A. Male (lateral view); B. Female (ventral view); C. Cephalic region and 1st thoracic somite (dorsal view); D. Typical thoracopod.

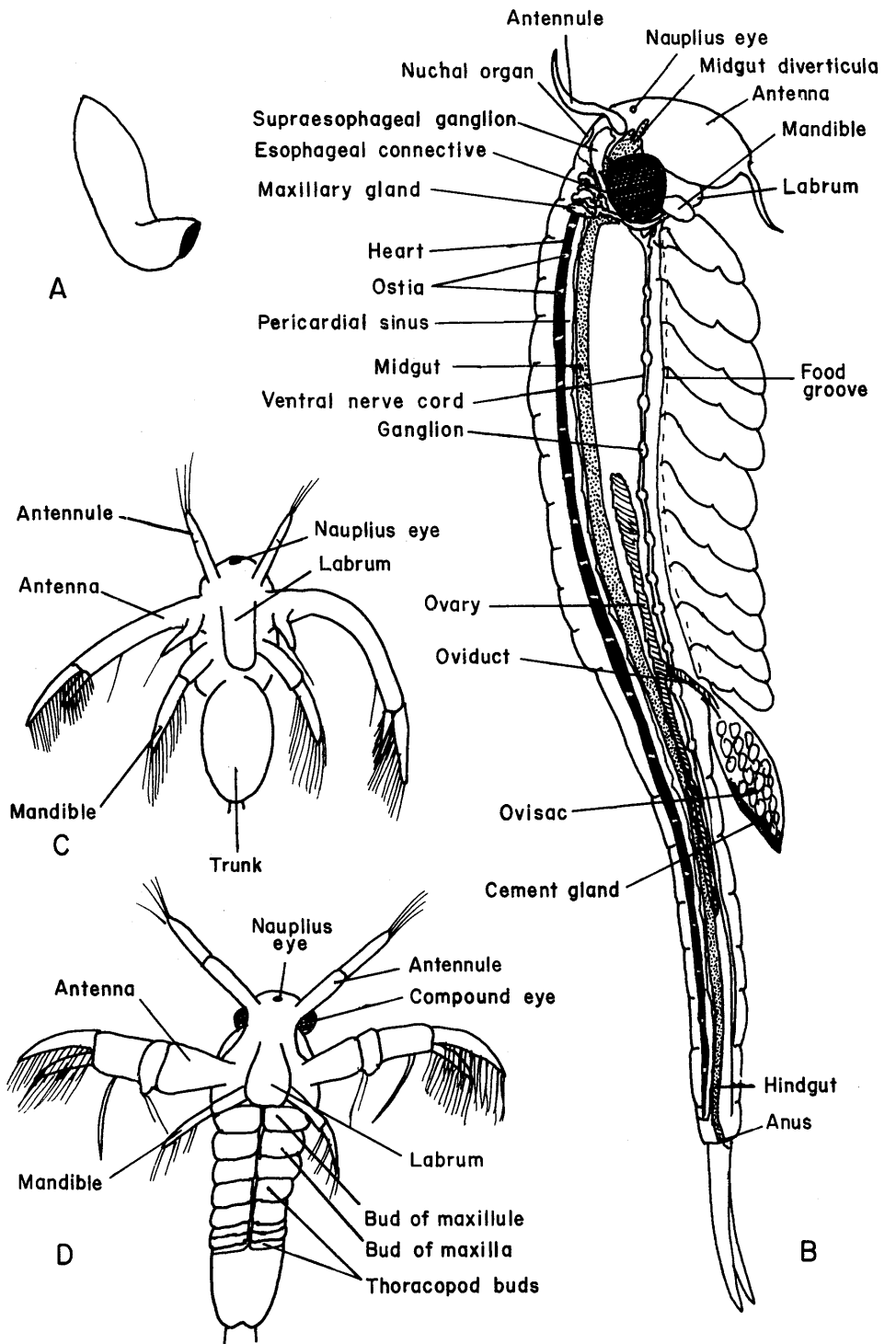


Figure 6 Anostraca: A. Left mandible; B. Diagrammatic anostracan in lateral view, illustrating major organ systems; C. Nauplius; D. Metanauplius [C and D after Snodgrass, 1956].

the hemocoel by a pericardial septum, but a series of openings provide for the return of blood to the sinus.

Directly beneath the heart and pericardial sinus, identify the midgut that extends almost the entire length of the body. Posteriorly the very short hindgut terminates in an anal opening located between the bases of the caudal rami. Food passes from the mouth through the short, vertically directed esophagus to the midgut; 2

cecalike diverticula, located in the head, join the midgut in the postesophageal region. Laterally and posteriorly the maxillary glands, which extend into the 1st thoracic somite, can be distinguished. The antennal glands, which in most crustaceans serve an excretory function, are present in larval anostracans but soon degenerate and are replaced in the adult by the maxillary glands. The ducts of these glands open between the maxillulae and

the 1st pair of thoracopods at the level of the vestigial or reduced maxillae.

Located between the lobes of the midgut diverticula, several sensory structures should be identified. In the dorsal midline observe the previously mentioned nuchal organ and more anterior nauplius eye consisting of 2 lateral and 1 ventral cups. In close proximity to the latter are the X-organ and paired ventral frontal organs; however, these structures will not be apparent without special staining. The latter structure is similar to but apparently not a homologue of the ventral frontal organ of the Malacostraca. Posteroventral to the nuchal organ is the supraesophageal ganglion and the esophageal connectives, which encircle the esophagus. As these nerve elements may be obscured by the midgut diverticula or the compound eyes, it is advisable to open the chitinous exoskeleton of the head and carefully remove or push aside the ceca. Trace the esophageal connectives to their junction with the subesophageal ganglia and ventral nerve cord. Ganglia are present in each somite through the 2nd postgenital somite.

The testes usually extend from the 3rd or 4th abdominal somite anteriorly into the 1st genital somite. Near the point of fusion of the 2 genital somites the paired vas deferens leave the testes and are directed ventrally and posteriorly to the penes. A large distention of the vas deferens near its junction with the penis serves as a seminal vesicle. The ovaries usually originate in the 4th or 5th abdominal somite and extend anteriorly to the 8th, or more often, 7th thoracic somite. The oviducts arise near the middle of the fused genital somite, or near the boundary between the 2 genital somites in instances where fusion has not occurred, and lead into the ovisac. The latter frequently will have a pair of cement glands dorsal and proximal to the egg mass.

Development in anostracans generally is anamorphic, with hatching occurring as either the nauplius or metanauplius. The naupliar stage is characterized by the presence of 3 pairs of appendages (antennules, antennae, and mandibles) and an unsegmented trunk. At the metanaupliar stage, not only are the 3 primary appendages present, but buds of the maxillulae, maxillae, and several thoracopods as well. Changes beyond the 1st metanaupliar stage are gradual and often between 14 and 17 instars are passed through before adulthood is reached.

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ORDER CONCHOSTRACA Sars, 1867

Recent species	Approximately 180 in six families.
Size range	Approximately 5–17 mm.
Carapace	Bivalve, laterally compressed, with or without growth lines; completely enclosing head, body, and appendages.
Eyes	Sessile, compound, dorsal, and usually closely set; and single nauplius eye.
Antennules	Uniramous, short; unsegmented or with 2 segments, usually with series of dorsal sensory papillae.
Antennae	Biramous; each ramus variously segmented according to taxa.
Mandibles	Without palp.
Maxillulae	Small, simple single lobe.
Maxillae	Vestigial or absent.
Maxillipeds	None.
Thoracic appendages	Thorax and abdomen not delimited; 10–32 pairs of trunk appendages.
Abdominal appendages	As above; generally phyllopod in structure, progressively decreasing in size posteriorly.
Telson	Broad, truncate, with pair of clawlike caudal rami or cercopods.
Tagmata	Head and trunk (postcephalic body).
Somites	Head with 5, trunk with 10–32 somites, excluding telson.
Sexual characters	Gonopores of both sexes on 11th trunk somite. Males with modified 1st and/or 2nd postcephalic appendages; carapace often exhibiting sexual dimorphism.
Sexes	Generally separate, but with some parthenogenetic reproduction.
Larval development	Primarily anamorphic; hatch as nauplii or metanauplii.
Fossil record	Lower Devonian.
Feeding types	Filter feeders on detritus and plankton.
Habitat	Free swimming in littoral regions of lakes, ponds, and temporary freshwater pools. Most seem to prefer warmer water than anostracans.
Distribution	Broadly distributed through temperate regions; however, certain species may be restricted to type localities or have very restricted distributional patterns.

The instructions for observations and dissections of conchostracans are based on specimens of *Caenestheriella*. Differences between this genus and the others in the family Cyzicidae are in the strength of the occipital point, the shape of the rostrum, and the number of antennal articles. Major taxonomic differences between the other conchostracan families will be pointed out when such differences are pertinent to the study of the general morphology of the group.

The conchostracan carapace is a bivalve shell, hinged in the midline, that encloses the head, trunk, and ap-

pendages (see Figure 7). A distinct umbonal region usually can be distinguished. Except in the Lynceidae, the shell is marked with a varying number of concentric lines, referred to as growth lines. As the carapace is not shed with the animal's exoskeleton during molting, the growth lines may reflect successive molts. The carapace is attached to the body anteriorly by an attachment ligament in the region of the umbones and by a pair of adductor muscles. By cutting the adductor muscle and ligament on one side, one valve of the carapace can be removed to expose the animal.

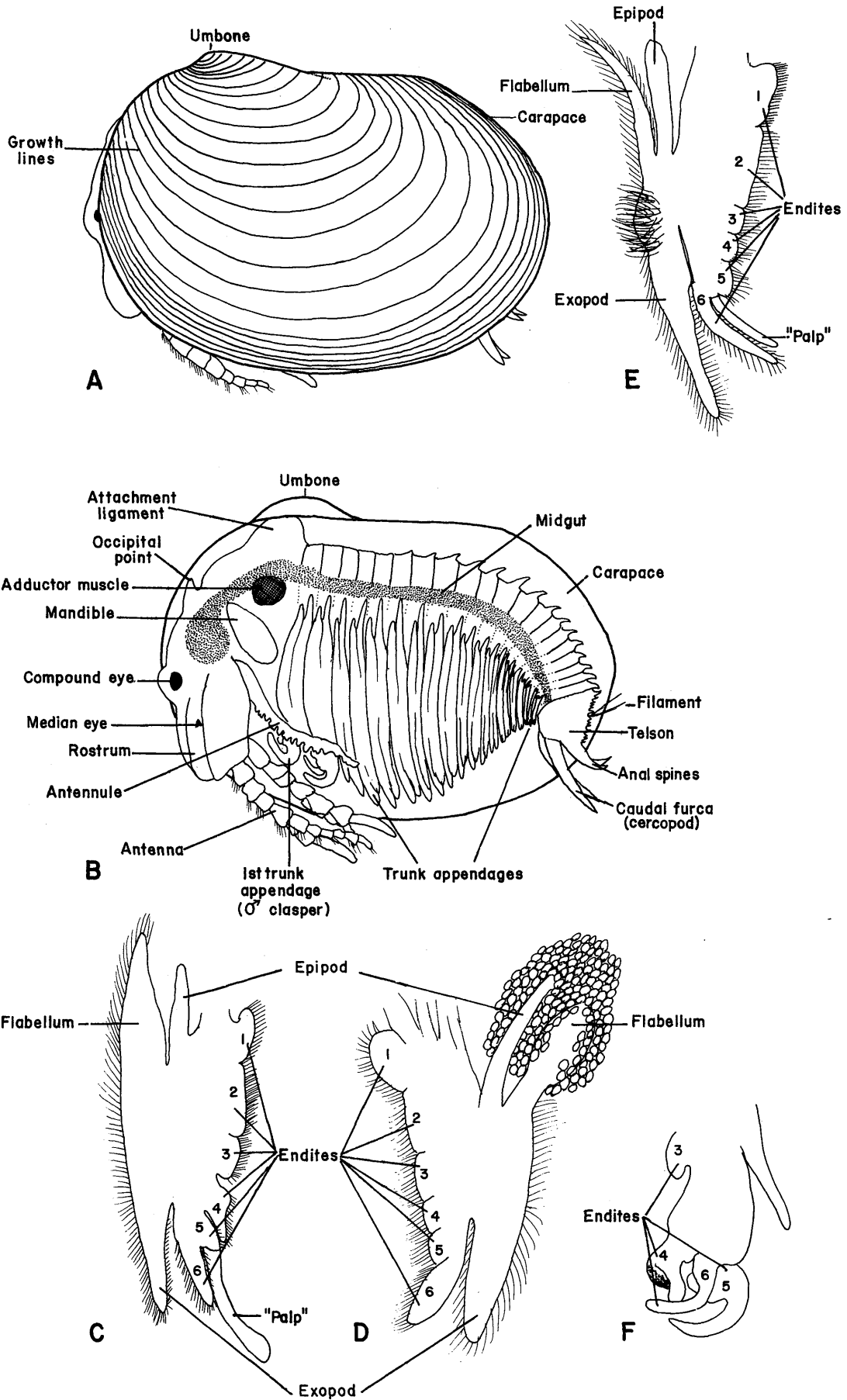


Figure 7 Conchostraca: A. Whole animal (lateral view); B. Animal with left valve removed; C. 10th thoracopod of male; D. 10th thoracopod of female; E. 1st thoracopod of female; F. 1st thoracopod of male.

The conchostracan body is divided into 2 parts, the head (cephalon) and trunk (postcephalic body). Several structures of the head will be immediately apparent. The sessile compound eyes usually are closely set but in a few taxa may be fused to form a single large eye. The median or nauplius eye is small and frequently triangular in shape. One of the most conspicuous structures of the head is the usually well-developed rostrum, which in many species is pointed, spatulate, and notched and may have a terminal spine. The occipital point and notch are not well developed in some species of *Caenestheriella* but in other taxa often are very prominent. In the family Limnadiidae a pyriform frontal organ projects from the middorsal surface of the head. This structure appears to be associated with the nauplius eye (cf. Elofsson, 1966). Note the moderately short uniramous antennules, the very well-developed biramous antennae, the prominent mandibles, and the small maxillulae. The abdomen is not distinguishable; the postcephalic body consists of 10 to 32 somites, excluding the telson. Each somite carries a pair of appendages, usually phyllopod in structure, but in males the 1st or the 1st and 2nd pairs are modified as claspers to grasp the female during copulation. In many species the dorsal surfaces of the posteriormost somites are drawn out into a series of spinelike projections. The telson is a broad structure terminating in a pair of caudal rami (cercopods or furcal claws). [Bowman (1971) considers only the triangular terminal lobe of the ultimate segment the telson; the remainder is an anal somite, and its appendages are uropods.] The morphological dorsal surface of the telson appears to be the posterior margin because of the flexure of the trunk. Usually it is armed with a series of spines; the most prominent posterior ones are referred to by some authors as "anal spines." A biramous filament also is present.

Begin your detailed examination by first removing the antenna and antennule from one side of the body. The biramous antenna has a stout protopod and moderately long, segmental rami. The antennule is uniramous, usually unsegmented, but may have 2 segments, with a series of dorsal sensory papillae. The chitinous mandibles are massive; the toothed margins usually are hidden by the labrum. The very small, single-lobed maxillulae carry only a few terminal setae. The maxillae are vestigial or absent.

Sexual dimorphism is most clearly expressed in the trunk appendages, so be sure to examine these appendages in both sexes. The 1st, sometimes the 1st and 2nd, pair in the male usually is modified for grasping. Compare one of these appendages with one of the more typical phyllopod appendages that follow. Identify the endites, epipods, and exopods of each. In the female the 1st and 2nd pairs of phyllopods are unmodified; however, modifications for egg carrying occur on the 9th to 11th pairs. The eggs are cemented in raftlike fashion to the slender and elongate flabellum and epipod. How do the

trunk appendages of conchostracans compare with the thoracopods of the anostracans and notostracans?

The conchostracan nauplius is atypical in that the antennules are reduced or vestigial. The shell typically is produced by a pair of integumental folds in the metanauplius; however, the nauplii of some have a broad dorsal shield resembling that of the Notostraca. The later larval stages frequently resemble the adult structure of the Cladocera.

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ORDER CLADOCERA Latreille, 1829

- | | |
|-----------------------|--|
| Recent species | Approximately 420 in eleven families. |
| Size range | 0.2–18 mm. |
| Carapace | Univalve, laterally compressed, and folded over; usually enclosing trunk and appendages; occasionally reduced. |
| Eyes | Sessile compound, coalesced, medial; occasionally absent; often with small nauplius eye; occasionally only with latter. |
| Antennules | Uniramous, usually short, slender, with tuft of terminal sensory setae; occasionally modified in males. |
| Antennae | Biramous, strong; principal appendages of locomotion. |
| Mandibles | Without palp. |
| Maxillulae | Small, simple. |
| Maxillae | Occasionally rudimentary or vestigial; usually absent. |
| Maxillipeds | None. |
| Thoracic appendages | Thorax and abdomen not readily delimited; 4–6 pairs of biramous trunk appendages, usually foliaceous; in some predatory species modified for grasping prey. |
| Abdominal appendages. | See above. |
| Telson | Usually not delimited; typically with clawlike caudal furca; occasionally with long caudal process or appendix. |
| Tagmata | Head and trunk; posterior portion of trunk recurved (postabdomen). |
| Somites | Variable, not easily distinguished. |
| Sexual characters | Genital ducts opening laterally on “thoracic” portion of trunk. Antennules usually more developed in males, occasionally modified for clasping female; rostrum sometimes exhibiting sexual dimorphism. |
| Sexes | Sometimes separate; parthenogenetic reproduction most common. |
| Larval development | Primarily epimorphic; in <i>Leptodora</i> , released from brood pouch as metanauplii. |
| Fossil record | Oligocene to Recent. |
| Feeding types | Primarily filter feeders; occasionally particulate feeders or predators. |
| Habitat | Generally restricted to fresh or brackish waters, occasionally marine. Representatives occasionally also found in acid bogs or mud and saline lakes. |
| Specialization | Cyclomorphosis, i.e., seasonal changes in morphology that drastically alter individual appearances. |
| Distribution | Worldwide. |

The instructions for observations and dissections of the Cladocera are based on species of *Daphnia*. Cladocerans do exhibit a considerable amount of interspecific morphological variation; however, with the exceptions of members of the families Leptodoridae and Polyphemidae, they generally follow the patterns described for species of *Daphnia*. Your attention will be directed to any major exceptions. If living specimens are not available for observation, some cleared or stained specimens also should be available, as the opaqueness of most preserved material makes study of the internal anatomy difficult. Some staining techniques, such as chlorazol black in lactophenol, frequently will distort the carapace.

Parthenogenesis is the most common form of reproduction among cladocerans, therefore samples may contain few if any males. Should males be present, they usually can be recognized by their smaller size, the longer and occasionally modified antennules, the somewhat modified postabdomen, and the 1st trunk appendage modified as a hook or claw for grasping the female.

Observe the general body features before attempting a dissection of the appendages and mouthparts (see Figure 8). The head is exposed; the body usually is enclosed in a bivalvelike carapace. Actually the carapace is a single valve arising from an integumental fold behind the head; it extends posteriorly and laterally to enclose the trunk and appendages. It may be extended posteriorly as a prominent carapace or shell spine. In a few taxa, the carapace is greatly reduced and serves only as a brood pouch. The junction of the head and body frequently is delimited by a depression, the cervical notch or sinus. Anteriorly the head usually is produced into a beaklike rostrum. The head region between the rostrum and the compound eye is referred to as the vertex. In addition to the large sessile compound eye (the result of the fusion of the typically paired eyes), many cladocerans also retain the small median or nauplius eye located in the midline between the mouth and the compound eye. Elofsson (1966) has reported that the frontal organ present in some taxa is probably an additional light-sensitive structure.

The appendages of the head consist of paired antennules, antennae, mandibles, and maxillulae. The maxillae are absent except in a few taxa where they are rudimentary. The antennules usually are quite short, situated in close proximity to the rostrum, and provided with sensory setae. The antennae are the very well-developed biramous appendages arising laterally from the head; they are the primary locomotory appendages in cladocerans.

Cut the carapace along the dorsal midline to expose the body and appendages on one side or remove it entirely. In most cladocerans the trunk segmentation is not apparent, but the posterior part of the abdomen is ventrally flexed. This region, referred to as the postabdomen, abreptor, or pygidium, usually terminates in a pair of caudal rami (caudal furca); occasionally a long caudal

process or appendix may be present. On the morphological dorsal surface of the postabdomen, which appears to be in a posterior position as a result of the abdominal flexure, are a series of small anal spines and a pair of abdominal setae. Frequently in females the brood pouch with developing embryos will be observed, and occasionally the developing ephippium and ephippial eggs will be present. Posterior to the brood pouch are a pair of abdominal processes. These are thought to aid in closing off the brood chamber. Depending upon the particular taxon under study, 4 to 6 pairs of trunk appendages will be present. Before beginning the dissection of the mouthparts and trunk appendages, observe the relationships of these appendages.

For ease of dissection it is recommended that you remove the antenna first. Then carefully remove the trunk appendages from one side of the body. In *Daphnia* and related taxa there are 5 pairs. These appendages usually are flattened and foliaceous; they are used for filtering food particles. In the Polyphemidae and Leptodoridae these appendages usually are prehensile. Examine each appendage and identify the structural elements. How do these appendages, particularly the 3rd and 4th pairs in *Daphnia* and related genera, compare with and/or differ from those of other Branchiopoda?

With the anterior trunk appendages and antenna removed, the mouthparts will be much more accessible. The prominent labrum lies in the midline and covers the median portions of the well-developed mandibles. Remove 1 of the mandibles and observe the toothed or ridged grinding surface. A pair of very small, simple maxillulae are located between the mandibles and the median, conical paragnath (lower lip).

Examine a cleared specimen and identify the components of the major organ systems. Dorsally the subovate heart is located anterior to the brood pouch. It may appear reddish in color as hemoglobin frequently is present. There are no arteries or well-developed sinuses in *Daphnia* and related genera, but an anterior aorta has been reported in *Leptodora*. In *Daphnia* blood flow is channeled through the hemocoel and into the appendages by thin membranes. Blood enters the heart through a single pair of ostia.

Food is passed along the food groove to the mouth and then through the short esophagus to the elongate, straight or coiled midgut. In *Daphnia* and related genera a pair of ceca, situated posteriorly in the head, join the midgut just posterior to its junction with the esophagus. In some genera these ceca are absent, and in others a 3rd cecum is present posteromedially. This cecum is thought to be derived from the hindgut. The latter is short and terminates in an anal opening at the base of the caudal furca.

In addition to the large compound eye, 1 to 4 small nauplius eyes may be present. These are innervated by nerves from the supraesophageal ganglion, which lies just anterior to the midgut-esophagus junction and

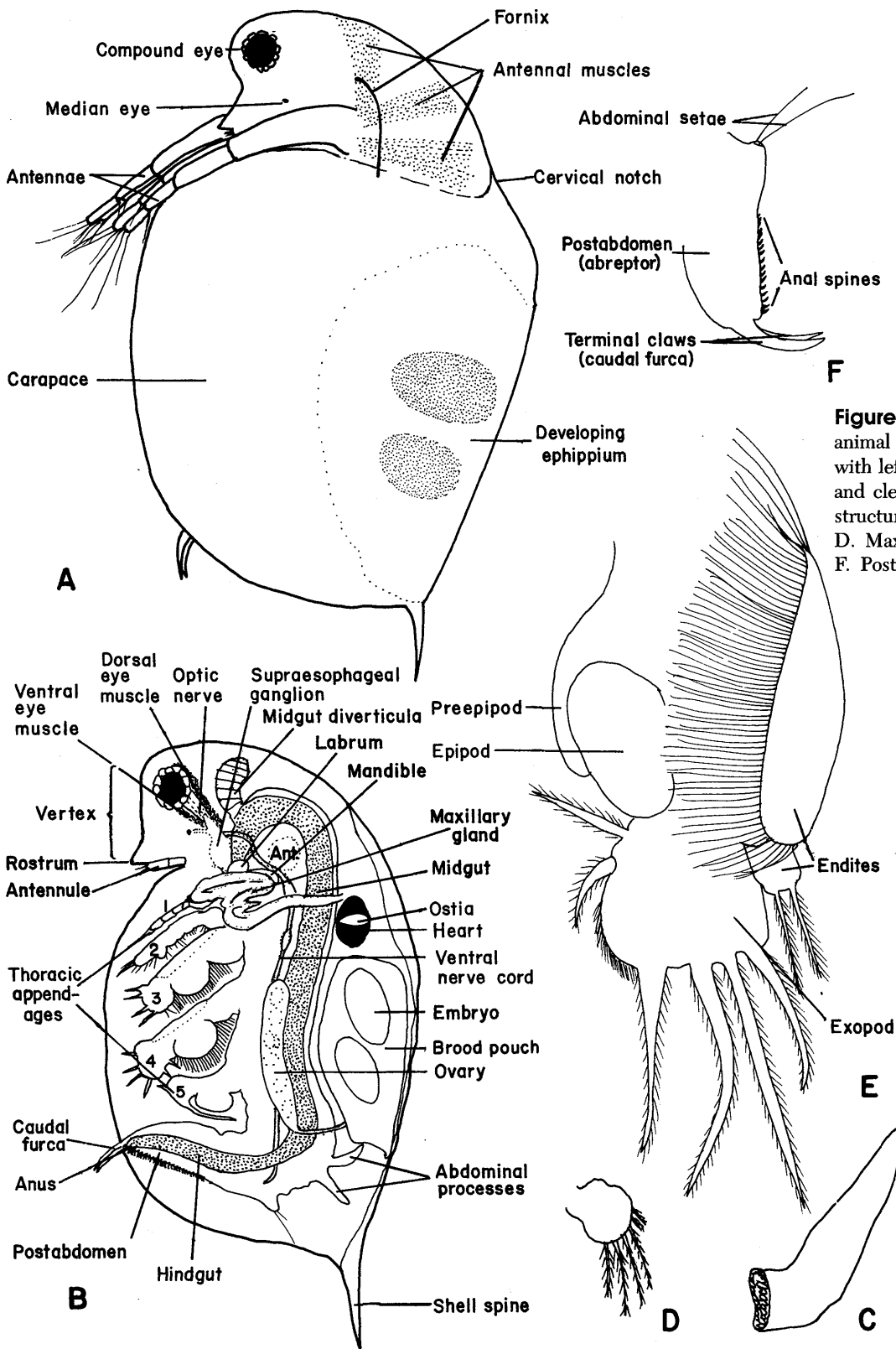


Figure 8 Cladocera: A. Whole animal (lateral view); B. Animal with left side of carapace removed and cleared to show internal structures; C. Mandible; D. Maxillule; E. 4th thoracopod; F. Postabdomen.

below the midgut diverticula. Trace the large optic nerve from the ganglion to the compound eye. The eye is moved by pairs of dorsal and ventral optic muscles. The pair of esophageal connectives that encircle the

esophagus, as well as the antennular and antennal nerves, may be difficult to identify unless the specimen has been stained with one of the vital stains. The ganglia of the ventral nerve cord usually can be distinguished

without special staining. In *Daphnia* 3 ganglia are present in the anterior part of the trunk.

Identify the paired ovaries lying behind the midgut in the posterior half of the trunk. A slender duct leads from each ovary to the brood pouch. In males the paired testes are in a similar position. The vas deferens are directed ventrally to gonopores on the furca, or occasionally to penes when present.

Only in *Leptodora* is a metanauplius hatched. In all other cladocerans complete development takes place within the egg. Under routine conditions one to several parthenogenetic generations may be produced without any males at all. This does not, however, mean that all parthenogenetic offspring will be identical. At least in some species of *Daphnia* there is a type of meiosis that occurs within the nuclear membrane and there may be some gene exchange before bivalents conjugate during anaphase. Under certain circumstances, presumably ones of stress, both males and haploid eggs that require fertilization are produced. These are ephippial eggs, rich in yolk, and capable of withstanding drying or freezing. They are enclosed in strongly sclerotized egg cases, or ephippia, which, after being discharged into the water, begin to float and can be transported by wind, birds, and other animals.

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CLASS OSTRACODA Latreille, 1806

Recent species	Approximately 2000.
Size range	0.4–30 mm.
Carapace	Bivalve, laterally compressed; completely enclosing head, body, and most appendages.
Eyes	Usually present; single nauplius eye, sometimes also sessile compound eyes.
Antennules	Uniramous; endopod with 5–8 segments (including 2 of propod); sometimes sexually dimorphic.
Antennae	Biramous; sometimes sexually dimorphic.
Mandibles	With endopodal palp, exopod, and gnathobase.
Maxillulae	Well developed, variable (usually referred to as maxilla).
Maxillae	None (1st thoracopod sometimes referred to as 2nd maxilla).
Maxillipeds	None (1st thoracopod sometimes referred to as maxilliped).
Thoracic appendages	One to 3 pairs of thoracopods, usually biramous; variously developed and specialized.
Abdominal appendages	None.
Telson	Not delimited; with caudal rami, variable in structure and form.
Tagmata	None delineated.
Somites	Segmentation indicated by paired appendages.
Sexual characters	Genital ducts opening anterior to caudal furca; usually on genital lobe; female often with sperm receptacle; male frequently with penes. Appendages and carapace sometimes sexually dimorphic.
Sexes	Separate; sometimes parthenogenetic reproduction.
Larval development	Anamorphic; eggs brooded beneath carapace or cemented to plants or substrate; 6 naupliar substages (nauplius atypical, with bivalve carapace).
Fossil record	Cambrian to Recent; approximately 12,000 fossil species described.
Feeding types	Diverse; filter feeders (plankton and detritus), predators, scavengers, and herbivores.
Habitat	Benthic and planktonic; in virtually all aquatic habitats, including sulfur springs, stagnant ponds, swamps, streams, brackish lagoons, estuaries, tide pools, salt marshes, epicontinental seas, and ocean basins. Two species are reported to be terrestrial in moss; one group is commensal with freshwater isopods, crayfish, and crabs.
Distribution	Worldwide.

The instructions for the examination of ostracod external morphology are based on a composite taken from examples of both Recent subclasses, the Myodocopa and Podocopa. Specific differences that may be encountered

by students having representatives of only one of the subclasses available for study will be pointed out. Although our present interest is with Recent crustaceans, fossil ostracods have played an extremely important role

in ostracod taxonomy, phylogeny, and morphology. Consequently, ostracod specialists have developed a terminology and vocabulary that is not necessarily applicable to other crustacean groups. This is particularly true with reference to the ostracod shell, and shell structure is given a great deal of attention by specialists of this class. An in-depth study of various types of ostracod carapace sculpture is beyond the scope of this text, so only the more generalized aspects of the shell morphology will be described.

The carapace is truly bivalved, being articulated dorsally along a hinge (see Figure 9). The 2 valves, which may be equal, subequal, or unequal in size, enclose the entire body of the animal. Generally the carapace is composed of a hard calcium carbonate layer and a soft epidermis, although some taxa possess very thin carapaces. The calcium carbonate layer is coated with a layer of chitin and the epidermis is enclosed in chitin. The calcium layer may be subdivided into an outer lamella and a duplicature. The duplicature (calcified inner lamella) extends along the free margin of the valve and is fused to the outer lamella. In contrast to conchostacans, ostracods shed their hard carapaces in a series of molts. Environmental conditions may contribute to shell thickness and to bizarre ornamentation developed after a molt. The shape and the outline of the carapace are of diagnostic significance. When the valves of the carapace are opened, a free edge and a contract margin can be determined. The latter is the narrow portion of each valve that comes in contact with its opposing valve upon closure. The contact margin can be simple or complex. In its simplest form, a single ridge, called the selvage, extends along the free margin. When the valves are closed, the selvage fits into the selvage groove of the opposite valve. When a duplicature is present, the contact margin is complex. Two other ridges may be present: a small ridge, the list, proximal to the selvage; and distal to the selvage a ridge (flange) that is part of the outer lamella. When both a selvage and a flange occur, they are separated by a flange groove. The lateral surfaces of the valves may be smooth or ornamented by granules, pustules, striae, costae, pits, spines, or reticula. The surface may also be pierced by pores or have lobes, sulci, furrows or sutures.

Remove one valve of the carapace and observe the animal while it is still attached to the other valve. Notice the general body form and the orientation of the appendages. The ostracod body is short, laterally compressed, and shows no trace of segmentation. Recent subclasses of ostracods may be separated, in part, by the development of the antennae. In the Myodocopa the antennae are strongly developed swimming appendages; in the Podocopa they are developed for walking. The latter lack a rostrum and rostral incisure that usually are present in the Myodocopa. Before removing the animal from its other valve, determine if sessile eyes, a nauplius eye, or a lens or pair of lenses are present dorsal, and usually

posterior, to the base of the antenna. A frontal organ also may be observed, usually in close proximity to the eyes.

Remove the animal from the other valve but do not discard the valve. Remove and examine the appendages of one side of the body. After the antennule and antenna have been removed, the thoracic appendages should be removed before attempting to dissect the mouthparts. Depending upon the taxon, 1 to 3 pairs of thoracopods are present. The protopod has 1, 2, or less frequently, 3 segments (coxa, basis, and possibly precoxa). They usually have an endopod and exopod and sometimes additional structures such as epipods and endites. Identify the structural components of the thoracopods of your specimen(s). The thoracopods usually are rather elongate in podocopid ostracods; in many myodocopids the 3rd pair of thoracopods are markedly altered in structure; they are multiarticulate and directed dorsally and posteriorly.

The mouthparts consist only of the mandibles and maxillulae. Remove and examine these appendages. The mouth is formed by an upper lip (labrum) and a lower lip (labium or hypostome). In most ostracods the latter is preceded by a pair of rake-shaped chitinous structures embedded in the tissue.

A definitive abdomen is lacking in ostracods; the body terminates in a caudal furca. [Bowman (1971) interprets the posteriorly produced terminal end of the abdomen in the podocopid genus *Loxococoncha* as a telson and the rounded lobes ventral to the anus and bearing setae possibly as nonarticulated uropods. He also suggests that the myodocopid furca may be a deeply incised telson.] Very frequently a genital lobe can be distinguished anteroventrally of the caudal furca. In some taxa, a very large and complex penial structure is developed in males.

Returning to the shell, examine the interior and identify the muscle scars and hinge structure. The patterns of these scars and the details of the hinge are of taxonomic importance.

The internal organ systems are quite variable in ostracods. The description presented is based on specimens of the myodocopid family Cypridinidae (see Figure 10). Major differences between cypridinids and other myodocopids, as well as differences between the Myodocopa and Podocopa, will be pointed out. Begin by removing one half of the carapace of a cleared specimen and observing the general musculature of the body and appendages. To examine the major internal organ systems, carefully remove the cephalic and trunk appendages from the exposed side of the body.

A heart is present only in myodocopids. In many taxa it is positioned just dorsal to the mandible; in the species illustrated it is located anterodorsally near the hinge. A single pair of ostia is present in the ostracod heart; blood flows from the heart either through an anterior opening or through a definitive aortic artery. Identifiable arteries are absent in podocopids and in many

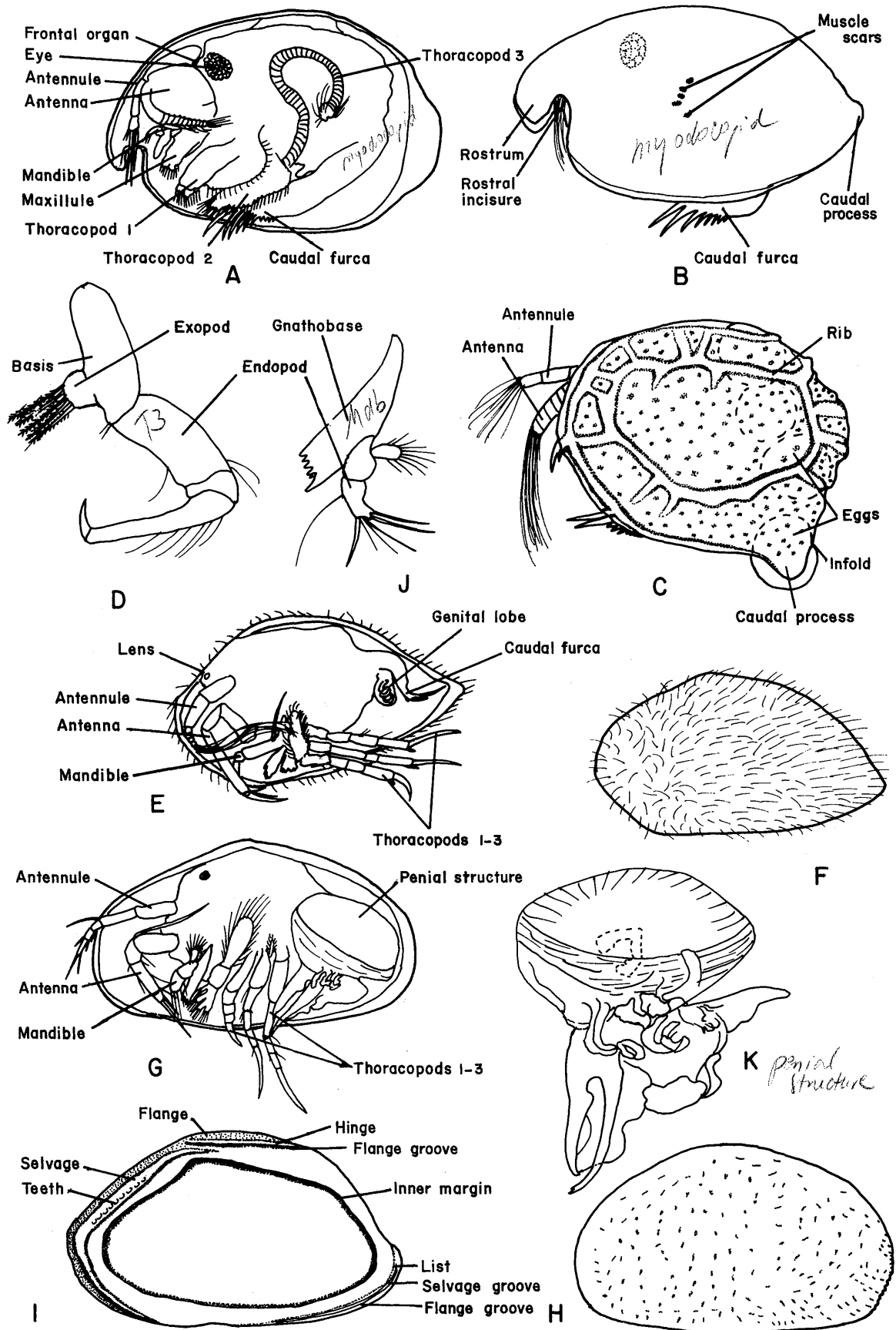


Figure 9 - Ostracoda: A-C, Myodocopa; D-K, Podocopa. A. Lateral view of animal with left valve removed; B. Whole animal (lateral view); C. Whole animal with sculptured carapace (lateral view); D. 3rd thoracopod; E. Lateral view of animal with left valve removed; F. Left valve (external view); G. Lateral view of animal with left valve removed; H. Left valve (external view); I. Right valve (internal view); J. Mandible; K. Penial structure enlarged.

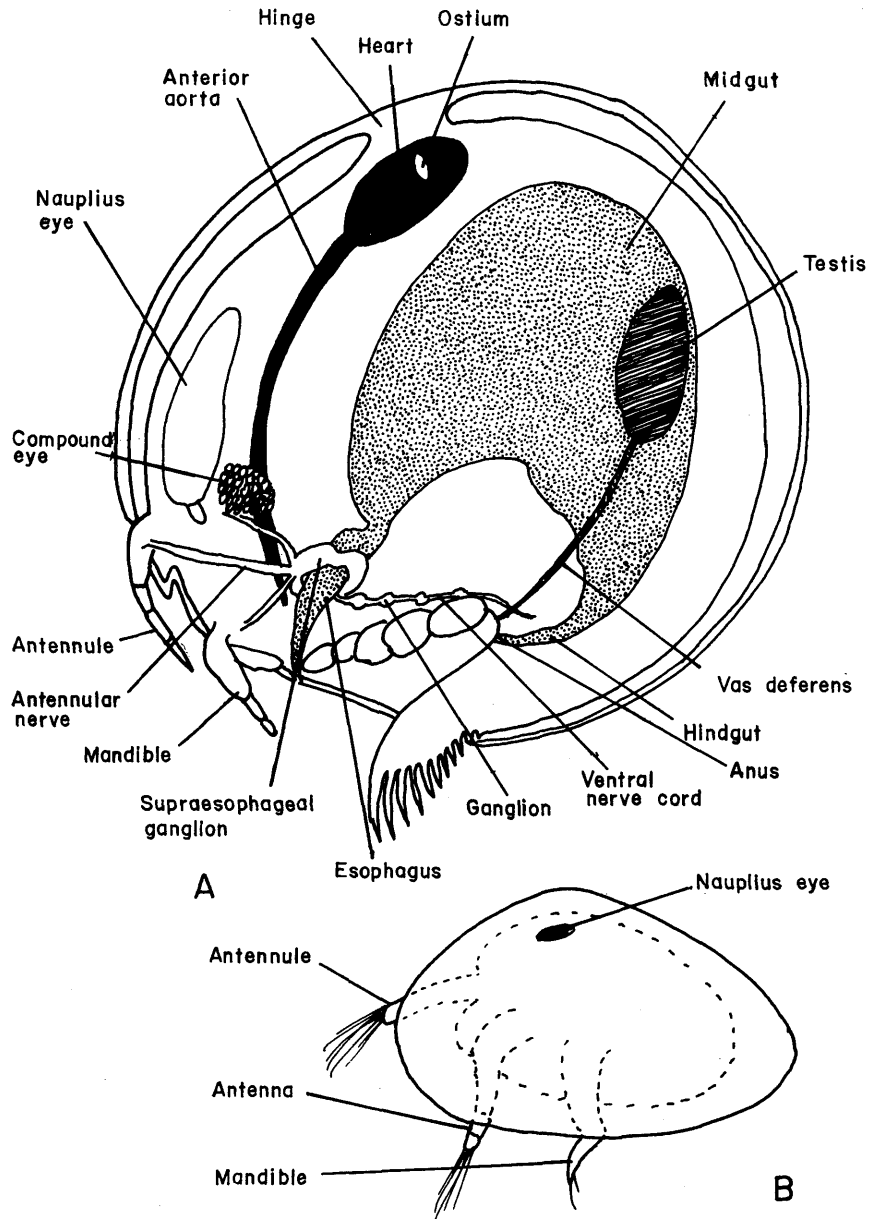


Figure 10 A. Diagrammatic myodocopid ostracod with musculature removed to show major organ systems; B. Nauplius.

myodocopids; blood circulation is through blood spaces or a network of blood channels.

Food is passed from the mouth through the muscular esophagus to the midgut or stomach. In myodocopids such as the species illustrated in Figure 10, the midgut is very large and occupies much of the body space; the hindgut is short and opens to the exterior through a ventrally positioned anus. In podocopids the midgut is small and usually subdivided by a constriction; the hindgut is enlarged and the anus is dorsal to the furca. A single large pair or numerous small midgut ceca are present in many ostracods, but are frequently absent in cypridinids. In some the gut appears to be surrounded

by parenchymal tissue. Excretory functions are carried out by antennal glands in some ostracods and by maxillary glands in others.

Observe the prominent "nerve ring" consisting of the supraesophageal ganglion and esophageal connectives encircling the esophagus. Trace the relatively large nerves leading from the nerve ring to the antennules, antennae, and mouthparts. From the nerve ring, follow the parallel branches of the ventral nerve cord posteriorly through the body, identifying the ganglia of the trunk appendages, which often lie in close proximity to the bases of the appendages. Frequently the ganglion of the last pair of thoracopods will be very small.

In females the ovaries usually are located in the posterior part of the body, although in the Cyprididae they are in the hypodermis. If possible, trace the oviducts from the ovaries to their openings, usually on a genital lobe anterior to the caudal furca. Are seminal receptacles present on your specimen(s)? The male reproductive system basically consists of paired testes, vas deferens, and usually penes; however, in many taxa ejaculatory ducts or a complex penial structure are present. In a male specimen locate the testes (simple in myodocopids, usually 4-lobed in podocopids) and trace one of the vas deferens. Are penes, penial apparatus, or ejaculatory ducts present?

Larval development in ostracods differs from that in other Crustacea in that the newly hatched nauplius possesses a bivalve shell. As with typical nauplii, the appendages of the 1st naupliar substage consist of the paired antennules, antennae, and mandibles. Usually the buds of a new pair of appendages appear after each molt. The number of larval instars varies among the taxa.

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CLASS MYSTACOCARIDA Pennak and Zinn, 1943

Recent species	Nine plus three subspecies in one genus, <i>Derocheilocaris</i> .
Size range	0.525–1.01 mm; stage 1 larvae reported greater than 2.0 mm (Hessler, 1969)
Carapace	Absent.
Eyes	Ocelli, generally 4; each typically with lens, usually without pigment.
Antennules	Uniramous, sometimes with terminal aesthetasc; primarily sensory in function, also used in locomotion.
Antennae	Biramous; used in locomotion and feeding.
Mandibles	Biramous; used in locomotion and feeding.
Maxillulae	Uniramous; used in locomotion and feeding.
Maxillae	Uniramous, without exopod; gnathobase usually well developed.
Maxillipeds	One pair; usually biramous; without exopod in 1 species.
Thoracic appendages	Four pairs of small, uniramous, unsegmented thoracopods; function as yet undetermined.
Abdominal appendages	None.
Telson	With clawlike caudal furca; used in grooming and as lever in movement.
Tagmata	Head, thorax, and abdomen; or preferably, head, maxilliped somite, and thoracoabdomen.
Somites	Head with 5; maxilliped somite (1); thoracoabdomen with 9, excluding telson.
Sexual characters	Gonopore on ventral surface of 3rd thoracoabdominal somite, or reportedly possibly paired on appendages of 3rd somite; 4th, sometimes also 3rd, pair of appendages exhibiting sexual dimorphism.
Sexes	Separate.
Larval development	Anamorphic; hatch as nauplii or metanauplii; 7–10 juvenile substages.
Fossil record	Recent.
Feeding types	Deposit feeders, feeding on detritus, bacterial film, and microorganisms.
Habitat	Interstitial on intertidal and subtidal beaches. Sand type and particle size appear to be important factors.
Distribution	Maine to Miami Beach, Florida; Gulf of Mexico; Mediterranean and Portugal; east and west coasts of Africa; west coast of South America.

Mystacocarids basically are very conservative in their morphology. Individual species can be distinguished by the characters of the antennular portion of the cephalon, the setation of the appendages, and the configuration and armature of the telsonic combs and caudal furca. The extremely small size, as well as the limited supply of

specimens, precludes individual student dissections. Consequently, the instructions are for observations of whole mounts and slide preparations of the appendages.

Observe the general body plan, both dorsally and ventrally, before studying the individual appendages (see Figure 11). In dorsal view, the cephalon will be seen to

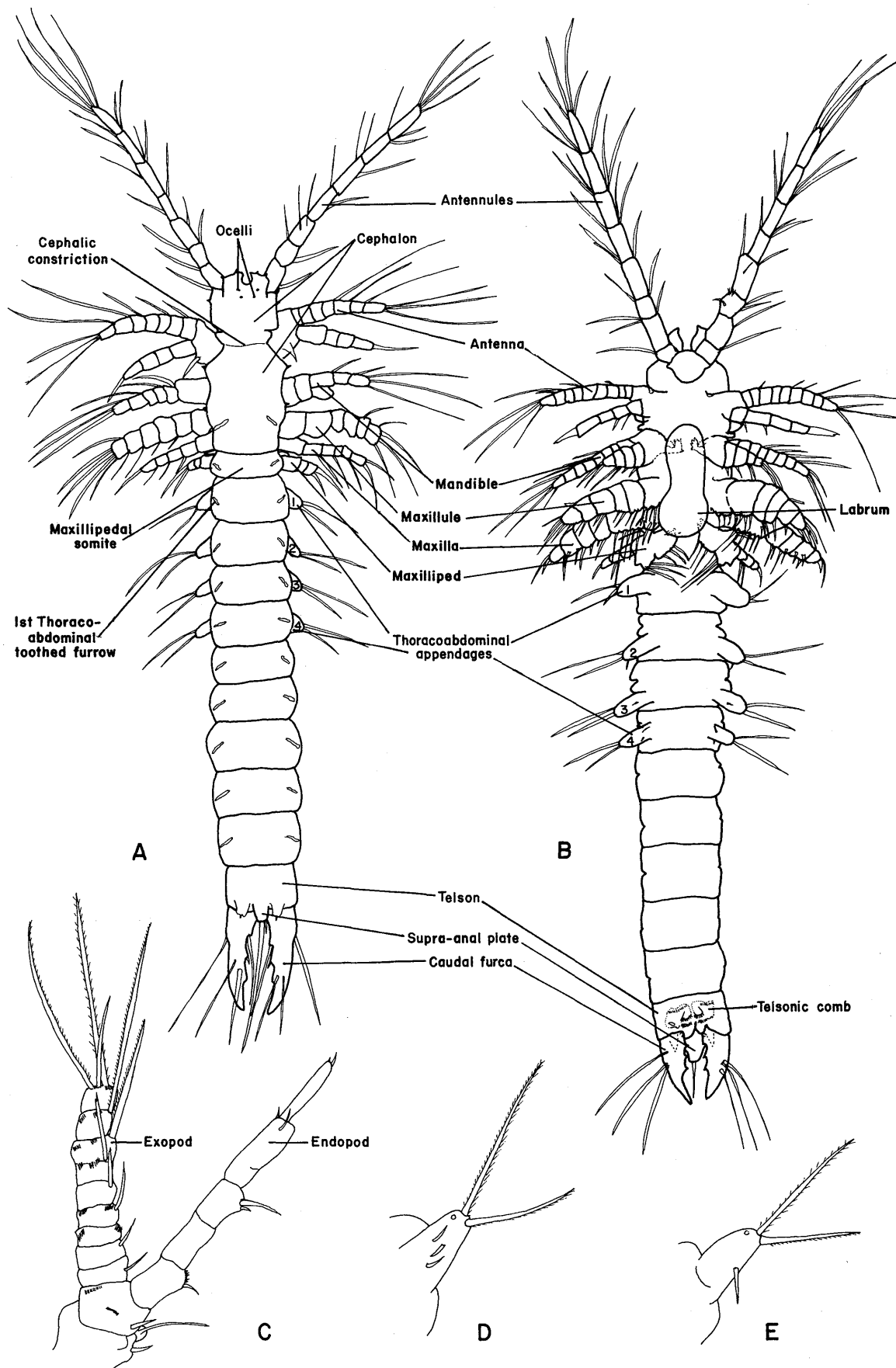


Figure 11 Mystacocarida: A. *Derocheilocaris* (dorsal view) [after Kaestner, 1970]; B. Whole animal (ventral view) [after Hessler and Sanders, 1966, and Hessler, 1972]; C. Antenna; D. Male 4th thoracopod (ventral view); E. Female 4th thoracopod (ventral view) [C–E after Hessler, 1969].

be very elongate, with an anterior or antennular part delineated by a cephalic constriction. The anterior and lateral margins of the antennular part are cleft, forming 2 prominent anteromedial lobes and 2 anterolateral lobes respectively. Usually 4 simple ocelli are present. In a few species neither lens nor pigment spots can be detected. Laterally on the posterior part of the cephalon, the 1st pair of toothed furrows can be observed. The structure and extent of the development of these furrows and the succeeding pairs may be diagnostic among the taxa. The function of the toothed furrows is not known.

Posterior to the cephalon are 10 body somites, excluding the telson and caudal furca. [Bowman (1971) considers the supra-anal plate to be the telson, and the caudal rami probably to be uropods; however, he subsequently has proposed that the thoracoabdomen consists of 11 somites and that the telson is absent (personal communication).] There has been additional disagreement among zoologists as to the proper subdivision of the somites. Some have included the maxilliped somite with the cephalon because the maxilliped functions as a cephalic appendage. Other zoologists have proposed that the maxilliped somite be considered the 1st thoracomere of a 5-somite thorax. A third alternative interpretation, and one that appears to have received support from the majority of mystacocarid specialists, is that the maxilliped somite, which is fused neither to the cephalon nor to the thorax, be considered as a distinct unit. The remaining 9 trunk somites then would be collectively referred to as thoracoabdominal somites, the first 4 of which bear small appendages. This latter interpretation has been adopted herein. A pair of lateral toothed furrows is present on each of the thoracoabdominal somites. The telson, dorsally, carries a median supra-anal process, flanked by a pair of spinous processes. The length of the major seta of the supra-anal process often is an important diagnostic character. Dorsal to the insertion of the major seta, 2 raised pores are apparent in some species.

In ventral view, the cephalic appendages and the 4 thoracoabdominal appendages can be distinguished more clearly. The antennules are relatively long; each consists of 8 segments, often also with a terminal aesthetasc. The antennae are relatively short and biramous. The biramous mandibles are similar in structure to the antennae but have gnathobases, which lie beneath the anterior part of the bulbous labrum. The maxillulae and maxillae are uniramous. The maxillipeds, except in one species, are biramous; the protopods often bear 2 to several endites. The thoracoabdominal appendages are small, single-segmented structures with only a few setae. In some species, a slight difference between the sexes can be observed in the 4th and occasionally also in the 3rd pair of appendages.

A genital pore may be observed on the ventral surface of the 3rd thoracoabdominal somite. In some species the possibility of a pair of genital pores at the bases of the

appendages of the 3rd somite has been reported. The ventral surface of the telson bears the anus and 2 pairs of ventral combs. The combs, which are variously developed, are one of the more distinct diagnostic characters for species determination. The ventral setae of the caudal furca or furcal claws also are important characters in identification.

Having examined the appendages on the intact animal, examine the slide preparations of the individual appendages. It would be well to sketch the cephalic appendages so that you can compare their structure with those of the other relatively primitive and conservative groups that you have studied, as well as with other members of the class.

Larval development in the mystacocarids is poorly documented. One species is known to hatch as a metanauplius, and 10 larval instars have been reported for a second species.

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CLASS COPEPODA H. Milne Edwards, 1840

Recent species	Approximately 7500.
Size range	< 0.26–17 mm in free-living species; up to 320 mm in some parasitic species.
Carapace	Absent; cephalic shield may project forward as rostrum.
Eyes	Usually nauplius eye; occasionally absent.
Antennules	Uniramous, sometimes markedly reduced; in males often well developed and geniculate.
Antennae	Uni- or biramous, well developed, or reduced; sometimes prehensile; occasionally absent.
Mandibles	Usually well developed, with biramous palp; sometimes reduced, absent, or modified as piercing stylet.
Maxillulae	Usually biramous; sometimes prehensile; occasionally reduced or absent.
Maxillae	Uniramous; sometimes reduced or absent.
Maxillipeds	One or 2 pairs; uniramous, sometimes prehensile; occasionally reduced or absent.
Thoracic appendages	Four or 5 pairs; last pair often modified, reduced, or vestigial; occasionally absent.
Abdominal appendages	None.
Telson	Absent; anal somite with caudal rami.
Tagmata	Cephalosome, metasome, and urosome; or prosome (cephalosome + metasome) and urosome.
Somites	Head with 5 + 1 or 2 thoracic (maxillipeds) [= cephalosome]; thorax basically with 5 or 4 (varying from 2–5) [= metasome]; abdomen with 5 or fewer, including genital and anal somites [= urosome].
Sexual characters	Gonopore(s) of female on ventral surface of genital somite (1st or fused 1st and 2nd abdominal somite), gonopore(s) of male also on genital somite. Female often with seminal receptacle(s); 5th pereopods of male usually modified as copulatory structures; male antennules sometimes also modified.
Sexes	Separate; occasionally parthenogenetic reproduction.
Larval development	Metamorphic; eggs carried in ovisacs or shed freely; 6 naupliar substages → 5 copepodid substages → adult.
Fossil record	L. Cretaceous to Recent.
Feeding types	Calanoids generally filter feeders; some calanoids and many cyclopoids predatory; harpacticoids generally grazers on sand grains. Parasitic orders adapted for piercing and sucking or absorption.
Habitat	Generally marine, although many species occur in freshwater; some terrestrial harpacticoids have been reported. Calanoids primarily pelagic, harpacticoids generally benthic or interstitial; approximately 2000 parasitic species with many kinds of hosts.
Distribution	Worldwide.

The members of this class have successfully adapted to a variety of habitats. Of the eight orders usually recognized, the members of four are parasitic, at least at some stage in the life cycle; that is, Notodelphyoidea, Monstrilloidea, Caligoida, and Lernaepodioida. Some representatives of the Cyclopoida and a few of the Harpacticoida also are parasitic. Members of the Calanoida and Misophrioida all are free-living. Kabata (in press) has proposed changes that will greatly alter the hierarchical classification, particularly of the parasitic groups, and

these changes appear to have a sound basis in morphological and phylogenetic fact (T. Bowman, personal communication). In Kabata's classification most parasitic taxa have been removed from the Cyclopoida; the names Poecilostomatoida and Siphonostomatoida have been reintroduced for those taxa having falcate and styletlike mandibles, respectively. The free-living and parasitic types will be discussed separately; the major characters of each taxon are given.

FREE-LIVING COPEPODA

ORDER CALANOIDA Sars, 1903

Antennules	16–26 articles; 1 antennule often modified.
Antennae	Biramous.
Mandibles	Biramous; with gnathobase.
Maxillulae	Biramous.
Maxillae	Uniramous; often modified.
Maxillipeds	Uniramous.
Flexure	Between 6th thoracic somite and abdomen.
Habitat	Free-living, usually planktonic.

ORDER HARPACTICOIDA Sars, 1903

Antennules	Ten or fewer articles; often geniculate in male.
Antennae	Biramous; exopod reduced.
Mandibles	Biramous; usually with gnathobase.
Maxillulae	Usually biramous; broad, platelike.
Maxillae	Uniramous.
Maxillipeds	Uniramous; sometimes subchelate.
Flexure	Between 5th and 6th thoracic somites.
Habitat	Usually free-living; primarily benthic; occasionally parasitic.

ORDER CYCLOPOIDA Sars, 1903

Antennules	10–16 articles; often geniculate in male.
Antennae	Usually uniramous; exopod absent or reduced.
Mandibles	Usually biramous.
Maxillulae	Usually biramous.
Maxillae	Uniramous.
Maxillipeds	Uniramous.
Flexure	Between 5th and 6th thoracic somites (except in Lernaecidae).
Habitat	Usually free-living; often planktonic; frequently in fresh water.

ORDER MISOPHRIODA Gurney, 1933

Antennules	Sixteen or fewer but not less than 11 articles; prehensile.
Antennae	Biramous.
Mandibles	Biramous; with gnathobase.
Maxillulae	Biramous.
Maxillae	Uniramous.
Maxillipeds	Uniramous.
Flexure	Between 5th and 6th thoracic somite.
Habitat	Free-living epibenthic.

The Calanoida, Harpacticoida, and Cyclopoida all have a great many marine and freshwater representatives; the Misophrioida is known from very few species. The discussion of copepod morphology that follows is quite general to facilitate its usefulness. Examine the sampling of copepods, which should be a mixture of several taxa. Two characters can be used to distinguish calanoid species from harpacticoid and cyclopoid taxa quickly: the number of antennular articles (15 or more) and the position of the body flexure or articulation (between the 6th thoracic somite and the genital somite). Distinctions between harpacticoid and cyclopoid copepods are not as easily made. In general, the antennular flagella of harpacticoid copepods have fewer articles (5–10) and only a slight constriction, if any, exists between the 5th and 6th thoracic somites (somites of the 4th and 5th pereopods). In cyclopoids, the flagella of the antennules usually have more articles (6–17) and the constriction between the 5th and 6th thoracic somites usually is pronounced. Another distinguishing character is the basal segment of the 5th pereopods. This segment is enlarged on the inner margin in harpacticoids but not in cyclopoids. Determine the order(s) to which the copepods in your sample belong.

Begin your study of copepods by examining the whole animal(s) (see Figure 12). A carapace is absent; however, the cephalic shield may be produced anteriorly to form a small rostrum. Eyes may be present or absent; when present, they frequently lack pigment. The cephalon is fused with the 1st thoracic somite (Calanoida) or with the 1st and 2nd (some Calanoida, Cyclopoida, Harpacticoida, and Misophrioida); the composite is referred to as the cephalosome. The remaining thoracic somites become progressively narrower posteriorly in some calanoids, cyclopoids, and the misophrioids, but remain generally the same width in harpacticoids. As previously indicated, a flexure of the body occurs between the 5th and 6th thoracic somites in all but the Calanoida. The flexure in the latter is between the 6th thoracomere and the genital somite. The free thoracic somites anterior to the flexure collectively are referred to as the metasome, and the somites (thoracic and abdominal) posterior to the

flexure as the urosome. The abdomen usually consists of 4 or 5 somites, the 1st of which is fused in females with the last thoracic somite to form a genital somite. The last or anal somite of the abdomen, called a telson by some authors, is not homologous with a true telson. A pair of caudal rami are terminal.

Examine the animal from a lateral or ventral view and identify the appendages before beginning your dissection. In most calanoids the antennules are very elongate; one antennule may be geniculate in males; in some species the maxillae may be extremely enlarged and/or modified. The 1st thoracopods are modified as maxillipeds. Four pairs of pereopods (thoracopods 2–5) are well-developed biramous appendages used in locomotion. The 5th pair (6th thoracopods) may be reduced or strongly modified, and are sometimes absent in females. The characters afforded by this pair in males frequently are of considerable importance in species determination. Remove the pereopods and identify the structural components, such as protopod, endopod, and exopod. Frequently both members of a pair will be removed simultaneously. This is because they are bound together by a basal connection that insures that they will move in unison.

Before removing the mouthparts, observe the position of the maxillipeds in relation to the maxillae. Usually they are attached medial to the maxillae. Remove the mouthparts from one side of the body and examine their structure. Would you expect your study specimens to be filter feeders, grazers, or predators? On what characters have you based your answer?

Using cleared specimens, it is possible to identify most of the major organ systems without extensive dissection (see Figure 13) unless the species under study is one with prominent lateral muscle bands. Carefully remove any cephalic or thoracic appendages that obscure a clear view of the body. If prominent lateral muscle bands are present carefully cut the integument and remove them from one side. In calanoids and misophrioids a heart is present dorsally in the midline of the body. It is a short organ with 1 pair of lateral ostia and 1 ventral ostium in calanoids. Blood is carried anteriorly to the head by a

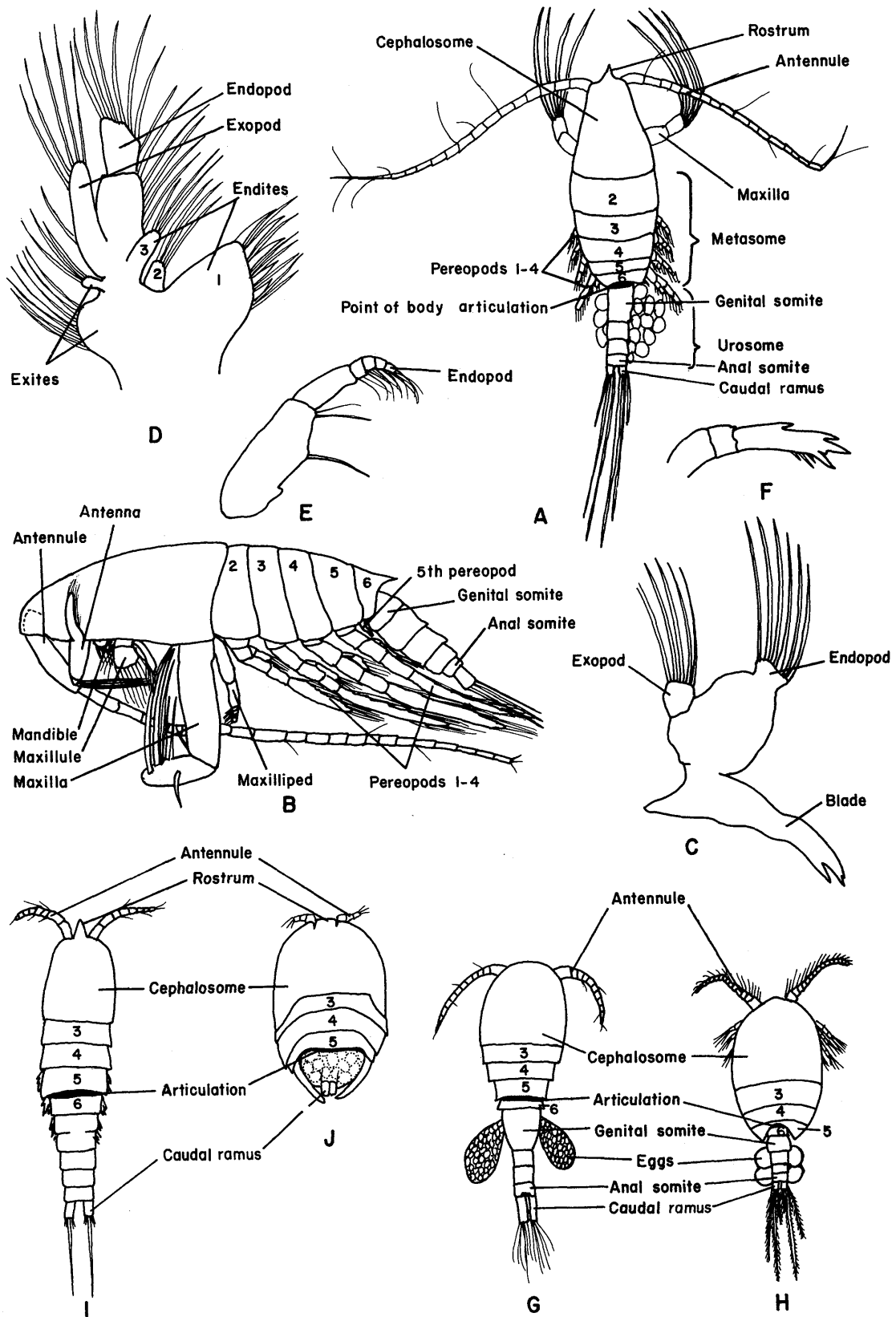


Figure 12 Copepoda, free-living: A–F, Calanoida. A. Female (dorsal view); B. Male (lateral view); C. Mandible of male; D. Maxilla of female; E. Maxilliped of male; F. 5th pereopod of male; G. Female Cyclopoida (dorsal view); H. Female Misophrioida (dorsal view [after Sars, 1903]); I. Male Harpacticoida (dorsal view); J. Female Harpacticoida (dorsal view).

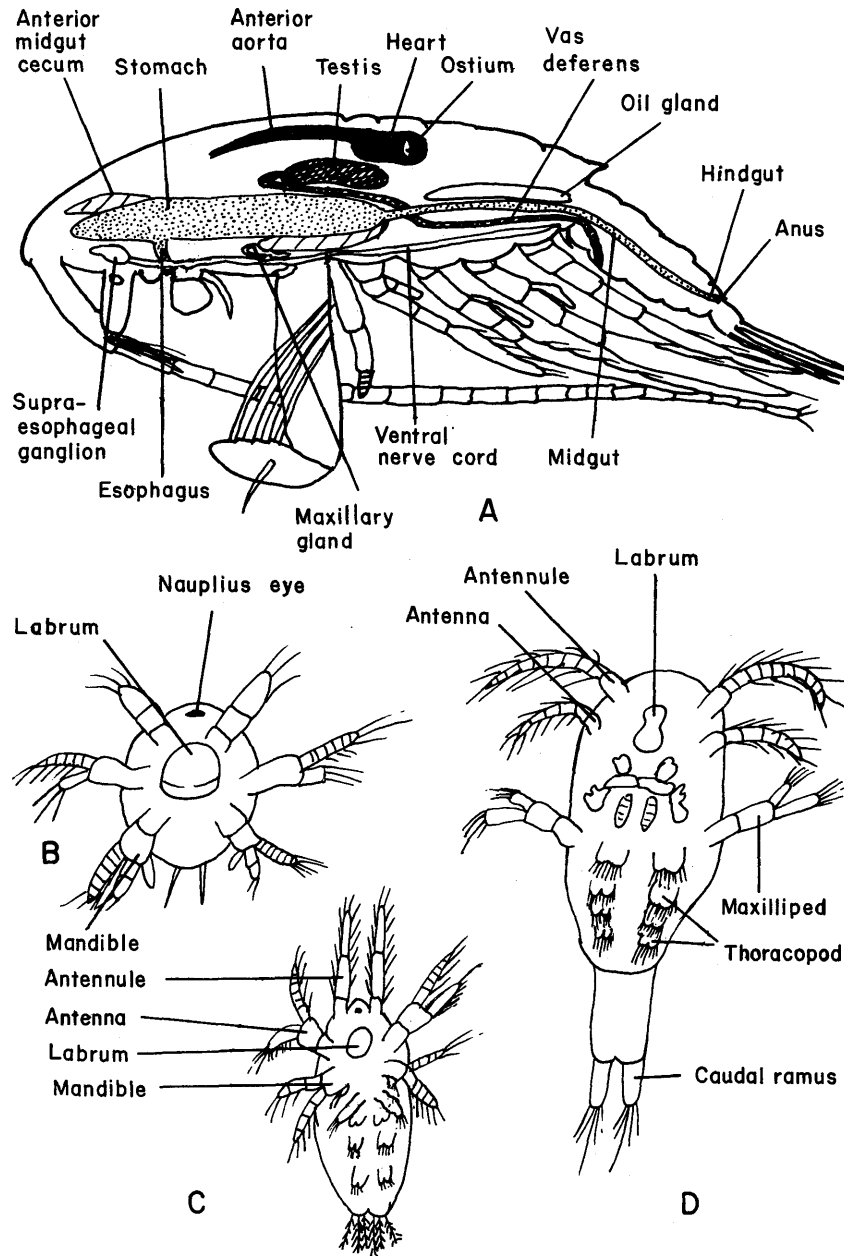


Figure 13 Copepoda, free-living: A. Diagrammatic calanoid copepod with musculature removed to show major internal organ systems; B. Diagrammatic nauplius I; C. Diagrammatic nauplius IV; D. Diagrammatic copepodid I.

short anterior aorta; no other blood vessels are present. Blood circulates to the thoracic appendages through a ventral sinus. In harpacticoids and cyclopoids no heart or arterial system are present; body movements and the pulsating movements of the gut provide the necessary movement of blood in the hemocoel.

The digestive system is simple, consisting of an esophagus, stomach, midgut, hindgut, and usually ceca. The anterior portion of the enlarged stomach, as well as the esophagus, are of ectodermal origin; the remainder

of the stomach and the midgut, of endodermal. The short hindgut extends approximately the length of the anal somite and terminates dorsally in the anus. One or a pair of midgut ceca usually arise at the junction of the stomach and midgut. In *Calanus* a prominent oil gland is present above the midgut in the metasome. Excretion is through maxillary glands in adult copepods, but through antennal glands in the nauplius.

In free-living copepods the gonad (ovary or testis) typically is an unpaired organ lying in the midline above the

midgut. Anteriorly from the ovary trace the pair of oviducts forward toward the head. In mature females large diverticuli from the oviducts occupy much of the dorsal region of the cephalosome. From the diverticuli follow the oviducts posteroventrally to the genital somite, where they join just before entering the atrium (calanoids) or separately open through a pair of gonopores (cyclopoids). Calanoids have a pair of seminal receptacles that open into the atrium; cyclopoids have a median seminal receptacle which connects with the gonopores via short, often kinked, fertilization ducts. A 3rd opening into this receptacle is a copulatory pore. In the male locate the testis in approximately the same position as the female's ovary was found. One (calanoids) or a pair (cyclopoids) of vas deferens leave the testis anteriorly and proceed posteriorly and then ventrally to the genital somite. Histologically it is possible to distinguish regions of the vas deferens as seminal vesicle, spermatophoric sac, and ejaculatory duct; it may also be possible to observe changes in the spermatophores as they pass from the testis to the genital somite.

Anterior to or anteroventrally of the stomach observe the supraesophageal ganglion. Typically innervation of

the sense organs of the head occurs from this ganglion but will be difficult to follow unless the specimen has been specially stained. From the supraesophageal ganglion follow one of the large esophageal connectives around the esophagus to the ventral nerve cord. If you are studying a specimen of *Calanus*, locate the giant nerve fibers that innervate the muscles of the pereopods and metasome. Posteriorly, identify the ganglia of the nerve cord. Ganglia are not present in the abdomen.

Larval development in copepods is metamorphic; young hatch as 1st substage nauplii having 3 pairs of appendages (antennules, antennae, and mandibles) but lacking external segmentation of the body. Additional appendages are added during successive naupliar substages. Six naupliar substages are present in most calanoids; in harpacticoids and cyclopoids 5 commonly occur, occasionally fewer. A metamorphic molt to the copepodid stage follows the last naupliar substage. The body form is more like that of the adult and body segmentation is apparent. Additional metameres and appendages are added during the 4 subsequent copepodid substages.

PARASITIC COPEPODA

ORDER NOTODELPHYOIDA Sars, 1903

Antennules	Often reduced, sometimes modified.
Antennae	Uniramous; 3-segmented or reduced; sometimes modified as claw.
Mandibles	Biramous; with gnathobase; occasionally reduced.
Flexure	Usually between 6th thoracic somite and abdomen.
Habitat	Parasitic or commensal in tunicates; males sometimes free-living.

ORDER MONSTRILLOIDA Sars, 1903

Antennules	Usually well developed.
Antennae	Absent in adults.
Mandibles	Absent in adults.
Flexure	Usually between 5th and 6th thoracic somites.
Habitat	Parasitic as larvae on polychaetes and rarely echinoderms; free-living, presumably nonfeeding as adults.

ORDER SIPHONOSTOMATOIDA Thorell, 1859

Antennules	Usually reduced or minute.
Antennae	Frequently prehensile; sometimes biramous with exopod reduced or vestigial.
Mandibles	Modified as piercing stylets.
Flexure	Between 4th and 5th or 5th and 6th thoracic somites; occasionally lacking.
Habitat	Parasitic on marine and freshwater fishes and invertebrates.

ORDER POECILOSTOMATOIDA Thorell, 1859

Antennules	Well developed or reduced.
Antennae	Uniramous.
Mandibles	Uniramous; falcate.
Flexure	Between 5th and 6th thoracic somites; often lost.
Habitat	Parasitic on fishes and invertebrates, usually marine.

Among the four orders of parasitic copepods, there is a great diversity of body form; in fact, in many instances it is difficult to recognize the parasite as being a copepod. The degree of specialization or the amount of reduction in appendages also varies greatly within individual orders. Examples showing some of this diversity have been illustrated in Figure 14. A caligid representative of the Siphonostomatoida will be described and may serve as a model if demonstration materials are available.

The term cephalothorax frequently is used in referring to the cephalon and fused thoracic somites of most parasitic copepods. The number of thoracic somites that are fused varies with the taxa. In dorsal view, it will be noticed that the cephalothorax is covered by a broad shield; this is not a true carapace. In certain taxa, a pair of lunules is present anteriorly and the 2- or 3-segmented antennules usually can be distinguished. A nauplius eye also may be observed in the midline anteriorly. In some taxa, the shield may be produced posteriorly as a pair of alae, as frequently also occurs in Branchiura. One or more pedigerous segments may be present. Posteriorly the genital somite is enlarged, particularly in sexually mature females, and varies in shape; the posterolateral surfaces may be expanded. Developing embryos are carried in a pair of egg strings. The abdomen may be segmented or not; the former condition is more typical in males. The abdomen terminates in a pair of caudal rami.

In ventral view, the antennules and lunules are more clearly observed. The antenna is reduced; 1 to 3 short segments frequently terminate in hooks or claws. Laterad of the antennae in many taxa is a pair of postantennal processes or "maxillary hooks," which are not,

however, components of the maxillulae or maxillae. The mandibles usually are small and obscurely implanted in the mouth cone (tube). The maxillulae typically are small, often nodular or prehensile, but may be reduced or vestigial. The maxillae usually have 1 or 2 segments and often terminate in weakly developed hooks or spines. Each maxilliped frequently terminates in a strong clawlike structure. A pair of post-oral processes and a sternal furca also may be present. The first 7 pairs of thoracic appendages are uni- or biramous and variously developed; the 5th and 6th pairs, on the genital somite, usually are greatly reduced and even may be absent.

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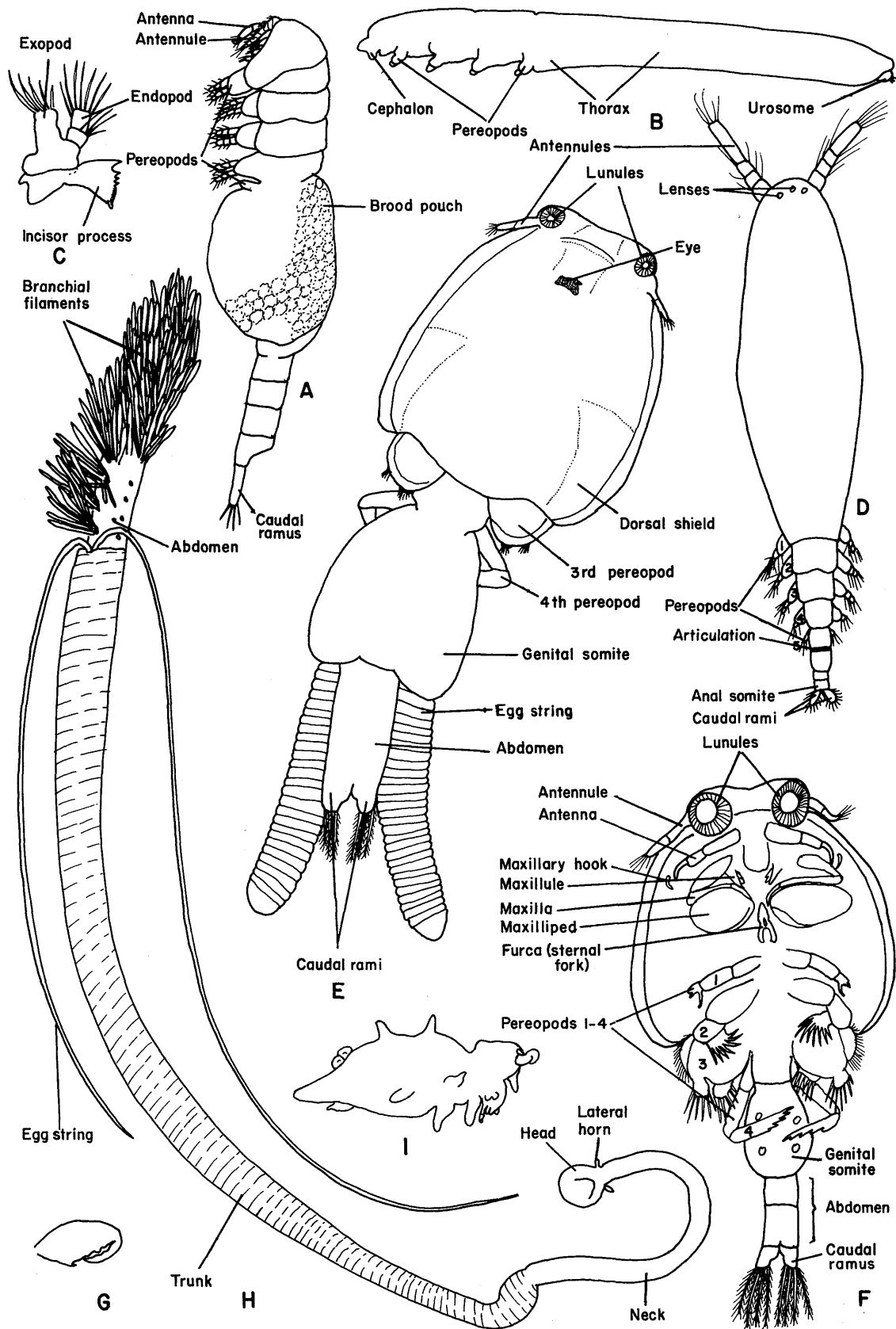


Figure 14 Copepoda, parasitic: A—C, Notodelphoidea [after Illg, 1958]. A. Female, *Notodelphys* (lateral view); B. Female, *Scolecodes* (lateral view); C. Mandible, *Notodelphys*; D. Monstrilloidea, female (dorsal view) [after Wilson, 1932]; E—H, Siphonostomata. E. Female (dorsal view); F. Male (ventral view); G. Maxilliped of male; H. Female, *Penella*; I. Poecilostomata, female [after Ho, 1972].

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CLASS BRANCHIURA Thorell, 1864

Recent species	Approximately 130 in four genera: <i>Argulus</i> , <i>Chonopeltis</i> , <i>Dolops</i> , and <i>Dipteropeltis</i> .
Size range	0.5–30 mm.
Carapace	Dorsoventrally flattened; usually broad.
Eyes	Sessile, compound, and usually 1–3 median nauplius eyes.
Antennules	Reduced, usually with small hooks or spines; sometimes absent.
Antennae	Uniramous; reduced or absent.
Mandibles	Highly modified; in <i>Argulus</i> , at least, usually incorporated in medial proboscis system.
Maxillulae	Uniramous, without endites; highly modified; with distal claws in <i>Dolops</i> ; other three genera with paired, stalked suction discs.
Maxillae	Usually with hooks or spines.
Maxillipeds	None.
Thoracic appendages	Four pairs of biramous thoracopods; used in swimming; usually sexually dimorphic.
Abdominal appendages	None.
Telson	Absent; anal somite terminating in caudal rami.
Tagmata	Cephalothorax and abdomen; or cephalon, pereon, and abdomen.
Somites	Head with 5 + 1st thoracic; thorax or pereon usually with 3; abdomen unsegmented.
Sexual characters	Gonopores of female at bases of 4th thoracopods (oviducts apparently function alternatively); male with single gonopore medially on ventral surface of last cephalothoracic somite; female with paired spermatheca on abdomen anteroventrally. Thoracic appendages usually sexually dimorphic.
Sexes	Separate.
Larval development	Anamorphic or epimorphic; eggs deposited on stones or plants; hatch as nauplius (some <i>Argulus</i> spp.) or naupliar and metanaupliar stages passed through in egg, hatch as juveniles.
Fossil record	Recent.
Feeding types	Parasitic, adapted for piercing and sucking.
Habitat	All are temporary to permanent ectoparasites of fishes, occurring in marine, brackish, and freshwater. Temporary parasites are good swimmers and apparently are not host specific.
Distribution	<i>Argulus</i> — worldwide; <i>Chonopeltis</i> — Africa; <i>Dolops</i> — primarily South America, but also known from Tasmania and Africa; <i>Dipteropeltis</i> — South America.

The instructions for the study of the Branchiura are based on specimens of *Argulus* (see Figure 15). The branchiurans are morphologically adapted for a parasitic existence. The somewhat flattened carapace arises at the

base of the cephalic region and extends posteriorly as a pair of lobes or alae, partially covering the thoracic somites. The carapace is fused only with the first thoracic somite. The cephalon is delineated posteriorly by the

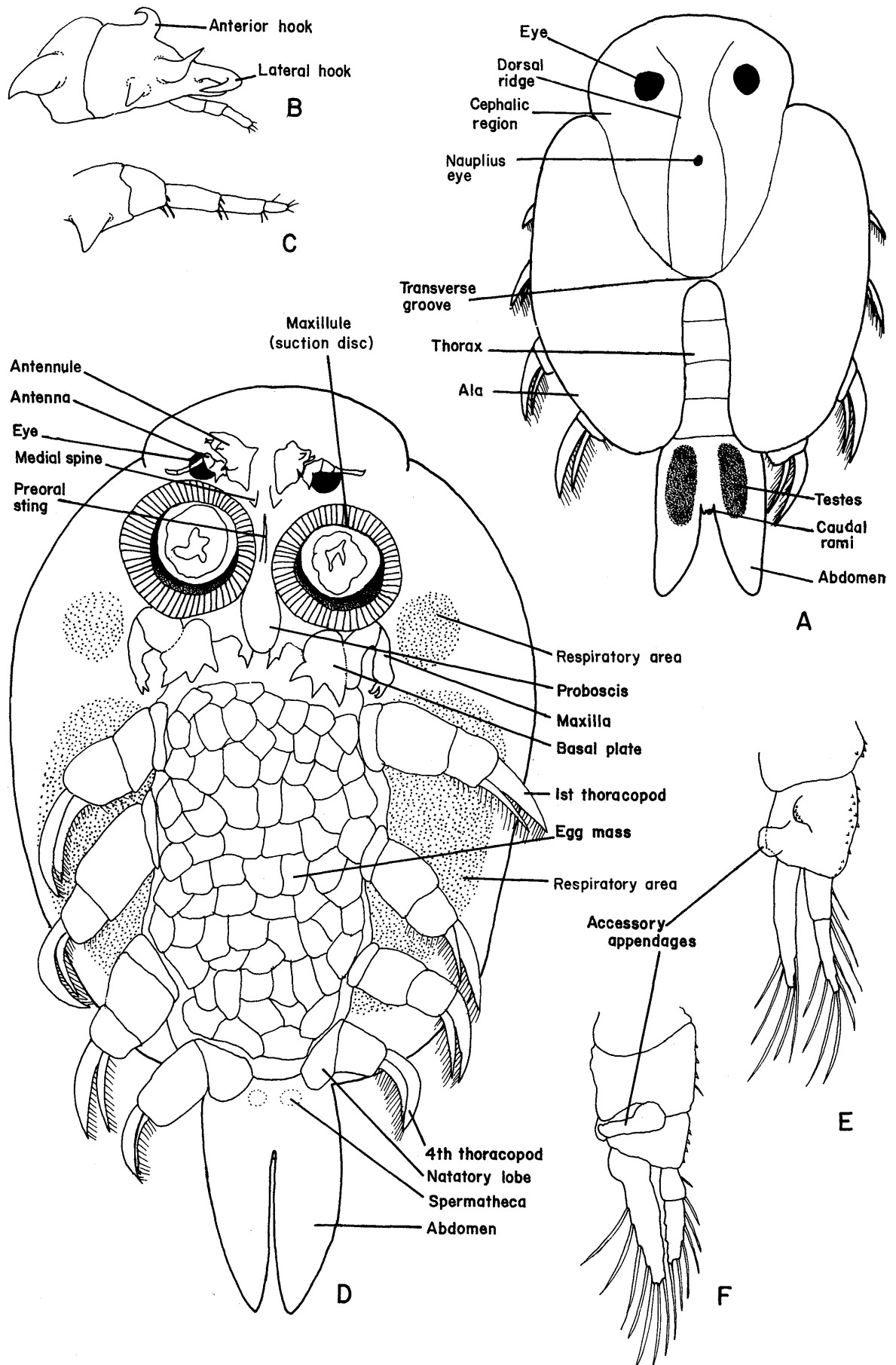


Figure 15 Branchiura: A. Male (dorsal view); B. Antennule; C. Antenna; D. Female (ventral view); E. Male 3rd thoracopod; F. Male 4th thoracopod.

transverse or cervical groove and laterally by ridges. In dorsal view, the prominent paired compound eyes will be clearly visible. Frequently a single small median or nauplius eye also is present. Usually a pair of longitudinal dorsal ridges, situated between the eyes, can be observed. In most specimens, a pair of respiratory areas, lying on the ventral surface of the carapace, may be distinguished from the ventral side. Between the alae the free thoracic somites also can be seen. The abdomen is unsegmented but lobed posteriorly. Distinguish the caudal rami between the lobes. [Bowman (1971) considers that these rami are uropods.]

In ventral view, examine the cephalic and thoracic appendages. The antennules and antennae usually are reduced in size or occasionally absent; in argulids, the basal segments of both generally are broadened and frequently armed with spines or hooks. The most prominent appendages are the maxillulae, which are modified as suction discs. In the midline and somewhat anteriorly, locate the preoral sting, a retractile piercing mechanism with a poison gland at its base. Posterior to the sting is the large proboscis. The mandibles are completely enclosed in the proboscis and thus are not easily observable. The maxillae usually have broadened, toothed basal plates and often 2 pairs of postmaxillary spines.

Remove and examine 1 or more of the thoracopods. The first 2 pairs may be provided with epipods. In the male, the 2nd through 4th thoracopods have accessory appendages that are used in copulation. The 4th thoracopods usually are basally expanded into natatory lobes.

In males the testes usually are very apparent as a pair of elongate bodies lying in the abdomen to each side of the midline. Be sure to examine specimens of both sexes. In females observe the pair of spermatheca located on the ventral surface of the abdomen.

Larval development in branchiurans may be one of two types. In the first, a form of anamorphic development occurs; the young hatch as nauplii, swim by means of the antennae, mandibles, and 1st thoracopods, and attach to a host by means of the distal hooks of the maxillulae. After one molt all 4 pairs of thoracopods are functional. The second type of development is epimorphic; the young hatch with functional appendages and usually are similar to the adult form except in size and sucker development.

The Branchiura were, until recently, classified as a taxon of the Copepoda. What characters can you find that justify the separation of this group of fish parasites into a separate class? In which characters do they agree with the Copepoda?

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CLASS CIRRIPEDIA Burmeister, 1836

The Cirripedia is a relatively large, highly successful group of sedentary crustaceans whose members are noted for their diversity in form and habitat. And, at least among free-living taxa, they also are the most uncommon-looking crustaceans in the superclass. Until the mid-nineteenth century, when the crustacean

affinities of their larvae were discovered, cirripeds were thought to be a type of mollusk. The class is comprised of four orders: Acrothoracica, Thoracica, Ascothoracica, and Rhizocephala. Representatives of the first two orders usually are free-living; those of the latter two are parasitic.

ORDER ACROTHORACICA Gruvel, 1905

Recent species	40–45 in eight genera.
Size range	0.4–20.0 mm.
Carapace	Mantle thin, rarely with 1 pair of calcareous plates.
Eyes	Nauplius eye in nauplius, with compound eyes in cyprid; nauplius eye sometimes retained in adult.
Antennules	Uniramous in cyprid and male; absent in female.
Antennae	Only in nauplius, biramous, occasionally absent.
Mandibles	With palp in adult female; absent in male.
Maxillulae	Present only in female.
Maxillae	Present only in female.
Maxillipeds	May be represented by pair of mouth cirri.
Thoracic appendages	In female, 3–5 pairs of uni- or biramous terminal cirri; absent in male.
Abdominal appendages	None.
Telson	Absent.
Tagmata	Head and thorax in adult female; not differentiated in male.
Somites	Head with 5 + 1 thoracic (= presoma); thorax usually with 6 (7 + 8 fused).
Sexual characters	Openings of oviducts near bases of 1st cirri in females; male with or without penis and with or without specialized attachment structures.
Sexes	Separate; males reduced.
Larval development	Metamorphic; nauplius → cyprid; frequently released as cyprid.
Fossil record	Carboniferous to Recent.
Feeding types	Filter feeders (female); male nonfeeding.
Habitat	Marine; in burrows in living and dead coral and limestone and shell.
Distribution	Worldwide.

The Acrothoracica differ from all other cirripeds in being burrowers. The female is permanently attached to the burrow and usually lacks calcareous plates. The reduced male lacks mouthparts. The Acrothoracica are more closely related to the Thoracica than to the other orders. They differ in several characters: (1) the posterior cirri (sometimes reduced in number) are terminal in position; (2) calcareous plates usually are not developed; (3) the entire exoskeleton, instead of only the inner lining and appendages, is molted. Sexes always are separate. Naupliar substages usually are passed through in the egg. Acrothoracicans always are free-living; their specialized habitats, such as burrows in coral and shell substrates, do not make them easy to study.

The acrothoracican usually is not visible, but its presence is marked by a tapered slit in the substrate. To remove the female acrothoracican from her burrow, one must either chip away the matrix surrounding the burrow or dissolve the matrix in acid. Shell material probably is best decalcified by placing the specimen in dilute hydrochloric acid (1 or 2%), unless the specimens have been collected alive. In the latter case, placement of the specimens in a large volume of Bouin's solution will serve both to preserve the animals and to decalcify the

shelly matrix. Even with decalcification, most specimens will not be freed completely and must be extracted gently with a pair of fine forceps. Specimens treated in either of the manners described usually will take on a dark red coloration that is an aid in their recognition.

Any more than a superficial examination of the gross morphology of the female will not be possible under routine classroom conditions (see Figure 16). Males may be attached to the female's body or to the walls of the burrow. The females are small but the males are even smaller, and care should be taken to examine both the burrow and the female for them. Males often are attached to the periphery of the "horny" attachment knob. This region of the mantle is firmly attached to the burrow and apparently is not cast routinely with each molt. Consequently, as the female grows, this area usually expands in a series of concentric rings.

The most obvious external features of the typical acrothoracican are the lips of the mantle aperture. The thickened plates may be homologous or analogous to the occludent margin of the mantle of the thoracicans. These lips frequently are armed with teeth, hooks, or spines. Observation of most taxonomically diagnostic characters requires treatment of the specimens with heated potas-

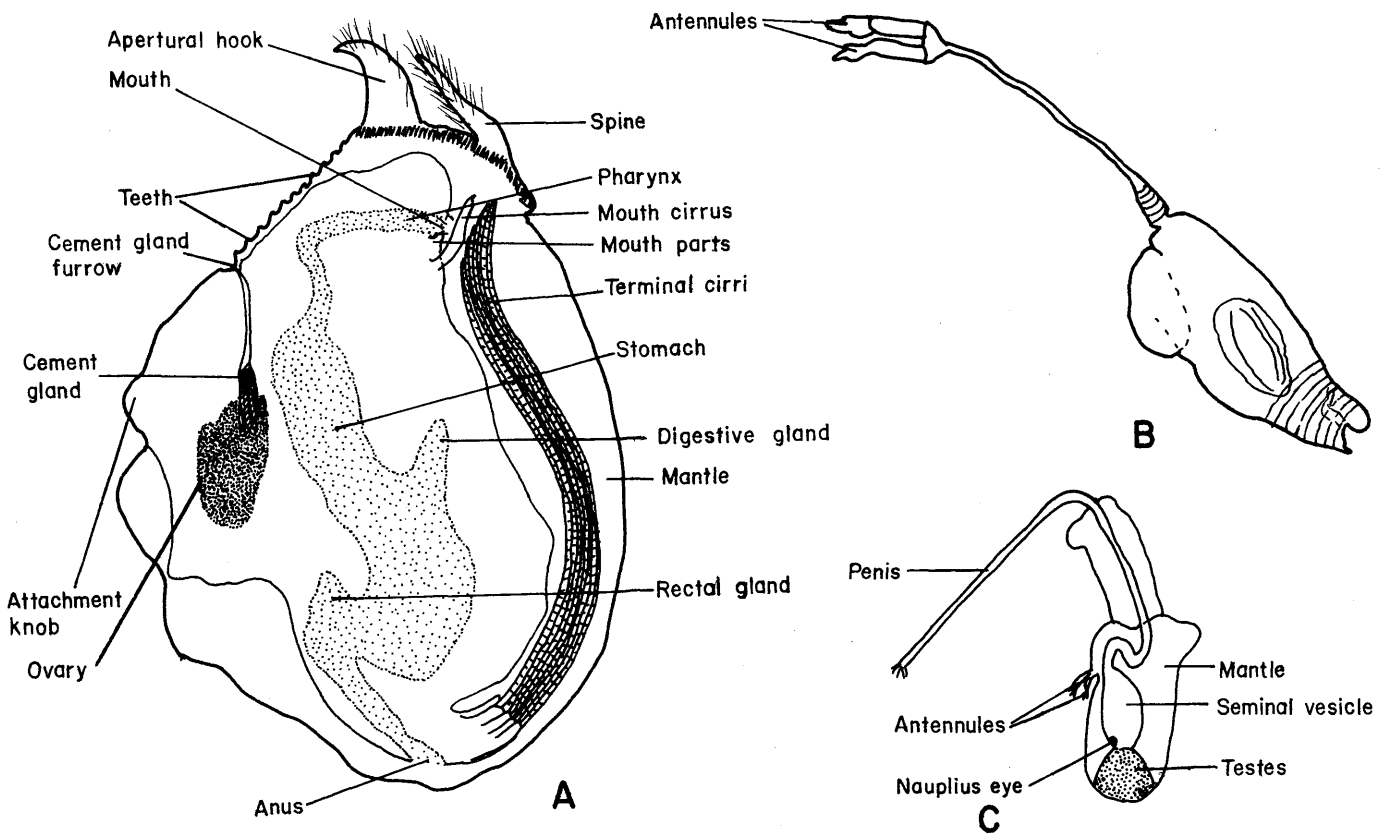


Figure 16 Cirripedia, Acrothoracica: A. Female, *Lithoglyptes* (lateral view); B. Male, *Lithoglyptes* [A, B after Tomlinson and Newman, 1960]; C. Male, *Trypetesa* [after Tomlinson, 1955].

sium hydroxide (10%) to remove the soft parts and then clearance in glycerin. If treated cleared specimens are available, you should examine the thoracic cirri, paying particular attention to the number of pairs and to the mouthparts and mouthcirri. The setation of the cirri is often of taxonomic significance, particularly the size and distribution of setae; however, it is not expected that you will be able to make specific identifications.

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ORDER THORACICA Darwin, 1854

Recent species	Approximately 800.
Size range	Up to 80 cm height; 20 cm diameter.
Carapace	Membranous “mantle” formed by bilateral folds of carapace; usually armed with calcareous plates; occasionally spinous or without plates or spines.
Eyes	Nauplius eye deeply embedded, rarely discernable in adult; nauplius and compound eyes present in cyprid.
Antennules	Vestigial in adult; uniramous in nauplius and cyprid; used for temporary attachment by cyprid.
Antennae	Absent in adult and cyprid; biramous in nauplius.
Mandibles	Without palp (mandibular palp shifted to labrum); with modified gnathobases.
Maxillulae	Modified gnathobase.
Maxillae	Modified gnathobase; pair sometimes fused.
Maxillipeds	None.
Thoracic appendages.	Usually 6 pairs of biramous cirri; in males, reduced, vestigial, or absent.
Abdominal appendages	None.

Telson	Absent.
Tagmata	Head and thorax.
Somites	Head with 5; thorax with 6.
Sexual characters	Openings of paired oviducts at bases of 1st cirri (1st thoracopods) in hermaphrodite and female; penis between bases of 6th cirri always present in hermaphrodite, sometimes in males.
Sexes	Rarely separate; usually functional hermaphrodites; occasionally with dwarf or complemental males attached to female or hermaphrodite respectively.
Larval development	Metamorphic; 6 naupliar substages → cyprid; occasionally naupliar substages passed through in egg.
Fossil record	U. Silurian to Recent.
Feeding types	Typically filter feeders; sometimes predators (free-living); occasionally absorption (parasites); males sometimes nonfeeding.
Habitat	Marine or brackish water, intertidal to abyssal, on rocks, pilings, shells, and other hard substrates, and on plants and other animals.
Distribution	Worldwide.

Thoracic cirripeds are attached permanently as adults. The mantle usually bears calcareous plates; the external surface, including the plates, is never molted. Six pairs of biramous appendages (cirri) are present and (except the 1st pair) are evenly distributed along the thorax. The 1st pair is closely associated with the mouthparts (trophi). Sexes usually are combined, rarely separate; males, when present, are reduced and associated with hermaphrodites as complemental males or with females as dwarf males. Thoracic cirripeds are primarily free-living, often commensal; occasionally they are symbiotic, rarely they are parasitic. Larval development is metamorphic and typically includes a nauplius stage with 6 substages and a cyprid stage. The nauplius is distinc-

tive in that it can be distinguished from other crustacean nauplii by the presence of frontolateral horns. With metamorphosis, the broad dorsal shield of the nauplius becomes the bivalved carapace of the cyprid. In the cyprid the antennules are prehensile, the antennae absent, the mouthparts rudimentary, and the thoracic appendages natatory. Occasionally the nauplius stage is passed through in the egg and the young hatch as fully developed cyprids.

The Thoracica includes three suborders, each sufficiently distinct to be treated individually. A brief synopsis of major diagnostic characters precedes the discussion of each suborder.

SUBORDER LEPADOMORPHA Pilsbry, 1916

Calcareous plates	Usually present on capitulum, sometimes also on peduncle; capitulum with 5 or 6 principal plates; sometimes also with 1 or 2 paired laterals in upper whorl; sometimes also with secondary whorl of 3 pairs of laterals; with or without subrostrum and subcarina; less often also with basal whorls of smaller laterals; occasionally with fewer than 5 principal plates, with spines or without plates or spines.
Primordial plates	Chitinous principal plates except rostrum, occasionally 1 or 2 additional plates present in cyprid; retained at umbos of adult.
Basis	Absent.
Labrum	Bullate.
Caudal appendages	Usually present.

Basidorsal point (penis)	Absent.
Filamentary appendages	Usually present.
Sexes	Usually hermaphroditic, occasionally separate; sometimes with complementary or dwarf males.

The Lepadomorpha are distinguished from the sessile barnacles by being attached to the substrate by a stalk or peduncle rather than by a membranous or calcareous basis. The capitulum that typically is distinguished from the peduncle encloses the body and usually bears calcareous plates. The number and arrangement of the plates are diagnostic characters. There are 5 or 6 principal plates: paired scuta and terga, which border the occludent margin of the orifice, and an unpaired carina and sometimes a rostrum. In addition, there may be a second whorl of 9 pairs of lateral plates and sometimes several basal whorls of small plates.

The directions for the study of pedunculate morphology are based on representatives of the genera *Pollicipes* and *Lepas* (see Figure 17). *Pollicipes* is a member of the family Scalpellidae, which includes many diverse groups principally found in deep water, and is characterized by a capitulum with more than 5 principal plates and a peduncle with calcareous scales. In contrast, *Lepas* is a member of the family Lepadidae, which is characterized by a capitulum with 5 or fewer plates and a naked peduncle. If available, compare and contrast representatives of both genera. Note that the peduncle of *Pollicipes* is quite flexible although the integument is thick and covered with very small scales. The capitulum has several whorls of plates that decrease in size from above downward to the peduncle; the lowest whorl may have over 100 small plates. Identify the 6 principal plates. The rostrum is below the scutum in the midline. There is a secondary plate, a latus, between the scutum and tergum at the rostral level. In the next whorl identify the subrostrum and subcarina. Compare these capitular plates with those of *Lepas*, in which the plates of the capitulum include only the 5 primary plates, that is, paired scuta and terga and unpaired carina. The lepadid peduncle is equally as flexible, but the integument is thinner and unarmed.

By making two incisions on one side of the animal, the first to the side of the rostrum and the second to the side of the carina, the capitulum can be laid back to expose the body of the animal within (see Figure 18). The thoracic appendages (cirri) are the most apparent structures. They are orientated in such a manner that they can be extended through the orifice toward the rostral side of the animal. Directly in front of the cirri are the trophi. The adductor muscle appears as a dark, very prominent ovoid structure directly behind the rostrum and in front

of the trophi. Below the pedicles of the cirri a series of (*Pollicipes*) or a few (*Lepas*) filamentary appendages can be observed. These appendages are not found in many other genera, nor even in all species of one genus. In *Lepas* they usually are limited to association with the 1st cirrus; their function is unknown. Remove the 6 cirri from one side in sequence while the animal is still within the capitulum, mounting them on a microscope slide. If a temporary mount is all that is desired, a medium such as glycerin is adequate; if you are making a permanent mount, a medium such as polyvinyl alcohol lactophenol is recommended. A method commonly used by cirripedologists is to mount the cirri from each side of the animal together under a single cover slip in the following manner:

Right side	I, II, III
	IV, V, VI
Left side	III, II, I
	VI, V, IV

By mounting the cirri in this way, you will be able to identify each cirrus. Observe that the anterior cirri (first 3 pairs) do not differ greatly from the posterior. Examine the pedicle (protopod) and rami (anterior and posterior, rather than endopod and exopod) of each cirrus. Are there differences in the setation of the cirri or of the two rami of one cirrus? The penis arises from between the bases of the 6th cirri. A pair of caudal appendages situated on each side of the anus are very small in *Pollicipes* and simple points continuous with the thorax in *Lepas*. Caudal appendages occur in all but a few genera and usually are more conspicuous, in some being long and multiarticulated. Free the specimen from the capitulum and remove the cirri from the other side before attempting to dissect out the mouthparts.

The trophi form a compact unit and can be removed, as such, from the rest of the body. First examine the trophi as a unit; the most apparent structure is the bulate labrum. Remove the paired mouthparts from the side opposite the labrum as follows: the maxillae (referred to by cirripedologists as the 2nd maxillae), the maxillulae (1st maxillae), the mandibles, and the labrum with palps. Mount the paired mouthparts with both members facing in the same direction so that both the outer and inner surfaces may be examined more easily. The maxillae are fused together basally and are best removed simultaneously, then separated when mounted.

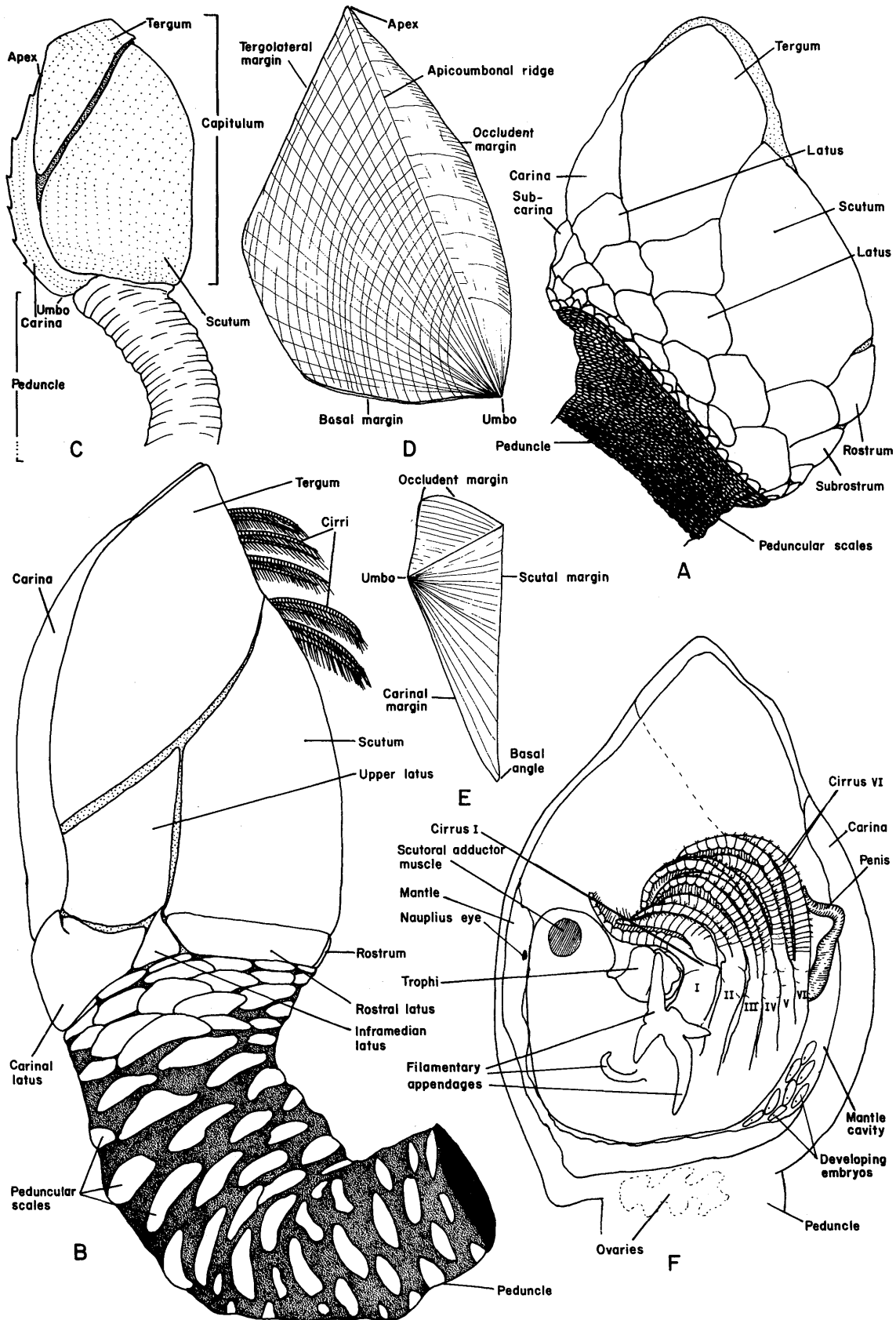


Figure 17 Cirripedia, Thoracica, Lepadomorpha: A. *Pollicipes* (lateral view); B. Scalpellid (lateral view); C. Lepadid (lateral view); D. Lepadid scutal valve; E. Lepadid tergal valve; F. Lateral view of animal within capitulum.

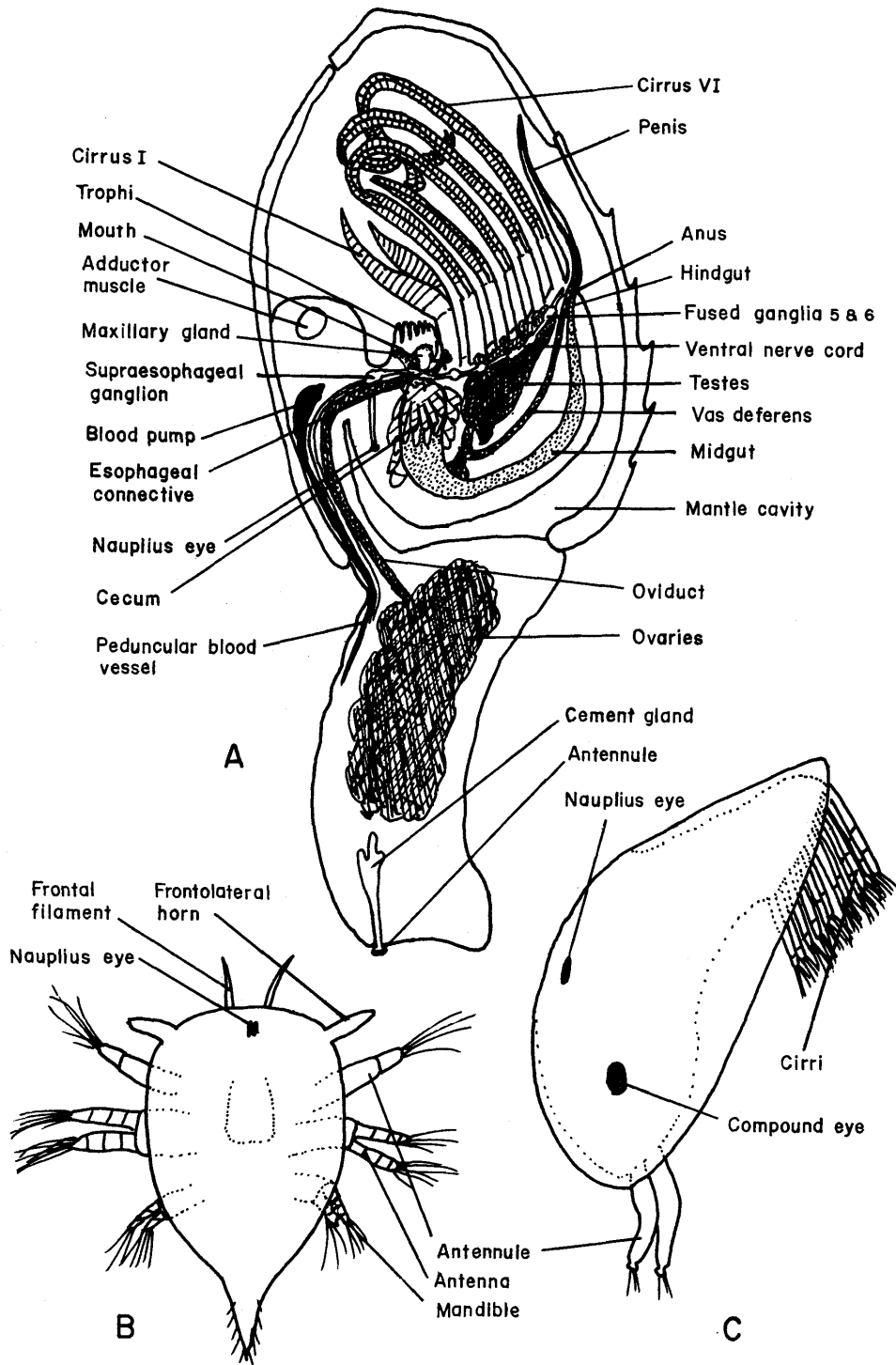


Figure 18 Cirripedia, Thoracica, Lepadomorpha: A. Diagrammatic lepadid with musculature removed to show major organ systems; B. Nauplius; C. Cyprid.

Remove the palps and much of the attached muscle and tissue from the labrum before mounting. The palps are attached to the lateral margins of the labrum rather than to the mandibles in all orders of the Cirripedia except the Acrothoracica.

The orientation of the cirriped body in the capitulum makes the study of the internal organ systems a little difficult. After removing the capitulum from one side, cut the peduncle on both the rostral and carinal sides and gently tease the integument away from the underlying

muscles. Carefully remove the external membrane and superficial muscles that cover the body of the animal. In the peduncle remove the muscle fibers to expose the ovaries and cement glands, being careful not to destroy the ducts of the glands that follow the muscle wall to the antennules. The cement glands usually are quite small and may be difficult to distinguish in poorly preserved material. The peduncular space largely is filled by the tubules of the ovaries. Toward the midline of the peduncle rostrally locate the paired oviducts, and if possible trace one as it leads from the ovary, along the rostral side of the peduncle into the capitulum, and to the 1st cirrus. The oviduct terminates in glandular tissue within the pedicle of the cirrus that can be seen by removing the external membrane and the muscles of the pedicle.

In close proximity to the oviduct near the rostral margin of the capitulum identify the large membranous blood pump; it extends into the peduncle as the peduncular blood vessel. Cirripeds lack a true heart, and the blood pump, through alternate compression and release of compression, serves as the propulsory mechanism. Blood flows from the pump into the peduncle by way of the peduncular blood vessel and is carried back to the

body through parenchymatous spaces into the blood sinuses in the mantle and body.

Often the most prominent structure in the body will be the greatly ramified testes. It may be necessary to remove the cirri from the exposed side of the body to be able to trace the vas deferens to the penis, as these tubes often are located near the midline of the body in close association with the midgut.

At the base of the labrum locate the mouth. Food is passed through the short esophagus or foregut into the U-shaped midgut, expanded anteriorly as a stomach, near which a pair of ceca are given off. Trace the midgut posteriorly; it will be difficult to distinguish the short hindgut from it as both are cuticularized. The anus opens near the base of the penis between the 6th pair of cirri. Adjacent to the esophagus is the end-sac of the maxillary gland with a duct opening on the maxilla.

Between the blood pump and the trophi locate the relatively small supraesophageal ganglion, which is connected with the ventral nerve cord and subesophageal ganglia by very long esophageal connectives. The ganglia of the 2nd to 4th cirri are distinct, whereas those of the 5th and 6th are fused in *Lepas*.

SUBORDER VERRUCOMORPHA Pilsbry, 1916

Calcareous plates	Asymmetrically arranged, forming wall and operculum; wall with 4 principal plates (rostrum, carina, fixed scutum, and fixed tergum); operculum with 2 principal plates (articulated scutum and tergum).
Primordial plates	Five chitinous plates (carina and paired scuta and terga).
Basis	Calcareous or membranous.
Labrum	Bullate.
Caudal appendages	Usually present.
Basidorsal point (penis)	Absent.
Filamentary appendages	Absent.
Sexes	Hermaphroditic.

These sessile barnacles exhibit pronounced asymmetry. In *Verruca*, the only Recent genus, the wall is composed of a rostrum and carina on one side and a fixed scutum and tergum on the other. The other scutum and tergum form the lidlike operculum. The basis is membranous or calcareous. In the characters derived from the body, *Verruca* resembles the lepadomorph cirripeds more than the balanomorphs, particularly in the mouthparts and the usual occurrence of caudal appendages. Verrucomorphs have a widespread distribution, primarily in deep water, usually on living organisms, less frequently on rocks.

Specimens of this suborder usually are not available for study; however, if some are, remove and clean the articulated scutum and tergum according to the instructions provided for the balanomorph opercular valves. Compare the verrucomorph shell with those of the balanomorphs, and, following the instructions given for the dissection and mounting of the lepadomorph animal, make a slide preparation of the appendages and mouthparts. What similarities and differences do you find between the verrucomorph and lepadomorph animals?

SUBORDER BALANOMORPHA Pilsbry, 1916

Calcareous plates	Symmetrically arranged, forming wall and usually operculum; wall with 2 principal plates (rostrum and carina) and 1–3 paired laterals; occasionally with plates wholly coalesced; rarely also with 1 or more basal whorls of small plates; operculum usually with 4 principal plates (i.e., articulated scutum and tergum on each side of aperture); occasionally opercular valves separate, fused, or absent.
Primordial plates	Absent.
Basis	Calcareous or membranous.
Labrum	Usually not bullate, notched; bullate in primitive members.
Caudal appendages	Present only occasionally.
Basidorsal point (penis)	Present only in Balanidae.
Filamentary appendages	Absent.
Sexes	Hermaphroditic; rarely with complementary males.

The Balanomorpha are differentiated from the other sessile suborder, the Verrucomorpha, by the symmetrical wall (see Figure 19). The 6 principal plates are homologous with those in the Lepadomorpha; that is, the rostrum and the carina in the shell wall and the paired scuta and terga that form the operculum. Basically the shell wall has, in addition, 3 pairs of lateral plates, but by loss or fusion of 1 or more plates, the shell typically has 6 or 4 plates; rarely the plates will be wholly coalesced. Each compartmental plate usually has 3 parts: a large central triangular area (paries, pl. parietes) and narrower segments on each side. If they are differentiated in structure from the paries, the one that overlaps the next compartment is called the radius, and the one that is overlapped, the ala. The carina and rostrum have alae on both sides; the rostralaterals and compound rostrum have radii on both sides; and the carinolaterals and laterals have radii on one side and alae on the other. Shell walls with 8 plates are found only in the most primitive group; rarely there are also 1 or more basal whorls of small plates. In the two most primitive groups the parietes are solid and the mouthparts resemble those of the lepadomorphs. The parietes become progressively more complex with an inner lamina and tubes between it and the outer lamina in progressively more advanced taxa. In the most advanced, the radii also are tubiferous.

A large number of balanomorphs should be available for comparative study. The description and instructions are based on specimens of *Balanus*. Begin your examination with the shell. First determine which plates are overlapped on 1 or both sides. In *Balanus* the rostrum is compound (rostralaterals fused, rostrum missing). If a specimen of *Chthamalus* (another balanomorph with 6 plates in the shell wall) is available, note that it has a true rostrum; it is the carinolateral plates that have been lost. Other diagnostic characters of the shell include the

structure of the basis, the parietes, radii, and sheath. Many of the characters require removing the surface by filing or grinding, but you can determine whether the basis is calcareous or membranous, and whether the parietes are solid or tubiferous without special equipment. After you have removed the animal, examine the inner lamina and sheath.

Having completed an examination of the shell, remove the opercular valves by cutting the opercular membrane and underlying muscles with a scalpel. The terga are held in place partly by a strong muscle attaching to the shell near the base, in close proximity to the carina; the scuta similarly are attached by muscles inserting in the region of the rostrum. In removing the opercular valves be careful not to break off the tergal spur; it is an important character. Carefully detach the animal from the valves; before dissection of it, place the opercular valves in 5% sodium hypochlorite (bleach) to remove the attached tissues, as significant characters will be obscured otherwise.

The orientation of the animal of the balanomorph is very similar to that of a lepadomorph, and the instructions for dissection are approximately the same. Note that the anterior and posterior cirri are, for the most part, easily distinguishable. However, the cirri of the 4th, 5th, and 6th pairs resemble one another. The number of setae on the anterior margins of the 6th pair is important; therefore, take the time to mount the cirri as you did for the lepadomorphs. Care should be exercised in separating the 6th cirrus from the penis and base of the opposing member of the pair. It is advisable to remove the trophi as a unit before removing the cirri from the second side, as it is easy to inadvertently discard the trophi with the body remnants. After the remaining cirri have been removed, sever the penis at its base. Balanids have a penial structure not present in other cirripeds, a

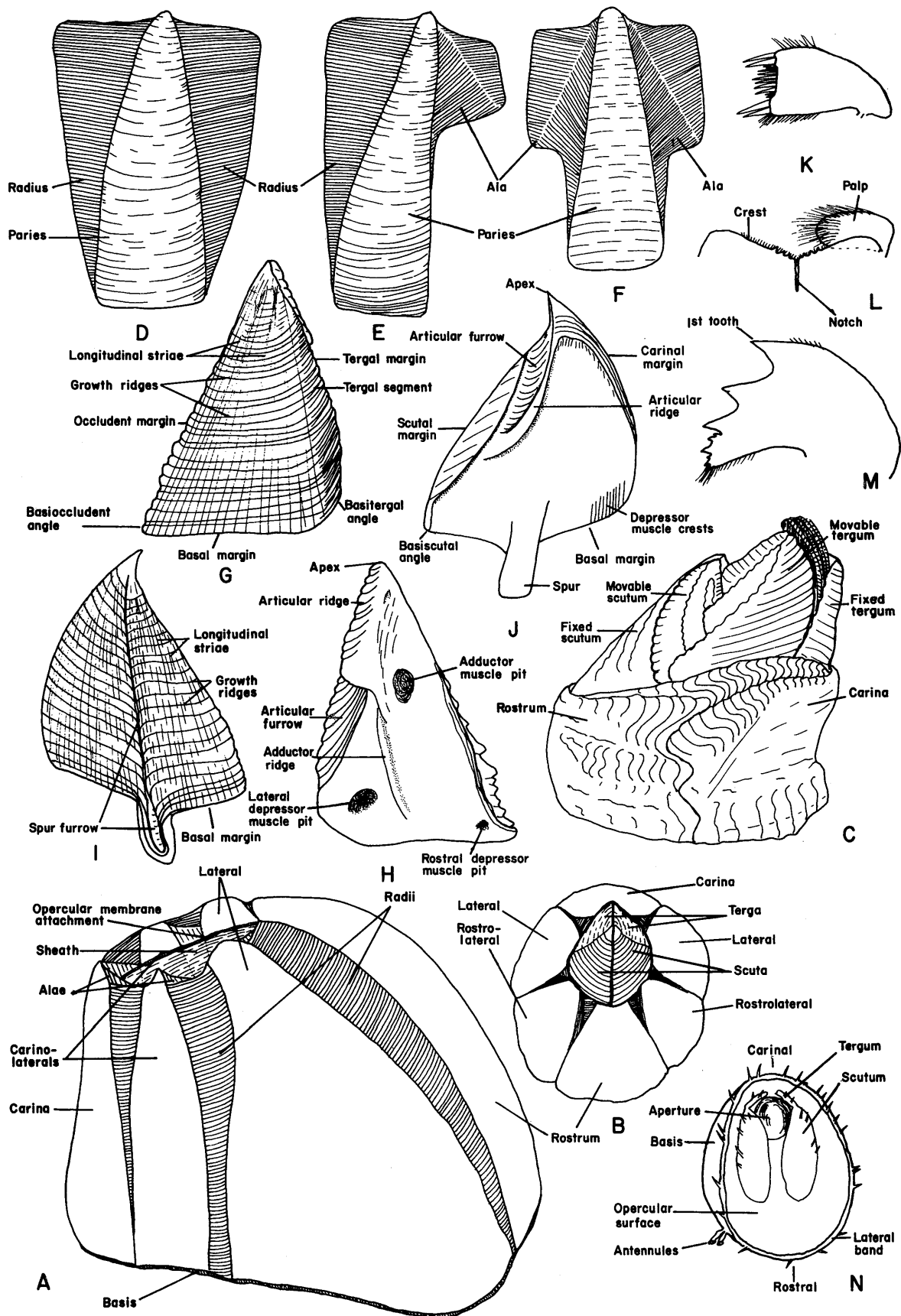


Figure 19 Cirripedia, Thoracica, Balanomorpha, Verrucomorpha: A. Balanid; B. Chthamalid; C. Verrucomorph; D–F, Parietes of shell. D. Pariet with paired radii, e.g., fused rostrum (rostrum + rostrolaterals); E. Pariet with radius and ala, e.g., lateral; F. Pariet with paired alae, e.g., carina; G. Balanid scutum (external); H. Balanid scutum (internal); I. Balanid tergum (external); J. Balanid tergum (internal); K. Maxillule; L. Labrum; M. Mandible; N. Complementary male of balanid.

basidorsal point located just distal to the penis' attachment to the body. The basidorsal point often has taxonomic significance. Next mount the mouthparts following the instructions given for the lepadomorphs: maxillae, maxillulae, mandibles, palps, and labrum. Examine the mouthparts and cirri under moderately high magnification. How does the labrum differ from that of *Pollicipes* or *Lepas*? Are the other mouthparts similar to those in the lepadomorphs? How do they compare with the verrucomorphs, if specimens are available?

Returning to the opercular valves, rinse them in water after the tissue has been dissolved. Examine each tergum and scutum (the valves usually will become disarticulated in the bleach, but if they have not, gently separate them). Using the reference illustrations in Figure 19 as a guide, identify the various elements of the terga and scuta.

If slides of complemental males are available, examine them and compare their structures with those of the hermaphrodites. The characters most readily observable are those of the opercular valves, orifice, lateral band, and perhaps the antennules. If the penis is extended, observe the armature. The vestigial cirri or mouthparts can rarely be distinguished without careful dissection.

The major organ systems of the balanomorphs differ only slightly from those of the lepadomorphs. The most significant difference is in the location of the ovaries, which are still preoral but located in the basal and parietal portions of the mantle.

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ORDER ASCOTHORACICA L.-Duthiers, 1880

Recent species	Approximately 30 in seven genera.
Size range	Up to 85 mm.
Carapace	Bivalved, open ventrally; occasionally absent.
Eyes	Nauplius eye in nauplius, with compound eyes in cyprid; both absent in adult.

Antennules	Uniramous; prehensile in cyprid and adult; often subchelate in adult.
Antennae	Biramous in nauplius; absent in cyprid and adult.
Mandibles	Without palp; part of protuberant oral cone modified for piercing and sucking.
Maxillulae	Part of protuberant oral cone.
Maxillae	Uniramous; part of protuberant oral cone; sometimes fused with paired stylet tips.
Maxillipeds	None.
Thoracic appendages	Three to 6 pairs of uni- or biramous thoracopods; sometimes reduced or absent.
Abdominal appendages	None.
Telson	Absent; caudal furca often present.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5 or 6 (1st thoracic somite sometimes fused to head); thorax usually with 5 or 6, occasionally obscure; abdomen with 4 or 5, or rarely coalesced with thorax.
Sexual characters	Female gonopore on conical papilla at base of 1st thoracopods; penis on 1st abdominal somite, at least in hermaphrodite.
Sexes	Typically separate; rarely hermaphroditic; males small.
Larval development	Nauplius → cyprid.
Fossil record	Cretaceous to Recent.
Feeding types	Parasitic; piercing and sucking.
Habitat	Marine; ecto- and endoparasites of coelenterates and echinoderms.
Distribution	Worldwide.

The Ascothoracica is the most primitive order of Cirripedia, as shown by the generalized form (see Figure 20). Prehensile antennules, a bivalved carapace, natatory thoracic appendages, and abdominal somites terminating in a furca are retained in the adult. [Bowman (1971) interprets the furca as uropods.] The sexes usually are separate, although hermaphroditism is known. Ascothoracicans are ecto- or endoparasites, and their mouthparts are adapted for piercing and sucking.

If infected coelenterates or echinoderms are available, a general study of ascothoracican morphology may be undertaken. Infection by *Ascothorax ophioctenis* produces a prominent swelling on the ophiuroid host; however, most species inhabit the gastric cavity of the host species and can be located only by the careful dissection of a large number of host specimens.

A thorough inspection of the female should be made for any attached males. If males are present, remove them to a separate container for subsequent examination. Carefully cut open the mantle of the female to reveal the body structure. In contrast to typical cirriped appendages, the thoracic appendages of the ascothoracicans are straight, natatory structures. Pay particular attention to the oral pyramid (mouth cone) and to the antennules, which usually are subchelate. In most species

the abdominal segmentation can be distinguished and usually a pair of caudal rami is present. The external anatomy of the males of *Ascothorax ophioctenis* differs markedly from that of the female. The male has a bivalve carapace or mantle that scarcely covers the body and a pair of subchelate antennules extending anteriorly. Posteriorly, the abdomen and caudal furca are clearly distinguished. The degree of development of the appendages and the number present is correlated to the parasitic mode of the species.

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ORDER RHIZOCEPHALA Müller, 1862

Recent species	Approximately 250 in ten genera.
Size range	As large as 10 × 5.5 × 3 cm.
Carapace	Absent.
Eyes	Nauplius eye in nauplius, with compound eye in cyprid; both absent in adult.
Antennules	Uniramous in cyprid; absent in adult.
Antennae	Biramous in nauplius; absent in cyprid and adult.
Mandibles	Absent.
Maxillulae	Absent.
Maxillae	Absent.
Maxillipeds	None.
Thoracic appendages	Absent.
Abdominal appendages	None.
Telson	Absent.
Tagmata	Not distinguishable.
Somites	Not distinguishable.
Sexual characters	Females with or without male-cell receptacle in mantle cavity.
Sexes	Usually hermaphroditic, occasionally separate, female and cyprid as functional male.
Larval development	Usually nauplius → cyprid → kentrogon; occasionally released as cyprid, with kentrogon.
Fossil record	Recent.
Feeding types	Parasitic; absorption through ramifying system.
Habitat	Marine; endo- or more rarely ectoparasites of Crustacea, particularly Decapoda.
Distribution	Worldwide.

The Rhizocephala are parasitic, greatly modified Cirripedia lacking appendages and a digestive tract in the adult. In part, the modification is so great that the affinity with the Cirripedia is determined only by the characteristic nauplius with frontal horns and/or the cyprid. Sexes until recently were thought to be combined; however, in some species the female invades the host and the spermatogenic material is provided by a male cyprid.

Very little, in terms of morphological studies, can be done with the rhizocephalans without histological sec-

tions. The various taxa, however, exhibit a variety of external reproductive capsules, and these should be examined. Rhizocephalans have been noted for the "parasitic castrating effect" they have on some hosts. Examine the host specimens and note any morphological changes that may have been induced by the rhizocephalan infection, such as the presence of female-type pleopods in males. Figure 20 illustrates the mode of reproduction of a species of *Peltogastrella*. The life cycle includes: (a) the female producing large eggs, which

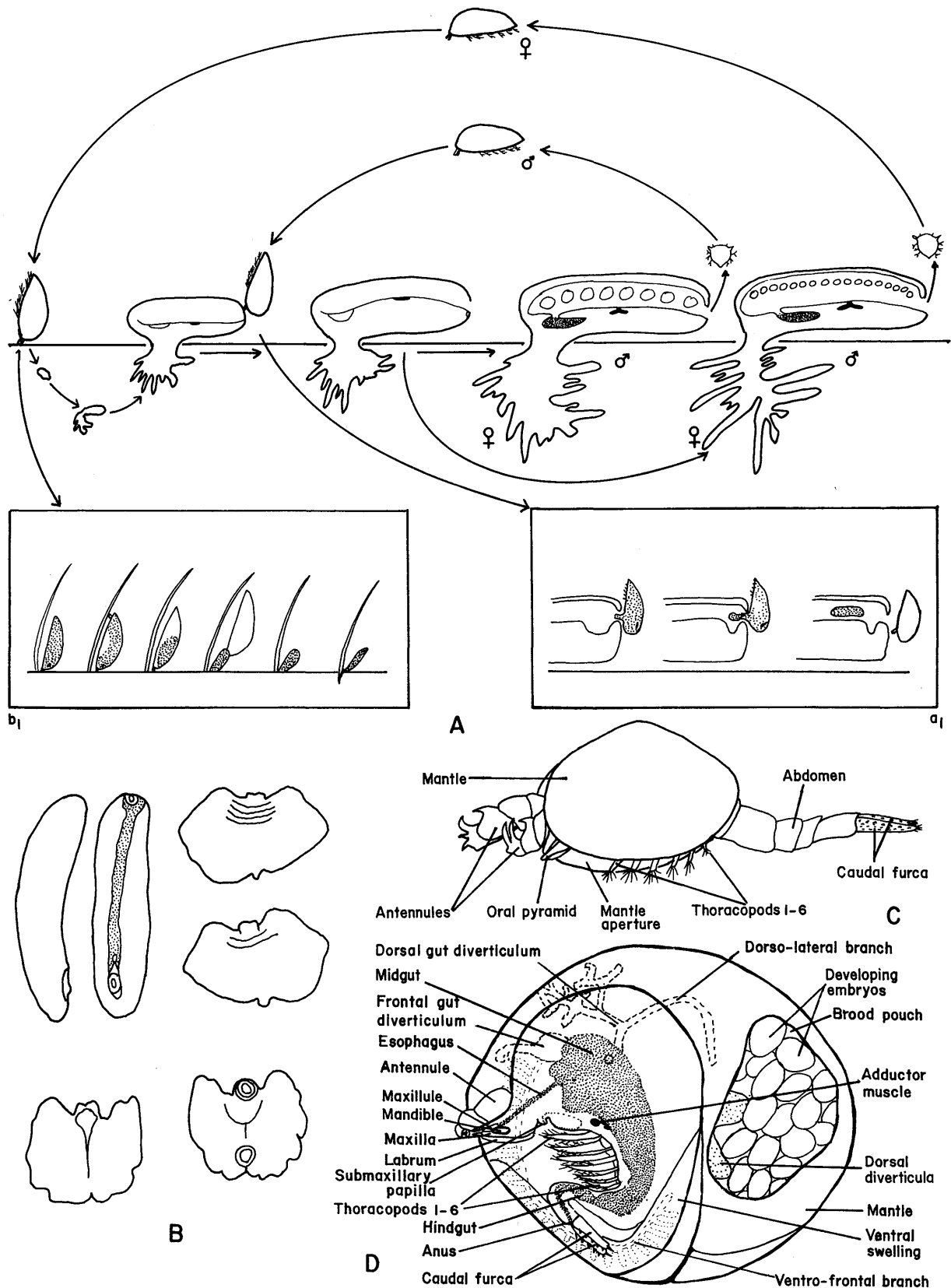


Figure 20 Cirripedia, Rhizocephala, Ascothoracica: A. Life cycle of a rhizocephalan parasite; a₁. Male spermatogenic cells injected into young female; b₁. Female cyprid attached at base of seta of host and casting cyprid shell prior to invasion of host [after Newman, Zullo, and Withers, 1969, from *Treatise on Invertebrate Paleontology*, courtesy of the Geological Society of America and University of Kansas]. B. Different forms of rhizocephalan reproductive sacs, *Peltogasterella*, *Sacculina*, *Lernaeodiscus* [after Boschma, 1950, 1952, 1959]; C. Ascothoracica, male; D. Ascothoracica, female [C, D after Wagin, 1946].

hatch as nauplii that become males; and (b) a female producing small eggs, which hatch as nauplii that become females. The male cyprid spermatogenic cells are injected into the young female and migrate to a receptacle (a_1); the female cyprid (kentrogon) attaches at the base of a seta of the host and casts the cyprid shell prior to invading the host's tissue (b_1).

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CLASS MALACOSTRACA Latreille, 1806

All remaining crustaceans are grouped in the class Malacostraca. Subclasses within this class include the Phyllocarida, Hoplocarida, and Eumalacostraca. The Phyllocarida and Hoplocarida are represented by the Recent orders Leptostraca and Stomatopoda respectively. The Eumalacostraca includes a number of superorders, orders, and suborders which, for discussion and study purposes, will be given equal attention.

General characters of the Malacostraca include paired

compound eyes; usually biramous antennules and antennae, the latter with the exopod usually developed as a scaphocerite; and well-developed mandibles. Five to 8 pairs of uni- or biramous thoracic appendages and 5 pairs of biramous pleopods usually are present. The female gonopore(s) are invariable on the 6th thoracic somite or its appendages; the male gonopores are on the 8th or its appendages. The sexes usually are separate although protandry and protogyny are known.

SUBCLASS PHYLLOCARIDA Packard, 1879

ORDER LEPTOSTRACA Claus, 1880

Recent species	Eleven, in four genera: <i>Nebalia</i> , <i>Paranebalia</i> , <i>Nebaliopsis</i> , and <i>Nebaliella</i> .
Size range	0.8–4.0 cm.
Carapace	Bivalve, laterally compressed; lacking hinge or hinge line; enclosing thorax but not cephalon; rostrum articulated.
Eyes	Stalked, compound, except nonfunctional in <i>Nebaliella</i> and <i>Nebalia typhlops</i> ; ocular scale sometimes present.
Antennules	Usually biramous; exopod scale or platelike, occasionally markedly reduced or absent.
Antennae	Uniramous, well developed; may be sexually dimorphic.
Mandibles	With palp; molar and incisor processes usually well developed, occasionally reduced.
Maxillulae	Paired endites and flagelliform palp; latter occasionally reduced.
Maxillae	Protopod usually with 4 endites; endopod and exopod usually well developed; occasionally endopod reduced, exopod vestigial.
Maxillipeds	None.
Thoracic appendages	Eight pairs of biramous foliaceous thoracopods, usually well developed, occasionally reduced; with or without epipods.
Abdominal appendages	Six pairs: 1st 4 pairs biramous, large, last 2 uniramous, reduced.
Telson	With caudal furca.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5, thorax with 8, abdomen with 7, excluding telson.
Sexual characters	Gonopores on coxae of 6th thoracopods of female, on 8th coxae of males. Antennules and antennae often sexually dimorphic.

Sexes	Separate.
Larval development	Epimorphic; usually hatch as postlarvae (manca stage); in <i>Nebaliopsis</i> as planktonic larvae.
Fossil record	Extensive, since Lower Cambrian. More than 50 fossil genera known; two orders known only from fossil record.
Feeding types	Generally filter feeder.
Habitat	Marine, usually between 10 and 400 m; most are benthic although one species is bathypelagic.
Distribution	Principally from Atlantic; one species from Puget Sound, Washington and one from Antarctic.

The Phyllocarida are represented by a single Recent order, the Leptostraca; it contains only the suborder Nebaliacea and family Nebaliidae with four currently recognized genera: *Nebalia*, *Paranebalia*, *Nebaliopsis*, and *Nebaliella*. Illustrations and the discussion of external morphology of this group are based primarily on specimens of *Paranebalia*; those of the internal anatomy are based on a composite. The few major morphological differences among the taxa will be pointed out. If an abundance of material is available, individual student dissections should be undertaken as these animals are easily manipulated, even when small in size. In cases where only very limited material is available, students should examine intact animals, then refer to slide preparations for the study of appendages, mouthparts, and internal organ systems.

The carapace is laterally compressed, forming a bivalvelike shell; however, no hinge or hinge line is present (see Figure 21). Anteriorly, the head is not covered by the carapace and the stalked compound eyes, as well as the articulated rostrum (also referred to as a rostral plate), are immediately apparent. The elongate antennules and antennae protrude from beneath the carapace. The number of articles in the antennular and antennal flagella are fewer in *Paranebalia* than in *Nebaliella* or *Nebalia* and generally also vary between the sexes. Although the virtually transparent carapace covers the entire thorax, it is attached only to the cephalon. The cephalic and thoracic appendages generally are visible beneath the carapace; however, for ease in distinguishing individual appendages, the carapace should be removed from one side of the body. After cutting the carapace along the dorsal midline, sever the prominent adductor muscle and remove one side of the carapace.

Before dissection, observe the thoracic and abdominal segmentation and the relationships of the appendages. Note that the abdomen bears pleopods on the anterior 6 somites but not on the 7th or the telson. [Bowman (1971) considers the abdomen 8-segmented; that is, the telson is lacking and the ultimate lobe is the anal somite. The caudal furca by his definition are uropods.]

Examine the stalked eyes; depending upon the genus, a scale or acicle may not be present at the base of each ocular peduncle. Remove the antennule and antenna from the exposed side of the body. The exopod of the antennule is extended as a denticulate plate or scalelike structure in *Paranebalia* and *Nebaliopsis*, reduced to a tuft of bristles in *Nebaliella*, and virtually absent in species of *Nebalia*. Sexual dimorphism is exhibited in the larger number of sensory bristles on the antennules and the considerably greater length and number of articles of the antennal flagella in males of some of the species. In a few species, the antennules and/or antennae of males are modified for grasping the female during copulation.

Remove one or more of the thoracopods. In *Paranebalia*, as figured, the thoracopods are unspecialized; the epipods are considerably reduced. In species of *Nebalia* both the exopods and epipods are very much flattened and inflated. In all species, except *Nebaliopsis typicus* G. O. Sars, the 8 thoracopods are very similar in structure. In *N. typicus* the 1st pair are slightly modified to act as interlimb space valves, and the subsequent 6 pairs are unsegmented and the epipods are represented by slight lobes on the outer margins; the last pair have very few setae. In most leptostracans, the tips of the thoracic endopods of the female carry long setae that curve inward toward the midline and form an effective brood pouch. The female gonopores open on the coxae of the 6th thoracopods but may be difficult to distinguish. The gonopores of the male open on low papillae on the coxae of the 8th pair of thoracopods.

Remove and examine one of the first 4 pairs and one of the last 2 pairs of pleopods. Observe that the endopods of the anterior pleopods are linked together by a small spinose structure, the appendix interna. The pleopods of the last 2 pairs are small, simple, and uniramous. The unsegmented caudal furca articulates freely with the telson.

Remove the mouthparts. You will notice that the mandible has a prominent molar process and palp but a weakly developed incisor process. The incisor process is

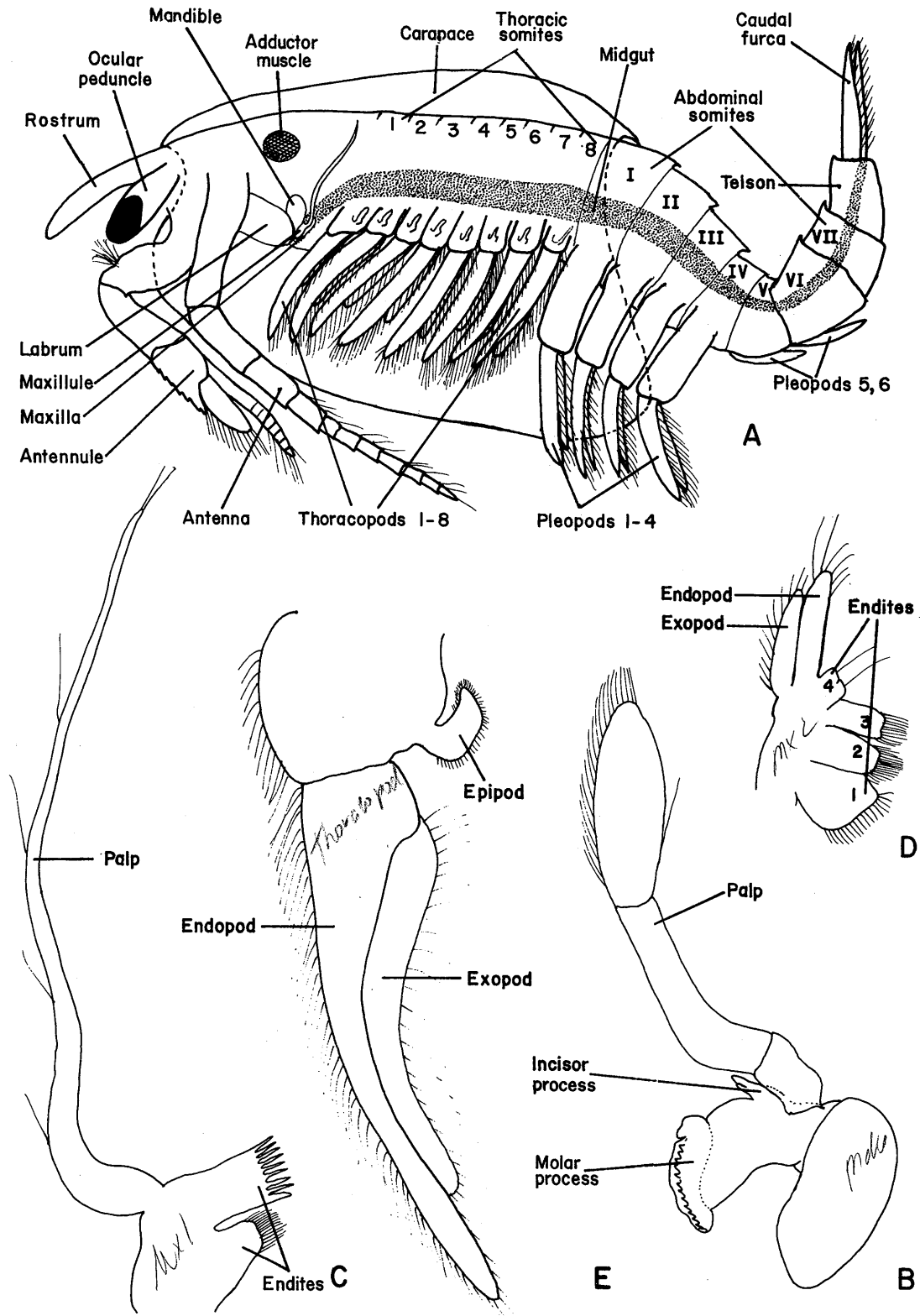


Figure 21 Phyllocarida: A. Lateral view of animal with left side of carapace removed; B. Mandible; C. Maxillule; D. Maxilla; E. Typical thoracopod.

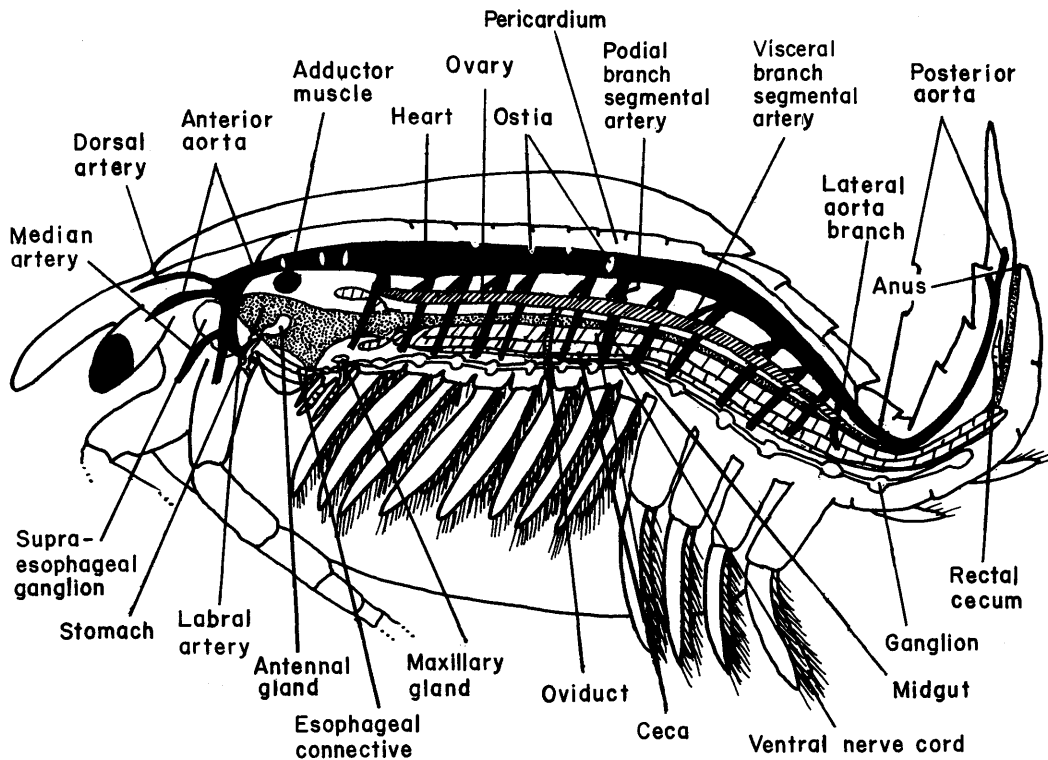


Figure 22 Phyllocarida: Diagrammatic leptostracan with musculature removed to show major organ systems.

also weakly developed in *Nebalia* and lacking in *Nebaliopsis*; however, it is well developed in *Nebaliella*. In all leptostracans, except *Nebaliopsis*, the maxillule has a well-developed, curved palp, which may represent a flagellate endopod. The maxilla usually has 4 endites and both an endopod and exopod as well; in *Nebaliopsis* the endopod is reduced and the exopod is vestigial.

The leptostracan body is quite muscular and these layers of muscle tissue must be removed before the major internal organ systems can be examined (see Figure 22). Begin dorsally in the midline and strip the muscles from each side of the body. Directly beneath the muscle layer is the tubular heart that extends from the cephalic region to the 4th abdominal somite surrounded by a pericardial sinus. Identify 3 pairs of lateral ostia in the cephalic portion of the heart and the 3 dorsal and 1 large lateral pairs in the thoracic region. Follow the anterior aorta forward; it gives off branches ventrally to the antennules, antennae, and mouthparts and dorsally to the dorsal artery of the head and rostrum. In the thoracic region the heart gives off 8 pairs of segmental arteries; an additional 4 pair are given off in the abdomen. Each artery has a visceral branch that provides blood to the body organs and a podial branch that supplies the extrinsic muscles of the thoracopods and pleopods. Posteriorly identify the posterior aorta and its pair of lateral branches that supply blood to the posterior abdominal somites.

Laterally and slightly beneath the heart are the ovaries or testes. These are paired, long tubular organs that extend from the region of the stomach to the 3rd or 4th abdominal somite. In females the paired oviducts lead from the ovaries to the genital openings on the 6th thoracopods. In males the short vas deferens opens on small papillae on the coxae of the 8th thoracopods.

In most leptostracans food passes from the mouth through an esophagus or foregut into an enlarged cardiac stomach. The cardiac portion of the stomach is provided with masticatory ridges moved by muscles; the posterior or pyloric part of the stomach is provided with setose lobes and a dorsal groove that leads into the midgut as a chitinous funnel. Anteriorly the midgut gives off 1 or 2 pairs of dorsally and ventrally directed short ceca. Two or 3 elongate tubular ceca arise from a pair of ventral openings in the midgut and extend almost the entire length of the body. A short dorsal cecum arises from the midgut just anterior to the short cuticularized hindgut. The anus opens ventrally between the caudal rami. In *Nebaliopsis* there is no cardiac stomach, the midgut is very narrow, and only 1 large midgut cecum is present. In leptostracans excretion is accomplished by means of both antennal glands and maxillary glands.

Beneath the anterior aorta identify the large supraesophageal ganglion and the short connectives encircling the esophagus. Carefully remove the stomach, midgut, and ceca to expose the large ventral nerve cord

and ganglia. Note that the nerve cord and ganglia terminate at the 6th abdominal somite. No ganglia are present in either the 7th somite or telson; however, 1 additional neuromere is present in the embryo and it has been assumed that the most posterior ganglion of the adult has resulted from the fusion of the two most posterior embryonic ganglia.

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SUBCLASS HOPLOCARIDA

ORDER STOMATOPODA Latreille, 1817

Recent species	Approximately 300 in four families.
Size range	5–55 cm.
Carapace	Well developed, laterally expanded; covering cephalon, except for acron and antennular somite, and anterior half of thorax.
Eyes	Stalked, compound; occasionally reduced.
Antennules	Peduncle with 3 segments; 3 flagella, dorsal and divided ventral.
Antennae	Peduncle with 2 segments; exopod with segment expanded as scaphocerite; endopod with flagellum.
Mandibles	With or without palp; well-developed toothed incisor and basal molar processes.
Maxillulae	Basal and coxal segments each with endite; endopod reduced; exopod absent.
Maxillae	With 4 segments, 1st and 2nd each with endite.
Maxillipeds	None.

Thoracic appendages	Eight pairs; first 5 subchelate, 2nd modified as powerful raptorial claw; all used in feeding; thoracopods 6–8 biramous, used in locomotion.
Abdominal appendages	Five pairs of biramous, laminar pleopods, often with gills; 6th somite with uropods.
Telson	Well developed, occasionally fused with 6th abdominal somite (pleotelson); usually well armed.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5, excluding acron; thorax with 8; abdomen with 6, excluding telson.
Sexual characters	Gonopores on 6th thoracic somite of female, 8th of male; male with well-developed penes. Armature of telson and size and armature of raptorial claw sexually dimorphic.
Sexes	Separate.
Larval development	Anamorphic; hatch as antizoea or pseudozoea; several pelagic substages before settlement.
Fossil record	Mississippian to Recent.
Feeding types	Predators.
Habitat	Usually marine, few reported from brackish water; usually inhabiting shallow water, but some deep-sea forms have been reported.
Distribution	Tropical and subtropical seas throughout world; sometimes temperate seas. In northern hemisphere as far north as Hokkaido, Japan; Massachusetts, U.S.A.; and southern North Sea. In southern hemisphere, South Australia and South Africa.

The figures and instructions for the study of the Stomatopoda are based on specimens of the family Squillidae; however, as the primary characters that distinguish the families are found in the armament of the telson, the use of species of other families will not invalidate the general discussion. You will notice immediately that stomatopods exhibit a number of characters that have not been present in the crustaceans that have been examined previously. Therefore, take time to examine the gross morphology of the animal before beginning your dissection (see Figure 23).

Examine the cephalon in dorsal view. Certain features of the ophthalmic area will be noticeably distinct. As in other stalk-eyed crustaceans, the eyes are situated on movable peduncles, the cornea broadly dilated. The ocular peduncles are attached to an articulated acron, also sometimes referred to as an ophthalmic somite, although it is doubtful that it is a true cephalic somite. It should be possible to distinguish 3 plates of the acron: the anteriormost plate, protruding in front of the basal margin of the ocular peduncles, is called the fastigial plate; the medial plate, at the bases of the peduncles, is the ocular plate; and the posterior plate, with dorsally directed small projections, the ocular scales, is the postocular plate.

Posterior to the acron is the antennular somite, also referred to as the posterior dorsal plate of the head; it is covered medially by the broad rostral plate or rostrum which articulates with the carapace. The antennular somite bears the 3-segmented antennules and, dorsolaterally, the antennular processes. The ventral flagellum of the antennule is subdivided into 2 flagella. The antennae arise lateral to the antennules and each consists of a 2-segmented peduncle, 2-segmented exopod, and 3-segmented endopod with flagellum. The terminal segment of the exopod is broadened and flattened, forming the antennal scale or scaphocerite.

The remaining cephalic somites and first 4 thoracic somites are covered dorsally by the carapace, which is broad and flattened. The surface of the carapace is variously sculptured in the different taxa but typically bears 3 grooves, that is, a transverse cervical groove on the posterior third and a pair of parallel, longitudinal gastric grooves. Usually there also is a median carina. A dorsal pit (median pore) between the cervical groove and the anterior bifurcation of the median carina may be easily distinguished in many species. The produced anterolateral angles may be armed or unarmed. In some species lateral and intermediate carinae between the gastric groove and the lateral margin on each side of the

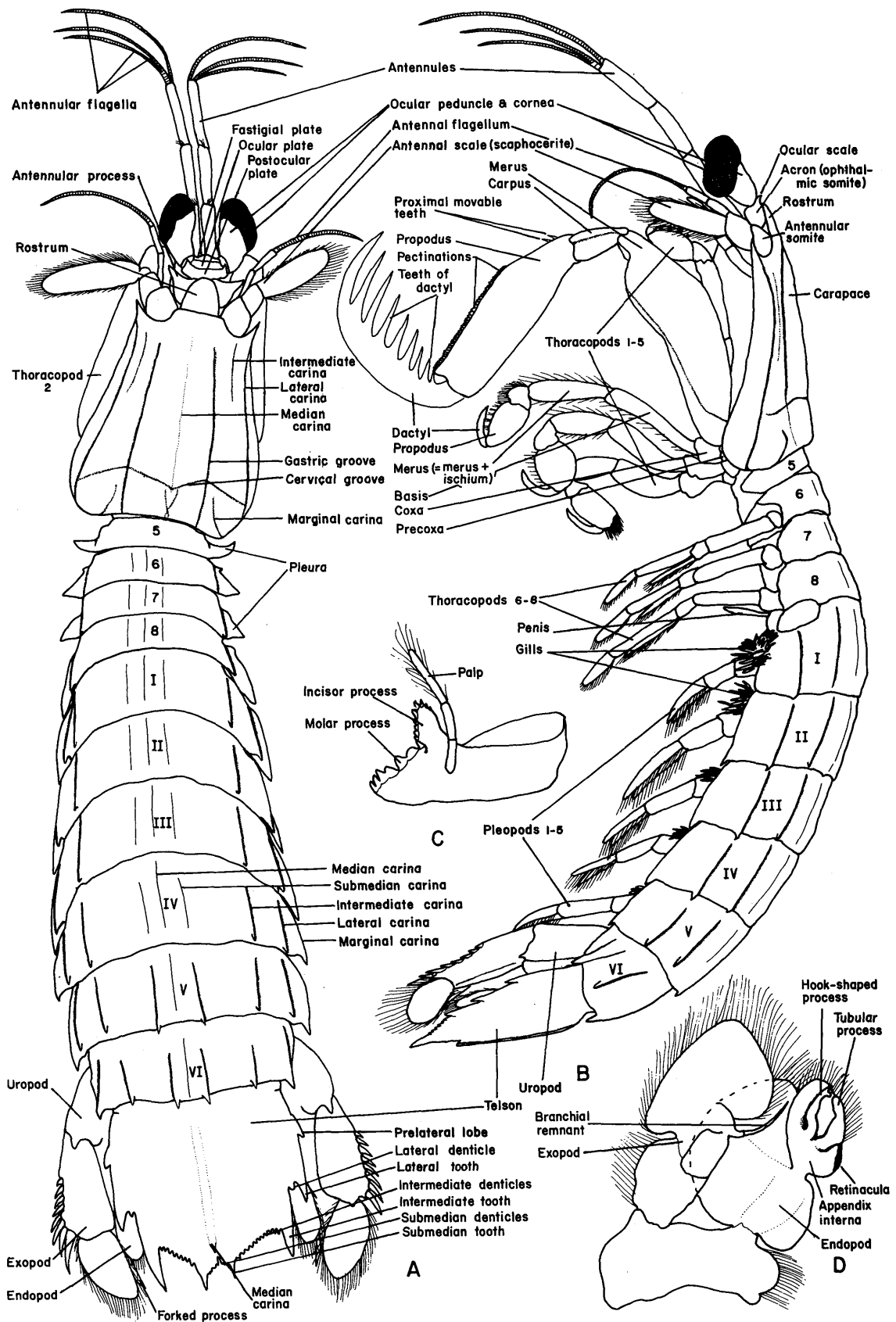


Figure 23 Stomatopoda: A. Whole animal (dorsal view); B. Male (lateral view); C. Mandible; D. 1st pleopod of male.

carapace, as well as a posterolateral marginal carina, also are present.

The last 4 thoracic somites are free (not covered by the carapace). They, as well as the first 5 abdominal somites, often have a number of longitudinal carinae, such as submedian, median, intermediate, lateral, or marginal. The 6th abdominal somite usually lacks marginal carinae. Identify the carinae present in your specimen(s). In some species secondary ridges may occur between the carinae. Not infrequently the carinae terminate in spines at the posterior margins of the somites. Denticles also may be present on the somites.

The telson usually is distinct from the 6th abdominal somite; however, fusion of the 6th somite and the telson occasionally does occur, resulting in a pleotelson. The telson usually is armed with teeth, denticles, or both. The teeth and denticles are identified according to their positions, such as lateral, intermediate, or submedian. Sketch the telson of your specimen(s) and identify the teeth and denticles present.

Place the specimen with its ventral surface up and examine the surfaces of the somites (the sternites), the appendages, and the telson. The first 5 pairs of thoracopods are modified for feeding, and the posterior pairs as walking legs. In older texts the anterior appendages often are referred to as maxillipeds; however, they are not equivalent to the maxillipeds of other crustaceans. Remove the anterior thoracopods from one side and observe their basic structure. All are subchelate and are composed of 7 segments. There is some disagreement about which are the fused segments; that is, whether the coxa and precoxa have fused or the ischium and merus have fused. Thus the thoracopods are thought to consist of either a coxa (fused), basis, ischium, merus, carpus, propodus, and dactyl, or a precoxa, coxa, basis, merus (fused), carpus, propodus, and dactyl. Notice how the dactyl is folded back on the propodus to form a subchela. Epipods may be present at the bases of the thoracopods. There is little difference in the 1st, 3rd, and 4th thoracopods except in size. The 2nd thoracopod is markedly stronger than the others, and the dactyl and propodus form a powerful and effective raptorial claw. The 5th thoracopod has a prominent tuft of stiff setae on the propodus that is used for cleaning the body. Remove one of the walking legs. You will observe that it is biramous. The protopod consists of 3 segments, the 2nd of which is elongate. The outer ramus consists of a single segment and, contrary to what should be expected, this ramus is the endopod. The inner ramus is the 2-segmented exopod; their relative positions have been reversed during development.

Five pairs of pleopods are present. They are biramous, broad, flattened, and provided with gills. In males the endopods of the 1st pair are modified markedly, and the second very slightly. Remove a 3rd pleopod, which may be considered typical, and examine the components.

There is a basal protopod from which arise an endopod and exopod, each of which is lamellar and membraneous and obscurely divided into 2 segments. The basal segment of the exopod has 2 filamentous structures protruding from the internal margin. These are the gills. The distal segment of the endopod also has a structure protruding from the internal margin. This is an appendix interna that carries a group of coupling hooks or retinacula, which serve to attach the pair of pleopods together so that they may move in unison. Examine the 1st pleopod of a male specimen and note the modifications of the endopod to form the so-called petasma, particularly the hook-shaped and tubular processes. In addition to the 1st pleopods, males may be distinguished by a pair of tubular copulatory structures (penes) arising at the bases of the last pair of thoracic legs, and females by the presence of gonopores located submedially on the 6th thoracic sternite.

You should be able to distinguish the anal pore on the anteroventral surface of the telson and, directly posterior to it, a short post-anal carina. Strong ventral carinae are present medially on the abdominal sternal plates. The uropods (appendages of the 6th abdominal somite) typically consist of a 1-segmented protopod or basal segment, a 2-segmented exopod, and a 1-segmented endopod. The basal prolongation of the uropod is a flattened, usually bifurcate ventral projection, referred to as a forked process. This structure has considerable diagnostic significance at the generic and specific levels. The proximal segment of the exopod is provided with a series of movable spines.

Three pairs of cephalic appendages that constitute the mouthparts lie in close proximity to the broad epistome and above the bulbous labrum. Remove the mouthparts from one side. The maxillae are the most external of the mouthparts. The maxilla is somewhat different in appearance from those of most other crustaceans. It consists of 4 segments; the 1st and 2nd are provided with endites and that of the 2nd is bilobed. The orifice of the maxillary gland can be observed on the basal segment. The maxillule directly overlaps one lobe of the bulbous, bilobed labium. The maxillule consists of 2 segments, the coxa and basis, and each has a distinct endite. The exopod is absent and the endopod is represented by a very small segment arising near the base of the basal endite. It is sometimes referred to as the palp of the maxillule. The calcareous mandible is very large and has a prominently toothed incisor process and basal molar process. The incisor process lies over the labrum, but the molar process protrudes beneath the labrum. The mandibular palp may be 3-segmented or reduced to 1 or 2 segments. By probing the labrum ventrally in the midline, the mouth can be observed.

The position and the action of the mandibles is somewhat unusual, in that they have weak dorsal articulations and strong ventral articulations with small condyles on

the posterior margins of the long lateral wings of the epistome that embrace the labrum. The fibers of the ventral muscles of the mandibles do not arise from a supporting ligament but are attached separately on large lateral expansions of an apodemal arch arising from pre-mandibular invaginations between the epistome and the doublure of the carapace. A corresponding apodeme has not been observed in other crustaceans. Manipulation of the mandibles will show that the only movement of these jaws can be a partial rotation on their vertical epistomal hinges between the 2 points of articulation.

To examine the major aspects of the internal anatomy (see Figure 24), carefully free the carapace by cutting along the ventrolateral body wall where the laterally expanded carapace connects and posteriorly at its point of attachment. With a pair of sharp scissors, cut away the dorsal integument of the acron and the antennular somite, being careful not to damage the underlying structures. Then remove the remainder of the dorsal exoskeleton. A median and two lateral cuts with sharp pointed scissors will allow you to separate the exoskeleton from its attached muscles without major damage to the latter.

The posterior thorax and the abdomen are very well provided with thick layers of circular and longitudinal muscles. Examine these muscle layers and then carefully remove the dorsal portions to expose the underlying organs. Anteriorly the principal muscles are those of the antennae, antennules, and ocular peduncles. Carefully separate these muscles and trace each into its respective appendage. In the midline between the muscle pairs locate the anterior aorta. As the circulatory system in stomatopods is particularly significant from an evolutionary viewpoint, it should be studied in considerable detail. The anterior aorta is a large vessel that can be traced easily, even in noninjected specimens. At the level of the antennae it gives off a pair of large branches that are the common origins of the antennal and antennular arteries. In the acron the anterior aorta gives rise to the paired ophthalmic artery and smaller vessels that provide blood to the supraesophageal ganglion. After identifying the cephalic arteries, cut the overlying membrane and trace the anterior aorta posteriorly to its junction with the heart. At this level the paired lateral cephalic arteries arise. Trace the heart from its anterior end at the level of the 2nd thoracic somite to its termination in the 5th abdominal somite. The presence of paired segmental lateral arteries and ostia (the latter difficult to identify in noninjected specimens) are original in the Stomatopoda and considered to be a primitive condition. Trace several of the lateral arteries to their respective limbs; their small branches to the musculature and surrounding tissues will be difficult to distinguish. Exceptions to the segmental pattern are the 1st pair, which supplies blood to the mouthparts; the 2nd pair, which supplies both the 1st and 2nd thoracopods; the 9th pair, which supplies

blood to the tissues and musculature of the 8th thoracic somite and the 1st abdominal somite; and the last pair, which serves both the last pair of pleopods and the uropods. Posterior to the heart the posterior aorta can be traced into the telson. Secondary branches of the lateral arteries connect with the large ventral subneural artery, which will not be observed until the digestive tract has been removed. Blood returning to the heart passes into the pleopodal gills through a large lacuna ventral to the gut. From the gills the blood flows into the pericardial sinus through segmentally arranged, dorsally directed sinuses. Details of the circulatory system will be difficult to observe in noninjected specimens.

Immediately beneath the heart are the reproductive organs. In females a pair of elongate ovaries are present with oviducts opening on the sternite of the 6th thoracic somite. In males a paired accessory gland is present anteriorly with ducts opening into the tubular copulatory appendages on the 8th thoracic somite. The testes extend from the 3rd abdominal somite to the telson, where the coiled pair fuse to form a single tube. Anteriorly from the testes trace the coiled paired vas deferens forward to their openings in the paired penes.

Return to the anterior part of the thorax and remove the muscles of the antennae and antennules. Observe the prominent anterior extension of the cardiac stomach. With careful teasing separate the stomach from the adjoining muscle bands. No clear distinction can be made between the esophagus and stomach in stomatopods. Near the anterior end of the heart observe the marked reduction in the size of the stomach. This is the pyloric part of the stomach that opens into the midgut and into a pair of digestive glands (ceca) through a structure called the *pars ampullaris*. Trace the midgut and one of the digestive glands posteriorly. In each segment the cecum is expanded into a large segmental pouch. In the telson the cecum branches into a series of tubules; the gut terminates at the anus, located anteroventrally on the telson. Cut the stomach free in the area of the mouth and at the beginning of the midgut, and remove and open it. Observe the structure of the filtering apparatus separating the cardiac and pyloric portions and the structure of the pyloric stomach itself. The former consists of a pair of sickle-shaped, finely toothed upper lateral plates, a pair of similarly shaped lower lateral plates, and a broad, ovate median plate. The pyloric stomach consists of a broad ventral filtering plate with anterior sclerite and right and left filtering plates with anterior sclerites. Each of the filtering plates is lined with rows of fine teeth that form a very efficient filtering apparatus.

With the cardiac stomach removed, the supraesophageal ganglion can readily be observed. Trace the nerves of the ocular peduncles, antennules, and antennae. The esophageal connectives in stomatopods are very elongate. Anteriorly the ventral nerve cord is enlarged by the fusion of the ganglia of the mouthparts and

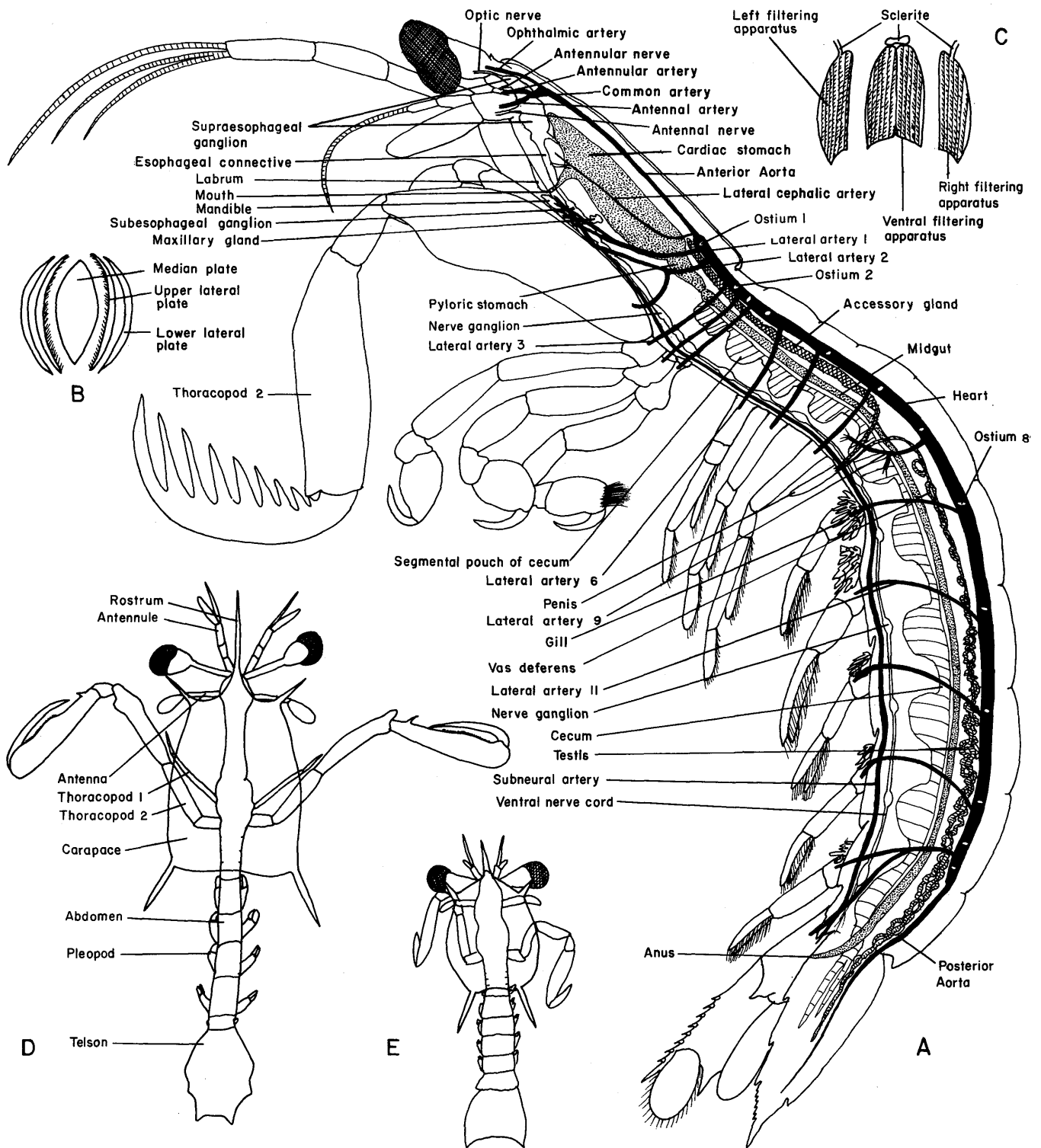


Figure 24 A. Diagrammatic stomatopod with musculature removed to show major organ systems; B. Filtering apparatus separating gastric from pyloric portions of stomach; C. Plates of pyloric stomach; D, E. Two forms of early stage pseudoscorpions.

first 5 thoracomeres to form the very elongate subesophageal ganglion. Paired ganglia of the subsequent thoracic and abdominal somites appear fused as median ganglia separated by long connectives. Trace the nerve cord and identify the segmental ganglia. Beneath the nerve cord is the large subneural artery. Trace this blood vessel from its origin in the mandibular somite to its termination in the 6th abdominal somite.

Larval development in stomatopods is anamorphic and may be regular or irregular. Most stomatopods hatch as pseudozoeae, characterized by the presence of 4 or 5 functional pleopods, biramous antennules, and 2 uniramous thoracopods. In two genera, *Lysiosquilla* and *Coronida*, the larvae hatch as antizoea, characterized by the lack of pleopods (which develop progressively later), uniramous antennules, and 5 pairs of biramous thoracic appendages. The number of propelagic and pelagic larval substages appears to be variable among species and genera. Usually a single postlarval stage represents the transitional period between the free-swimming larvae and the benthic adults.

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SUBCLASS EUMALACOSTRACA Grobben, 1892

The Eumalacostraca includes the three superorders Syncarida, Peracarida, and Eucarida. Collectively eumalacostracans can be distinguished from phyllocarids by the absence of a bivalve carapace and the lack of a 7th abdominal somite. Characters that distinguish the

Eumalacostraca from the Hoplocarida are the absence of an acron and the lack of 5 pairs of subchelate, feeding thoracopods, the 2nd of which is extremely powerful and raptorial.

Superorder SYNCARIDA Packard, 1885

The Syncarida is a relatively small taxon possessing a unique combination of characters, the most outstanding of which is the complete absence of any vestige of a carapace or cephalic shield. The body plan is simple and

quite fundamental; the biramous thoracopods are considered to represent the original primitive condition. The three orders, Anaspidacea, Stygocaridacea, and Bathynellacea, are discussed individually.

ORDER ANASPIDACEA Calman, 1904

Recent species	Seven or eight in three families.
Size range	2–50 mm.
Carapace	Absent.
Eyes	Stalked or sessile, rarely absent.
Antennules	Biramous; with statocyst.
Antennae	Uni- or biramous; latter with scaphocerite.
Mandibles	With palp.
Maxillulae	With 2 endites and vestige of (?) endopod.
Maxillae	With 2 endites and bilobed terminal segment.
Maxillipeds	One pair.
Thoracic appendages	Seven pairs of thoracopods; 1st through 5th biramous, with epipods; 6th and 7th with or without exopods; 6th sometimes without epipods; 7th without epipods.
Abdominal appendages	Five pairs of pleopods usually with endopods reduced or absent; endopods of 1st and 2nd pleopods modified as copulatory structures (gonopophyses) in males. Uropods well developed, biramous, spatulate, or slender.
Telson	Sometimes spatulate.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5 + 1 thoracic (maxilliped); thorax with 7; abdomen with 6, excluding telson.
Sexual characters	Gonopores on 6th thoracic somite of female, 8th of male. Endopods of 1st and 2nd pleopods modified as copulatory structures in males; females with spermatheca.
Sexes	Separate.
Larval development	Epimorphic.
Fossil record	Triassic to Recent.
Feeding types	Primarily filter feeders on detritus and algae; sometimes predators.
Habitat	Freshwater mountain lakes and streams.
Distribution	Tasmania and southern Australia.

The restricted distribution (Tasmania and Australia) of Recent species makes it probable that no more than demonstration materials of anaspidaceans will be available for study. However, this is a generally basic group of higher crustaceans and its morphological patterns will provide a basis for subsequent modifications. The discussion and instructions for study are based on specimens of *Anaspides tasmaniae* Thomson; but major differences between this species and others in the order will be pointed out.

Observe the whole animal from both dorsal and ventral aspects (see Figure 25). Dorsally, the cephalon is produced into a broad, ventrally deflected rostrum; it may be considerably reduced in other taxa. A pair of prominent stalked eyes project from beneath the rostrum; in *A. tasmaniae* they are directed almost laterally, but in other taxa more anteriorly. Anaspidids all have stalked eyes, but the eyes in the koonugids are sessile; *Micraspides* is blind. A small tubercle, commonly found in mysids, has been reported on the eyestalk of *Allanaspides*. The antennular peduncles are very broad and the flagella biramous. A slitlike opening of the statocyst may be observed on the 1st peduncular segment. The antennal flagellum is moderately long; the exopod is developed as a scaphocerite in the Anaspididae but is absent in the Koonugidae. The cephalon and 1st thoracic somite are fused, but a mandibular or cervical groove or sulcus is very prominent in *Anaspides* and *Allanaspides*. It is less pronounced in *Paranaspides* and virtually obscured in *Koonuga*. In the midline, anterior to this groove, a small pigmented area can be observed. It is frequently referred to as a "4-celled sense organ"; its function is unknown. Some carcinologists have suggested that it might be similar to or homologous with the dorsal organ of some nonmalacostracans. The thorax consists of 7 somites (2–8), each with a pair of thoracopods. The first 5 pairs (thoracopods 2–6) are biramous and usually have a pair of epipods developed. The exopod of thoracopod 7 is reduced or absent in the Anaspididae and absent in the Koonugidae; 1 or 2 epipods are present. The last pair of thoracopods are uniramous and without epipods in all taxa.

The 6 somites of the abdomen are very well developed; the telson usually is spatulate. Five pairs of biramous pleopods are present in the Anaspididae, but endopods are lacking in the Koonugidae, except for the first 2 pairs in males. The first 2 pairs of pleopods are modified for reproductive purposes in all males. The biramous uropods are spatulate in *Anaspides*, and together with the telson form a tailfan. In other taxa the uropods may be styliiform or reduced but are always biramous.

Examine the ventral aspects of the whole animal before making a detailed study of the appendages and mouthparts. In males the vas deferens open through a pair of oblique slits on the sternite of the 8th thoracomere in *Anaspides* or through a single opening in *Al-*

lanaspides. In addition to paired gonopores that open on the medial faces of the coxae of the 6th thoracopods, females have the anterior margin of the 8th thoracic sternite produced to form a sperm receptacle or spermatheca. In females particularly, the coxal segments of the thoracopods have setose medial lobes projecting in toward the midline.

Examine a thoracopod from one of the anterior pairs and compare its structure with that of the 7th and 8th. Typically, each thoracopod consists of a 2-segmented protopod, an exopod and endopod. A pair of epipods arise laterally from the coxa. The endopod, in contrast to most malacostracans, is 6-segmented; that is, preischium, ischium, merus, carpus, propodus, and dactyl. Basis-preischium fusion is progressive in the thoracopods of *Allanaspides*. The exopod consists of a basal stipe and an annulated terminal segment. What differences from this typical pattern do you find in the last 2 pairs of thoracopods? Examine the first 2 pleopodal endopods of the male. In *A. tasmaniae* the remaining 3 pairs in males and all 5 pairs in females have reduced, 1-segmented endopods. Endopods are lacking, except for the modified first 2 pairs in males, in *Allanaspides*.

Examine slide preparations of the mouthparts. The mandible is large, with well-developed incisor and molar processes; the mandibular palp has 3 segments. The maxillule has 2 endites and a small lobe that may be a vestige of either the endopod or exopod. The maxilla has 2 small endites and 1 that is large and bilobed. The maxilliped is not appreciably modified from a typical thoracopod, except for 2 articulated endites (gnathobases) on the coxa. These structures are absent in *Koonuga*, but the maxilliped is distinguishable by its much stouter appearance.

From a carefully dissected specimen, in sagittal view it will be possible to examine the major organ systems (see Figure 26). Dorsally the heart, which lies in close proximity to the very thin exoskeleton, extends from the 1st thoracic to the 4th abdominal somite. A single pair of ostia is present at the level of the 3rd thoracomere. Anterior from the heart, the prominent anterior aorta extends into the cephalon. Also arising anteriorly from the heart is the 1st of 7 pairs of lateral arteries. Almost immediately each lateral artery gives off a branch to the viscera, the remaining branch continuing to supply blood to the appendages. The 2nd pair of lateral arteries arises at the level of the 8th thoracomere. The lateral branch of only one of the pair is well developed, the descending aorta, which supplies blood to the thoracopods via the supraneural artery. The 3rd pair of lateral arteries provides blood to the body tissues, while the remaining 4 pairs provide blood to the pleopods and uropods.

The digestive system consists of an esophagus, stomach, midgut, hindgut, and ceca. The stomach is divided into cardiac and pyloric parts; a pars ampullaris at

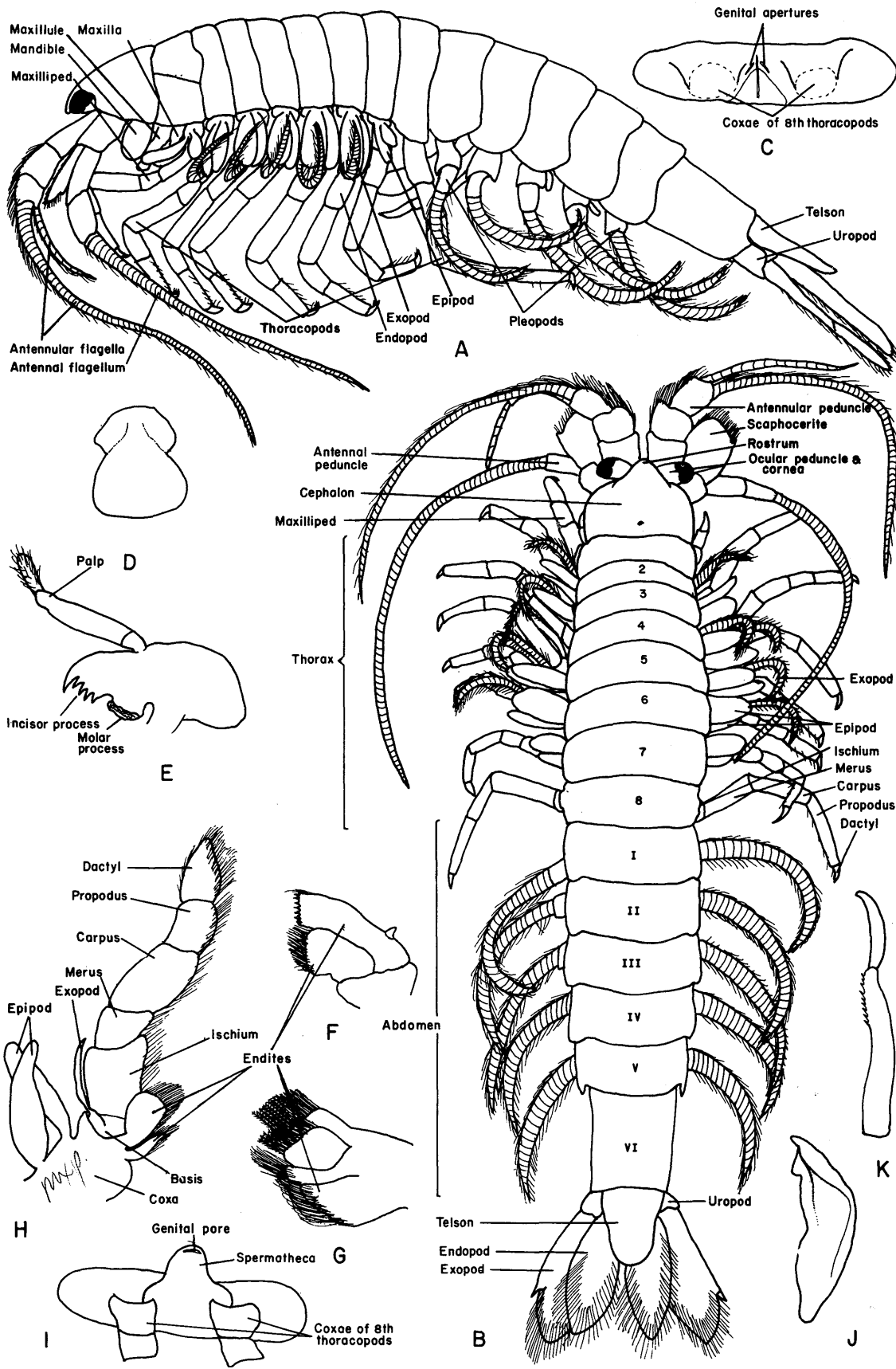


Figure 25 Anaspidacea: A. Whole animal (lateral view); B. Whole animal (dorsal view); C. 8th sternite of male; D. Labrum; E. Mandible; F. Maxillule; G. Maxilla; H. Maxilliped; I. 8th sternite of female; J. Endopod of 1st male pleopod; K. Endopod of 2nd male pleopod.

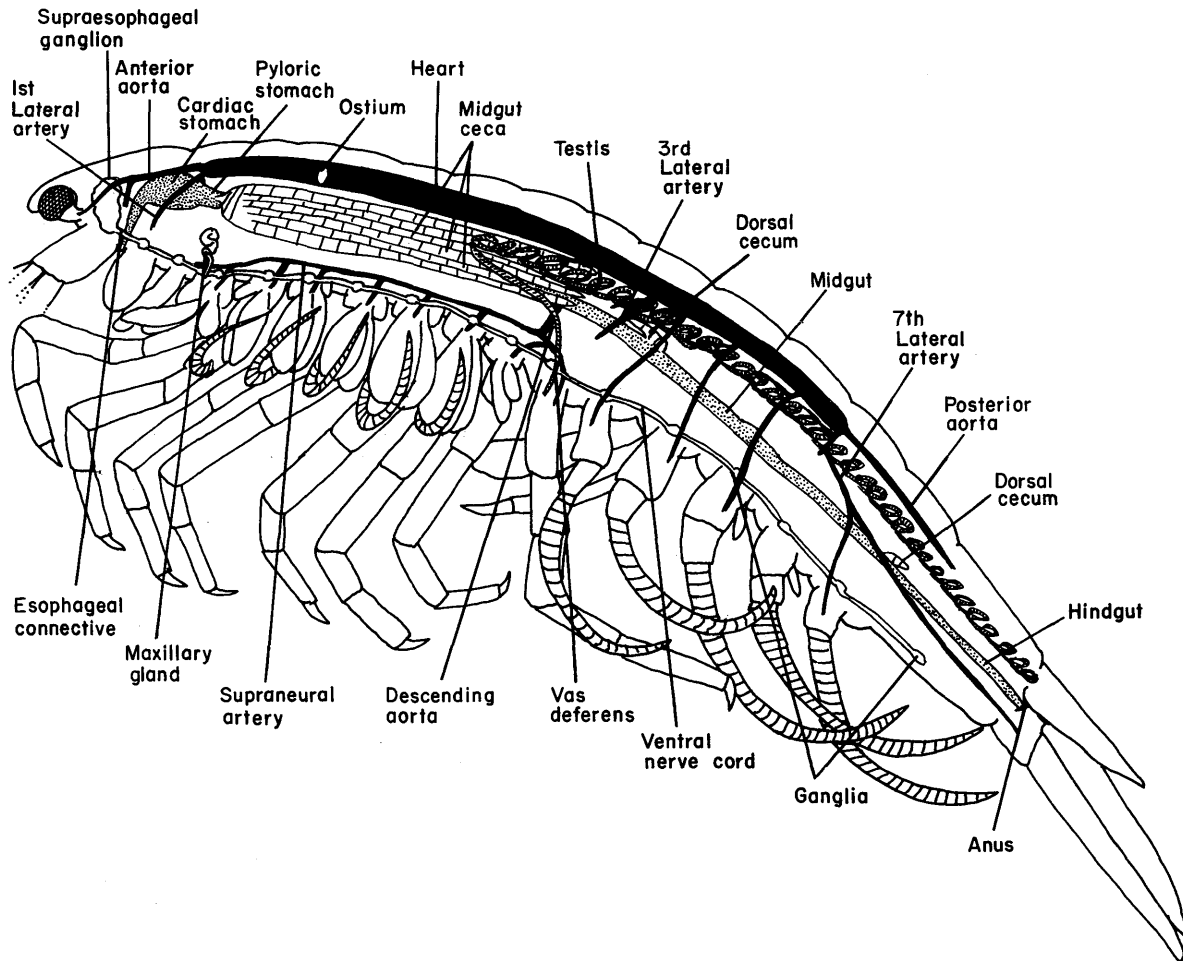


Figure 26 Anaspidacea: Diagrammatic *Anaspides* with musculature removed to show major organ systems.

the entrance of the ceca is homologous with that of stomatopods. In *Anaspides* the numerous ceca are thin tubules extending the length of the thorax. At the level of the 1st abdominal somite a short, anteriorly directed dorsal cecum arises from the midgut, and a second dorsal cecum often is present at the level of the 5th somite. A change in the muscular wall of the gut at the level of the 6th somite suggests the beginning of the hindgut. The anus opens at the base of the telson. Excretion is by means of a maxillary gland, the tubules of which are easily recognized.

The large supraesophageal ganglion is located anterodorsally in the cephalon and the prominent optic, antennular, and antennal nerves and the esophageal connectives leading from it can be distinguished without difficulty. In contrast to other malacostracans, no subesophageal ganglion is present; the ganglia of the mouthparts all are distinct. The ventral nerve cord, lying directly beneath the supraneural artery in the thorax, consists, in *A. tasmanica*, of a broad band of parallel fibers with ganglia in each somite.

The reproductive system in the male consists of paired, thin coiled testes that extend from the 5th thoracic somite to the telson. Anteriorly from the testes paired vas deferens lead to the gonopores on the 8th thoracic sternite. In *Allanaspides* the vas deferens unite before opening into the median gonopore. In the female the ovaries are a pair of broad tubular structures that lie on either side of the midgut. Although typically extending from the 6th thoracic to the 6th abdominal somite, they often extend anteriorly to the region of the 2nd thoracomere. A pair of oviducts lead from the ovaries to the gonopores on the coxae of the 6th thoracopods. The sternite of the 8th thoracomere is produced anteriorly to form a spermatheca.

Development in anaspidaceans is epimorphic, with the young hatching with the full complement of body somites and appearing quite similar to the adult. At the time of hatching, young *Anaspides* have sessile eyes, a vestigial nauplius eye, and a deeply cleft telson; the endopods of the pleopods have not developed. The complete adult form is attained in successive molts.

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ORDER STYGOCARIDACEA Noodt, 1964

Recent species	Five in two genera, <i>Stygocaris</i> and <i>Parastygocaris</i> .
Size range	2.0–4.2 mm.
Carapace	Absent.
Eyes	Absent.
Antennules	Biramous; with statocyst.
Antennae	Uniramous; nephropore absent.
Mandibles	Without palp; dentate setae (penicillae) present; incisor and molar processes well developed.
Maxillulae	With 2 endites.
Maxillae	With 4 enditic lobes.
Maxillipeds	One pair.
Thoracic appendages	Seven thoracopods, 2–8; 2–6 with or without exopods; 7 and 8 uniramous; 2–7 with 2 epipods.
Abdominal appendages	Pleopods usually absent; 1st and 2nd pairs present in males, forming petasma. Uropods biramous.
Telson	With rudimentary caudal furca.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5 + 1 thoracic (maxilliped); thorax with 7; abdomen with 6, excluding telson.

Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female also with spermatheca between bases of 8th thoracopods; male with petasma; head, antennules, and antennae sometimes exhibiting sexual dimorphism.
Sexes	Separate.
Larval development	(?) Anamorphic.
Fossil record	Permian to Recent.
Feeding types	Probably grazers on sand grains.
Habitat	Interstitial in fresh water.
Distribution	South America and New Zealand.

The Stygocaridacea is a very small order, with only four described species in a single family, all from interstitial habitats. It is probable that material will not be available for detailed study of this group; thus description and illustrations will be used to explain the general morphology of the order (see Figure 27).

The body is elongate and vermiform, with little distinction between thoracic and abdominal somites, except in the appendages. A carapace and eyes are lacking. The rostrum is a thin, platelike structure either quadrate or strap-shaped, occasionally deeply cleft. The cephalon is fused with the 1st thoracic somite. The cephalic appendages include the biramous antennules, each with a well-developed statocyst on the 1st segment, the uniramous antennae, mouthparts, and 1 pair of maxillipeds. There are 7 pairs of thoracopods. Exopods are present on thoracopods 2 to 6 in species of *Parastygocaris* but are absent in *Stygocaris*. A pair of epipods is present on each thoracopod except the last pair in all species.

Abdominal appendages are absent except for the modified first 2 pairs in males. These appendages form a petasma, which is distinctly structured in each species. The uropods have a basal protopod, a 1-segmented endopod, and usually a 2-segmented exopod. Remnants of a caudal furca are present as small setose protuberances from the terminal margin of the telson. [Bowman (1971) interprets these protuberances as lobes of a slightly incised telson.]

The mandible has a well-developed incisor process with a toothlike structure directly beneath it. One or 2 penicillae usually are present between these structures

and the prominent molar process. The maxillule consists of a pair of endites; the maxilla has 4 enditic lobes. The maxilliped is provided with a setose endite and a 7-segmented endopod.

The larval development of stygocaridaceans is not known, but is assumed to be similar to that of the bathynellaceans.

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ORDER BATHYNELLACEA Chappuis, 1915

Recent species	Approximately 69 in three families: Bathynellidae, Parabathynellidae, and Leptobathynellidae.
Size range	0.5–5.4 mm.
Carapace	Absent.

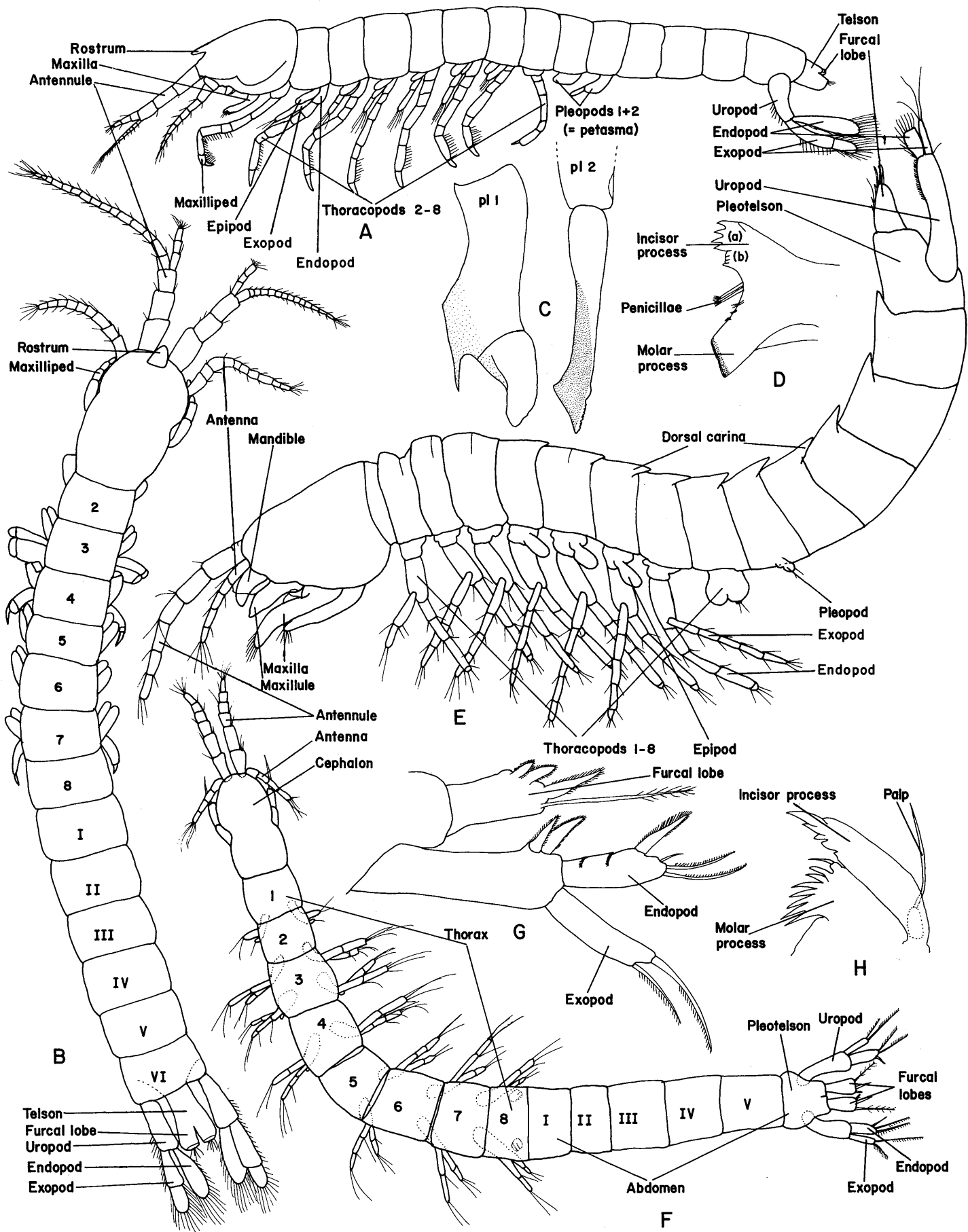


Figure 27 Stygocaridacea, Bathynellacea: A—D, Stygocaridacea; E—H, Bathynellacea. A. *Stygocaris* (lateral view) [after Kaestner, 1970]; B. *Parastygocaris* (dorsal view) [after Brooks, 1969, from *Treatise on Invertebrate Paleontology*, courtesy of the Geological Society of America and University of Kansas]; C. Petasma of *Stygocaris gomezmillasi* Noodt [after Noodt, 1970]; D. Mandible of *Parastygocaris andina* Noodt [after Gordon, 1964]; E. *Allobathynella* (lateral view) [after Ueno, 1961]; F. *Leptobathynella* (dorsal view) [after Noodt, 1972]; G. Left uropod and furcal lobe of telson [after Noodt, 1972]; H. Mandible of *Parabathynella fagei* Delamare Deboutteville and Chappuis [after Gordon, 1964].

Eyes	Absent.
Antennules	Uniramous; without statocyst.
Antennae	Uni- or biramous; nephropore absent.
Mandibles	With palp; incisor and molar processes well developed.
Maxillulae	With 2 basal endites.
Maxillae	With 2 or 3 endites.
Maxillipeds	None.
Thoracic appendages	Usually 7 biramous thoracopods, 1–7; 8th reduced or vestigial, occasionally absent; 1 or 2 epipods frequently present on thoracopods 1–7.
Abdominal appendages	Usually 1st or 1st and 2nd pairs of pleopods; occasionally absent. Uropods biramous.
Telson	Fused with 6th abdominal somite (pleotelson); with furcal lobes.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5; thorax with 8; abdomen with 5, excluding pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th thoracopod of male; 8th thoracopods sexually dimorphic.
Sexes	Separate.
Larval development	Anamorphic.
Fossil record	Recent.
Feeding types	Detritus feeders.
Habitat	Interstitial in fresh water.
Distribution	Africa, Madagascar, southwestern Asia, Japan, New Zealand, South America, United States, and Europe.

Like the rather closely related stygocaridaceans, species of Bathynellacea are very small interstitial crustaceans. They are, however, somewhat better known than the former order, with some 69 species within the three families. The typically small size and the relative paucity of specimens in teaching collections make it necessary to study this group from demonstration materials. If these are not available, at least familiarize yourself with the general morphology from Figure 27 and the discussion.

As in other syncarids, the carapace is lacking. The eyes also are absent, as is a rostral plate. The cephalon is not fused with the first thoracic somite; however, the number of body somites is the same as in the stygocaridaceans as a result of the fusion of the 6th abdominal somite with the telson to form a pleotelson. [Bowman (1971) interprets the abdominal segmentation as

6 unfused somites, with the terminal lobes representing a divided telson rather than caudal rami.]

The cephalon generally is more elongate than any of the individual body somites. The antennules are uniramous; the antennae have a small exopod in the Bathynellidae, a rudimentary exopod in the Leptobathynellidae, and lack an exopod in the Parabathynellidae. The 1st thoracopod is not modified as a maxilliped.

Eight pairs of thoracopods often are present; however, this number sometimes is reduced to 7 and occasionally to 6. The 8th pair, when present, is markedly smaller and usually modified as gonopods in males. Typically both endopods and exopods are present and most thoracopods also carry epipods, which may be reduced in size. Pleopods may be absent, or present only on the 1st or the 1st and 2nd abdominal somites. The pleotelson has a

pair of biramous uropods and a pair of setose or spinose caudal lobes (caudal rami).

The mandible is well developed, with an incisor process, molar process, and 1- to 3-segmented mandibular palp that frequently is prehensile. The maxillule typically has a pair of endites, and the maxilla 2 or 3 endites. Paragnaths often also are present.

A newly hatched bathynellid has antennules, antennae, mouthparts, and 1st thoracopods, but only 10 body somites. Following the first molt 11 somites are present in addition to the 2nd thoracopods and limb buds of the 3rd and 4th thoracic and 1st abdominal appendages. Usually 6 juvenile substages occur, and one or two additional molts are required for the animal to reach sexual maturity.

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Superorder PERACARIDA Calman, 1904

General characters of the Peracarida include a carapace that is never fused to all the thoracomeres (the carapace in isopods and amphipods secondarily has been lost); an antenna typically with a 3-segmented protopod; and a mandible usually with a lacinia mobilis. At least the 1st pair of thoracopods is modified as a pair of maxillipeds; the pleopods lack an appendix interna; and females have a brood pouch usually formed by medial lamellar out-

growths of the coxae of some of the thoracopods.

Seven orders are included in the Peracarida: Mysidacea, Thermosbaenacea, Spelaeogriphacea, Cumacea, Tanaidacea, Isopoda, and Amphipoda. Of these, the suborders of the Isopoda and Amphipoda are sufficiently distinctive and important that they each warrant specific consideration. Therefore, diagnoses of these taxa are presented as diagnoses of the individual suborders.

ORDER MYSIDACEA Boas, 1883

Recent species	Approximately 450.
Size range	10–350 mm.
Carapace	Well developed; covering head and most of thorax; fused with first 3, rarely also 4th, thoracic somites.
Eyes	Stalked, compound.
Antennules	Biramous.
Antennae	Biramous; exopod scalelike.
Mandibles	With well-developed palp.
Maxillulae	Usually with pair of endites and 1 exite; occasionally also with endopod.
Maxillae	With endopod, endites; usually also with exopod.
Maxillipeds	One or 2 pairs.
Thoracic appendages	Usually 6 or 7 pairs; exopods usually present.
Abdominal appendages	Biramous when present, often reduced or absent in females; uropods frequently with statocysts.
Telson	With uropods forming well-developed tailfan.
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 1 or 2 thoracic (maxillipeds); thorax with 6 or 7; abdomen with 6, excluding telson.
Sexual characters	Gonopores on coxae of 6th thoracopods of female, on genital papillae or penes of 8th thoracomere of male; pleopods often absent in females, sometimes modified as gonopods in male; female with oostegites.
Sexes	Separate.
Larval development	Epimorphic; released as miniature adults.
Fossil record	Mississippian to Recent.
Feeding types	Filter feeders or predators.
Habitat	Primarily marine, some brackish and freshwater species; pelagic, epibenthic, or sometimes benthic.
Distribution	Worldwide.

The Mysidacea include two suborders, the Lophogastrida and the Mysida. The Lophogastrida is considered the more primitive suborder; its representatives gen-

erally inhabit deep water and may attain a large size. The description of lophogastrid mysidaceans has been based primarily on characters exhibited by the genera

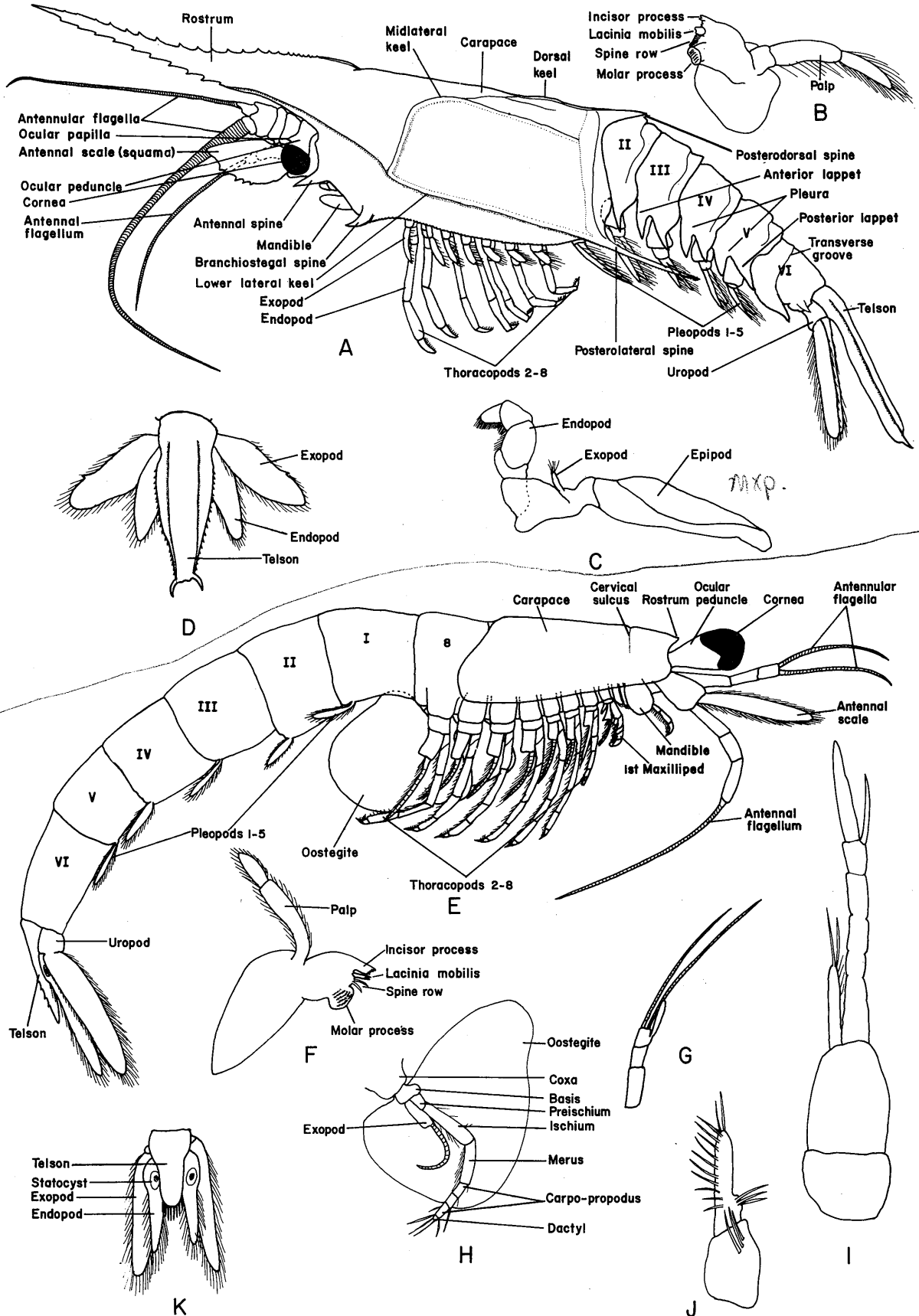


Figure 28 Mysidacea: A–D, Lophogastrida; E–K, Mysida. A. Whole animal (lateral view); B. Mandible; C. Maxilliped; D. Telson and uropods; E. Whole animal (lateral view); F. Mandible; G. Antennule of male; H. Thoracopod with oostegite; I. 1st pleopod of male; J. 2nd pleopod of male; K. Uropods and telson.

Lophogaster and *Gnathophausia*, as these taxa are more frequently available for study (see Figure 28). The carapace is very well developed, usually ornamented with dorsal and lateral keels and marginal and posteromarginal spines, and is produced anteriorly into a very prominent, elongate rostrum. At least in some species of *Lophogaster*, the rostrum is often more elongate in adult females than in males and immature specimens. The eyes are usually well developed, even if occasionally of small size. The ocular peduncle, at least in species of *Gnathophausia*, carries a moderately prominent papilla. The antennular peduncle is 3-segmented; in *Lophogaster* the 3rd segment has a scalelike process that often is referred to as an antennular lamella. The antennular flagella are paired; 1 flagellum often is much stronger than the other. The exopod of the antenna is developed into a prominent scale.

In the lophogastrids the 1st thoracopod is modified as a maxilliped, and the 2nd through 8th are well developed. The form of these latter thoracopods is one of the characters used to separate the two families of Lophogastrida. In the Lophogastridae all 7 thoracopods are similar in structure; in the Eucopiidae the 2nd to 4th are short and subchelate, the 5th to 7th are long and subchelate, and the 8th is typical in structure. Gills of 3 or 4 branches are present on the 2nd to 7th thoracopods; when present on the 8th, gills are reduced or rudimentary. Females have oostegites on all 7 pairs of thoracopods.

The abdomen of lophogastrids is well developed and the tergites are laterally produced to form prominent pleura, which, in *Gnathophausia* at least, are subdivided into anterior and posterior lappets. The 6th abdominal somite is transversely grooved, which has led to speculation that this somite primitively may have represented a fusion of the 6th with a 7th somite. Five pairs of biramous pleopods are present in both sexes and usually are not modified in males, although some modifications have been reported in species of *Eucopia*. The uropods and telson are well developed and form a tailfan. The telson frequently carries a pair of terminal spines. No statocysts are present on the endopods of the uropods in lophogastrids.

The mouthparts consist of paired mandibles, maxillulae, and maxillae in addition to the pair of maxillipeds. The left mandible bears a lacinia mobilis between the incisor and molar processes; the right has a fixed cusp in this position. The maxillule has a large, swollen proximal endite with few setae; the distal endite has a row of blunt spines. No palp is present. The maxilla is provided with 2 endites (not subdivided in *Lophogaster*), an exite, and a palp.

If specimens are available for dissection, remove, examine, and illustrate the mouthparts, maxilliped, and 1 thoracopod. Pay particular attention to the structure of the right and left mandibles. Compare the mouthparts

and appendages of the lophogastrids with those of the mysids and the euphausiids, a superficially similar group of planktonic crustaceans at one time classified with the Mysidacea. Differences in internal organ systems will be discussed with the Mysida.

The description and instructions for the study of the suborder Mysida have been based on a composite of species. If you have been able to examine specimens of lophogastrids, the differences in carapace shape and development will be apparent immediately. In typical mysids the carapace is much more weakly developed and does not cover the bases of the thoracopods laterally. A rostrum may be present but is never appreciably elongate. Begin your examination of the external morphology by observing the animal from a dorsal view. The stalked eyes are prominent but there is no movable acron or ophthalmic somite such as was observed in the stomatopods. In the anterior portion of the carapace locate the transverse cervical sulcus. It is possible that this groove may be homologous with the cervical groove of anaspidaceans. Frequently not all of the thoracic somites are covered by the carapace; lift the posterior margin of the carapace and see if you can determine the number of thoracic somites to which it is fused. Even in preserved specimens numerous chromatophores usually can be observed, and these serve as an aid in the recognition of many mysids. In lateral view, observe the antennules, antennae, and appendages. The flagella of the antennule frequently are relatively short and of equal strength; the 3rd peduncular segment may have an accessory lobe in males. The exopod of the antenna is produced into a prominent scale, which may be diagnostic both in its shape and in its segmentation. The lateral part of the mandible frequently can be recognized without dissection. The 1st or in some cases the 1st and 2nd thoracopods are modified as maxillipeds. Thoracopods 3 to 8 may vary among themselves depending upon the taxa under study. After you have completed your general examination of the specimen, remove several thoracopods and identify the components. As in anaspidaceans, the endopod will consist of 6 segments, a preischium being present in addition to the typical components. In some taxa the carpus and propodus may be fused and may be multiarticulate in addition, the number of carpopropodal articles varying from 1 to 8. Exopods may be present or absent; epipods are present on the 1st thoracopod only. In females, 2 or 3 posterior thoracopods have oostegites developed.

The abdominal tergites of typical mysids are not laterally produced to form pleura. Pleopods generally are reduced or absent in females; in males they sometimes are normally developed, biramous, highly modified, or by a combination of conditions. Depending upon the taxon, the 1st, 2nd, 3rd, and 5th may be well developed or reduced; usually the 4th is modified, presumably for

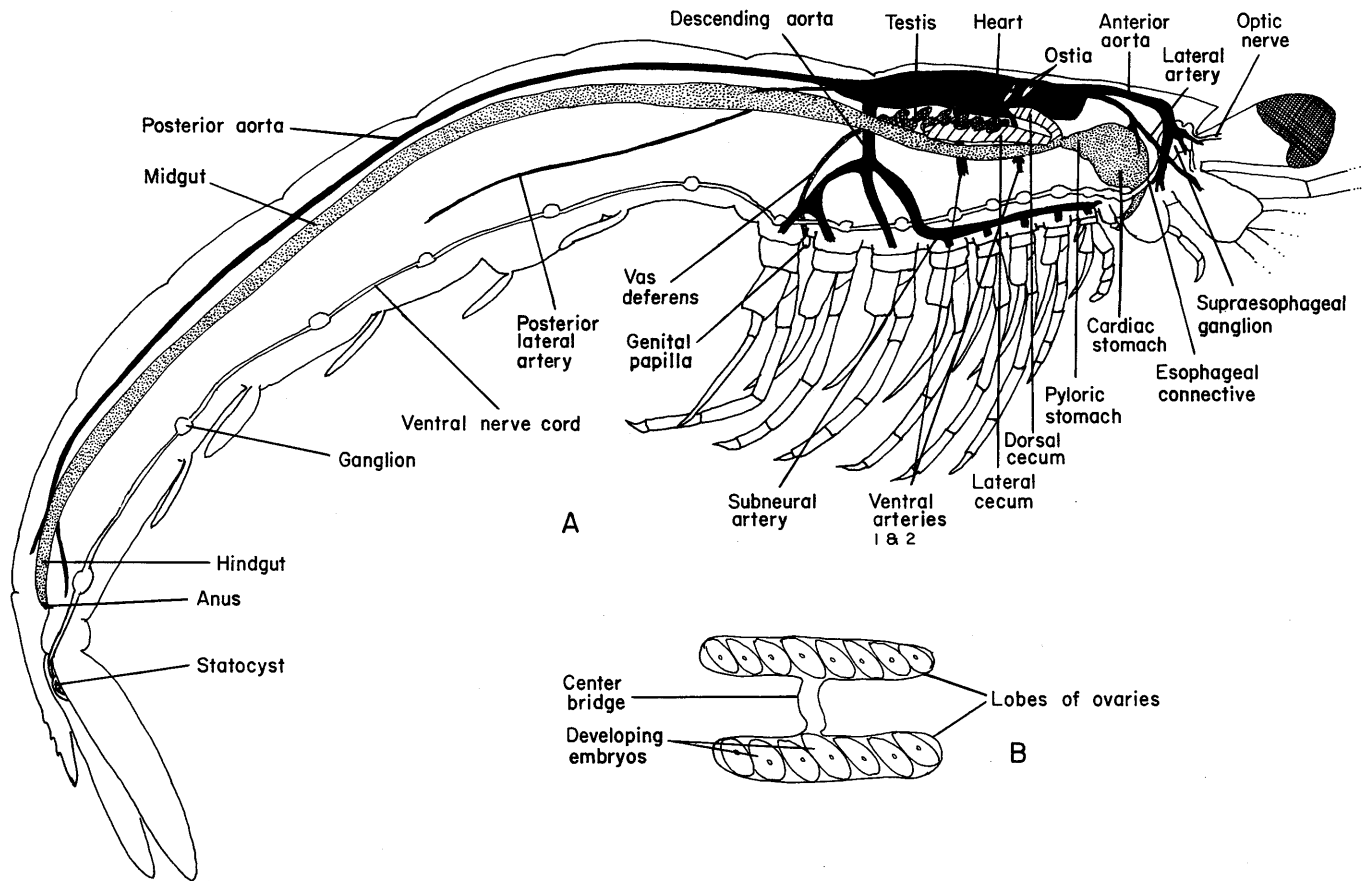


Figure 29 Mysidacea: A. Diagrammatic mysid with musculature removed to show major organ systems. B. Diagrammatic mysid ovaries.

copulation. The uropods have a prominent statocyst on each endopod. The telson is well developed, and with the uropods forms a tailfan.

Remove and examine the mouthparts. A mandibular palp is well developed. How do the mandibles compare with those of the Lophogastrida? The maxillule consists usually of 2 endites. The maxilla has an exopod, 2-segmented endopod, and paired endites, the distal one bilobed. Identify the epipod of the maxilliped. Compare the maxilliped with one of the anterior thoracopods and determine the feeding adaptations of this appendage.

The major internal organ systems of mysidaceans exhibit marked differences between the two suborders, particularly the circulatory system. The description is based on the condition found in mysids, but differences in lophogastrids will be pointed out (see Figure 29). Begin your study by teasing the carapace free of the anterior thoracic somites. With fine scissors or a microscalpel cut the integument of the abdomen and carefully remove the exoskeleton from one side. The mysid body is quite muscular, particularly in the abdominal region; this musculature must be removed from one side to expose the organs.

Dorsally in the cephalothorax locate the heart. It is moderately elongate, but rarely extending beyond the cephalothorax. In mysids 2 pair of ostia are present at the level of the 4th and 3rd thoracomeres; in lophogastrids a 3rd pair is present at the level of the 2nd thoracomere. Anteriorly a pair of lateral cephalic arteries and the unpaired anterior aorta lead from the heart and provide blood to the cephalic appendages, nervous system, and stomach. In mysids 3 unpaired ventral arteries arise from the heart medially. The first 2 provide blood to the gut sinus; the 3rd, the large descending aorta, divides into 3 branches. The 1st branch continues anteriorly as the subneural artery with branches to the first 5 pairs of thoracopods. The 2nd branch provides blood to the 6th thoracopods, and the 3rd branch supplies the 7th and 8th thoracopods. In lophogastrids 9 pairs of lateral arteries are present. The 1st pair are the lateral cephalic arteries also present in mysids; the 8th pair constitute the descending aorta (right branch) that contributes to the gut sinus and the subneural artery (left branch) that supplies blood to all the thoracopods. The 9th pair are the posterior lateral arteries leading posteriorly with the posterior aorta into the abdomen. In mysids these are the

only vessels providing blood to the tissues and appendages; in lophogastrids a pair of lateral branches from the posterior aorta lead to each of the paired pleopods. Blood returns to the heart via sinuses.

The digestive system consists of an esophagus, stomach, midgut, hindgut, and a variable number of ceca. The stomach is divided into an enlarged cardiac and smaller pyloric part. At the junction of the pyloric stomach and midgut frequently an unpaired dorsal cecum is present; 1 to 5 pairs of short to moderately long ceca opening through a pair of common ducts also may be present. The midgut is elongate; the cuticularized hindgut quite short, terminating in an anus on the ventral surface of the telson. The excretory organ in mysids is the antennal gland; in lophogastrids both antennal and maxillary glands are present.

The nervous system exhibits some variation among different taxa. The supraesophageal ganglion always is well developed; a subesophageal ganglion is present in lophogastrids, but apparently not in mysids. The ventral nerve cord in *Mysis* consists of a coalesced ribbon of ganglia and connectives extending the length of the cephalothorax; in *Boreomysis* individual pairs of cephalothoracic ganglia can be distinguished. Six pairs of abdominal ganglia always are present. In mysids the statocysts on the endopods of the uropods are innervated from the ventral nerve cord.

The female reproductive system in mysids differs from that of lophogastrids in that the ovaries in the former are connected by a narrow to moderately well-developed bridge. Each ovary is a moderately short tubule; posteriorly an oviduct leads to a gonopore on the coxa of the 6th thoracopod. The testes are paired coiled structures located in the cephalothorax that are easily identified by their pyriform follicles. A pair of vas deferens leads to genital papillae on the sternite of the 8th thoracomere. Oostegites form a brood pouch in females.

Larval development in the Mysidacea is epimorphic. Embryos hatch in the brood pouch of the female and remain there until all appendages have developed. The young, when released, resemble miniature adults.

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ORDER THERMOSBAENACEA Monod, 1927

Recent species	Eight in four genera: <i>Monodella</i> , <i>Thermosbaena</i> , <i>Halosbaena</i> , and <i>Limnosbaena</i> .
Size range	1.5–4.0 mm.
Carapace	Present; short, fused to 1st thoracic somite and covering adjacent 2 or occasionally 3 somites; dorsally enlarged to form brood pouch in females.
Eyes	Greatly reduced or absent; sometimes discernible only in sections.
Antennules	Biramous; sometimes with aesthetascs.
Antennae	Uniramous; flagella with few articles.
Mandibles	With palp; molar and incisor processes; lacinia mobilis well developed.
Maxillulae	With 2 endites and palp.
Maxillae	With 3 endites, palp, and rudimentary lobe possibly representing exopod.
Maxillipeds	One pair; uni- or biramous; sometimes sexually dimorphic.
Thoracic appendages	Biramous; 5–7 pairs; epipods absent.
Abdominal appendages	Two anterior pairs of uniramous pleopods; uropods biramous.
Telson	Well developed; freely articulated or fused with ultimate abdominal somite (pleotelson).
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5 + 1 thoracic (maxilliped); thorax with 7; abdomen with 6, excluding telson, or 5, excluding pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with dorsal brood pouch, without oostegites; male with paired penes. Maxilliped sometimes sexually dimorphic.
Sexes	Separate.
Larval development	Epimorphic; manca stage; when released sometimes without 6th and 7th thoracopods.
Fossil record	Recent.

Feeding types	Plant detritus feeders (although mandibles have biting capabilities).
Habitat	Thermal springs, fresh and brackish subterranean lakes, and brackish coastal interstitial areas.
Distribution	Southern Italy, Dead Sea, Tunisia, West Indies, and Hays County, Texas.

The Thermosbaenacea is a small order from a generally restricted habitat. Representatives of this order were known only from brackish waters with temperatures in excess of 30°C until a species from fresh cool water recently was described from Texas.

The small size, as well as the lack of reference specimens, restricts the classroom study of this very interesting group. Examine demonstration slides if available or, if not, study the general morphological characters of the order from the illustration in Figure 30. The two families have some major differences that will be pointed out.

The carapace, which is fused with the 1st thoracic somite, covers the cephalon and in some taxa several thoracic somites; in females it is expanded to provide a dorsal brood pouch. Eyes usually are absent or can be distinguished only in serial sections. The antennules are well developed, biramous appendages; the antennae are uniramous and considerably smaller. The 1st pair of thoracopods are modified as maxillipeds.

In the Monodellidae thoracopods 2–8 are well developed biramous appendages; the first 4 pairs are much shorter than the last 3. In the Thermosbaenidae only thoracopods 2–6 are present; they also are biramous but are relatively small and generally equal in length. The endopods have been interpreted as frequently having a fused or partially fused basis-ischium in the maxilliped and a fused ischium-merus in some thoracopods. Often the dactyl terminates in an elongate claw referred to as an unguis.

Six abdominal somites and a telson are present in the Monodellidae; 5 abdominal somites and a pleotelson occur in the Thermosbaenidae. In both families the uropods each consist of a protopod, a 1-segmented endopod, and a 2-segmented exopod; the uropods of the monodellids usually are much larger.

Of the mouthparts the mandible perhaps is the most structurally complex. It consists of a well-developed molar process bearing a series of fine guide setules at the anterior angle. The incisor process and lacinia mobilis are borne on a keel-like projection. The relatively broad space separating these structures from the molar process is occupied by a row of "lifting spines," also referred to in certain other taxa as a setal row. A very well-developed mandibular palp also is present. The maxillule consists of 2 endites and a palp; the maxilla has 3 endites, a palp, and a rudimentary structure considered by some investigators to represent the exopod.

The pair of 1st maxillipeds are sexually dimorphic in some species. In these the maxillipeds each consist of 2 endites, an exopodal palp, and an epipod in the female; the male endopod is a 5-segmented prehensile structure presumably functioning as a clasping structure.

Larval development has been observed in *Thermosbaena* and *Monodella*. In the former, the young hatch as miniature adults; in the latter, hatching occurs at the manca stage and the young pass through a postmarsupial stage during which the 6th and 7th thoracopods and the pleopods develop.

The thermosbaenaceans have been related, by various carcinologists, to the Hoplocarida, Syncarida, and Peracarida. What similarities and differences do you find among these orders and to which, if any, would you relate the Thermosbaenacea?

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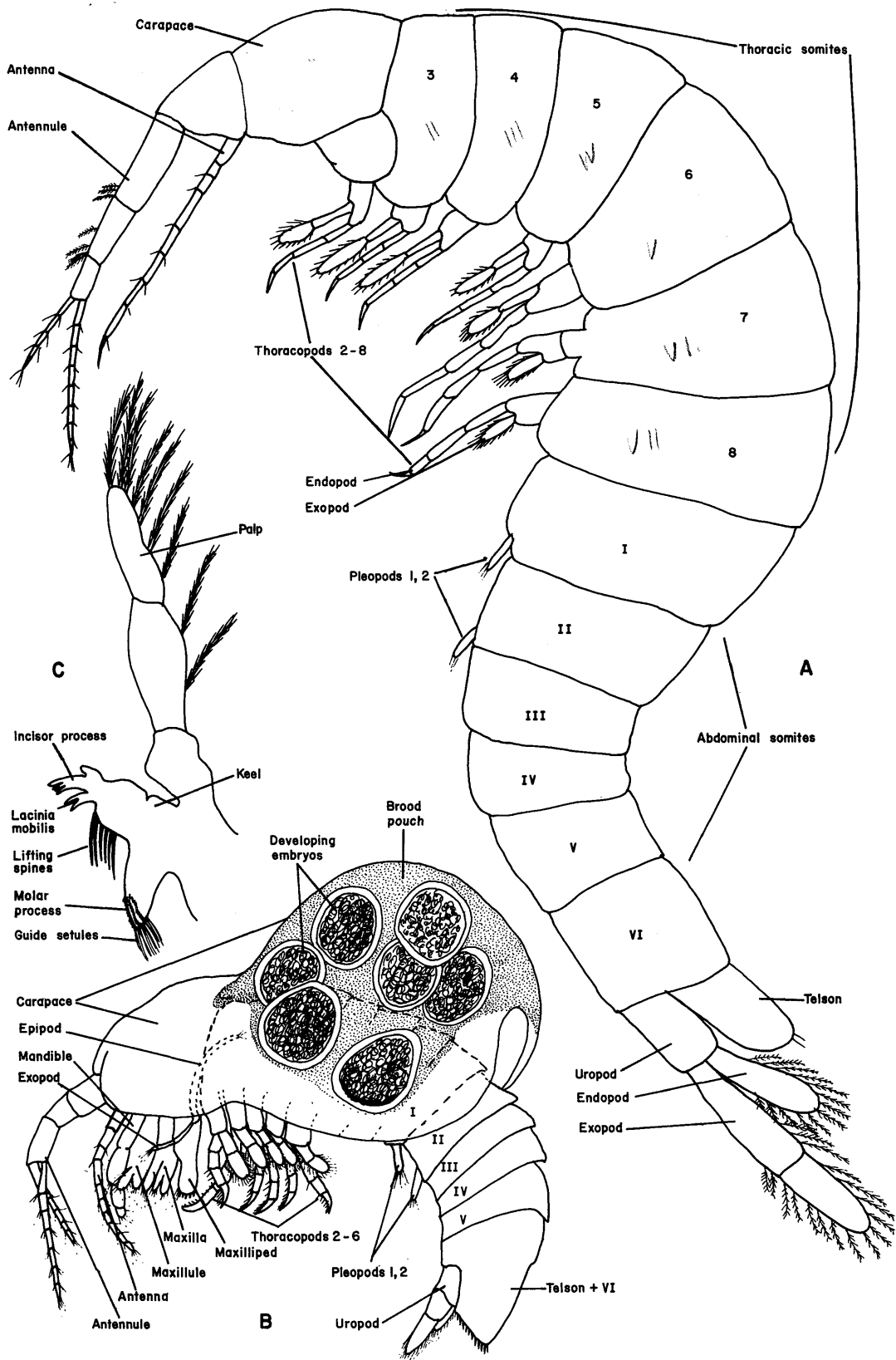


Figure 30 Thermosbaenacea: A. *Monodella* (lateral view) [after C. Delamare Deboutteville: *Biologie des eaux souterraines littorales et continentales* (Hermann, Paris, 1960)]; B. *Thermosbaena*, ovigerous female (lateral view) [after Barker, 1962]; C. Mandible of *Monodella relicta* Por [after Por, 1962].

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ORDER SPELAEGRIPHACEA Gordon, 1957

Recent species	One.
Size range	7.5–8.6 mm.
Carapace	Present; short; fused dorsally to 1st and covering most of 2nd thoracic somite.
Eyes	Stalked, nonfunctional.
Antennules	Biramous.
Antennae	Biramous; exopod scalelike.
Mandibles	With palp; lacinia mobilis well developed.
Maxillulae	With 2 endites, innermost slightly bilobed.
Maxillae	With 3 endites, 3rd strongly bilobed.
Maxillipeds	One pair.
Thoracic appendages	Seven pairs; anterior 3 pairs with ventilatory exopods; thoracopods 5–7 with gills.
Abdominal appendages	Pleopods 1–4 biramous, well developed; 5th vestigial; uropods biramous, broad.
Telson	Present.
Tagmata	Head, thorax, and abdomen.
Somites	Head with 5 + 1 thoracic (maxilliped); thorax with 7; abdomen with 6, excluding telson.

Sexual characters	Gonopores at bases of 6th thoracopods of female, 8th of male; female with 5 pairs of oostegites on thoracopods 2–6; male with pair of penes on coxae of 8th thoracopods, antennules sexually dimorphic.
Sexes	Separate.
Larval development	(?) Epimorphic.
Fossil record	Mississippian, Recent.
Feeding types	Apparently detritus feeders.
Habitat	Freshwater stream, bottom dwelling, and pelagic.
Distribution	Bats Cave, Table Mountain, South Africa.

As the Spelaeogriphacea is a monotypic order represented by only a single species, known only from the type locality, study material of this group will usually not be available. However, from the description and illustrations provided you should be able to draw some general comparisons between this order and others within the Peracarida (see Figure 31).

The carapace, which is fused with the 1st thoracic somite, is short and laterally expanded to enclose the branchial cavity and effectively conceal the mouthparts. Anteriorly, the carapace is produced into a broadly triangular rostrum. A cervical groove is present, but frequently is indistinct. A pair of ocular lobes is present, although spelaeogriphaceans lack functional eyes. The cephalon bears a pair of rather closely set, short antennules, a pair of more robust antennae with scalelike exopods, and mouthparts, including a pair of maxillipeds.

The 2nd through 8th thoracic somites are free, although the 2nd is partially covered by the carapace. The 7 pairs of thoracic appendages are simple and ambulatory, and are divisible into 2 types. The anterior 3 pairs each bear ventilatory exopods; the exopods of thoracopods 5–7 are reduced and modified as gills, and those of the last pair usually are absent. The 3 anterior pairs usually are more robust in males. Males have a

simple penial process on the coxa of each 8th thoracopod.

The abdomen is elongate, usually exceeding half the total body length; the somites bear pleura that are quite delicate and not easily distinguished, except on the 5th somite. The first 4 pairs of pleopods are well developed and natatory; the 5th pair is reduced and concealed by the epimere of the somite. The uropods are elongate. The telson is short and terminally rounded.

Females have oostegites on the first 5 pairs of thoracopods, and it is assumed that development is epimorphic; however, juvenile stages have not been observed.

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ORDER CUMACEA Kröyer, 1846

Recent species	Approximately 800.
Size range	0.5–4.0 mm.
Carapace	Well developed; covering anterior part of thorax.
Eyes	Sessile, compound, fused, usually dorsomedial; sometimes absent.
Antennules	Uni- or biramous.
Antennae	Uniramous; short in female and juvenile, well developed in mature male.
Mandibles	Without palp; lacinia mobilis well developed.
Maxillulae	With 2 endites and palp.

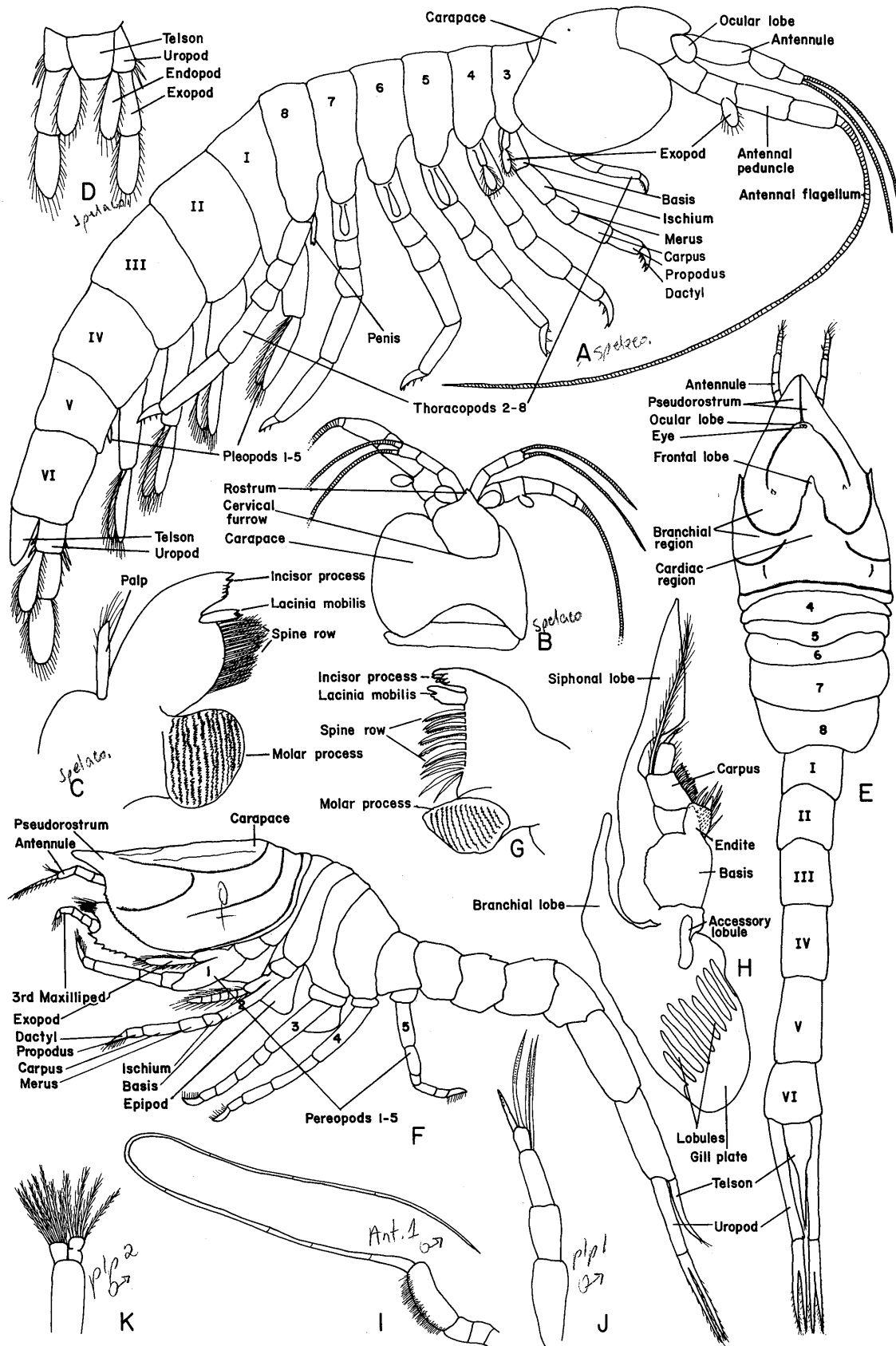


Figure 31 Spelaeogriphacea, Cumacea: A–D, Spelaeogriphacea; E–K, Cumacea. A. *Spelaeogriphus lepidops* Gordon (lateral view) [after Gordon, 1957]; B. Dorsal view of carapace and cephalic appendages [after Kaestner, 1970]; C. Mandible [after Gordon, 1957]; D. Telson and uropods [after Kaestner, 1970]; E. Whole animal (dorsal view); F. Female (lateral view); G. Left mandible; H. 1st maxilliped; I. Antenna of male; J. 1st pleopod of male; K. 2nd pleopod of male.

Maxillae	With pair of endites and lamellar exopod.
Maxillipeds	Three pairs.
Thoracic appendages	Five pairs of pereopods, with or without exopods.
Abdominal appendages	Absent in female; present in varying numbers in male; uropods elongate, biramous, styliform.
Telson	Present; occasionally fused with 6th abdominal somite (pleotelson).
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 3 thoracic (maxillipeds); thorax with 5 [= cephalothorax]; abdomen with 6, excluding telson, or 5, excluding pleotelson.
Sexual characters	Gonopores on coxae of 3rd pereopods of female, on sternite of last thoracic somite (8th) of male; female with oostegites forming marsupium or brood pouch; male with numerous secondary sexual characters.
Sexes	Separate.
Larval development	Epimorphic; manca stage → postlarva.
Fossil record	Permian to Recent.
Feeding types	Grazers on sand grains or filter feeders.
Habitat	Primarily marine, few brackish and freshwater species; burrowers.
Distribution	Worldwide.

The general body shape of cumaceans is characteristic of the order; all members have an inflated cephalothorax and a very slender abdomen with styliform uropods (see Figure 31). The telson frequently is reduced in size or fused with the 6th abdominal somite to form a pleotelson. Pleopods are absent in females but may be present in variable numbers in males. A very specialized character is the development of the anterior carapace. It is produced in 2 prominent plates to form a structure called a pseudorostrum that covers the anterior extension of the branchial cavity. Within the cavity, or channel, the greatly developed exopods of the 1st maxillipeds unite to form a siphon. The antennules usually each have a single flagellum, or in some taxa an inner flagellum may be reduced or vestigial. The antennae exhibit sexual dimorphism; in the female they are very small or vestigial and in the male they are well developed and the flagella may exceed the length of the body.

The last 3 to 5 cephalothoracic somites are not covered by the carapace; however, in the female, the oostegites often appear to be continuations of the carapace. The pereopods usually are similar in structure and generally are considered to be fossorial in function. The 1st pereopods usually are strongly developed; the 2nd pereopods sometimes have a reduced number of segments. Remove the appendages from one side of the body so that the distinctive structure of the carapace and branchial chamber can be observed. The 3 pairs of maxil-

lipeds lie in the midline. Laterally the carapace is fused to the body wall to form a relatively closed branchial chamber. The epipod or branchial lobe of the 1st maxilliped is considerably enlarged and lies in the branchial chamber. Usually it is furnished with respiratory processes or it may only be vascularized. Notice the narrow channel anteriorly that is covered by the pseudorostrum. Observe the development of the exopod of the maxilliped that forms a siphonal structure capable of being extended in front of the head.

The abdomen is elongate and considerably narrower than the cephalothorax. The telson may be free or fused with the 6th abdominal somite to form a pleotelson. [Bowman (1971) considers that certain families (e.g., Nannastacidae, Leuconidae, Bodotriidae) lack telsons rather than having pleotelsons.] Pleopods are absent in all females and occasionally also in males. When present, they vary in number according to taxa. Uropods are present in both sexes and usually are elongate and styliform.

The mouthparts of most cumaceans are small and rather difficult to remove. If sufficient magnification is available, remove and examine not only the maxillipeds but the other mouthparts as well. The 2nd maxilliped lacks an exopod, although the female usually has a small plate bearing a fringe of setae that projects backward into the marsupial chamber; it is thought to aid in keeping the eggs and embryos in motion. The maxilla has a pair of

endites. The endopod of the maxillule is usually retroverted. The mandible lacks a palp, but has a lacinia mobilis and spine or setal row between the incisor and molar processes.

Larval development in cumaceans is epimorphic. After hatching, the young remain in the brood pouch of the female until the manca or postlarval stage is reached. At this stage they resemble the adult cumacean but lack the last pair of pereopods. Secondary sexual characters (e.g., the male antennae, exopods of the pereopods and pleopods, and the female oostegites) develop gradually with successive molts.

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ORDER TANAIDACEA Dana, 1853

- Recent species Approximately 800.
- Size range 5–20 mm.
- Carapace Short; fused dorsally with first 2 thoracic somites.
- Eyes Compound, usually on produced lobe; frequently absent.
- Antennules Uni- or biramous.

Antennae	Uni- or biramous.
Mandibles	With or without palp; lacinia mobilis sometimes only on left mandible.
Maxillulae	With endopod and 1 or 2 endites; occasionally absent.
Maxillae	Developed or vestigial.
Maxillipeds	One pair.
Thoracic appendages	Usually 7 pairs, uni- or biramous; 1st pair often chelate.
Abdominal appendages	Often 5 pairs, biramous; sometimes reduced, both in size and number; occasionally absent; uropods small, slender.
Telson	Present; fused with 6th or occasionally 5th and 6th abdominal somites (pleotelson).
Tagmata	Head, thorax (pereon), and abdomen (pleon).
Somites	Head with 5 + 1 thoracic (maxilliped); thorax with 7; abdomen with 4 or 5, excluding pleotelson.
Sexual characters	Gonopores on coxae of 6th thoracopods of female, on 8th thoracic somite of male; female with oostegites forming marsupium; male with single or pair of genital cones. Chelipeds sexually dimorphic (greatly enlarged in mature males).
Sexes	Separate or hermaphroditic; gonochoristic and protogynous females.
Larval development	Epimorphic; manca stage → postlarva.
Fossil record	(?) Mississippian, Pennsylvanian to Recent.
Feeding types	Usually filter feeders on detritus and plankton; sometimes predators.
Habitat	Primarily marine, occasionally brackish and freshwater; burrowers or tube dwellers, occasionally inhabiting gastropod shells.
Distribution	Worldwide.

The Tanaidacea is an order of small peracaridan crustaceans that until recently was classified with the Isopoda. The extreme degree of sexual dimorphism exhibited among taxa of the Tanaidacea has resulted in considerable taxonomic chaos. The situation is further complicated by the probability that both protandry and protogyny exist in this group. Another source of difficulty in interpreting morphological characters comes from the fact that a series of structurally different stages in both juveniles and adults occur in most species.

The description of the morphology and instructions for the study of tanaidaceans have been based on species of *Pagurapseudes* and *Leptochelia*; however, major differences between these and other representatives of the two suborders Monokonophora and Dikonophora will be pointed out (see Figure 32).

Eyes frequently are lacking; when present they usually are set on small ocular lobes. The carapace covers the cephalon, which is fused with the 1st thoracic somite. The carapace is also fused with the 2nd thoracic somite and is laterally expanded to enclose the branchial

chambers. Both the antennules and antennae may be uni- or biramous; the number of peduncular segments varies among taxa. In the Monokonophora the antennal scale (exopod), when present, is small. The thorax, also referred to as the pereon, contains 7 somites, of which the posterior 6 are free. Disagreement among carcinologists exists as to the numbering of the somites and their accompanying appendages. As previously indicated, in this text the numbering of somites refers to the actual morphological somites; thus in tanaidaceans, the first free somite is the 3rd thoracic somite (the 1st is fused to the cephalon and the 2nd is covered by and fused to the carapace). Traditionally, when a maxilliped is present on the 1st true thoracic somite and the number 1 is assigned to a somite other than the morphological 1st, the pair of appendages associated with the former somite is also assigned the number 1. Some recent carcinologists have changed the designation of thoracic appendages in the tanaidaceans. The chelipeds (appendages of the 2nd thoracic somite) have been referred to simply as the chelipeds and the appendages of the following somite

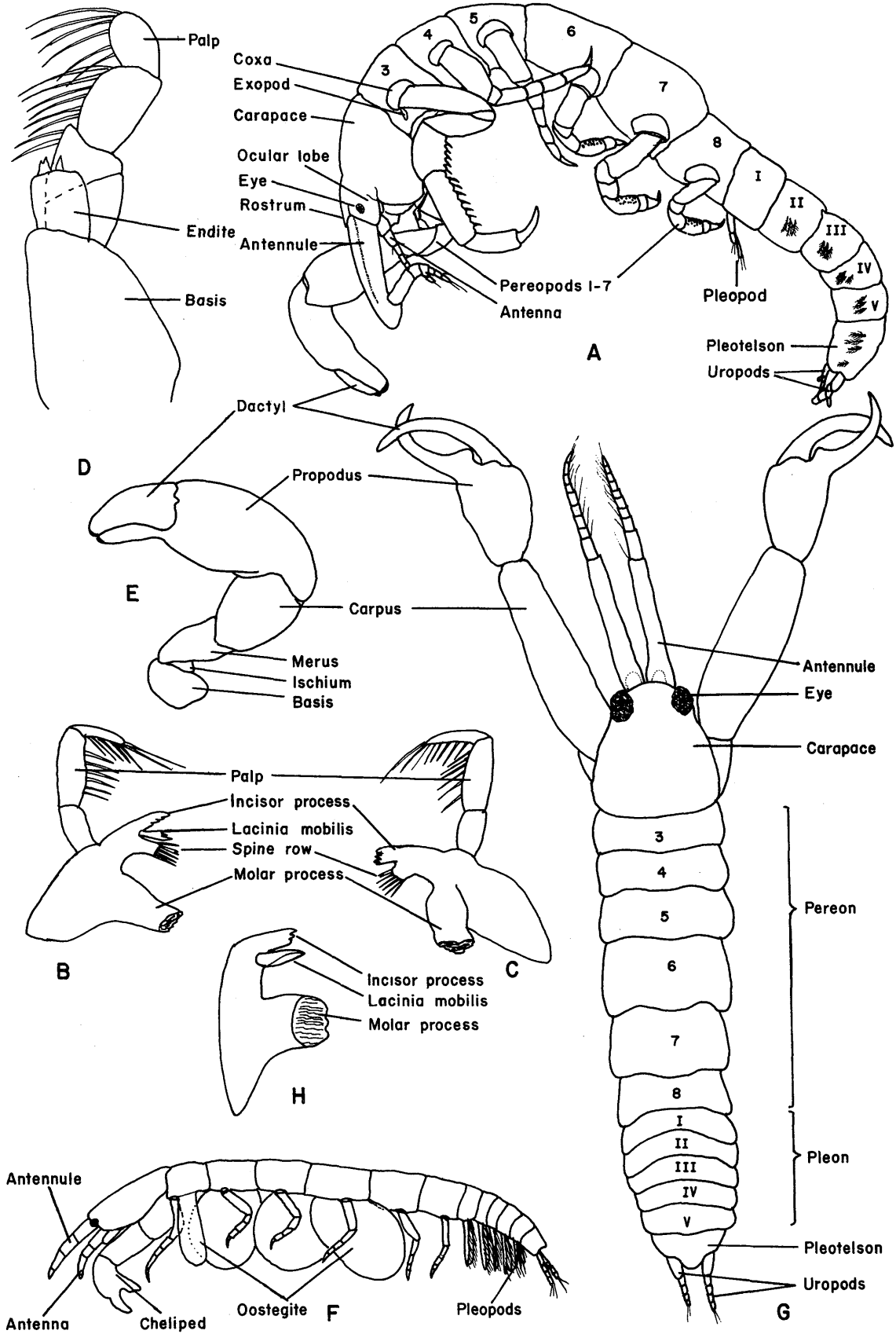


Figure 32 Tanaidacea: A—E, Monokonophora (*Pagurapseudes*); F—H, Dikonophora (*Leptocheilia*). A. Whole animal (lateral view); B. Left mandible; C. Right mandible; D. Maxilliped; E. Right cheliped of male; F. Female (lateral view); G. Mature male (dorsal view); H. Left mandible.

(3rd thoracic somite) as the 1st pereopods. Such a numbering system is not used in this manual. The chelipeds are considered to be the 1st pereopods (2nd thoracopods); and the subsequent pereopods are numbered 2 through 7. The chelipeds are usually moderately well developed in juveniles and females but become massive, and often asymmetrical, in mature males. The 2nd pereopods often are stronger than the succeeding 5 pairs. Exopods are present on the 1st and 2nd pairs of pereopods in the Monokonophora but absent from the posterior pairs; exopods are lacking on all pereopods in the Dikonophora. The 2nd pereopods in the Kalliapseudidae often have sensory structures either on the dactyls or in place of them; the remaining pereopods also often carry sensory structures. Examine the chelipeds, 1 or 2 of the anterior pereopods, and 1 of the posterior pairs of each sex. In species of *Pagurapseudes*, the last 3 pairs are distinctly different from the preceding pairs; each carries a rasp of chitinous scales or spines, similar to the propodal rasps of hermit crabs.

The abdomen usually consists of 4 or 5 slender, usually compressed, somites and a pleotelson (telson + 1 or 2 pleomeres). Biramous pleopods usually are well developed on the 5 pleomeres, but in some taxa, such as *Pagurapseudes* or *Tanais*, the number of pleopods may be reduced to 3 or fewer; occasionally they are completely lacking. The uropods are uni- or biramous, depending upon the taxon.

The mouthparts are variable among the tanaidacean taxa. The labrum usually is a large bulbous structure lying in close proximity to the epistome, which occasionally carries a prominent spine. The mandible is well developed, often with a palp, incisor process, lacinia mobilis, spine row, and molar process. However, the palp is absent in the Dikonophora and not infrequently the lacinia mobilis is present only on the left mandible. Be sure to examine the appendages from both sides of the animal.

Mature females have genital apertures (gonopores) opening on the coxae of the 6th thoracopods (5th pereopods). On the ventral surface of the 8th thoracic somite, a genital cone (Monokonophora) or a pair of cones (Dikonophora) are present in males. Successive stages in the morphological series have been reported for both sexes. In females these include 1 or 2 preparatory stages prior to stages of brood pouch development. Depending upon the taxon, females may develop from 1 to 4 pairs of oostegites, which form the brood pouch.

Larval development is epimorphic. Newly hatched embryos are held in the brood pouch for 1 or 2 weeks, during which time limb development takes place. They are released at the 1st submanca stage lacking only the last thoracic appendages and pleopods. With the molt to the 2nd manca substage these remaining appendages appear and are completely developed with the next molt to the 1st juvenile or neuter stage.

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ORDER ISOPODA Latreille, 1817

The Isopoda includes the suborders Valvifera, Anthuridea, Flabellifera, Microcerberidea, Asellota, Phreatoicoidea, Gnathiidea, Oniscoidea, and Epicaridea; the latter is exclusively parasitic. Although there are major differences among the other eight suborders, their

overall general morphology is sufficiently similar so that they do not need to be discussed separately. The major points of difference are indicated in the tabular review of the characters of the suborders.

Free-Living Isopoda

SUBORDER VALVIFERA Sars, 1882

Recent species	Approximately 600.
Size range	5–30 mm.
Carapace	Absent.
Eyes	Sessile, compound, usually well developed.
Antennules	Uniramous.
Antennae	Uniramous; peduncle with 5 segments; sometimes raptorial.
Mandibles	Usually without palp.
Maxillulae	Usually with 2 endites.
Maxillae	Typically with 3 endites.
Maxillipeds	One pair, usually with reduced number of segments.
Thoracic appendages	Thoracopods 3–8 with coxae developed as coxal plates and usually fused to pereon; sometimes ambulatory or prehensile, occasionally reduced in number.
Abdominal appendages	Biramous, branchial; covered by operculate uropods.
Telson	Fused with pleomeres 4–6 (pleotelson).
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon fused with telson or with 1–3 free somites + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with appendix masculina and usually stronger spination.
Sexes	Separate.
Larval development	Epimorphic; released at manca stage.

Fossil record	Oligocene to Recent.
Feeding types	Herbivores, scavengers, and predators.
Habitat	Marine; intertidal to abyssal.
Distribution	Worldwide.

SUBORDER ANTHURIDEA Leach, 1814

Recent species	Approximately 100.
Size range	1.5–47.0 mm.
Carapace	Absent.
Eyes	Sessile, compound; usually well developed; occasionally with increased number of ocelli in male.
Antennules	Uniramous.
Antennae	Uniramous, peduncle with 5 segments.
Mandibles	Usually with palp; occasionally reduced or absent.
Maxillulae	Usually absent.
Maxillae	Modified for piercing in some taxa.
Maxillipeds	One pair, highly variable, with 3–7 segments.
Thoracic appendages	Thoracopods 2–8; 1st pair usually strongly subchelate (except in some females), following 2 pairs usually weakly subchelate, and 5–8 simple.
Abdominal appendages	Biramous, elongate; 1st pair operculate in some taxa; 2nd modified in males. Uropods partially overlapping telson.
Telson	True telson in many (not fused with 6th pleomere); often with 1 or 2 statocysts at base.
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon with 6, excluding telson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with appendix masculina and more developed antennules.
Sexes	Separate or protogynic hermaphrodites.
Larval development	Epimorphic; released at manca stage.
Fossil record	Recent.
Feeding types	Little known.
Habitat	Marine, estuarine, and freshwater; benthic.
Distribution	Worldwide.

SUBORDER FLABELLIFERA Sars, 1882

Recent species	Approximately 1400.
Size range	Up to 350 mm.
Carapace	Absent.
Eyes	Sessile, compound, usually well developed; sometimes reduced or absent.
Antennules	Usually uniramous; occasionally vestigial.

Antennae	Uniramous; peduncle with 5 or 6 segments; sometimes reduced.
Mandibles	Usually with palp; molar processes often reduced or modified.
Maxillulae	Usually with 1 endite; sometimes modified for piercing or sucking.
Maxillae	Usually with 2 endites; sometimes modified for piercing or sucking.
Maxillipeds	One pair, variously developed.
Thoracic appendages	Thoracopods 3–8 with coxae developed as plates; ambulatory and/or prehensile.
Abdominal appendages	First 2 or 3 pairs often natatory; posterior pairs branchial. Uropods lateral, with pleotelson forming tailfan.
Telson	Fused with variable number of pleomeres (pleotelson).
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon variable + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, 8th of male; female with oostegites; male with appendix masculina.
Sexes	Separate or protandrous hermaphrodites.
Larval development	Epimorphic; released at manca stage.
Fossil record	Triassic to Recent.
Feeding types	Omnivorous scavengers and predators; temporary or permanent parasites adapted for piercing and sucking.
Habitat	Marine to freshwater; intertidal to moderate depths, sometimes cave dwellers.
Distribution	Worldwide.

SUBORDER MICROCERBERIDEA Chappuis and Deboutteville, 1960

Recent species	Approximately 22 in one genus.
Size range	0.5–1.4 mm.
Carapace	Absent.
Eyes	Absent.
Antennules	Uniramous.
Antennae	Uniramous; peduncle with 5 or 6 segments.
Mandibles	Usually without palp.
Maxillulae	With 3 endites.
Maxillae	With 2 reduced endites.
Maxillipeds	One pair; endopod with 5 segments.
Thoracic appendages	Thoracopods 2–8; 1st pair prehensile.
Abdominal appendages	Biramous; uropods with exopods reduced or absent.
Telson	Fused with 4 or fewer pleomeres (pleotelson).
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped), pereon with 7; pleon with 2 or more + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with appendix masculina.

Sexes	Separate.
Larval development	(?) Epimorphic.
Fossil record	Recent.
Feeding types	Unknown.
Habitat	Marine, freshwater; interstitial.
Distribution	Eastern Pacific, South America, Africa, Mediterranean, India.

SUBORDER ASELOTA Latreille, 1803

Recent species	Approximately 450.
Size range	1–15 mm.
Carapace	Absent.
Eyes	Sessile, compound; frequently absent.
Antennules	Uniramous.
Antennae	Uniramous; peduncle with 6 segments.
Mandibles	Usually with palp.
Maxillulae	Usually with 1 or 2 endites.
Maxillae	Typically with 3 endites.
Maxillipeds	One pair; usually well developed.
Thoracic appendages	Typically thoracopods 2–8, but number sometimes reduced; 1st often subchelate; coxae usually small.
Abdominal appendages	First 1 (female) or 2 (male) pairs operculate, remainder branchial and enclosed. Uropods terminal, uni- or biramous.
Telson	Pleotelson usually of 4–6 pleomeres + telson.
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon typically with 7, often fewer; pleon usually with 1–3 free + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with appendix masculina.
Sexes	Separate.
Larval development	Epimorphic; released at manca stage.
Fossil record	Recent.
Feeding types	Typically herbivores or detritivores.
Habitat	Marine to freshwater, interstitial to abyssal.
Distribution	Worldwide.

SUBORDER PHREATOICIDEA Stebbing, 1893

Recent species	Approximately 50.
Size range	5–45 mm.
Carapace	Absent.
Eyes	Sessile, compound; sometimes absent.
Antennules	Uniramous.
Antennae	Uniramous; peduncle with 5 segments.
Mandibles	Usually with palp.

Maxillulae	Usually with 2 endites.
Maxillae	Usually with 3 endites.
Maxillipeds	One pair; usually well developed.
Thoracic appendages	Thoracopods 2–8; last 3 pairs directed backwards; coxae not developed as coxal plates.
Abdominal appendages	Usually subequal, natatory as well as branchial. Uropods biramous.
Telson	Fused with 6th pleomere (pleotelson).
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon with 5 + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, 8th of male; female with oostegites; male with appendix masculina.
Sexes	Separate.
Larval development	Epimorphic; released at manca stage.
Fossil record	Permian to Recent.
Feeding types	Plant detritus feeders.
Habitat	Freshwater; occasionally semiterrestrial.
Distribution	South Africa, India, New Zealand, Australia.

SUBORDER GNATHIIDEA Leach, 1814

Recent species	Approximately 75.
Size range	2–17 mm.
Carapace	Absent.
Eyes	Sessile or rarely on small peduncles, compound; occasionally absent.
Antennules	Uniramous.
Antennae	Uniramous; peduncle with 4 segments.
Mandibles	Absent in adult female; well developed, nonfunctional in male.
Maxillulae	Reduced or vestigial.
Maxillae	Reduced or vestigial.
Maxillipeds	Two pairs, 2nd modified as operculum.
Thoracic appendages	Thoracopods 3–7 (8th absent), not chelate or subchelate.
Abdominal appendages	Usually biramous, unmodified. Uropods well developed, biramous.
Telson	Fused with 6th pleomere (pleotelson).
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 2 thoracic (maxillipeds); pereon with 6; pleon with 5 + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, 8th of male as single median cone; female with oostegites; male with mandibles greatly enlarged, modified for burrowing; without specialized copulatory structures.
Sexes	Separate.
Larval development	Metamorphic; segmented larva → praniza (postlarva).

Fossil record	Recent.
Feeding types	Juveniles adapted for piercing and sucking; adults scavengers or nonfeeders.
Habitat	Marine; juvenile, temporary ectoparasites of fish; adult, burrowers (burrows dug by male).
Distribution	Worldwide.

SUBORDER ONISCOIDEA Latreille, 1803

Recent species	Approximately 900.
Size range	Up to 50 mm.
Carapace	Absent.
Eyes	Sessile, compound; usually present.
Antennules	Uniramous, usually reduced.
Antennae	Uniramous; peduncle with 4 or 5 segments.
Mandibles	With palp.
Maxillulae	Typically with 2 endites.
Maxillae	Usually with 3 endites.
Maxilliped	One pair; terminal segments often reduced.
Thoracic appendages	Thoracopods 3–8 with coxae expanded as coxal plates.
Abdominal appendages	Biramous; at least first 2 pairs, sometimes all 5 pairs with pseudotracheae. Uropods sometimes operculate, with broad exopod and small, ventral endopod.
Telson	Usually fused with 6th pleomere (pleotelson); occasionally not fused with pleomere.
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon with 5 + pleotelson or 6 + telson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with 2nd, sometimes also 1st, pair of pleopods modified for copulation.
Sexes	Separate.
Larval development	Epimorphic; released at manca stage.
Fossil record	Recent.
Feeding types	Usually herbivores or detritivores.
Habitat	Amphibious and terrestrial; several commensal in termite and ant nests.
Distribution	Worldwide.

With few exceptions (Anthuridea, Phreatoicoidea), the isopod body is dorsoventrally compressed, a character used as a rule of thumb for distinguishing isopods from amphipods. Another very significant character of isopods is the adaptation of the pleopods for respiration. Examine the intact specimen(s) before beginning a more detailed study of individual appendages, mouthparts, and major organ systems (see Figures 33–35). In dorsal

view the typical isopod cephalon is small, usually with small, sessile compound eyes; in *Bathynomus giganteus* A. Milne Edwards, the eyes are very large and occupy much of the anterior part of the cephalon. Uniramous antennules and antennae generally can be observed projecting from the cephalon; however, in species of the Oniscoidea, the antennules are exceptionally short and usually do not protrude beyond the cephalic margin. A

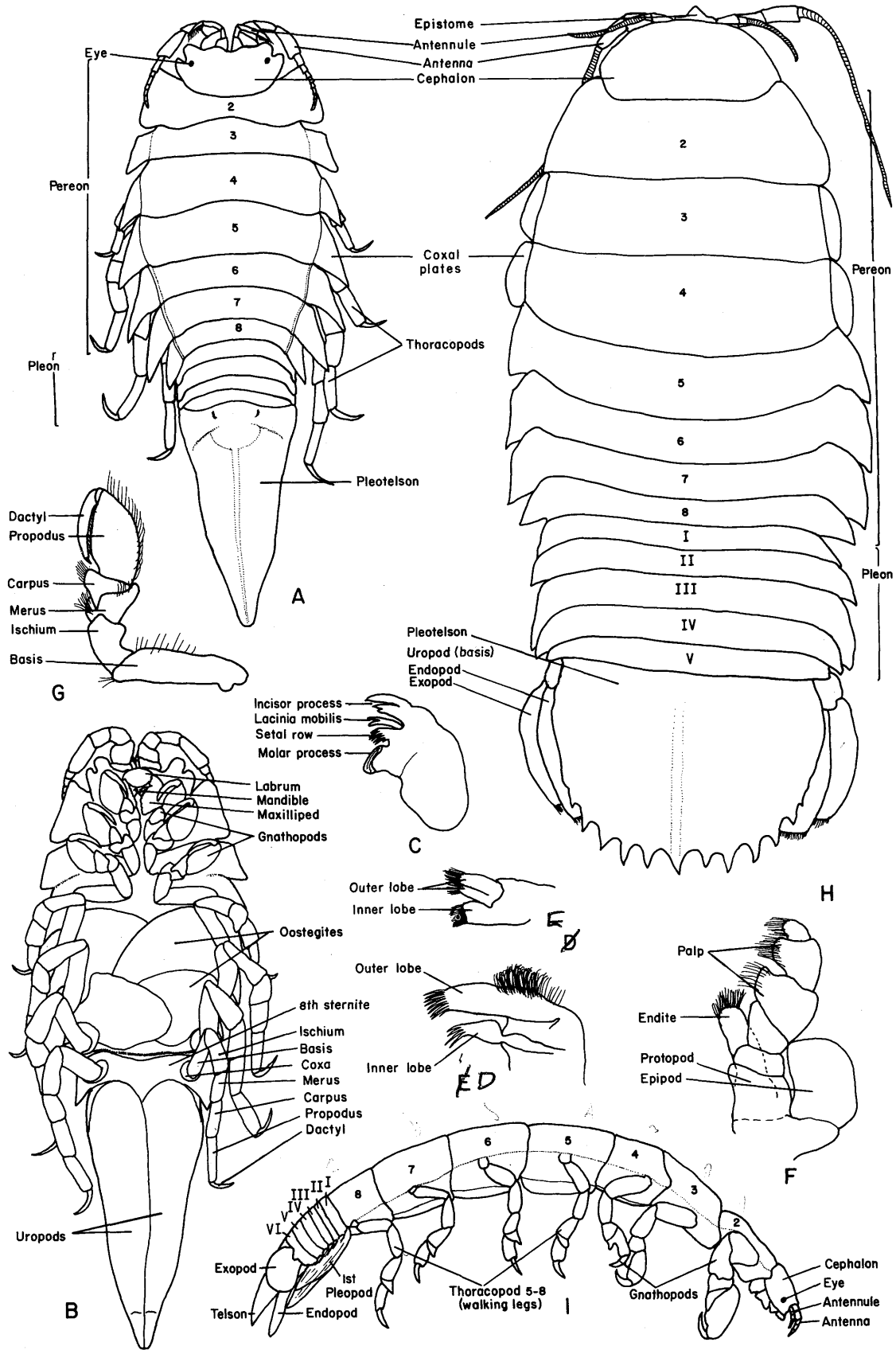


Figure 33 Isopoda: A—G, Valvifera; H, Flabellifera; I, Anthuridea. A. Whole animal (dorsal view); B. Female (ventral view); C. Mandible; D. Maxillule; E. Maxilla; F. Maxilliped; G. Gnathopod; H. Typical flabelliferan (dorsal view); I. Typical anthuridean (lateral view).

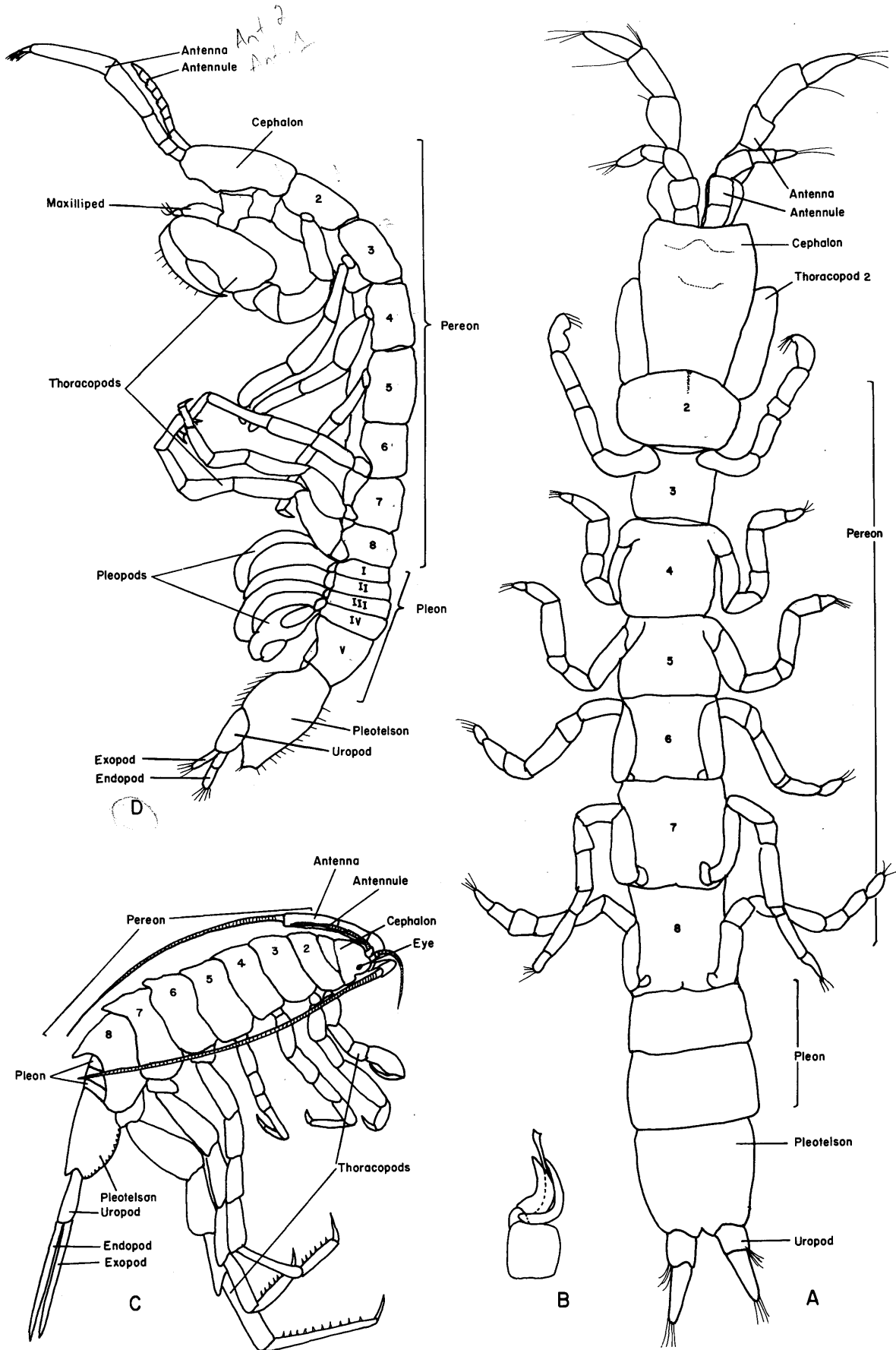


Figure 34 Isopoda: A, B Microcerberidea; C, Asellota; D, Phreatoicidea. A. *Microcerberus* (dorsal view); B. 2nd pleopod of male [A, B after Chappuis and after C. Delamare Deboutteville: *Biologie des eaux souterraines littorales et continentales* (Hermann, Paris, 1960)]; C. Typical asellotan; D. Typical phreatoicidean [after Birstein, 1962].

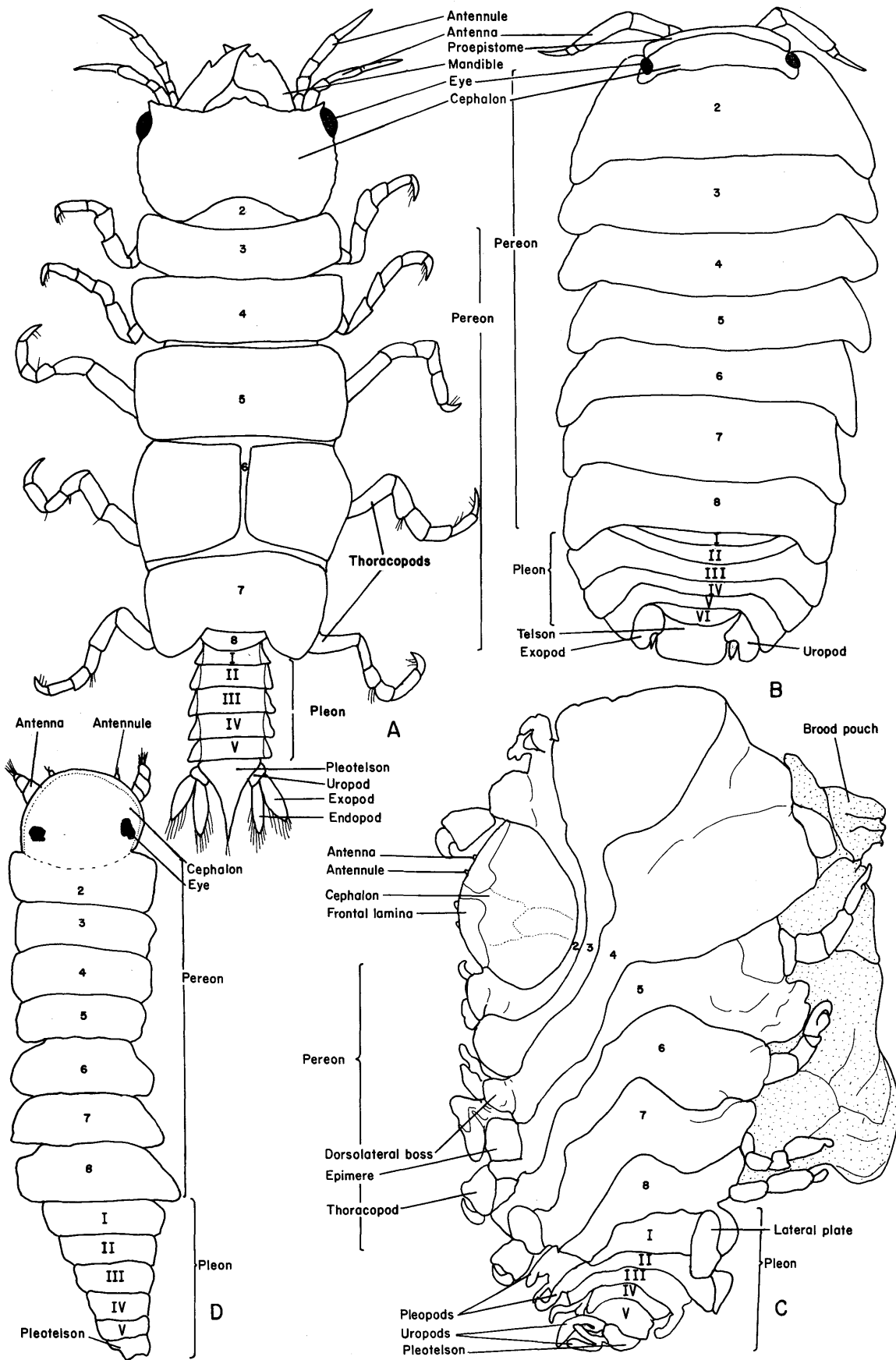


Figure 35 Isopoda: A, Gnathiidea; B, Oniscoidea; C, D, Epicaridea. A. Typical gnathiidean [after Hessler, 1969, from *Treatise on Invertebrate Paleontology*, courtesy of the Geological Society of America and University of Kansas]; B. Typical oniscoidean; C. Female bopyrid (dorsal view); D. Male bopyrid (dorsal view) [C, D after Markham, 1975b].

carapace is lacking but this is a secondarily derived condition. The 1st, rarely also the 2nd, thoracic somite is fused with the cephalon. Although some carcinologists refer to this condition as a cephalothorax, the preferred terminology is cephalon and pereon, as in the tanaidaceans. Seven, or less frequently 6, thoracic somites are free; occasionally 1 or more of these somites may be fused with an adjoining somite. The tergal plates of the somites often are laterally expanded. Very frequently the abdominal somites (pleomeres) are appreciably narrower than those of the pereon; as in tanaidaceans the abdomen is referred to as the pleon. One or more pleomeres usually fuse with the telson, forming the pleotelson. How many thoracic and abdominal somites can you distinguish in your specimen(s)?

In ventral view examine the sternites and appendages. Each pereonite typically carries a pair of appendages modified as walking legs (pereopods); in the Gnathiidea the last pair are absent. The coxal segments of pereopods 2–7 (thoracopods 3–8) often are laterally expanded to form dorsal coxal plates reminiscent of epimeres of other crustaceans and insects. The basal segments usually are directed toward the midline of the body; the remaining segments are directed laterally. A great deal of variation exists in the structure of the pereopods. Frequently the 1st pair is modified either for food gathering or, in males, as an accessory copulatory structure for grasping the female. One to 3 pairs of pereopods frequently are subchelate but never chelate as in the tanaidaceans. In some taxa of every suborder, but particularly in the Anthuridea and Phreatoicoidea, 2 groups of pereopods are differentiated: the anterior 3 pairs are directed anteriorly, the posterior 4 pairs posteriorly. In mature females, some thoracic sternites often are covered by large platelike oostegites; typically these are present on the coxae of the 1st to 4th or 5th pereopods, rarely on all 7 pairs. In certain species, the females carry their eggs not in the brood pouch but in paired hypodermal pockets formed by invaginations of the intersternal membranes into the body cavity. These invaginations open to the exterior by narrow slits. Oviducts open through a single median gonopore on the 6th thoracic sternite. The vas deferens of the males usually open through a pair of papillae on the 8th thoracic sternite; in the Gnathiidea and most Oniscoidea the papillae are fused into a median cone.

Five pairs of pleopods usually are present even if the number of pleonal somites has been reduced through fusion. Only rarely are all pleopods lacking, although in some taxa the number may be reduced. Pleopods in isopods serve a respiratory as well as natatory function, and as such, may be modified from the typical pleopodal form. The biramous condition generally persists, and when modifications occur, they usually are modifications of the endopods. In the male, the endopods of the 2nd pleopods bear modified copulatory structures, the ap-

pendix masculina. In most Oniscoidea the pleopods are specifically adapted for aerial respiration. If specimens of both aquatic and terrestrial isopods are available, compare the pleopodal adaptations of both groups. The uropods may be uni- or biramous, spatulate or styliform, well developed or reduced, and in a few instances absent. They sometimes are modified for special functions. In valviferans, they are modified as branchial covers. In the Oniscoidea the exopods usually are moderately large and are visible in dorsal view, but the endopods are very small and are ventrally positioned under the telson.

Remove the mouthparts and examine them. The maxilliped frequently is operculate, with a broadened proximal segment; endites frequently are present. The maxilla and maxillule both lack palps. The mandible usually is well developed, with incisor and molar processes, lacinia mobilis, and setal or spine row. The mandibles of male gnathiideans usually are very prominent and modified for burrowing. Occasionally some or all of the mouth appendages are reduced or greatly modified.

The internal anatomy of relatively few isopods has been studied in detail; therefore, the variations among major taxa cannot be predicted. The description of the major organ systems presented is based on *Bathynomus*, one of the more primitive taxa (see Figure 36). Begin your examination by removing the exoskeleton from the dorsal surface and one side of the animal. The tergites of each somite usually will have to be cut and removed individually. Isopods are unique among crustaceans in that the heart is located almost exclusively in the pleon (abdomen). Blood from the venous sinuses is returned to the heart through 2 pairs of ostia, or in the case of most terrestrial isopods, 1 pair. Anteriorly from the heart, trace the unpaired anterior aorta forward; just posterior of the cephalon the walls of the artery are expanded to form a cor frontale or accessory heart that aids in circulation of blood to the cephalon and its appendages. The several branches of the anterior aorta supply blood to the eyes, supraesophageal ganglion, foregut, and cephalic appendages. A ventral branch of the aorta joins the subneural artery anteriorly. Laterally from the heart locate the 5 pairs of lateral arteries. The most anterior pair provides blood to the ventral nerve cord and through large branches to the anterior 4 pairs of thoracic appendages (pereopods 1–4); blood to the following 3 pairs is provided by the 2nd to 4th lateral arteries respectively. Posteroventrally the posterolateral pair of arteries provides blood to the telson and uropods and branches to the abdominal musculature. These blood vessels do not enter the pleopods; blood to the pleopods is supplied by blood sinuses from the gut region and a pair of ventrolateral lacunae. Notice that the lateral arteries leave the heart generally in its anterior half in *Bathynomus*. In some other isopods the arteries are spaced equidistantly along the length of the heart. In terrestrial isopods, not

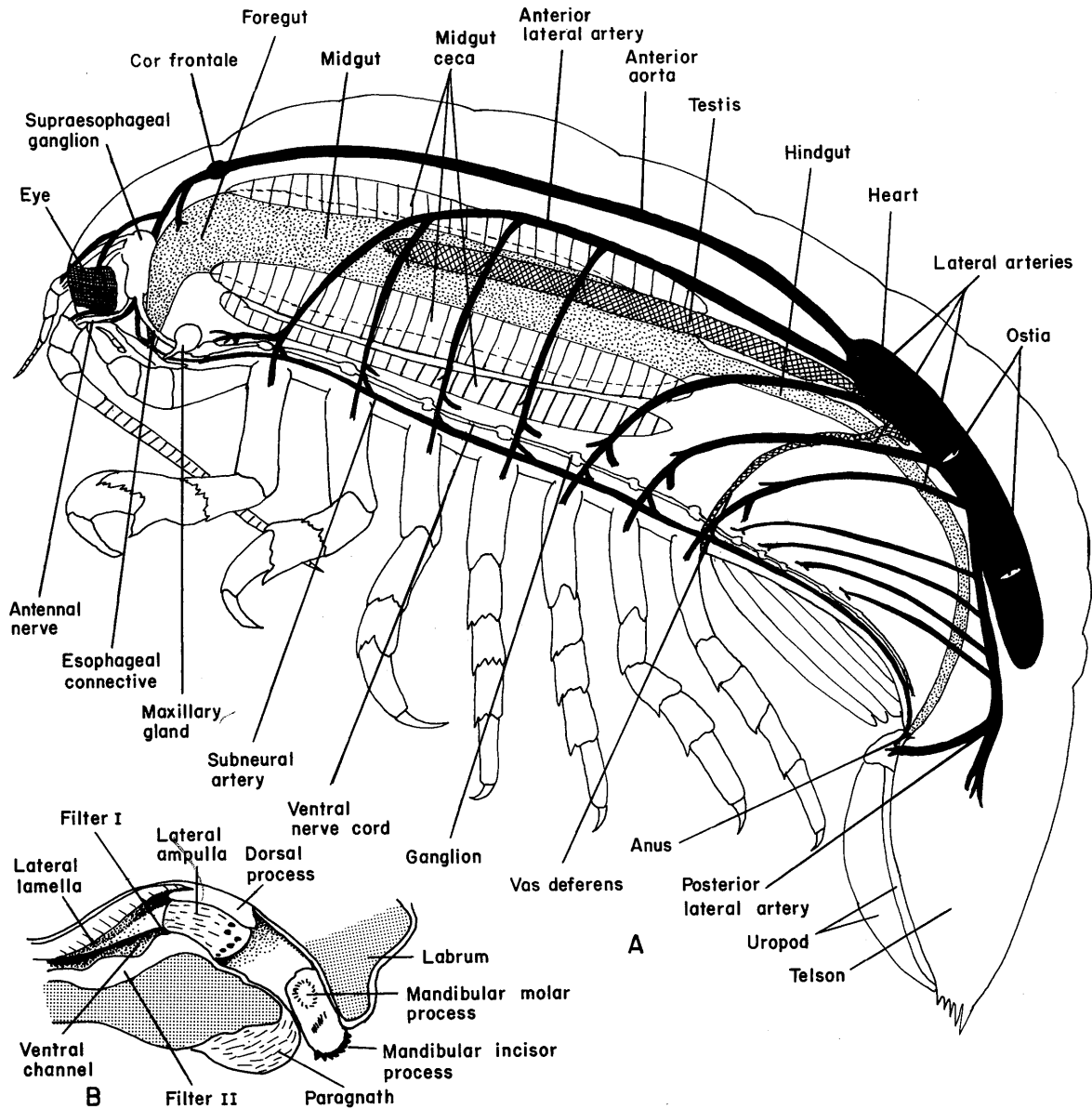


Figure 36 Isopoda: A. Diagrammatic flabelliferan with musculature removed to show major internal organs; B. Diagrammatic valviferan foregut showing internal structure [after Naylor, 1955].

only is there only a single pair of ostia (except in *Ligia*), but the heart tends to be longer and thicker and the arterial system is simpler.

The reproductive system in isopods typically consists of tubular paired ovaries or testes lying dorsolaterally of the gut. Oviducts leave the ovaries posteriorly at the level of the 5th or 6th thoracic somite, turn ventrally, and open individually in a median pore on the sternite between the 6th thoracopods (5th pereopods). Paired vas deferens leave the testes posteriorly and turn ventrally to open through a pair of median papillae or a single median cone on the sternite of the 8th thoracic somite.

The digestive system consists of a foregut, midgut,

hindgut, and usually from 1 to 3 pairs (3 in *Bathynomus*) of midgut or hepatic ceca of variable length. In *Bathynomus* the hindgut is the longest part of the digestive tract, commencing at the level of the 4th pereonite and continuing to the anus on the ventroproximal surface of the telson. Near the junction of the midgut and foregut are the ducts of the ceca. The foregut is specialized as a chewing or filtering stomach or, in the cases of isopods adapted for piercing and sucking, as a pumping stomach. As described for *Idotea*, the foregut has a pair of lateral ampullae on each side wall which crush the food material so that fluid can be sifted from the solid matter through paired, ventral, bristled plates

into a midventral channel (Filter I). This channel is formed by anterior lamellae (flaplike valves) and divided medially at its posterior end by a second filtering structure (Filter II). On either side of the channel, parallel with its upper margin, is a groove covered with strong bristles. Posteriorly these grooves open into the hepatic or midgut ceca of each side; fluids pass between the setae and into the ceca; a backward projection from the 2nd filter acts as a valve over the opening from the ceca into the midgut. Remove the foregut from your specimen, open it, and compare the structure of the chewing and filtering or pumping mechanisms with that described. Excretion in isopods is via maxillary glands.

With the foregut removed, locate the supraesophageal ganglion and identify the large optic, antennal, and antennular nerves radiating from it. Trace one of the esophageal connectives around the base of the foregut. In *Bathynomus* part of the ventral nerve cord is obscured by a pair of sternal alar plates. Remove part of these plates to expose the subesophageal ganglion, which rep-

resents the fusion of the ganglia of the mouthparts. Trace the nerve cord posteriorly, identifying the ganglia of the thoracic appendages and somites. The abdominal ganglia have moved somewhat closer together and no longer appear segmental.

Larval development generally is epimorphic, with the young held for some time after hatching in the brood pouch of the female. At the time of release, the manca stage, the young resemble the adult form a great deal, but usually lack the 7th pereopods. In some isopods (e.g., Gnathiidea, Cymothoidae), development is metamorphic. In Gnathiidea, the larvae are parasitic and quite different in body form from the adults. After release, the larva seeks out a fish host and attaches with its biting mouthparts. Once gorged with blood, the larva drops off the host, sinks to the bottom, and molts to the typical benthic adult. In contrast, the larvae of the Cymothoidae (Flabellifera) are free-living, while the adults are ectoparasites of fishes.

Parasitic Isopoda

SUBORDER EPICARIDEA Latreille, 1831

Recent species	Approximately 375.
Size range	1.5– 10.0 mm.
Carapace	Absent.
Eyes	Sessile, compound, frequently present in male; reduced or absent in female.
Antennules	Reduced in male; reduced or absent in female.
Antennae	Often with 3-segmented peduncle in male; reduced or absent in female.
Mandibles	Reduced, absent, or suctorial.
Maxillulae	Reduced, absent, or suctorial.
Maxillae	Reduced, absent, or suctorial.
Maxillipeds	Reduced, absent, or suctorial.
Thoracic appendages	Thoracopods 2– 8 in male, often with strong claws; reduced or absent in female.
Abdominal appendages	Usually reduced or absent; if present, branchial. Uropods usually biramous, not well developed in females, variously developed in males.
Telson	Fused with 6th pleomere (pleotelson).
Tagmata	Cephalon, pereon, and pleon.
Somites	Head usually with 5 + 1 thoracomere; pereon usually with 7; pleon usually with 5 + pleotelson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; males extremely reduced in size, without specialized copulatory structures.
Sexes	Separate.

Larval development	Metamorphic; epicaridum or microniscus → cryptoniscus → bopyridum.
Fossil record	(?) U. Jurassic to Recent.
Feeding types	Parasitic, feeding on body fluids of host.
Habitat	Parasitic on other crustaceans, particularly decapods; frequently host specific.
Distribution	Worldwide.

The Epicaridea are ectoparasites of other Crustacea; the best known family is the Bopyridae (see Figure 35). As adults, members of this family are parasitic on decapods, usually lodging in the gill chamber of the host. Juveniles use copepods as intermediate hosts. Sexual dimorphism is extreme. Males retain a general isopodlike appearance, although they are greatly reduced in size. Females are greatly altered. A cephalon usually is present but may be difficult to distinguish. Eyes, when present, are small; cephalic appendages usually are reduced or absent. The thorax generally is segmented and thoracic appendages (pereopods) usually are present, at least on one side, but are considerably reduced in size. The pleon generally also is present, but its segmentation and appendages often are difficult to distinguish. Frequently the greatly enlarged oostegites obscure much of the female's morphology. Examine representatives of several taxa if available, and observe the varying degrees of degeneration of the female.

Larval development is metamorphic. The larvae are released at a stage referred to as the microniscus or epicaridum. At this stage the larva has typical mancalike segmentation, but swims with the antennae and pleopods. It is at this stage that it seeks out the intermediate copepod host. After several molts, sexual differentiation begins, and the maturing juvenile detaches itself from the copepod host. This cryptoniscus is once again planktonic; its pereopods become developed as holdfasts. At this stage the larva seeks its permanent host, usually a decapod. If the host is already infected with a parasite of the same species, the newly arriving larva attaches, molts, and becomes a male. If the host is uninfected, the larva undergoes a series of molts until the adult female form is reached.

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ORDER AMPHIPODA Latreille, 1816

The nearly 5000 amphipod species are divided into four major taxa, the Gammaridea, Hyperiidea, Caprellidea, and Ingolfiellidea. The gammarideans are the most successful and, while primarily members of the benthos,

have adapted to a variety of habitats. The morphological specializations exhibited by the suborders are of sufficient interest that they are presented separately.

Gammaridea and Hyperiidea

SUBORDER GAMMARIDEA Latreille, 1803

Recent species	Approximately 4500.
Size range	1–150 mm.
Carapace	Absent.
Eyes	Sessile, compound; usually not very large.
Antennules	Usually biramous; 2nd flagellum sometimes reduced or absent.
Antennae	Uniramous.
Mandibles	With palp.
Maxillulae	With endopodal palp and basal endite.
Maxilla	Usually reduced.
Maxillipeds	One pair; usually with 7 segments.
Thoracic appendages	Uniramous; thoracopods 2–8, each often with large coxal plate; 2nd and 3rd usually subchelate.
Abdominal appendages	Pleopods and uropods usually biramous, easily differentiated.
Telson	Entire or bilobed.
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon with 6 excluding telson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with paired penes. Eyes, antennae, and 2nd gnathopod sexually dimorphic.
Sexes	Separate.

Larval development	Epimorphic; without postlarval stage.
Fossil record	U. Eocene to Recent.
Feeding types	Scavengers, filter feeders, often microphagous and predators; sometimes parasitic, adapted for piercing and sucking.
Habitat	Marine, brackish, and freshwater; primarily benthic; few semi-terrestrial.
Distribution	Worldwide.

SUBORDER HYPERIIDEA Latreille, 1831

Recent species	Approximately 450.
Size range	1–90 mm.
Carapace	Absent.
Eyes	Sessile, compound; often very large.
Antennules	Uniramous; usually reduced or vestigial in female.
Antennae	Uniramous; often vestigial in female.
Mandibles	With or without palp.
Maxillulae	Usually with palp; may be reduced or absent.
Maxillae	Often reduced, occasionally absent.
Maxillipeds	One pair, with 1 to 4 segments; usually without palp.
Thoracic appendages	Uniramous; thoracopods 2–8 with coxal plates small or fused to body; 6th sometimes raptorial.
Abdominal appendages	Pleopods and uropods usually well developed.
Telson	Entire.
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon with 5, excluding telson (urosomites 2 and 3 fused).
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with oostegites; male with small paired penes. Antennae of female reduced or vestigial.
Sexes	Separate.
Larval development	Epimorphic; usually without postlarval stage.
Fossil record	Recent.
Feeding types	Predators and parasites; usually associates of gelatinous plankton.
Habitat	Marine, pelagic; usually commensal or parasitic on tunicates, coelenterates, ctenophores and colonial radiolarians.
Distribution	Worldwide.

Of the four suborders of the Amphipoda, the two largest, both in size and in number of species, the Gammaridea and Hyperidea, generally are typical of the conceptual amphipod. The two smaller suborders, the Caprellidea and Ingolfiellidea, will be discussed separately. Undoubtedly the most abundant amphipods available for dissection and study are members of the Gammaridea. The following instructions and discussion have been suf-

ficiently generalized so that they are applicable to most taxa. Basic differences between gammaridean and hyperiidean morphology will be pointed out (see Figure 37).

In contrast to the Isopoda, the amphipod body usually is laterally compressed; however, a few gammarideans are more or less dorsoventrally compressed. Usually the 1st thoracic somite is fused to the cephalon and its pair of appendages modified as maxillipeds, which often are

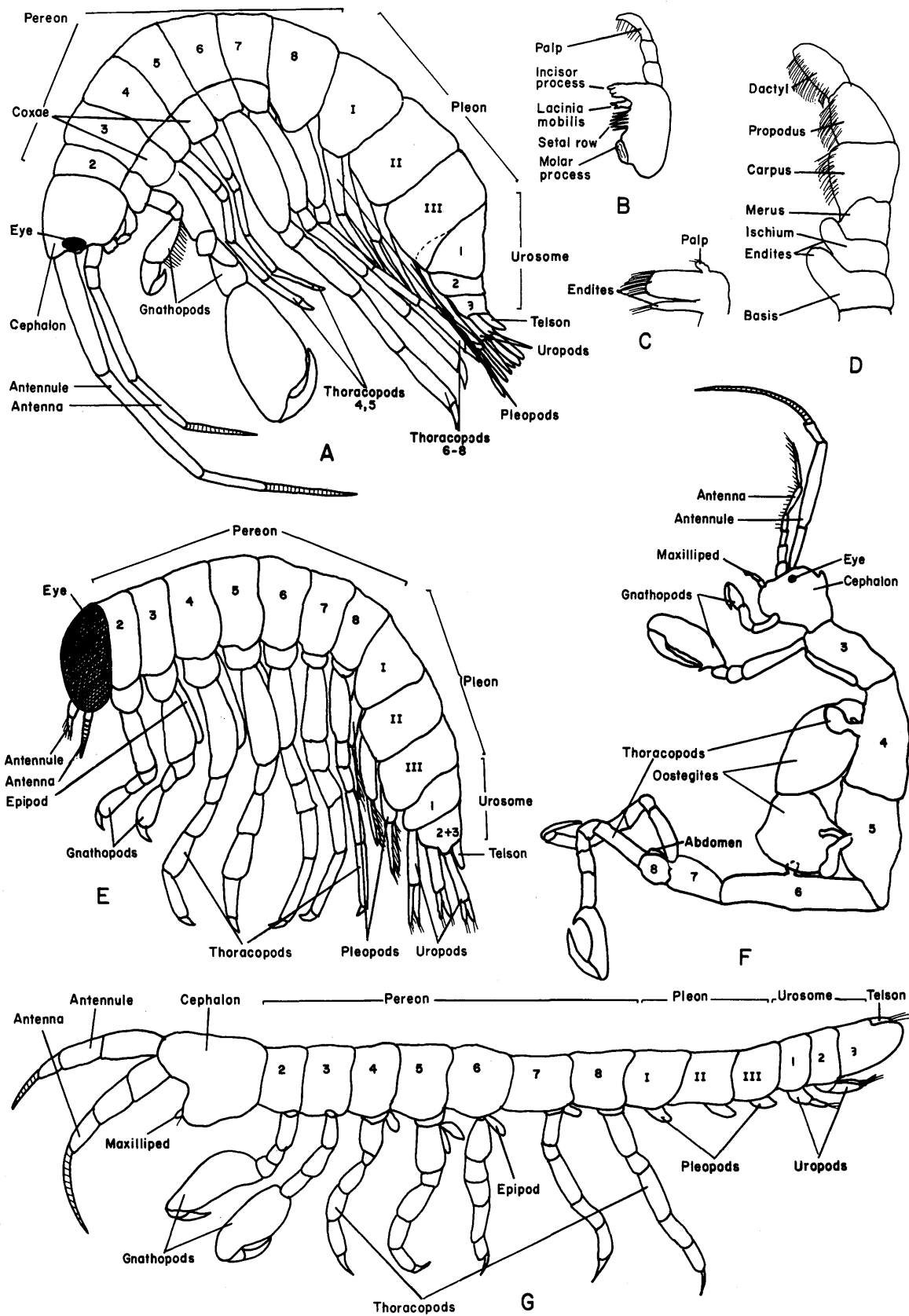


Figure 37 Amphipoda: A–D, Gammaridea; E, Hyperiidea; F, Caprellidea; G, Ingolfiellidea. A. Typical gammaridean (lateral view); B. Mandible; C. Maxillule; D. Maxilliped; E. Typical hyperiidean; F. Typical caprellidean; G. *Ingolfiella* [after C. Delamare Deboutteville: *Biologie des eaux souterraines littorales et continentales* (Hermann, Paris, 1960)].

fused basally. Eyes usually are present and moderately small in gammarideans, but in hyperiideans the eyes frequently occupy the major portion of the cephalon. The antennules have a 1- to 3-segmented peduncle and flagellum. A second, accessory flagellum also usually is present in living specimens, but often is broken off in preserved material. Inspect your specimen(s) closely to see if an accessory flagellum is, or has been, present. The antennae are uniramous, each consisting of a 1- to 5-segmented peduncle and a flagellum. The flagella of both antennules and antenna may carry sensory structures such as calceoli. The 7 thoracic somites collectively, as in isopods and tanaidaceans, are referred to as the pereon. The thoracopods are uniramous, with the coxae ventrally expanded to form coxal plates that cover and protect the gills, which are thoracic rather than abdominal as in isopods. Typically the first 2 pairs of pereopods (thoracopods 2 and 3) are subchelate and are referred to as gnathopods; the 2nd gnathopod, in particular, may be sexually dimorphic in mature males. The shape of this gnathopod has been used extensively as a taxonomic character; however, in many species it is polymorphic, thus it is not always a valid diagnostic character. The following 5 pairs of pereopods (thoracopods 4–8) are commonly called walking legs, although amphipods rarely use them for this purpose. Most obtain their mobility by swimming, usually on one side or the other. Frequently these appendages are differentiated into two types; the first 2 pairs are relatively short, often quite setose; the last 3 pairs are longer and directed posteriorly.

The abdomen or pleon is typically 6-segmented, not exhibiting the fusion of the pleomeres seen in isopods; however, there is a major distinction between the first 3 pleomeres and the last 3. The first 3 somites are generally normal in size and carry paired, multiarticulate, setose pleopods, well adapted for swimming. The posterior 3 somites usually are smaller and the paired appendages have fewer setae and only 1 or 2 segments. In hyperiideans only 2 posterior somites are apparent as a result of the fusion of the 2nd and 3rd. By convention, the last 2 or 3 somites are collectively referred to as the urosome, and their appendages as uropods. The uropods are often adapted for pushing or jumping. Only the last pair actually is homologous with uropods of other peracaridans. The telson may be entire or bilobed in gammarideans but is always entire in hyperiideans. Remove and examine 1 of each pair of appendages. If several stages of males of the same species are available, study the polymorphism exhibited by the 2nd gnathopods.

Not only are the 2nd gnathopods sexually dimorphic; the eyes and antennae of males frequently are larger than those of females. Males also possess a pair of penes, sometimes quite small and rather inconspicuous, on the sternite of the 8th thoracomere. In the female oostegites

are attached to the coxae of the 2nd through 5th pereopods; gonopores are present on the sternite of the 6th thoracomere.

In hyperiideans, the body, at least anteriorly, frequently is inflated or subcircular. The number of segments of the maxillipeds and thoracic appendages is reduced or they may be fused to their somites, and the coxal plates usually are much smaller than in gammarideans.

Remove and examine the mouthparts. The maxillipeds usually have 7 segments, a peduncle and four-segmented palp, and moderately well-developed endites in gammarids. In hyperiids the number of segments usually is reduced to 3 or 4 and the palp is absent. Quite frequently the maxillipeds in both groups are fused basally. The maxillae each have a pair of endites, but often they are reduced and occasionally may be absent. The maxillulae generally are well developed. A palp is present in gammarids and at least in some hyperiids (mouthparts have not been described for many species in the latter group). A pair of well-developed endites usually are present in gammarids, but the basal endite may be absent in hyperiids. The mandibles usually are well developed, with strong incisor and molar processes, lacinia mobilis, and setal row. A mandibular palp may be present or absent in both gammarideans and hyperiideans.

The following discussion of major amphipod organ systems has been based on gammarideans (see Figure 38). The gammarid exoskeleton adheres very closely to the body somites and is not easily detached. To avoid damage to the internal body structures use a pair of microscissors or a sharpened dissecting needle to cut the exoskeleton. Beginning at the 8th thoracic somite and proceeding anteriorly, cut the cuticle of each somite just above the coxal plate and carefully tease it free of the underlying muscles. Be particularly careful in the dorsal midline as the heart and pericardium attach to the epidermis directly beneath the exoskeleton. You need remove the exoskeleton from only one side of the body. To remove the cuticle from the head, make a shallow incision in the midline dorsally, anteriorly, and ventrolaterally. Carefully free the integument from the underlying tissue and remove it. Damage to the sessile eye is usually unavoidable; however, enough ocelli probably will remain to mark its position. Remove the exoskeleton from one side of the abdomen by making a lateral cut approximately at the level of the thoracic coxal plates and teasing it free. To observe the ventral nerve cord in the thorax it may be necessary also to remove carefully several of the thoracic appendages.

In the dorsal midline observe the elongate heart that extends from the 2nd to the 7th thoracic somite. Pairs of ostia are located in the 3rd to 5th somites respectively. Three pairs of lateral arteries lead from the heart to the stomach and midgut ceca. The heart is enclosed in a pericaridal sinus, which in gammarideans often extends

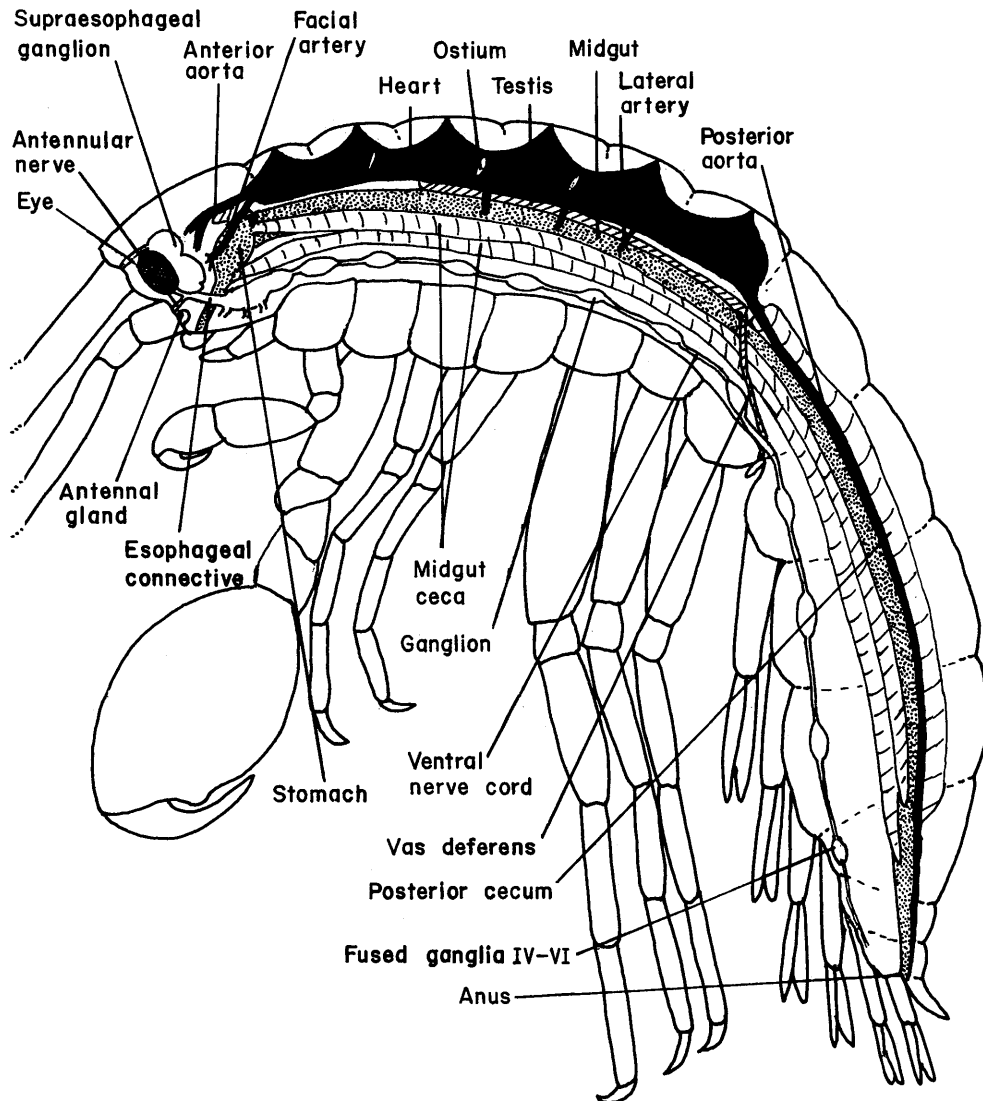


Figure 38 Amphipoda: Diagrammatic gammaridean with musculature removed to show major organ systems.

to the telson. Anteriorly identify the anterior aorta that provides blood to the cephalic region and an anterior lateral or facial artery that ramifies beneath the cephalic integument. Blood from the head enters the ventral or sternal sinus that bathes the ventral nerve cord and the hepatic ceca. From the sinus blood is provided to the appendages by subdivided channels (podopericardial channels); blood is returned from the appendages to the pericardium. Posteriorly identify the posterior aorta; it may be paired or a single vessel that extends the length of the abdomen. At the level of the telson it branches, turns downward, and empties into the ventral sinus. There is no definitive ventral or subneural artery in amphipods.

Beneath the heart and lateral to the midgut above the hepatic or midgut ceca observe the paired, elongate, tubular gonads. If your specimen is a male, locate one of the vas deferens at the posterior end of the testis and

trace it to the ejaculatory duct at the tip of one of the penial papillae on the 8th thoracic sternite. If your specimen is a female locate the oviduct and trace it from an ovary to its opening on the 6th thoracic sternite.

Food enters the body through a small, often slitlike mouth and passes through a short wide esophagus into the stomach. The stomach is thin walled, but armed internally with a pair of vertical plates anteriorly, cuticular toothed ridges, and a ventral groove covered in part by horizontal overlapping plates. The stomach opens posteriorly into the elongate midgut. Anteriorly from the midgut arise a forwardly directed short cecum and 2 to 4 posteriorly directed, elongate tubular ceca. Trace these ceca to their terminations. In the 1st urosomal somite, the midgut gives off a forwardly directed posterior pair of ceca. The hindgut may be distinguished posteriorly to the ceca. The digestive tract terminates in a ventrally directed anus at the base of the telson. Remove the

stomach, being careful to leave the esophagus intact, and examine the internal structure. The excretory organ in amphipods is the antennal gland.

Anteriorly in the head distinguish the supraesophageal ganglion. It may be possible also to trace the antennular, antennal, and optic nerves. Follow the esophageal connective around the esophagus to the ventral ganglia.

Note that the ganglia of the mouthparts have fused to form a large subesophageal ganglion. Trace the ventral nerve cord and segmental ganglia through the body. Note that the ganglia are fused in each somite, but between somites the nerve cords are widely separated. The ganglia of the urosomal somites are fused.

Ingolfiellidea and Caprellidea

SUBORDER INGOLFIELLIDEA Hansen, 1903

Recent species	Several in 1 genus.
Size range	1–14 mm.
Carapace	Absent.
Eyes	Absent; with articulated ocular lobes.
Antennules	Uniramous.
Antennae	Uniramous.
Mandibles	?
Maxillulae	?
Maxillae	Usually reduced.
Maxillipeds	One pair; with 6 or 7 segments.
Thoracic appendages	Uniramous; thoracopods 2–8 with small coxae; 2nd and 3rd with large subchelae.
Abdominal appendages	Pleopods vestigial; uropods 1 and 2 biramous, 3rd reduced or absent.
Telson	(?) Reduced or absent.
Tagmata	Cephalon, pereon, and pleon.
Somites	Head with 5 + 1 thoracic (maxilliped); pereon with 7; pleon with 6 excluding telson.
Sexual characters	Gonopores on 6th thoracic somite of female, on 8th of male; female with small oostegites; male probably with small paired penes.
Sexes	Separate.
Larval development	Epimorphic; without postlarval stage.
Fossil record	Recent.
Feeding types	Unknown.
Habitat	Marine, interstitial; abyssal to shallow; also cave dwellers.
Distribution	Worldwide.

SUBORDER CAPRELLIDEA Leach, 1814

Recent species	Approximately 300.
Size range	1–32 mm.
Carapace	Absent.
Eyes	Sessile, compound.
Antennules	Uniramous.

Antennae	Uniramous.
Mandibles	With or without palp and molar process.
Maxillulae	With endopodal palp; without basal endite.
Maxillae	Usually reduced.
Maxillipeds	One pair; usually with 7 segments, occasionally reduced.
Thoracic appendages	Uniramous; thoracopods 2–8, with 4th and 5th pairs reduced or absent; 6th pair occasionally reduced or absent.
Abdominal appendages	Usually absent in female; male with 1–3 pairs, often vestigial.
Telson	Vestigial or absent.
Tagmata	Cephalon and pereon; pleon reduced or vestigial.
Somites	Head with 5 + 2 thoracic (maxilliped); pereon with 4–6; pleon reduced or vestigial.
Sexual characters	Gonopores of female on 6th thoracic somite, of male on 8th; female with oostegites on 4th and 5th thoracic appendages only; male with paired penes.
Sexes	Separate.
Larval development	Epimorphic; without postlarval stage.
Fossil record	Recent.
Feeding types	Predators; sometimes parasitic.
Habitat	Marine, benthic, usually clinging to plants; 1 family parasitic on whales.
Distribution	Worldwide.

The Ingolfiellidea are interstitial inhabitants. The body is elongate and cylindrical (see Figure 37). The cephalon, which is fused with the 1st thoracic somite, has a small pair of ocular lobes but lacks eyes. A pair of maxillipeds is present; the thoracic appendages consist of 2 pairs of gnathopods and 5 pairs of pereopods. The coxal segments are small, as are the females' oostegites. The pleon and urosome are nearly equal in size; the pleopods are reduced but the first 2 pairs are biramous. The first 2 pairs of uropods also are reduced, but not as much as the pleopods; the last pair of uropods is vestigial.

The Caprellidea are the most structurally modified of all the amphipods. Despite their small size, they are easily recognized. The cephalon and first 2 thoracic somites are fused. Free-living caprellids have elongate bodies, while the bodies of parasitic species are dorsoventrally flattened. The pleon and telson are extremely reduced or vestigial in all but a few taxa. Although the first 2 thoracic somites are fused with the cephalon, only the 1st pair of thoracopods is modified as maxillipeds. The following 2 pairs usually are gnathopods. Of the remaining 5 pairs of pereopods, occasionally all are well developed, but most frequently the first 2 pairs are vestigial or absent. Occasionally even the 3rd pereopod (6th thoracopod) is reduced. The last 3 pairs (or as indicated above, 2 pairs) are well developed and adapted for holding the animal on the substrate. The cephalon carries small or moderately small compound sessile eyes, elon-

gate antennules, short antennae, and relatively well-developed mouthparts. Examine several specimens, if possible, from different genera. Very often the only structures apparent on the 4th and 5th thoracic somites are small gills, or in females, oostegites. The segments of the pereopods may be difficult to distinguish because of fusion, but see if you can determine the number of segments present.

Remove and examine the mouthparts. These structures are important in caprellidean systematics. Typically the maxilliped, including palp, consists of 7 segments, although this number may be reduced. The palp is present in most free-living taxa; occasionally it is reduced or more rarely absent. As in other amphipod taxa, the maxillae are reduced. In all species for which the maxillulae have been described, a palp is present but the basal endite is absent. The mandible is an especially valuable diagnostic character. A mandibular palp may be present or absent, as may the molar process. Although not as asymmetrical as seen in tanaidaceans, the right and left lacinia mobilis often differ. Not infrequently the right is 5-toothed, either serrate or smooth, while the left is 5-toothed apically. In some taxa accessory plates have been developed in addition to the lacinia mobilis. Do you find differences in the mandibular structure of your specimen(s)? In parasitic forms all the mouthparts are modified as piercing structures.

Larval development in all amphipods is epimorphic

and only in a few of the hyperiideans do the young hatch as postlarvae. In these cases, the appendages of the pleon are only buds and develop through 4 or 5 juvenile stages.

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Superorder EUCARIDA Calman, 1904

The eucarids are highly evolved and developed eumalacostracans. The carapace is fused to all the thoracomeres to form a cephalothorax; the eyes typically are carried on movable stalks; the mandible lacks a lacinia mobilis; and larval development is typically metamorphic.

This taxon includes the orders Euphausiacea, Amphionidacea, and Decapoda. The latter, representing the familiar shrimps, lobsters, and crabs, is so large and diverse that discussions of the different morphological groups are provided at the levels of infraorder, superfamily, and family.

ORDER EUPHAUSIACEA Dana, 1852

Recent species	Approximately 85, in eleven genera.
Size range	Up to 80 mm.
Carapace	Well developed; fused to all thoracic somites; gills not covered.
Eyes	Stalked, compound, usually well developed; sometimes subdivided by constriction.
Antennules	Biramous; sometimes sexually modified in males.
Antennae	Biramous; exopod scalelike. <i>5 segmented peduncle</i>
Mandibles	Usually with palp; without lacinia mobilis in adult.
Maxillulae	Usually with 2 endites and unsegmented endopodal palp; palp 3-segmented <i>Bentheuphausia</i> , 2-segmented in some larvae.
Maxillae	Typically with 4 segments; exopod, endopodal palp, and 2 endites, often bi- or trilobed.
Maxillipeds	None.
Thoracic appendages	Usually 8 biramous thoracopods; often 8th, sometimes 7th and 8th reduced or vestigial; sometimes 1st and 2nd or 2nd and 3rd elongate, occasionally chelate-like.
Abdominal appendages	Pleopods biramous, usually with appendix interna; 1st and 2nd pairs of males modified for copulation. Uropods biramous.
Telson	Well developed, usually with movable subterminal spines; together with uropods forms tailfan.
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5; thorax with 8; abdomen with 6, excluding telson.
Sexual characters	Gonopores on coxae of 6th thoracopods of female or on separate coxal plate; on 8th thoracomere of male; copulatory structures developed on 1st and 2nd pleopods of male. Antennules sometimes sexually dimorphic.

Sexes	Separate; female sometimes with ovisac(s).
Larval development	Anamorphic: nauplius → calyptopis → furcilia
Fossil record	Recent.
Feeding types	Usually planktonic filter feeders; occasionally predators.
Habitat	Marine, planktonic; often occurring in dense swarms; usually inhabiting open ocean waters.
Distribution	Worldwide.

The euphausiaceans have a relatively straightforward body plan; therefore, they are a comparatively simple group to study. The euphausiid depicted for external morphology is a specimen of the genus *Thysanopoda* in the family Euphausiidae (see Figure 39). The illustrated internal structures represent a composite. Your attention will be directed to the major differences among taxa. (Also see Table 1 on generic characters.) The number of thoracopods is variable. In several genera either the 8th or the 7th and 8th thoracopods are reduced or vestigial. Because of the development of filamentous gills on the coxae of the thoracopods, particularly the posteriormost pairs, reduced or vestigial appendages may be difficult to distinguish. A good rule of thumb is to start to count the number of appendages at the posterior end of the cephalothorax. A prominent luminescent organ is located on the base of the 7th thoracopod, except in *Bentheuphausia*.

Begin your study with an examination of the intact animal. The compound eyes are either simple or divided into anterodorsal and lateral parts. The antennular peduncle is either simple or the 1st segment has a flap-like lappet. The antennular flagella always are paired. The antenna carries a single flagellum; the exopod is developed into a broad scale or squama. Note that the carapace, which may be produced into a prominent rostrum, covers the thorax but does not enclose the gills. Frequently the lateral margins of the carapace have an interior or posterior spine or occasionally both. The gills are developed from the coxae of the 2nd through 8th thoracopods; those of the anterior appendages consist of a single branch. The posterior gills have several branches. Your attention already has been directed to the prominent luminescent or light organ at the base of the 7th thoracopod; similar luminescent organs generally also are present on each eyestalk and on the bases of each of the 2nd through 6th thoracopods. Additional luminescent structures can be observed on the ventral surfaces of each of the first 4 abdominal somites.

Generally all the thoracopods are similar in structure; however, in certain genera either the 2nd or the 3rd pair, or less frequently both the 1st and 2nd pairs, is extremely elongate. Most often these appendages terminate in a series of bristles; however, in the genus *Stylo-*

cheiron the ultimate and penultimate segments may form a chela-like structure.

The abdomen bears 5 pairs of well-developed pleopods used for swimming. In males, the endopods of the 1st and 2nd are modified as copulatory organs. The development of the 1st pair is more elaborate and their structure is an important taxonomic character. The appendages of the 6th abdominal somite are the uropods, which, together with the telson, form a tailfan. In most species the telson bears a pair of subapical movable spines. At the posteroventral margin of the 6th somite, a preanal spine frequently is present. Dorsally the abdominal somites may be armed with spines or produced to form prominent keels.

Once you have identified all of the major morphological structures of the euphausiid, remove one of the first 2 thoracic appendages. Generally the basis, ischium, and merus bear a series of closely set, plumose setae that join with the opposing members to form a food basket. If your specimen(s) belongs to one of the genera with specialized 1st, 2nd, or 3rd thoracopods, remove them and compare their modifications with the structure of the more typical thoracopods. What function would you ascribe to these specialized appendages?

Among the Eucarida, the euphausiaceans are the only group in which maxillipeds are not developed. The mouthparts consist of a labrum, labium, and paired mandibles, maxillulae, and maxillae. Examine each and identify the individual structural parts. How do the euphausiid mouthparts, particularly the mandibles, compare with those of the Peracarida you have studied?

Remove and make a temporary slide mount preparation of the male copulatory structure from the 1st pleopod. The processes vary, depending upon the species under study. Identify the structural elements of your particular specimen. A sketch may be helpful for comparison with the copulatory structure illustrated in Figure 39D.

Well-preserved, relatively large specimens should be used for a study of the major internal organ systems (see Figure 40). With a fine scalpel or sharpened microneedle sever the lateral muscle attachments of the carapace. Dorsally the carapace is held by a pair of prominent muscles and must be teased free very carefully, as the

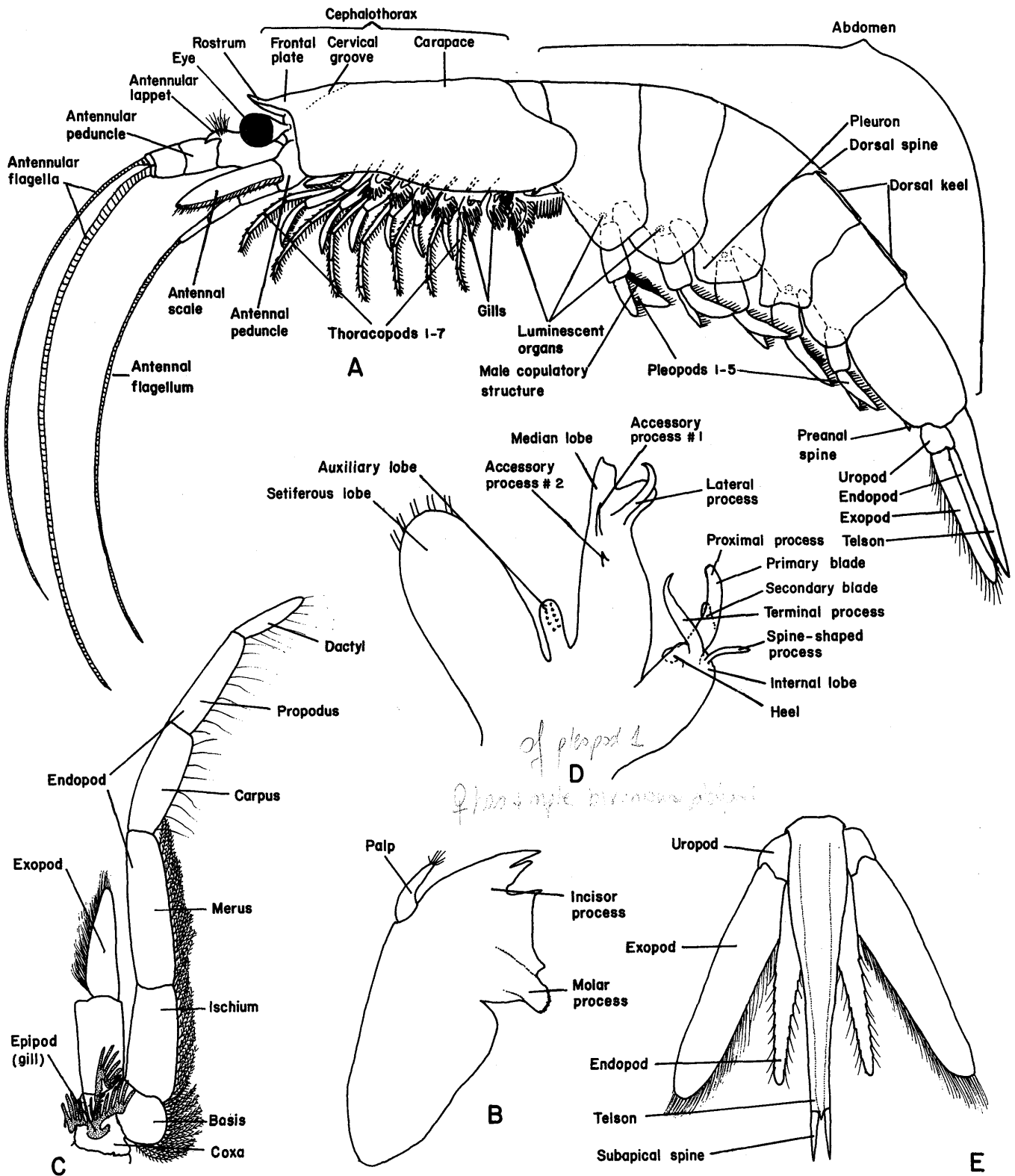






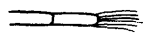




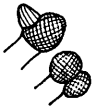


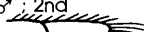



Figure 39 Euphausiacea: A. Male *Thysanopoda* (lateral view); B. Mandible; C. Typical thoracopod; D. Male copulatory structure; E. Telson and uropods.

TABLE 1 GENERIC CHARACTERS OF ADULT EUPHAUSIACEA

Genus	Thoracopods	Eyes	Rostrum	Ovisacs	Luminescent Organs
I <i>Bentheuphausia</i>	8 pairs, well developed	Imperfect 	Triangular, weakly produced	Unknown	None
II <i>Euphausia</i>	7th and 8th rudimentary, 5th and 6th similar		Variable	Absent	Typical distribution
<i>Meganyctiphanes</i>	8th rudimentary		Obsolete or weakly produced	Absent	Typical distribution
<i>Nyctiphanes</i>	8th rudimentary; exopod 6th and 7th in ♀, terminal segments 7th in ♂, all absent		Variable	Double	Typical distribution
<i>Pseudoeuphausia</i>	7th and 8th rudimentary; 6th distal segments reduced		Absent; frontal plate truncate	Double, fused	Typical distribution
<i>Thysanopoda</i>	8th endopod reduced, exopod normal; 7th short		Variable	Absent	Typical distribution
III <i>Nematobranchion</i>	8th rudimentary; 7th short; 3rd greatly elongate 		Variable, or rostral process	Unknown	Typical distribution
<i>Nematoscelis</i>	8th vestigial; 7th endopod biarticulate in ♀, exopod only in ♂; 2nd elongate 		Variable	Single	Typical distribution
<i>Stylocheiron</i>	1st and 2nd feeble; 8th rudimentary; 3rd greatly produced 		Variable	Single	Present on 7th thoracopod and 1st abdominal somite
<i>Tessarabrachion</i>	8th vestigial; 7th endopod absent in ♂; 2nd and 3rd elongate 		Absent; frontal plate short, triangular	Unknown	Typical distribution
<i>Thysanoessa</i> *	8th vestigial; 7th endopod absent in ♂; 2nd elongate 		Well developed, long to very long	Absent	Typical distribution

*Included in group III because, although variable, the majority of species exhibit characters of this group.

delicate blood vessels and heart lie directly beneath and posterior to this pair of muscles. The carapace in the rostral region often will have to be cut to free it. Remove the carapace, but before beginning your examination of

the cephalothoracic region cut open the abdominal exoskeleton. Returning to the cephalothorax, observe the antennal and mandibular muscles as well as the very prominent lateral and dorsal muscles. Anteriorly be-

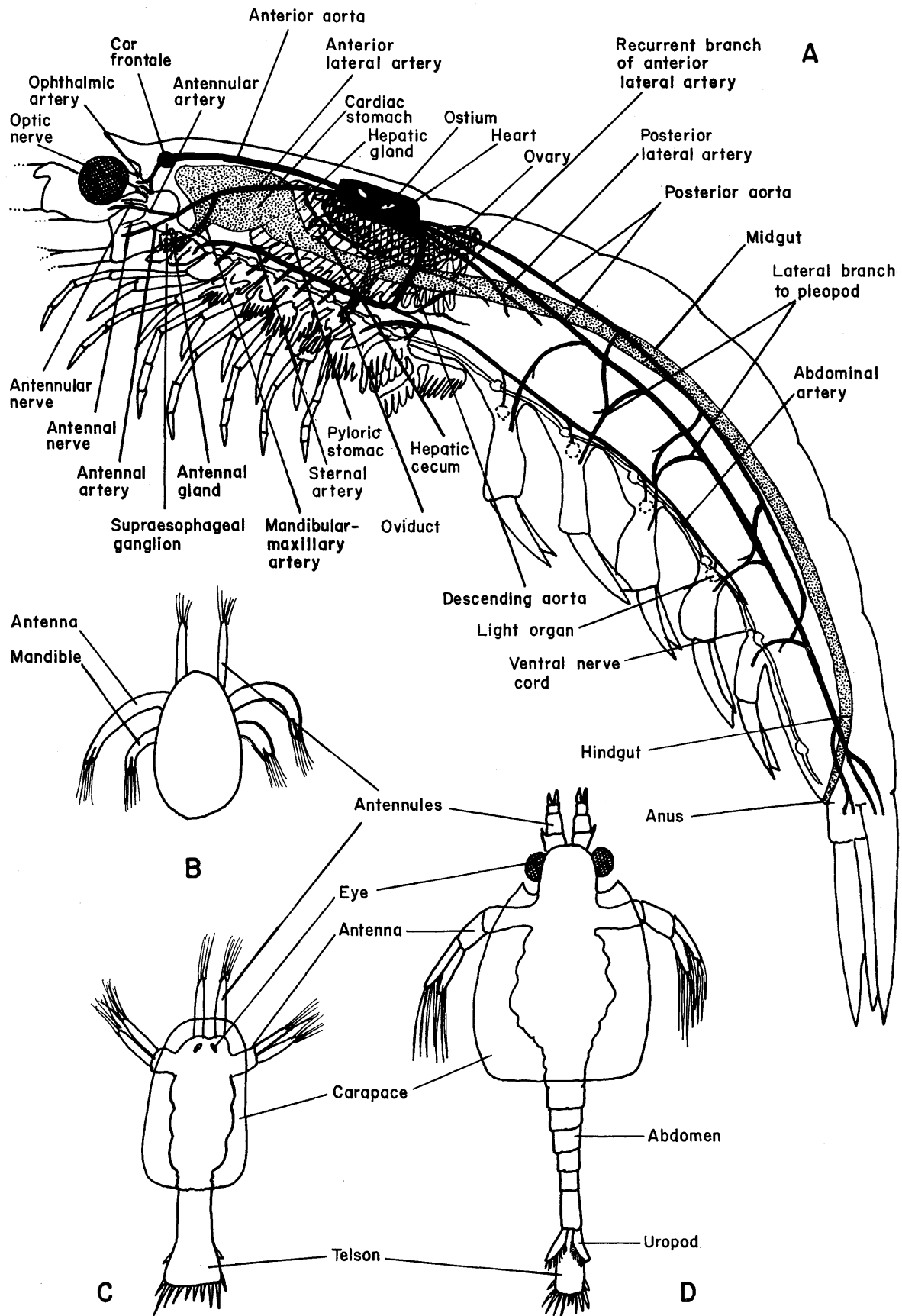


Figure 40 Euphausiacea: A. Diagrammatic euphausiacean with musculature removed to show major organ systems; B. Nauplius; C. Calyptopis; D. Furcilia.

tween the separated dorsal muscles note the dorsal surface of the cardiac stomach. The anterior aorta overlies the stomach, but will be difficult to detect until it can be traced from the heart. Carefully separate the dorsal muscles posteriorly to determine the position of the heart and the numerous blood vessels leaving it. Remove the dorsal and lateral muscles from one side of the body with caution, being careful in male specimens not to destroy the vas deferens, which crosses the musculature exteriorly on its course to the 8th thoracic somite. Removal of the musculature often will destroy the terminal portions of the anterior lateral artery, but its main path from the heart can be followed for some distance. Trace the anterior aorta over the cardiac stomach; anteriorly an enlargement of the vessel, a *cor frontale*, provides an additional pumping mechanism to improve circulation to the head. The anterior aorta provides blood to the eyes and anterior head region, while the anterior lateral artery serves the cephalic appendages. A lateral recurrent branch of the lateral artery and a small hepatic artery from the heart may be difficult to distinguish. The heart itself is subrectangular in shape, relatively small, and opens to the pericardium through 2 pairs of ostia. Observe the blood vessels leaving the heart posteriorly. The posterior aorta, which can be traced into the abdomen when the pair of dorsal abdominal muscles are removed, may be single or paired. A pair of posterior lateral arteries leads into the abdomen beside the midgut ceca, where they give off numerous small branches. Ventrally from the heart observe the descending aorta. This artery also may be paired, but if so, the second artery is much smaller and probably will not be discernable. The descending aorta provides blood to the sternal artery anteriorly and the abdominal artery posteriorly; however, neither of these blood vessels will be visible until you have removed the midgut and ceca. Blood from the sternal artery is supplied to the maxillae and first 6 pairs of thoracopods through lateral branches; branches of the abdominal artery supply the last 2 pairs of thoracopods and the luminescent organs of the abdomen. Follow the posterior aorta posteriorly. In each abdominal somite branches are given off to the appendages, musculature, and body tissues.

Return to the cephalothorax and examine the reproductive system. In the male the testes may be paired tubular structures lying to either side of the ceca and midgut, or a single testis may be horseshoe-shaped with lateral diverticula. The vas deferens may be coiled or straight. Trace this duct from the testis to its opening on the 8th thoracic somite. In the female, the ovaries lie posteroventrally of the heart and extend anteriorly over the anterior midgut, midgut ceca, and pyloric stomach. The posterior arteries from the heart often pass between the pair posteriorly. Trace an oviduct from the ovary to its opening on the coxa of the 6th thoracopod.

The euphausiid digestive system consists of an esophagus, cardiac and pyloric sections of the stomach, midgut, midgut ceca, and hindgut. The short esophagus leads from the mouth into the enlarged cardiac stomach. The structure of the cardiac stomach differs between filter feeding and predatory euphausiaceans. The cardiac stomach opens into the pyloric stomach through a cardiopyloric valve. At the entrance of the midgut a pair of hepatic ceca arise, which are highly convoluted and occupy much of the thoracic body cavity. Follow the midgut posteriorly. The beginning of the hindgut varies among taxa, but usually is at the level of the last abdominal somite. In some taxa a short blind diverticulum arises from the hindgut. The digestive tract terminates in a muscular anus. Excretion in euphausiaceans is by means of antennal glands.

The cardiac stomach frequently need not be removed to examine the nervous system, but the hepatic ceca should be, as should the lateral abdominal muscles from one side of the abdomen. Anteroventral to the cardiac stomach, observe the supraesophageal ganglion and the larger cephalic nerves. Follow the esophageal connective around one side of the esophagus to the fused ventral ganglia of the 3 pairs of mouthparts; then follow the ventral nerve cord the length of the body, distinguishing the individual segmental ganglia. In close proximity to the ventral nerve cord identify the sternal artery in the thorax and the abdominal artery in the abdomen.

Euphausiaceans pass through several stages and many instars during their larval development. Young hatch from eggs as free-swimming nauplii. This stage is followed by a metanauplius stage and then by a calytopis stage with several instars or substages. The 4th stage and its instars is referred to as the furcilia stage. The nauplius is characterized by the presence of 3 pairs of appendages: the antennules, antennae, and mandibles; no eyes are present and the body lacks segmentation. One or 2 instars or substages frequently occur. The metanauplius stage may be a single instar in some taxa or several substages. The metanauplius is characterized by the development of rudiments of the other cephalic appendages and the 1st thoracopods; eyes begin development and the mandibles become reduced. Neither the nauplius nor the metanauplius feeds. The calytopis stage is characterized by the presence of the carapace, the elongation of the trunk, and, in progressive instars or substages, the differentiation of somites. The appendages already present become more fully developed and subsequent limb buds develop. The furcilia stage with its several substages is characterized by the eyes being exposed and movable, the development of the thoracic and abdominal appendages, including the uropods, and by the development of the antennules toward the adult form. In the older literature a final cyrtopia stage, characterized by the adaptation of the pleopods for

swimming, was described; however, this stage now is included in the furcilliae as the 3rd of 4 phases. With the 4th phase the telson exhibits a reduction in the number of terminal spines. Some euphausiaceans have an abbreviated larval development in which one or more naupliar stages are passed through in the egg.

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ORDER AMPHIONIDACEA Sars, 1867

Recent species	One, <i>Amphionides reynaudii</i> (H. Milne Edwards, 1832).
Size range	2–3 cm.
Carapace	Cylindrical; extremely thin.
Eyes	Stalked, compound; with large inner tubercle.
Antennules	Biramous; without statocyst; with terminal dorsal papilla.
Antennae	Presumably with 5-segmented peduncle and with broad scale.
Mandibles	Vestigial.
Maxillulae	Vestigial.
Maxillae	Biramous; endites vestigial.
Maxillipeds	One pair.
Thoracic appendages	Six biramous pairs, with exopods reduced, in females; 7 pairs, 2–7 biramous with exopods reduced, 8th uniramous in males.
Abdominal appendages	Five biramous pairs of pleopods in males; 1st uniramous, 2nd–5th biramous in females. Uropods biramous.
Telson	Together with uropods forms tailfan.

Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 1 thoracic (maxilliped); thorax with 7; abdomen with 6, excluding telson.
Sexual characters	Gonopores of female on coxae of 6th thoracopods, presumably 8th of male. Female with enlarged uniramous 1st pleopods.
Sexes	Separate.
Larval development	Metamorphic; zoea → megalopa.
Fossil record	Recent.
Feeding types	Adults presumably do not feed.
Habitat	Marine, pelagic.
Distribution	Worldwide.

Although *Amphionides reynaudii* has a broad distribution, relatively few specimens are present in collections and thus available for study. The species is best known from its larvae. There are 9 to 12 larval substages, all bearing a general resemblance to the zoeal larvae of caridean shrimp, and for this reason *Amphionides* often has been classified among the Caridea. However, both larvae and adults have a number of characters that differ so greatly, not only from the carideans but from decapods in general, that the taxon is now classified as a distinct order of the Eucarida. Of particular import is the very specialized brood chamber of the female, formed by the elongate broad 1st pleopods and the single pair of maxillipeds. *Amphionides* is distinguished from the Caridea by the fact that the 2nd abdominal pleuron never overlaps the 1st. In this character the species agrees with the Dendrobranchiata, but can be distinguished from members of this suborder by the presence of an appendix interna, lack of a petasma in the male and thelycum in the female, in particular.

Adult females have an extremely thin carapace with well-developed postrostral spine and frequently also a rostral spine (see Figure 41). The eyes are small and a large tubercle, presumably a photophore, is present on the inner side. The antennules lack statocysts but do each have a terminal dorsal papilla. The scaphocerite of the antenna is very large and almost circular.

The thoracopods (2–7) are quite distant from the mouthparts; the 2nd are much shorter than the following pairs. Although the thoracopods are biramous, the exopods are small and apparently functionless; the endopods are segmented. The 5th pair is elongate. The 8th thoracomere lacks appendages in the female.

The 1st pair of pleopods in the female is elongate, reaching to the bases of the 2nd thoracopods, and uniramous; the fringe of setae and the shape, proximally concave and distally flat, suggest its function as a brood chamber. The remaining 4 pairs of pleopods are biramous swimming appendages; the endopods are each provided with an appendix interna.

The mandible and maxillule are vestigial; the maxilla and maxilliped are biramous but small. The degenerate condition of the digestive system suggests that the adult animals do not feed, or obtain food through absorption.

Adult males have been captured only rarely; therefore, descriptions of their morphology are limited. The 8th thoracopods are developed; the 1st pair of pleopods is biramous and adapted for swimming.

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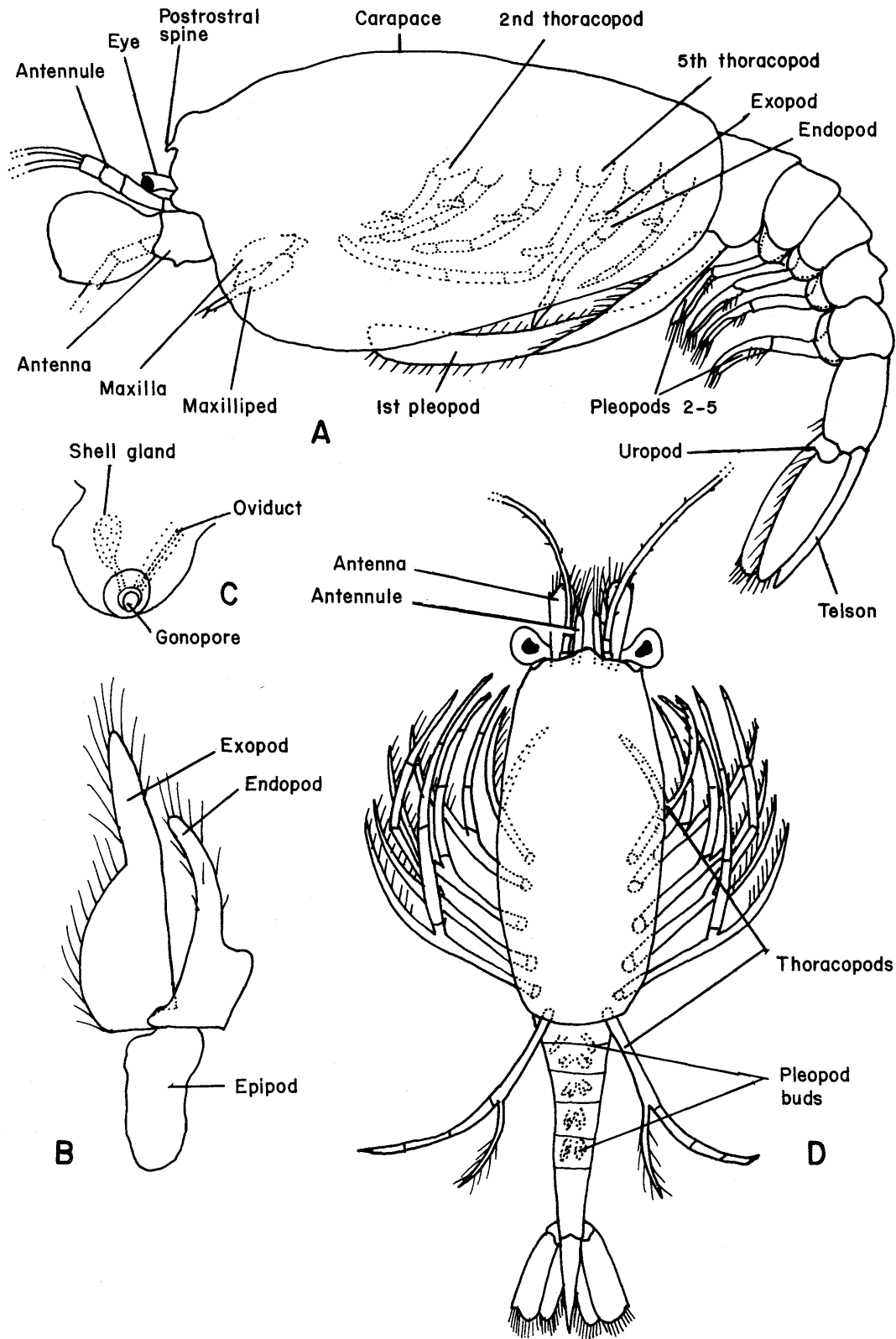


Figure 41 Amphionidacea: A. Diagrammatic *Amphionides*, adult female; B. Maxilliped; C. Base of 6th thoracopod showing gonopore, shell gland, and oviduct [A—C after Williamson, 1973]; D. Stage 2 larva [after Gurney, 1936].

ORDER DECAPODA Latreille, 1803

The Decapoda includes a great diversity of marine, freshwater, and semiterrestrial taxa characterized by the presence of a carapace developed to enclose the branchial chambers (branchiostegites) and by the modification of the 1st 3 pairs of thoracopods as maxillipeds; the remaining 5 pairs are typically walking legs or pereopods.

Within the Decapoda in general there is a basic gill pattern: a series of 4 gills are attached to each somite and/or appendage of the thorax; the gills have been named according to their positions. The gill attached to the lateral wall of the somite above the articulation of the appendage is called a pleurobranch; the 2 gills attached to the articular membrane between the body wall and the coxa are arthrobranchs; and the gill (a differentiation of the distal lobe of the epipod) that is inserted on the coxa is a podobranch. The proximal lobe of the epipod, when retained, often is referred to as a mastigobranch. There are 3 basic types of gills: dendrobranchiate, trichobranchiate, and phyllobranchiate. The phyllobranchiate gill (see Figure 42A) is the simplest in structure,

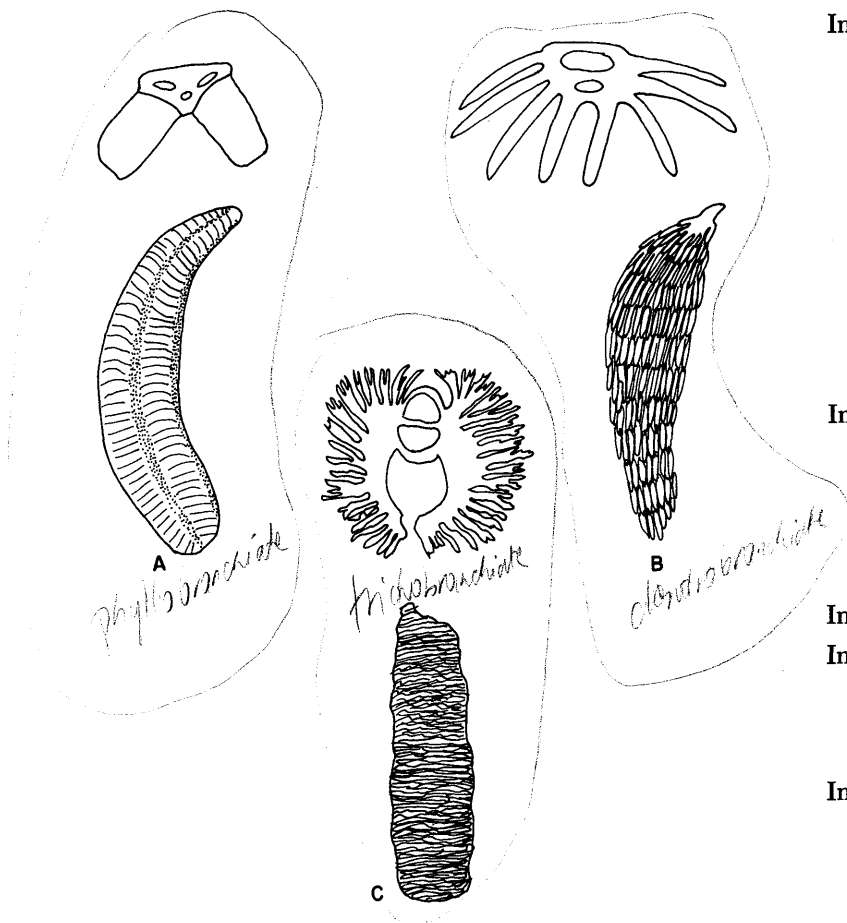


Figure 42 Gill structure of decapods: A. Phyllobranchiate, in transverse section (upper) and entire (lower); B. Trichobranchiate, in transverse section (upper) and entire (lower); C. Dendrobranchiate, in transverse section (upper) and entire (lower) [after Calman, 1909].

consisting of an axis with blood vessels and a pair of flattened branches. The trichobranchiate gill (see Figure 42B) consists of a series of filamentous branches arranged in several series around the axis. In dendrobranchiate gills (see Figure 42C) the primary biserial branches are divided into arborescent bunches.

As previously indicated, discussions of the major decapod groups will be at unequal levels within the taxonomic hierarchy. For reference and orientation the classification, as used in the text, is given below; taxa marked with an asterisk are discussed in detail.

Suborder Dendrobranchiata

Superfamily Penaeoidea

Family Penaeidae*

Superfamily Sergestoidea

Family Sergestidae

Suborder Pleocyemata

Infraorder Stenopodidea

Family Stenopodidae*

Infraorder Caridea*

Superfamily Procaridoidea

Superfamily Oplophoroidea

Superfamily Bresilioidea

Superfamily Stylodactyloidea

Superfamily Pasiphaeidea

Superfamily Palaemonoidea

Superfamily Psalidopodoidea

Superfamily Alpheoidea

Superfamily Pandaloidea

Superfamily Crangonoidea

Superfamily Phyetocaridoidea

Infraorder Astacidea

Superfamily Astacoidea*

Superfamily Parastacoidea

Superfamily Nephropoidea

Family Nephropidae

Family Thaumastocheilidae

Infraorder Austroastacidea

Infraorder Palinura

Superfamily Glypheoidea

Superfamily Eryonoidea

Superfamily Palinuroidea

Infraorder Anomura

Superfamily Thalassinoidea

Superfamily Coenobitoidea

Superfamily Paguroidea*

Superfamily Galatheoidea

Superfamily Hippoidea

Infraorder Brachyura

Section Dromiacea

Superfamily Dromioidea

Superfamily Homoloidea

Section Oxystomata
 Superfamily Dorippoidea
 Superfamily Calappoidea
 Superfamily Raninoidea
 Section Oxyrhyncha
 Superfamily Majoidea
 Superfamily Mimilambroidea
 Superfamily Parthenopoidea
 Section Cancridea
 Superfamily Crystoidea

Section Brachyrhyncha
 Superfamily Portunoidea*
 Superfamily Xanthoidea
 Superfamily Bellioidea
 Superfamily Grapsidoidea
 Superfamily Pinnotheroidea
 Superfamily Potamoidea
 Superfamily Ocypodoidea
 Superfamily Hapalocarcinoidea

Classification from Bowman and Abele (personal communication); incomplete at family level.

SUBORDER DENDROBRANCHIATA Bate, 1888

Recent species	Approximately 350.
Size range	Up to 31 cm.
Carapace	Laterally compressed or cylindrical.
Eyes	Stalked, compound; rarely reduced.
Antennules	Biramous; with stylocerite.
Antennae	With 5-segmented peduncle and scaphocerite.
Mandibles	With palp.
Maxillulae	With segmented endopodal palp.
Maxillae	Biramous; with 2 bilobed endites.
Maxillipeds	Endopods of 1st with 5 segments; without crista dentata.
Thoracic appendages	First 3 pairs chelate; sometimes without exopods.
Abdominal appendages	Pleopods biramous; usually with petasma, sometimes also with appendix masculina; without appendix interna. Uropods biramous.
Telson	Together with broad uropods forms tailfan.
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 3 thoracic (maxillipeds); thorax with 5; abdomen with 6, excluding telson.
Sexual characters	Gonopores on coxae of 3rd pereopods (6th thoracopods) of female, 5th of males (8th thoracopods); male with petasma, female with thelycum; eggs shed into sea.
Sexes	Presumably separate.
Larval development	Metamorphic; nauplius → protozoa → zoea → postlarva.
Fossil record	Permotriassic to Recent.
Feeding types	Various.
Habitat	Marine, brackish, or freshwater; often benthic, sometimes burrowing in mud.
Distribution	Worldwide.

Although differences are present between the penaeoids (superfamily Penaeoidea) and sergestoids (Superfamily Sergestoidea), the instructions given for the study of the Dendrobranchiata have been made sufficiently general so they will be applicable to most of the taxa. The il-

lustrations presented have been based on species of *Penaeus*.

Begin your study with an examination of the general morphology of the animal (see Figure 43). The carapace completely covers the cephalothorax and encloses the

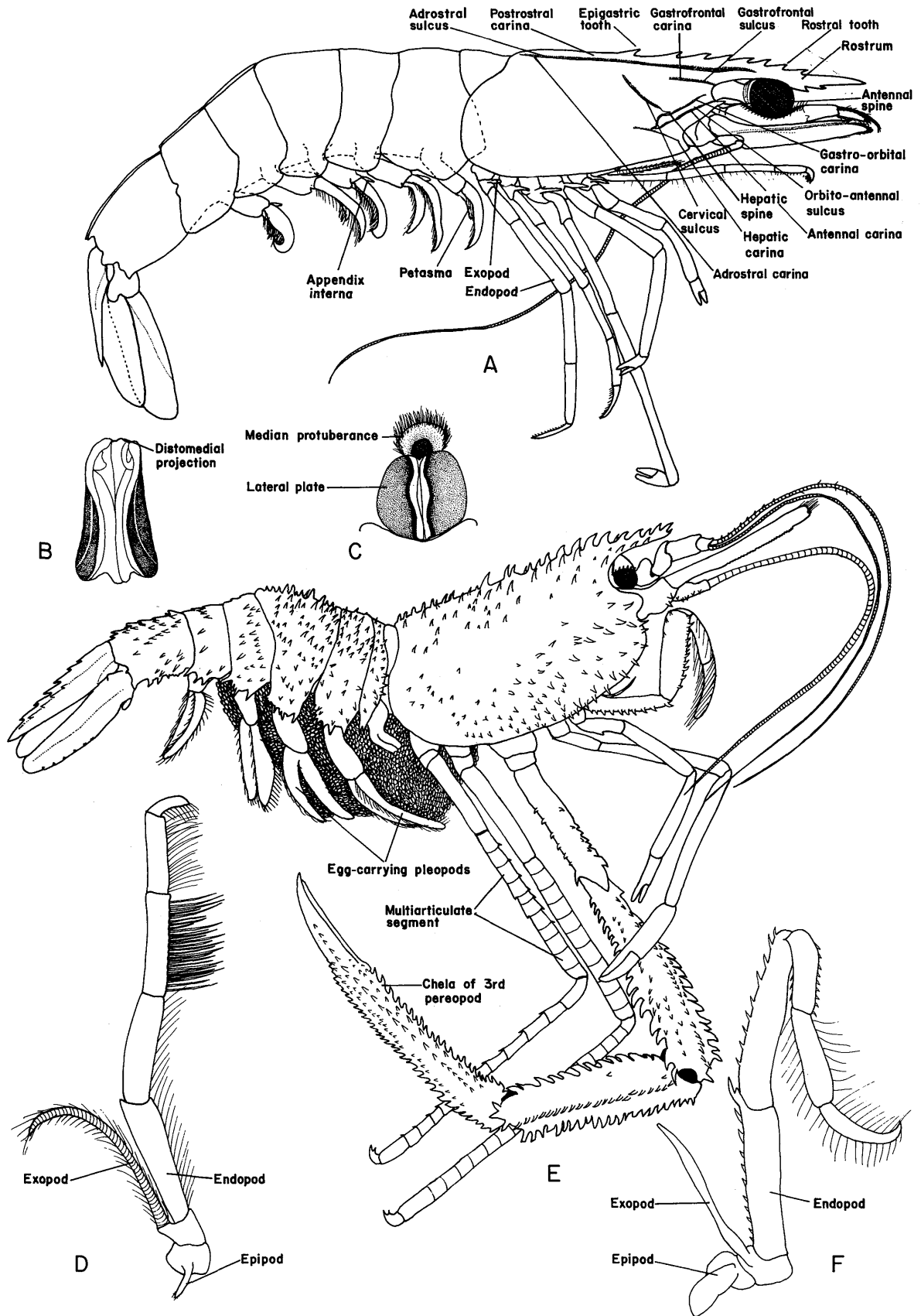


Figure 43 Decapoda: A—D, Dendrobranchiata; E—F, Stenopodidea. A. Typical penaeoidean (lateral view), showing carapace armature and ornamentation; B. Representative petasma of male; C. Representative thelycum of female; D. 3rd maxilliped; E. Typical stenopodidean (lateral view); F. 3rd maxilliped.

gills; it is fused dorsally to all the thoracic somites. The carapace usually is produced anteriorly to form a well-developed, elongate rostrum that is armed with dorsal and sometimes also ventral marginal spines. Posterior to the rostrum, in the dorsal midline, a postrostral carina or median ridge very frequently separates a pair of rostral grooves. The carapace usually is provided with a hepatic spine and frequently with 1 or more lateral carapace grooves. The compound eyes are set on a pair of movable peduncles and usually are directed laterally during life.

The antennules each consist of a basal peduncle or protopod of 3 segments and a pair of flagella. Very frequently the anterolateral angle of the 1st peduncular segment is produced into a small acute spine, the stylocerite. Examine the dorsal surface of the 1st segment and locate the opening to the statocyst. This segment also contains a depression for the eye accompanied by a dense row of setae often called an eye brush or pro-artema. The antennular flagella appear to serve a chemoreceptory function; frequently in males the median or inner flagellum is sexually modified through a dorsoventral flattening of the flagellum and the addition of a number of stout processes on the dorsal margin. It is presumed that these modifications aid the males in locating mature females. Each antenna is represented by a basal 2- or 3-segmented endopod, a scalelike exopod, and a long flagellum. It is customary to refer to the segments of the protopod and endopod together as the antennal peduncle and to the exopod as the scaphocerite or antennal acicle or scale. The antennal peduncle usually consists of a coxa, basis, and 3 endopodal segments. The flagellum is long, often 2 or 3 times the length of the body, straight in penaeoids, but with a bend in sergestoids.

The 1st pair of pereopods usually are short and often are used more for food manipulation than for locomotion. The first 3 pairs are chelate; the 4th and 5th may be subchelate or simple, well developed or, as in sergestoids, reduced. The pereopods usually consist of a 2-segmented protopod (coxa and basis) and 5-segmented endopod (usually ischium, merus, carpus, propodus, and dactyl). Exopods may be present or absent, but when present usually are quite small. The gills are dendrobranchiate; the gill formula typically is $19 + 6$ mastigobranchs (7 pleurobranchs, 11 arthrobranchs, and 1 podobranch). Examine your particular specimen and list the number and types of gills that you find associated with each appendage.

As in other eucarideans the abdomen is well developed and elongate. Each tergite is laterally expanded as a latero-tergal plate or pleuron. Each successive pleuron is overlapped by the preceding one. The abdomen consists of 6 somites, each usually with a pair of biramous appendages, and a well-developed telson. The first 5 pairs of appendages are developed as pleopods, the

primary swimming structures. In males, the endopods of the 1st pair are strongly modified to form a copulatory structure, the petasma. The medial margin of each half of the petasma is joined to its counterpart by a series of minute knobs. The structural details of the petasma frequently are used as diagnostic characters of species. In some genera the 2nd pair of pleopods also are modified. In these the endopods form the appendix masculina. Be sure to examine male specimens and study the details of these appendages. In females the sternal plates of the 7th and 8th thoracic somites develop a series of grooves and protuberances to form a sperm receptacle called the thelycum. The shape and configuration of the thelycum also is an important diagnostic character for species determination. The appendages of the 6th abdominal somite are the biramous uropods, which are well developed, and together with the telson form the tailfan.

As previously mentioned, the mouthparts of decapods include 3 pairs of maxillipeds. Remove and examine each of the maxillipeds from one side of the body. Identify the segments of the endopod. How does the 1st maxilliped compare with the 1st maxillipeds of the peracaridans you have examined? Be sure that you can distinguish endites from exites. Internal to the 1st maxilliped is the maxilla. Care should be taken when removing the maxilla, as the scaphognathite lays considerably laterad, in the incurrent water channel of the gills; it acts as a water pump for the gills. Removal of the maxilla will expose the maxillule. Between the maxillule and the mandible observe the fleshy paragnath. Remove the maxillule and then the mandible. Identify the incisor and molar processes, which often are separated only by a narrow groove. In some, however, a setal row also may be present. The mandibular palp is well developed.

The description of the major organ systems of the Dendrobranchiata is based on species of the Penaeidae (see Figure 44). Begin your examination by removing the carapace and the abdominal pleura from one side of the animal. To remove the carapace, which in decapods is fused to all the thoracic somites, make a shallow incision along the adrostral sulcus and gently free the carapace from the underlying membrane. Care is required in removing the carapace because the heart and pericardium are very close to the dorsal surface.

The penaeid body is quite muscular, and while we will not attempt a detailed description of the musculature, certain prominent muscles will have to be removed before the organ systems can be observed. Dorsolateral and lateral to the heart are the lateral thoracoabdominal muscles. Carefully remove enough of the muscle fibers to clearly observe the heart and its arteries. The heart receives blood from the pericardium through 3 pairs of ostia, 2 dorsal pairs and 1 lateral pair. From the anterior apical end of the heart a small unpaired artery extends a short distance; this may be the vestige of the anterior aorta of lower malacostracans. Anteriorly from the heart

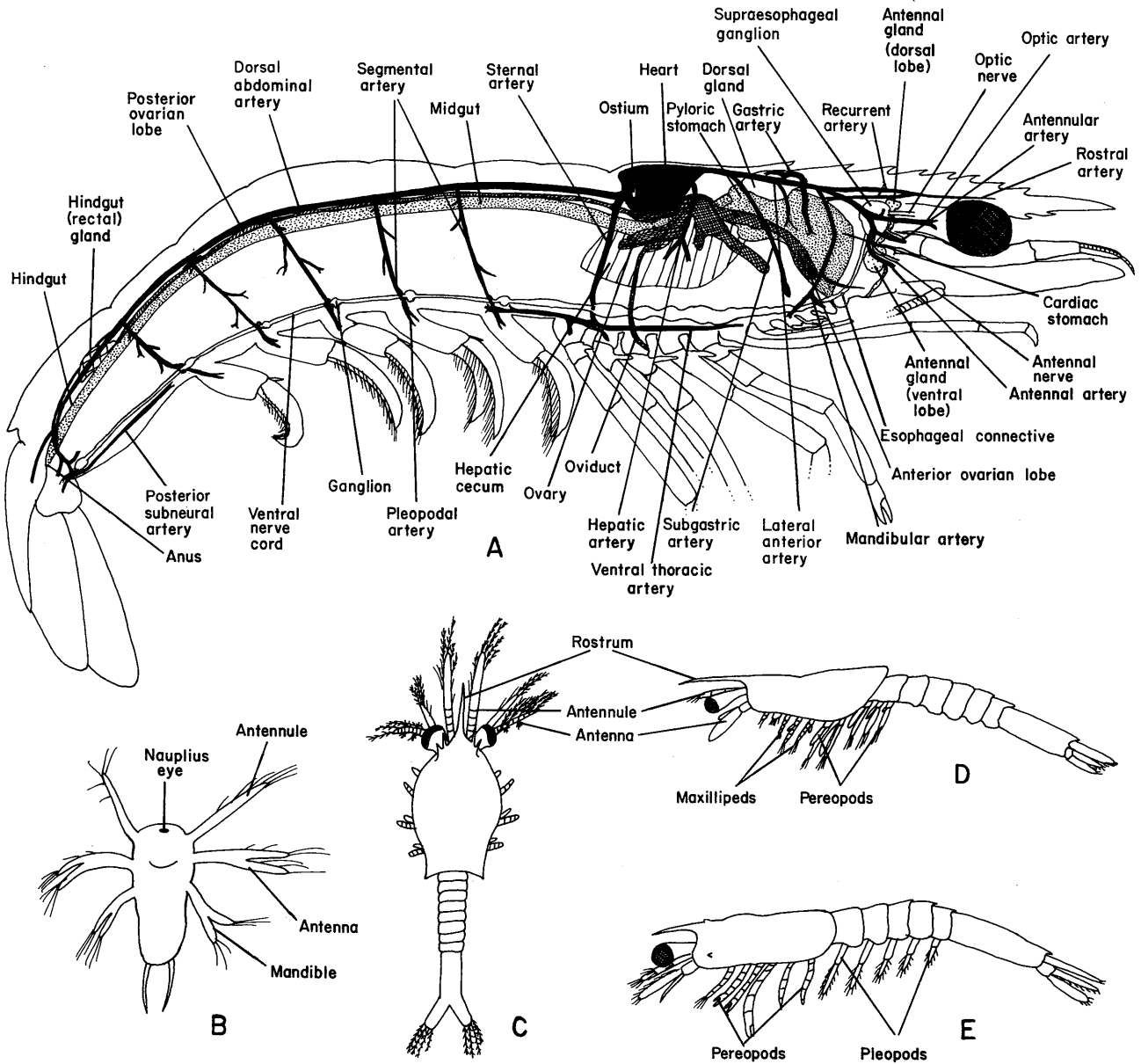


Figure 44 Decapoda, Dendrobranchiata: A. Diagrammatic penaeoidean with musculature removed to show major organ systems. B. Nauplius I; C. Zoea I; D. Mysis I; E. Postlarva I.

trace one of the pair of lateral anterior arteries and its several branches. The first to branch off is the subgastric artery that provides blood to the glandlike organ beneath the cardiac stomach. A short distance anteriorly locate the gastric artery, which serves the dorsal and ventral regions of the cardiac stomach, and the dorsal gland (a structure of unknown function). Further rostrad the lateral anterior artery turns toward the midline and joins its counterpart from the opposite side to form a median longitudinal vessel. At the point of fusion, or slightly before, a pair of optic arteries proceed to the ocular peduncles, giving off the cephalic arteries to the supraesophageal ganglion enroute. The anterior part of the

lateral anterior artery continues into the rostrum as the rostral artery and the posterior part turns posteriorly (as the recurrent artery) to the cardiac stomach. Other branches of the lateral anterior arteries are the mandibular and antennal arteries that supply blood to the muscles of the mandibles, antennules, and antennae. Returning to the heart, identify the pair of hepatic arteries that also leave the heart anteriorly. These vessels provide the blood supply to the hepatic cecum or hepatopancreas.

From the posterior end of the heart locate the large, unpaired posterior abdominal artery. Almost immediately the sternal artery is given off; in some malacostracans this artery arises from the heart itself.

Follow the sternal artery ventrally; it passes through the ventral nerve cord between the ganglia of the 3rd and 4th pereopods. Beneath the nerve cord the sternal artery divides into the two branches of the ventral thoracic artery. The anterior branch provides blood to the anterior thoracic appendages and to the nerve cord; the posterior branch provides large vessels to the 4th and 5th pereopods and then proceeds into the abdomen. Return to the posterior abdominal artery and trace its course posteriorly between the dorsal abdominal muscles. At the level of each somite it gives off a pair of segmental arteries that supply blood to the musculature, pleopods, and ventral nerve cord. Posteriorly the dorsal abdominal artery bifurcates around the hindgut or rectal gland and proceeds along the hindgut as a paired vessel, fusing again near the end of the hindgut. Branches are provided to the telson, uropods, and muscles of the region before the fused artery turns anteriorly beneath the ventral nerve cord as the posterior subneural artery. This latter artery appears to extend only into the 6th abdominal somite. Blood is returned to the pericardium and heart through a series of sinuses in the appendages and hemocoel.

The reproductive system of the male consists of a pair of testes lying on the dorsal surface of the hepatic cecum (hepatopancreas) ventral to the heart. Each testis is comprised of several lobes, frequently extending over the surface of the cecum. From the posterior end of the testis the vas deferens extends ventrally to a terminal ampoule situated above the male gonopore on the sternum of the 8th thoracic somite. This ampoule is primarily a glandular structure that secretes the spermatophore. In the female the ovaries also are paired. Usually an anterior projection of the ovary can be traced along the cardiac stomach, and several lobes can be distinguished on the dorsal surface of the hepatic cecum. An additional lobe, the dorsal ovarian lobe, should be located posterior to the heart; trace this lobe into the abdomen dorsolateral to the midgut. Locate the oviduct and follow it to the female gonopore on the coxa of the 3rd pereopod.

The penaeid digestive system consists of a muscular esophagus, prominent stomach with well-defined cardiac and pyloric sections, midgut, hindgut, and digestive gland. The cardiac stomach contains the grinding part of the stomach, the gastric mill, and this structure should be examined when the stomach is removed. The primary digestive gland is the hepatic cecum, also referred to by some as the hepatopancreas. It is a large gland situated in the posterior region of the thorax beneath and somewhat anterior to the heart, consisting of a mass of closely packed tubules. Juices from the gland enter the pyloric stomach ventrally near its junction with the midgut. In penaeids the midgut is elongate, extending nearly the entire length of the abdomen. Near the beginning of the hindgut, a small hindgut or rectal gland arises. The func-

tion of this gland is not known, but a role in osmotic regulation has been proposed for it. The hindgut terminates in a muscular anus. Returning to the stomach, remove it to reveal the nervous system and ventral blood vessels. Be sure to examine the gastric mill, which in penaeids is relatively simple; it consists of a strong median tooth and series of lateral denticles. Excretion is via antennal glands, but the glands themselves are diffused and not easily recognized. Externally the excretory pore can be identified.

Anteriorly in the cephalon beneath the rostrum locate the supraesophageal ganglion. Identify the large optic, antennal, and antennular nerves leaving the ganglion. The smaller oculomotor and tegumental nerves may not be as easily distinguished. Trace the esophageal connectives around the esophagus to the ventral nerve cord. The ganglia of the mouthparts are conspicuously fused; those of the first 3 pereopods are indicated by segmental swellings. The nerve cord is divided into 2 longitudinal tracts between the 3rd and the coalesced 4th and 5th ganglia to allow for passage of the sternal artery. Trace the nerve cord into the abdomen; each of the anterior 5 ganglia gives off a pair of nerves, one to the musculature and one to the pleopod on each side of the body.

Larval development in the Dendrobranchiata is metamorphic and has been described best for commercial species of *Penaeus*. All penaeid species have 3 distinct larval stages and numerous substages. The principal stages are the naupliar, zoeal, and mysis stages followed by metamorphosis to postlarvae. The naupliar stage usually consists of 5 or 6 substages during which the antennules, antennae, and mandibles are the only well-developed appendages. During the 3 zoeal substages the maxillulae and maxillae become functional, stalked eyes develop, and abdominal segmentation appears. During the 3 mysis substages the body takes on a shrimplike appearance, the pereopods become well developed and functional, and toward the conclusion to this stage the pleopods develop. Postlarvae may be recognized by the appearance of chelate first 3 pairs of pereopods; locomotion is a function of the pleopods.

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SUBORDER PLEOCYEMATA Burkenroad, 1963

INFRAORDER STENOPODIDEA Huxley, 1879

Recent species	Approximately 30.
Size	2–7 or 8 cm.
Carapace	Usually cylindrical.
Eyes	Stalked, compound.
Antennules	Biramous.
Antennae	With 5-segmented peduncle and scaphocerite.
Mandibles	With palp.
Maxillulae	With endopodal palp.

Maxillae	Biramous; with 2 bilobed endites.
Maxillipeds	Endopod of 1st with 2 segments; without crista dentata.
Thoracic appendages	First 3 pairs chelate; without exopods.
Abdominal appendages	Pleopods biramous; usually with appendix masculina; without appendix interna. Uropods biramous.
Telson	Together with broad uropods forming tailfan.
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 3 thoracic (maxillipeds); thorax with 5; abdomen with 6, excluding telson.
Sexual characters	Gonopores on coxae of 3rd pereopods of female; on 5th of male; male usually with appendix masculina; eggs carried on female pleopods.
Sexes	Presumably separate.
Larval development	Metamorphic; protozoa → zoea → postlarva.
Fossil record	Recent.
Feeding types	Usually particulate.
Habitat	Marine; frequently commensal.
Distribution	Tropical or subtropical.

Of the infraorders of the Pleocyemata, the Stenopodidea is by far the smallest, with only a little more than three dozen species described. It is probably best known by one of its more conspicuous members, *Stenopus hispidus* Olivier, the largest of the cleaner shrimp. Stenopodideans share a number of characters in common with the Dendrobranchiata, but are separated immediately by their trichobranchiate gills and by the massive, elongate 3rd pereopods (see Figure 43). If specimens are available, compare the general morphology of the stenopodideans with that of the dendrobranchs. Note particularly the development of the rostrum and scaphocerite and the armature of the cephalothorax and abdomen. Multiarticulate carpi and propodi of the 4th and 5th pereopods are characteristic of the genus *Stenopus*.

Larvae hatch as inert pre- or protozoae, but within hours molt into the 1st zoeal substage. At this stage the rostrum is well developed; the carapace lacks spines but several abdominal spines are present. All cephalic appendages are present, as are the 3 pairs of maxillipeds and 1st pereopods. Six zoeal substages or instars are followed by metamorphosis to the megalopa or postlarva, in which the pleopods are used for locomotion.

INFRAORDER CARIDEA Dana, 1852

Recent species	Approximately 1600.
Size range	Up to 32 cm.
Carapace	Cylindrical, laterally compressed, or slightly compressed dorso-ventrally.

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Eyes	Stalked, compound; occasionally reduced or absent.
Antennules	Bi- or triramous; with stylocerite.
Antennae	With 5-segmented peduncle and scaphocerite.
Mandibles	With or without palp.
Maxillulae	With endopodal palp.
Maxillae	Biramous; usually with bilobed distal and entire proximal endites.
Maxillipeds	Endopod of 1st with 2 or fewer segments; without crista dentata.
Thoracic appendages	First 2 pairs usually chelate; sometimes without exopods.
Abdominal appendages	Pleopods usually biramous; often with appendix masculina; usually also with appendix interna. Uropods biramous.
Telson	Together with broad uropods forms tailfan.
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 3 thoracic (maxillipeds); thorax with 5; abdomen with 6, excluding telson.
Sexual characters	Gonopores on coxae of 3rd pereopods of female, 5th of male; male often with appendix masculina; eggs carried on pleopods of female.
Sexes	Separate; protandry and protogyny occur.
Larval development	Metamorphic; protozoa → zoea → megalopa; sometimes abbreviated.
Fossil record	M. Jurassic to Recent.
Feeding types	Various.
Habitat	Marine, brackish, or freshwater; planktonic or benthic; sometimes commensal; rarely semiterrestrial.
Distribution	Worldwide.

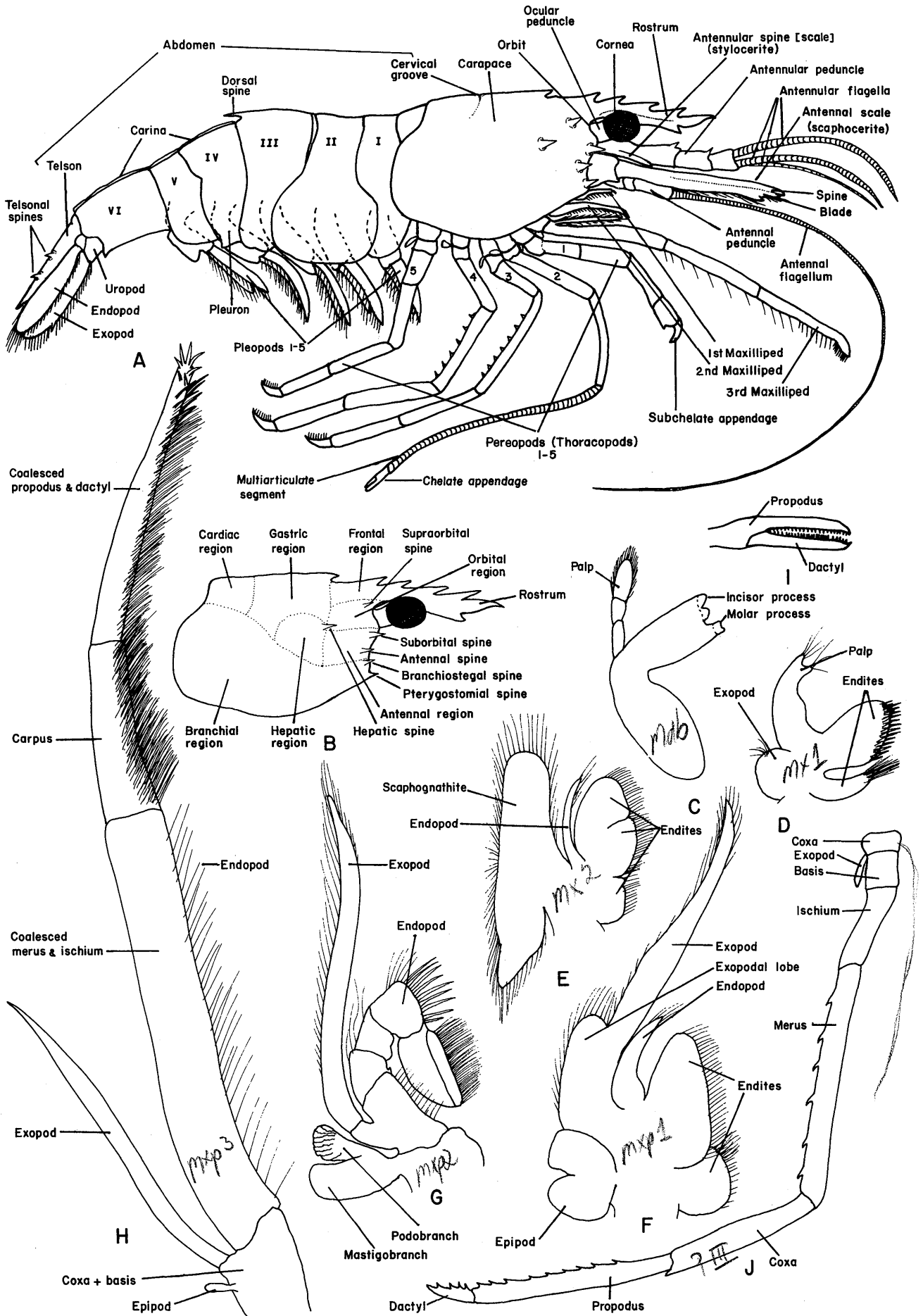
Although the Caridea resemble the Penaeoidea, Sergestoidea, and Stenopodidea in general body form, two important characters serve immediately to distinguish caridean taxa (see Figure 45). Examine the pleura of the first 3 abdominal somites. In contrast to the condition observed in penaeoids, sergestoids, and stenopodids, the 2nd abdominal pleura overlap the pleura of both the 1st and the 3rd somites in all carideans. The other important difference is the lack of terminal chelae on the 3rd pereopods.

The carapace of carideans is subdivided into regions (see Figure 45B), and for ease in understanding and working with descriptions of the numerous and diverse caridean taxa, you should commit these regions to memory. The basic subdivisions of the cephalothorax can be recognized through the number of changes in body shape that occur within the Decapoda. Note the number of carapace spines, not present in penaeoids, that occur

in the various caridean taxa. The presence or absence of particular spines is of generic and specific import. The caridean rostrum is extremely variable in both length and armature, and in some taxa it even is articulated with, rather than fused to, the carapace. In the Alpheidae the carapace forms a broad platelike covering over the eyes, thus restricting their movement; the rostrum, when present, is a small spine between the orbital hoods.

As in dendrobranchs and stenopodids, the antennules consist of a 3-segmented peduncle and a pair of flagella; however, in some caridean taxa the lateral (outer) flagellum is subdivided distally for part of its length, causing the impression that there are 3 flagella. A stylocerite usually is present. The antennal peduncle consists of a 2-segmented protopod and a 3-segmented endopod. The scaphocerite (exopod) usually is made up of a sharp spinelike process and a broad blade; however, one or the

Figure 45 Decapoda, Caridea: A. Typical caridean (lateral view); B. Cephalothorax (lateral view) showing carapace regions and armature; C. Mandible; D. Maxillule; E. Maxilla; F. 1st maxilliped; G. 2nd maxilliped; H. 3rd maxilliped; I. Chela with pectinate fingers; J. 3rd pereopod.



other, or occasionally both, may be absent. The antennal flagellum usually is very long.

The 5 pairs of pereopods generally consist of 2 chelate pairs (1st and 2nd) and 3 simple; however, there are many variations. The Crangonoidea, for example, all have subchelate 1st pereopods; in the Pandalidae, if chelae are present on the 1st pereopods, they are microscopic in size. In contrast, the first 2 pairs in the Alpheidae are considerably larger than the other pereopods, and one usually is massive. Examine the first 2 pairs of pereopods of your specimens and identify the individual segments. Depending upon the taxon, the carpus of the 2nd pereopod consists of a single article or may be subdivided into 2 to many articles. The cutting edges of the dactyl and propodal finger of the chela also are diagnostic in certain taxa. In your specimens are the edges pectinate? Exopods may be present or absent, depending upon the taxon. The gill formulae among carideans is extremely variable. In some species of *Pandalus*, for example, the formula is 12 + 7 mastigobranchs, whereas in *Hippolyte* spp. it is 5 + 2 mastigobranchs. Determine the gill formulae for your specimens.

The abdomens of carideans frequently are armed with spines or sometimes developed into carinae, and the telsons frequently carry several small spines. Observe the abdominal armature and ornamentation of your specimens. Examine the first 2 pairs of pleopods of a male specimen. A petasma, such as occurs in penaeoids, is absent; however, an appendix masculina often is developed on the 2nd pair. In both sexes the pleopods of each pair usually are coupled by an appendix interna (a pair of outgrowths from the endopods, provided with a series of small coupling hooks, or retinacula) enabling them to stroke simultaneously.

Remove the mouthparts, examine each, and compare them with the mouthparts of the penaeoids examined previously. Frequently the number of segments of the maxillipeds is reduced by the coalescence of 2 or more segments. In some taxa the terminal segment of the 2nd maxilliped articulates with the external margin of the penultimate segment rather than with the distal margin. The endopod of the 1st maxilliped is short; the exopod frequently has an epipod. The maxilla has a well-developed scaphognathite and endites. The maxillule has a pair of endites and an endopodal palp. The mandible may or may not have a palp.

Internally the organ systems are similar to those described for the Penaeidae; however, your attention is called to certain differences. In some caridean hearts 5 pairs of ostia are present. A median ophthalmic artery (or anterior aorta) also may be present and may be provided with a cor frontale. The lengths of the midgut and hindgut vary among taxa. The diverticula of the hepatic cecum usually are much longer in carideans than in penaeids. Excretion in carideans is via the antennal

glands; however, the length of the excretory canal varies considerably.

Larval development in the Caridea also is metamorphic, but more abbreviated than in the Penaeoidea. The naupliar stage is passed through in the egg and the young hatch as zoeae. One to several zoeal substages usually are followed by the mysid stage and then metamorphosis to postlarval form. The degree of development in each of the stages is comparable with that of the Penaeidae.

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INFRAORDER ASTACIDEA Latreille, 1803

Recent species	Approximately 750.
Size range	Up to 64.3 cm.
Carapace	Usually subcylindrical or subovoid.
Eyes	Stalked, compound; occasionally reduced or absent.
Antennules	Biramous; peduncle with 3 segments.
Antennae	Peduncle with 5 segments; with or without scaphocerite.
Mandibles	Usually with palp.
Maxillulae	With endopodal palp.
Maxillae	Biramous; with 2 bilobed endites.
Maxillipeds	Endopod of 1st with 2 or fewer segments; usually with crista dentata.
Thoracic appendages	Uniramous; first 3 pairs chelate, 5th often chelate.
Abdominal appendages	Pleopods uni- or biramous; often with appendix masculina or other copulatory structures in males. Uropods biramous.
Telson	Together with broad uropods forms tailfan.
Tagmata	Cephalothorax and abdomen.
Somites	Head with 5 + 3 thoracic (maxillipeds); thorax with 5; abdomen with 6, excluding telson.
Sexual characters	Gonopores on coxae of 3rd pereopods of female, on 5th of male; male often with appendix masculina or other copulatory structures; female often with annulus ventralis.
Sexes	Presumably separate.

Larval development	Metamorphic or epimorphic.
Fossil record	Permotriassic to Recent.
Feeding types	Various; often on plant material in freshwater species.
Habitat	Marine, brackish, or freshwater; usually benthic.
Distribution	Worldwide, except for Africa and parts of Asia.

This infraorder is subdivided into three superfamilies; the Astacoidea, containing the freshwater crayfishes of the northern hemisphere; the Parastacoidea, the freshwater crayfishes of the southern hemisphere; and the Nephropoidea, the marine lobsters. Several species of North American crayfishes are classical laboratory study animals, so you probably have examined specimens in general invertebrate courses. Your present study of the crayfish and marine lobsters, if specimens are available, should include not only the examination of the morphology of this group but also a comparison with similar structures of the previously studied decapods.

Most crayfish are relatively unspecialized morphologically, although their successful adaptation to fresh water has been accompanied by some physiological specializations and adaptations. The cephalothorax typically is divided into anterior and posterior regions by the cervical groove (see Figure 46). The rostrum is a large, broad, and dorsoventrally flattened structure that is flanked posterolaterally by a pair of postorbital ridges. The branchiostegites are delineated laterally. The anterior carapace frequently is armed with small orbital or hepatic spines. The posterior carapace is marked dorsally by a pair of branchiocardiac grooves; the area between the grooves usually is referred to as the areola. If specimens of nephropoideans are available, compare the carapaces of the two taxa. Characteristically the nephropoidean carapace is marked by numerous grooves, ridges, spines, teeth, and tubercles, all of which are of considerable diagnostic importance (see Figure 47B). The carapace lines and grooves also are especially significant in paleontological studies.

Of the 5 pairs of pereopods, the first 3 always are chelate in this infraorder; the 1st pair usually is much more massive than the others. The pleopods generally are not as well developed as in the Dendrobranchiata and other infraorders of the Pleocyemata studied previously. In some taxa the 1st pair of pleopods is absent. The males frequently have the 1st and 2nd pairs modified as copulatory structures, or an appendix masculina is developed on the 2nd pair (Nephropidae). In females, a median sternal sclerite between the last 2 thoracic somites often is modified to form a sperm receptacle, the annulus ventralis (Astacoidea and Parastacoidea) or a thelycum is developed on the sternite of the 4th pereopods (Nephropoidea). This structure is functionally equivalent to the thelycum of the female penaeoidean.

Before removing the mouthparts, remove the branchiostegite from one side and expose the gills. What type of gills are present and what are the gill formulae for your specimens? Remove the maxillipeds and other mouthparts. The crista dentata on the ischium of the 3rd maxilliped is well developed in most crayfishes and frequently in nephropoideans as well. The mandible usually is well developed and usually has a palp. Note the absence of a lacinia mobilis. Are the incisor and molar processes distinguishable?

The major organ systems are described for species of Astacoidea (see Figure 47). Before beginning your dissection, carefully remove the carapace and proximal region of the rostrum. At this time it would be advisable also to remove the pleura dorsally and laterally from one side of your specimen. Although we will not discuss the musculature in detail, 2 pairs of prominent muscles immediately are apparent dorsally in the anterior part of the cephalothorax when the carapace is removed. The anteriormost are the muscles of the proventriculus or stomach; the posterior pair are the adductor muscles of the mandibles. These muscles will have to be removed to expose the underlying organs.

Posteriorly in the cephalothorax just beneath the hypodermis locate the heart. Blood enters the heart from the pericardial sinus or pericardium through 3 pairs of ostia, 1 dorsal, 1 lateral, and 1 ventral. From the anterior end of the heart follow the unpaired median ophthalmic artery forward over the stomach. A swelling in the artery (the cor frontale or accessory heart) aids in circulating blood to the cephalic region. Beyond the cor frontale the artery branches to provide blood to the eyes, antennules, and supraesophageal ganglion. A pair of large antennary arteries leaving the heart anteriorly parallel the ophthalmic artery for a short distance before turning ventrolaterally. Branches from the antennary arteries supply blood to the gonads, branchiostegites, hepatic cecum, stomach, and musculature of the cephalic appendages. Trace as many of these branches as possible. Anteroventrally from the heart locate one of the pair of hepatic arteries that carry blood to the hepatic cecum (hepatopancreas). From the posterior margin of the heart locate the large dorsal abdominal artery. As this artery leaves the heart a pair of asymmetrical arteries are given off. Both of these arteries provide blood to the gonads; the larger gives rise to the sternal artery. Trace the sternal artery ventrally as it passes to one side of the

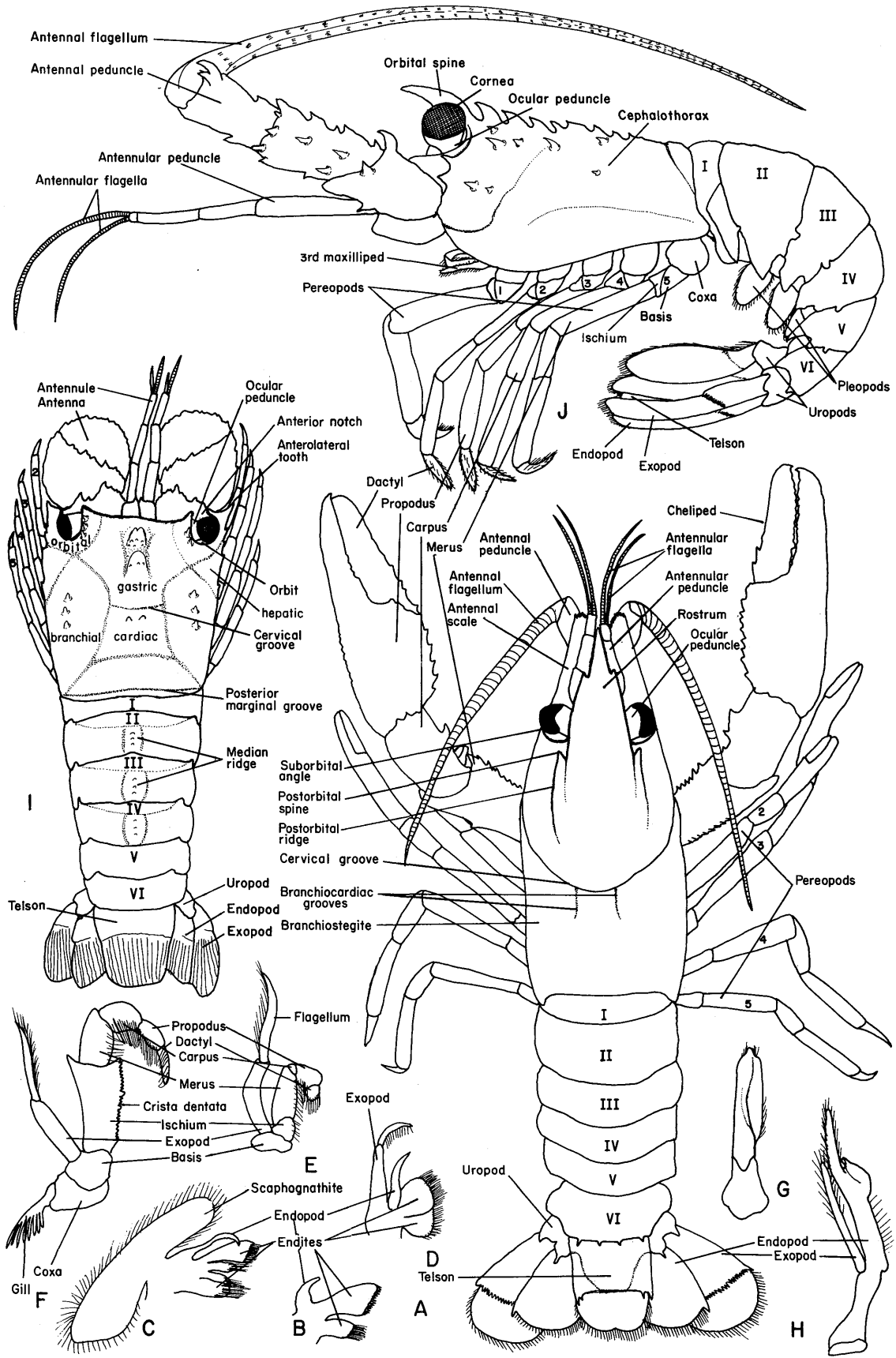


Figure 46 Decapoda, Astacidae and Palinura: A—H, Astacidea; I, J, Palinura. A. Typical astacidean (crayfish); B. Maxillule; C. Maxilla; D. 1st maxilliped; E. 2nd maxilliped; F. 3rd maxilliped; G. 1st pleopod of male; H. 2nd pleopod of male; I. Typical scyllaridean (slipper lobster); J. Typical palinuridean (spiny lobster).