

SUBORDER DENDROBRANCHIATA BATE, 1888¹⁾

BY

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INTRODUCTION

General remarks

The suborder Dendrobranchiata includes shrimp that have an important role in estuaries and marine ecosystems. The approximately 500 extant species range from shallow waters in the tropics to depths of 1000 m or more on the continental slopes (Pérez Farfante & Kensley, 1997).

The history of attempts to classify the group is long and somewhat confusing. In 1880, Boas divided Decapoda into Natantia, a group that included all shrimp, and Reptantia, for the remaining decapod species. Bate (1888) recognized that there are different types of branchiae (gills) among the natantians, and he divided this group into three subgroups: Dendrobranchiata, Phyllobranchiata, and Trichobbranchiata. However, by that time Dendrobranchiata included other groups in addition to the tribe Penaeidea. Bate included two families within Penaeidea: Penaeidae and Sergestidae (further divided in the subfamilies Sergestinae and Luciferinae). Wood-Mason & Alcock (1891) recognized the major differences among groups of Penaeidae and separated them into three clusters: Aristeina,

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Benthesicymina, and Solenocerina. Calman's (1909) classification of Dendrobranchiata (as Tribe Penaeidea) contained two families: Penaeidae (subfamilies Aristeinae, Sicyoniinae, Penaeinae) and Sergestidae (subfamilies Sergestinae and Luciferinae). Subsequently, Crosnier (1978) raised Aristeina to family status, including Aristeinae, Benthesicyminiinae, and Solenocerinae as subfamilies, and pointed out that the majority or all subfamilies of Penaeidae should be raised to familial level. Pérez Farfante & Kensley (1997) took this action and raised those subfamilies to family level. However, that change has been criticized for not including consistent genetic differences (see more under Biogeography below).

Diagnosis

According to most previous authors (Burkenroad, 1981, 1983; Pérez Farfante & Kensley, 1997; Dixon et al., 2003), the suborder is defined by the following characters: (1) the presence of **dendrobranchiate gills**; (2) the appearance during development of pleurobranchiae after the arthrobranchiae and podobranchiae; (3) the possession of (usually) chelae on the first three pairs of pereopods; (4) the second pleomere with pleura that do not overlap those of the first; (5) prominent hinges between the pleomeres; (6) eggs that are released directly into the water (as opposed to being carried by females) and that hatch as a lecithotrophic nauplius or protozoa; (7) the presence of a petasma in males; and (8) pleopods that lack an appendix interna, with the exception of vestigial structures found in some males.

EXTERNAL MORPHOLOGY

General habitus

The dendrobranchiates are all shrimp and thus exhibit the typical "**caridoid facies**" (fig. 63.1). The body is divided into two tagmata, a cephalothorax and the pleon, and they are generally somewhat laterally compressed. For the most part dendrobranchiates have a robust body form (although the cuticle itself can be somewhat soft and flexible), except for members of Luciferidae, which are small and not well sclerotized.

Cephalothorax

The **carapace**, which exhibits significant traits and characters that are important for understanding the taxonomy of Dendrobranchiata, is well developed with many spines, grooves, carinae, and sutures (Kubo, 1949) (fig. 63.2). It completely covers the cephalothorax, encloses the gills, and is fused dorsally to all the thoracic somites (McLaughlin, 1980). Its importance in higher-level taxonomy can be seen, for example, in the presence of the unique **postorbital spine** that defines Solenoceridae. Carapace features are also important in defining genera, such as in Aristeidae, where the presence of the **postcervical sulcus** is unique for the genus *Pseudaristeus*.

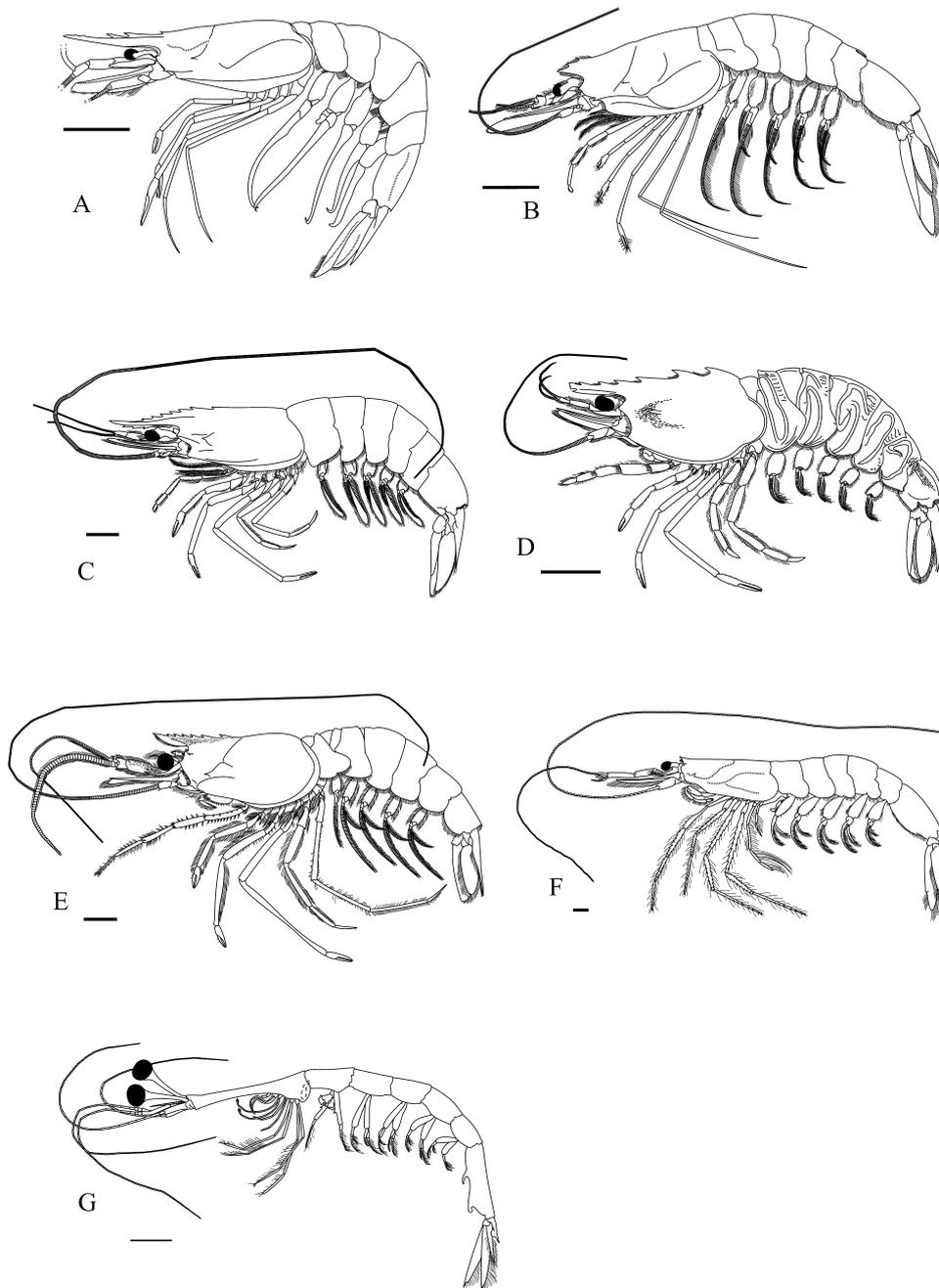


Fig. 63.1. Families of Dendrobranchiata. A, Aristeidae; B, Benthesicymidae; C, Penaeidae; D, Sicyoniidae; E, Solenoceridae; F, Sergestidae; G, Luciferidae. [Modified after Pérez Farfante & Kensley, 1997.]

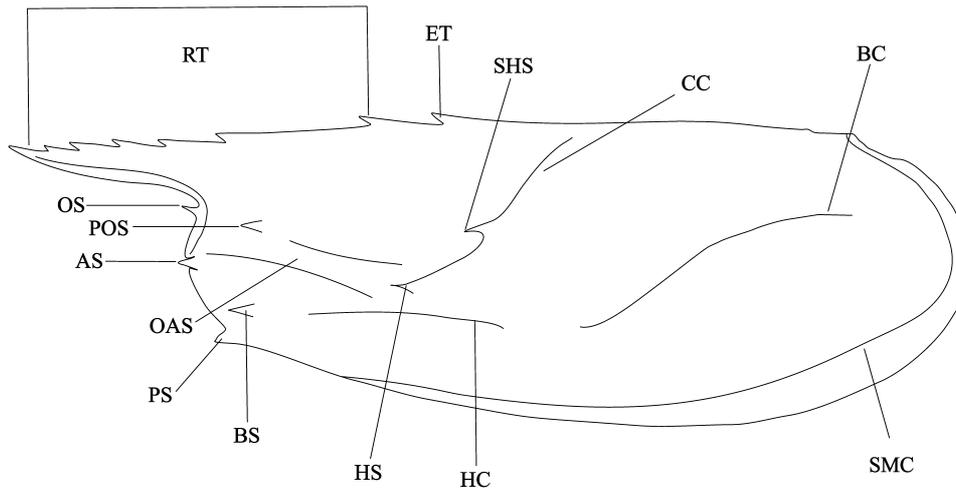


Fig. 63.2. Schematic dendrobranchiate, showing the main spines and carinae on the carapace. Abbreviations: AS, antennal spine; BC, branchiocardiac carina; BS, branchiostegal spine; CC, cervical carina; ET, epigastric tooth; HC, hepatic carina; HS, hepatic spine; OAS, orbitoantennal sulcus; OS, orbital spine; POS, postorbital spine; PS, pterygostomial spine; RT, rostral teeth; SHS, suprahepatic spine; SMC, submarginal carina. [Modified after Pérez Farfante & Kensley, 1997.]

The carapace usually is produced anteriorly to form an extension, the **rostrum**, which is variable in length ranging from short (approximately the same length as the eyes) to long (extending well beyond the length of the **antennular peduncles**). Benthescymidae, Luciferidae, Sergestidae, and some penaeids and solenocerids are examples of short rostrum groups, while Aristeidae and some penaeids and solenocerids are examples of long rostrum groups. Different types of **rostral ornamentation** are found among Dendrobranchiata. Aristeidae, Benthescymidae, Sicyoniidae, the majority of Solenoceridae (*Hymenopenaeus*, *Solenocera*, and *Hadropenaeus*), and some Penaeidae (*Artemesia*, *Parapenaeus*, and *Xiphopenaeus* are examples) possess spines only on the dorsal surface of the rostrum. Some species of the solenocerid genus *Haliporoides* and some Penaeidea (*Farfantepenaeus*, *Litopenaeus*, and *Pelagopenaeus*) possess dorsal and ventral rostral spines. The number of spines in both cases is variable. Sergestidae and Luciferidae show no such ornamentation; their rostra completely lack spines. Some sexual dimorphism is observed in some genera of Aristeidae, in which the rostrum is longer in females and juvenile males than in adult males.

Eyes consist of the **eyestalk** and the **cornea**. The eyestalk is the peduncle or unifacted part of the eye supporting the cornea (Pérez Farfante & Kensley, 1997), and it can bear either a tubercle (as in Benthescymidae, Aristeidae, and some Solenoceridae), or an **ocular scale** (as in most Solenoceridae and Penaeidae) on the basal segment (fig. 63.3A). An ocular **stylet** (as in Sicyoniidae) can arise from the ocular plate (fig. 63.3B). During life, eyes are usually directed laterally (McLaughlin, 1980).

Posteriorly, two or three thoracic sternites are modified into the female genitalia or **thelycum**. The thelycum consists of a series of prominences, depressions or grooves,

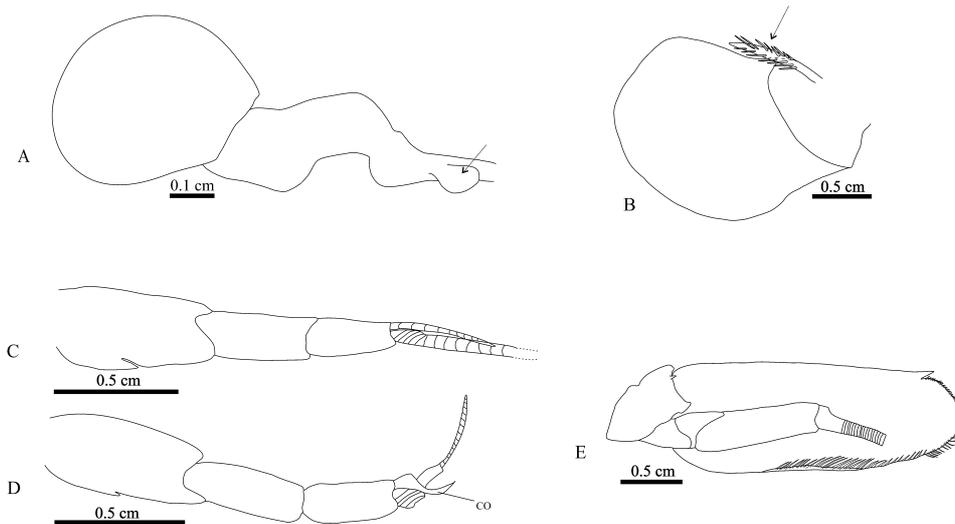


Fig. 63.3. Eyes: A, *Farfantepenaeus paulensis*: the arrow indicates the ocular scale; B, *Sicyonia typica*: the arrow indicates the ocular stylet. Antennules: C, *Sergia regalis*, female; D, *Sergia regalis*, male with clasper organ (CO). Antennae: E, *Hepomadus tener*.

plates, and sacs modified from the sternites of the sixth to eighth thoracic somites (Kubo, 1949; Bauer, 1994) (fig. 63.6A). The thelycum can be classified into two types: open, in which the seminal receptacles are absent, and closed, in which seminal receptacles are present.

Gills

The name Dendrobranchiata (from the Greek “dendron”, tree, and “branchia”, gills), coined by Bate (1888), refers to the highly branching “tree-like” nature of the gills. Each gill consists of a long central axis, sometimes called the **rachis**, from which arises a series of paired **branches** (secondary branches). These secondary branches curve slightly toward one another, creating something of a central hollow longitudinal space between them. Each branch in turn is subdivided into smaller fingerlike processes (tertiary branches) that arise from the distal surfaces of the branch, and each fingerlike process is also branched (dendritic). These gills are referred to as dendrobranchiate or simply “dendrobranchs” (Martin et al., 2007) (fig. 63.4A, B). However, there are some variations on this basic pattern among the families. In the study of Martin et al. (2007), Aristeidae, Penaeidae, *Pleoticus*, and some *Benthescymus* (except for part of the genus *Solenocera*) show the classical pattern, while the other families display some variations. Sicyoniidae are dramatically different from the classic **dendrobranch gill pattern**, with secondary branches extremely flattened and plate-like, and the tertiary elements are very flattened and show none of the “dendritic” branching seen in the tertiary process of “classic” dendrobranchiate gills (fig. 63.4E, F). In the gills of *Gennadas*, the secondary branches do not curve medially to create a central longitudinal hollow space as described above, and,

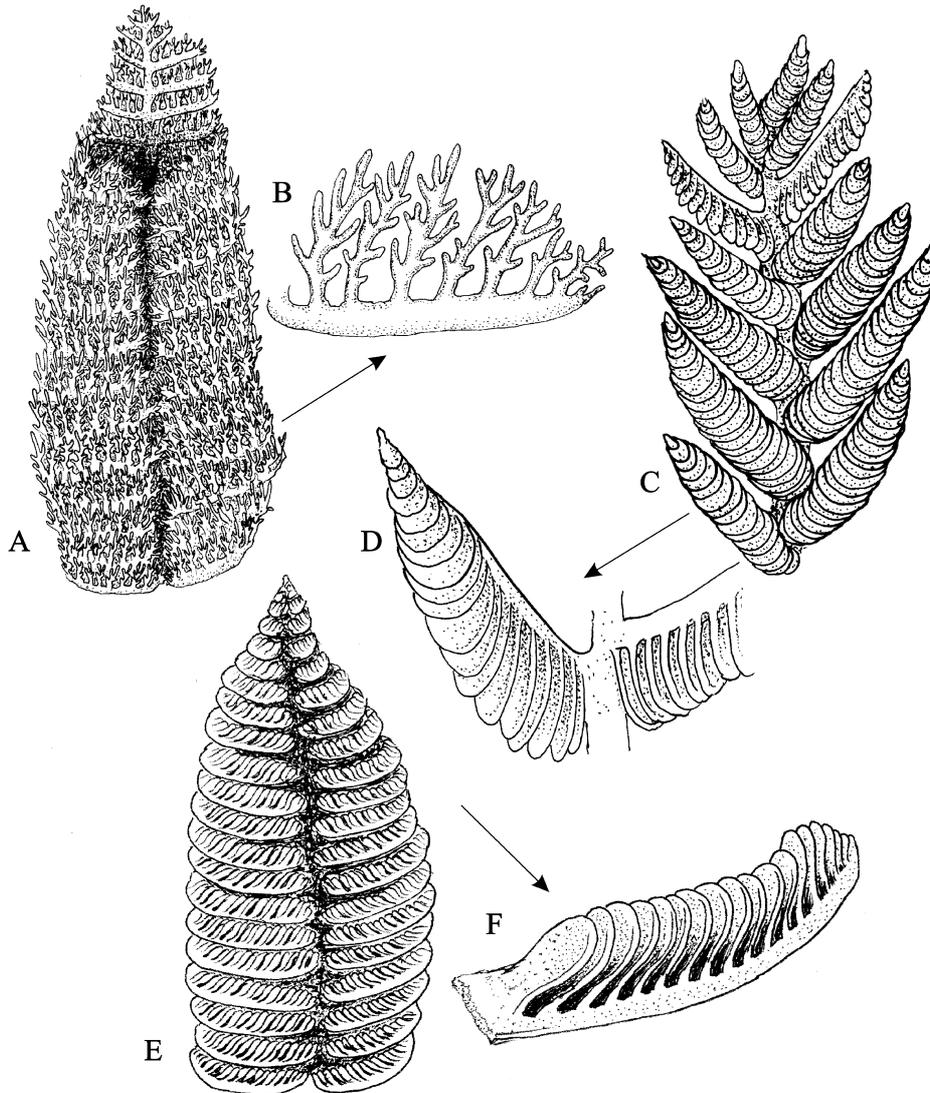


Fig. 63.4. Schematic illustrations of some of the more extreme variations seen among “dendrobranchiate” gills. A, “classical” dendrobranchiate gill found in penaeids, aristeids, and at least some benthescyemids and solenocerids, seen in lateral view, with secondary arms curving off the main gill axis toward the viewer and meeting at the midline; B, part of a single secondary gill branch of the gill type shown in A, with tubular, dendritic tertiary gill elements directed distally; C, gill of the sergestid genus *Sergestes* in lateral view, with secondary branches arising in an alternating pattern off the main gill axis and with flattened, oval tertiary elements directed laterally and basally; D, parts of two secondary gill branches coming off the main gill axis in the *Sergestes* gill, with each branch bearing flattened, oval tertiary elements; E, “plate-like” dendrobranchiate gills of the Sicyoniidae (*Sicyonia*) in lateral view; F, distal part of a single secondary branch of the sicyoniid gill showing a flattened secondary gill branch giving rise to flattened tertiary elements directed distally. Not drawn to scale. [Modified after Martin et al., 2007.]

furthermore, the tertiary elements that arise from these branches are much more flattened and have the overall appearance of “book gills”. In *Sergestes*, the secondary branches appear to arise in an alternating (rather than paired) pattern from the main gill axis, and they are wider basally than they are distally; in addition, the tertiary elements that arise from these branches are not tube-like and dendritic but instead are flattened, oval plates (fig. 63.4C, D). In some *Solenocera*, there appears to be some flattening of the tertiary elements, and these elements are indeed branched. Gills are absent in adult Luciferidae.

Depending on where the gill is attached, it is termed a **pleurobranch**, **arthrobranch**, or **podobranch**. Pleurobranches are attached to the thoracic pleura; generally one is present on the third maxilliped through pereopod 5 except in Sicyoniidae, where a pleurobranch gill appears only on pereopod 2, and in Sergestidae, where there are no pleurobranches. Arthrobranches are attached to the articular membrane between the body wall and the coxa; generally one is present on the first maxilliped, and two are present on the second maxilliped through the fourth pereopod. Podobranchs are inserted on the coxa, generally only on the second maxilliped, as in Penaeidae and Sicyoniidae, sometimes from the second maxilliped through the third pereopod, and never on the fourth and fifth pereopods. Regarding the timing of their development, pleurobranches appear later than do podobranchs and arthrobranches (Burkenroad, 1983).

Bauer (1999) observed the **gill-cleaning mechanism** in a penaeoid shrimp, *Rimopenaeus similis*. It was demonstrated that setiferous epipods compose the major tools for gill cleaning. In this species, epipods on the second maxillipeds and on pereopods 1-3 are equipped with long setae bearing an array of digitate scale setules. These multidenticulate setae reach to most gills and are jostled among them during limb movements. Other important structures in gill cleaning are the pereopodal exopods. They are equipped with long multidenticulate setae like those on the epipods; exopods sweep back and forth over the gill filaments just under the gill cover, areas not reached by the epipods.

Pleon

The pleon is laterally compressed; in most cases it is longer than or almost the same size as the cephalothorax. The **pleura** (lateral extensions) of the second pleonal somite (**pleomere**) do not overlap those of the first, which serves to separate dendrobranchiate from caridean shrimp. The pleomeres often display several kinds of **ornament**. A dorsal carina can be variable in length. For example, in *Sicyonia dorsalis* the carina extends from pleomeres 1 to 6, in *Mesopenaeus tropicalis* from pleomeres 2 to 6, and in *Benthesicymus bartletti* from pleomeres 4 to 6. Each pleomere can have posterodorsal spines, e.g., as in *Aristaeomorpha foliacea* on pleomere 5, *Penaeopsis serrata* on pleomere 6, and *Parapenaeus americanus* on pleomeres 4-6, and/or anterodorsal spines, e.g., as in *Sicyonia burkenroadi* and *Gordonella paravillosa* on pleomere 1. The pleurae of each pleomere also can be ornamented, e.g., with mid-carinae (as in *Haliporus thetis*, *Gordonella kensleyi*, and *Sicyonia dorsalis*) or posterior spines (as in *Sergestes armatus* on pleura 6 and *Sicyonia typica* on pleura 5-6). Some species have **photophores** in different parts of the pleon.

Appendages

ANTENNULES

In Dendrobranchiata, the antennules have a 3-segmented **peduncle** that gives rise to a dorsolateral and a ventrolateral **flagellum** (biramous antennule) (fig. 63.3C), except in Luciferidae, which have only one flagellum (uniramous antennule). The function of the flagella has not been fully established, but it is traditionally regarded as being chemosensory (Young, 1959) as is the case with other decapods. The angle on the proximal region of the antennular peduncle is often produced into a small acute spine, the **stylocerite**. Except for Sergestidae and Luciferidae, a distolateral spine on the outer margin of the first antennular peduncle is present. Solenoceridae, Sicyoniidae, and Penaeidae have a scalelike process called the **prosartema** arising from the inner margin of the first antennular peduncle. The only family with noticeable sexually dimorphic antennules is Sergestidae, in which males have a **clasper organ** consisting of a modification of the ventral antennular flagellum that results in a sharply pointed protrusion at the base of the limb (fig. 63.3D). In some members of Penaeidae, e.g., the genera *Artemesia*, *Penaeopsis*, *Parapenaeus*, and *Metapenaeopsis*, there is a parapenaeid, or ventromesial, spine that projects from the mesial or distal position of the ventromesial margin of the first antennular segment.

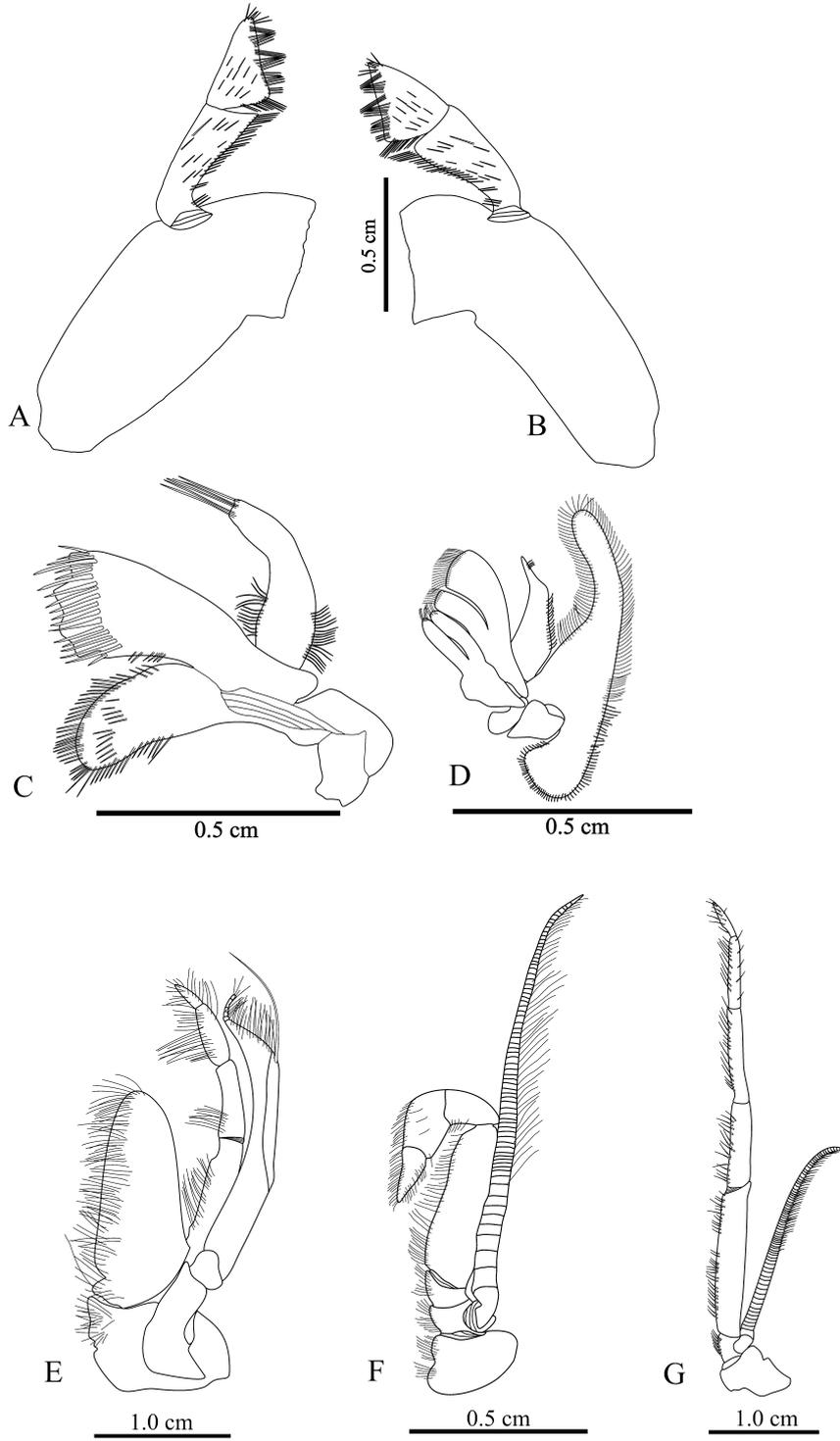
ANTENNAE

Lateral, but lying in a ventral position, to the antennules are the antennae. Each antenna consists of a **protopod** of two segments: a basal carpus and a distal basis. The latter bears two structures, a large inner **scaphocerite** (antennal scale) and an **endopod** consisting of three segments and the long multi-articulate flagellum (Dall et al., 1990) (fig. 63.3E). The scaphocerite, or antennal acicle or scale, ends in a spine on the outer margin. The scaphocerite functions as a laterally directed stabilizing fin. Its articulation enables it to be moved laterally during the “backward flip” or **caridoid escape reaction** (Dall et al., 1990). The flagellum is long, often 2 or 3 times the length of the body and is straight in penaeoids but has a bend in sergestoids (McLaughlin, 1980).

MANDIBLES

Mandibles in Dendrobranchiata conform to the basic malacostracan pattern, with discrete **incisor** and **molar processes** in the same plane (fig. 63.5A, B). An exception is the penaeid *Funchalia villosa*, in which the molar process is totally suppressed and the incisor process is greatly enlarged and sickle-shaped. A 3-segmented mandibular **palp** is present, except in the Luciferidae.

Fig. 63.5. *Hepomadus tener*, some appendages. A, right mandible; B, left mandible; C, maxillule; D, maxilla; E, maxilliped 1; F, maxilliped 2; G, maxilliped 3. [Modified after Tavares & Serejo, 2007.]



MAXILLULAE

Each maxillule consists of a **basal** and a **distal endite** and an endopodal **palp** (fig. 63.5C). The endopodal palp is absent in Luciferidae.

MAXILLAE

Each maxilla consists basically of **endites**, **endopodal palp**, and **exopod** (fig. 63.5D). Most often there are two bilobed setose endites, as in Aristeidae, Benthescymidae, Luciferidae, Penaeidae, and Solenoceridae, but in Sergestidae and Sicyoniidae only the distal endite is bilobed, whereas the basal endite has only one lobe. The endopodal palp is absent only in Luciferidae.

THORACIC APPENDAGES

Maxillipeds

The **first maxilliped** consists of an endite, endopod, and exopod (fig. 63.5E). The endite is sub-oval in shape, and it is absent in Luciferidae.

The **second maxilliped** consists of an endopod and an exopod (fig. 63.5F). The exopod is absent in Sergestidae, Luciferidae, and in some other species such as *Artemesia longinaris* and *Sicyonia dorsalis*.

The **third maxilliped** is totally **pediform** and consists of an endopod and an exopod (fig. 63.5G). The endopod consists of 5 articles plus the protopod, but the articles can be fused, as in Luciferidae (*Lucifer faxoni* has 4 articles + protopod). The dactyl can be entire or 5-segmented as in *Sergestes armatus*. The exopod is present in Aristeidae, Benthescymidae, Penaeidae, and Solenoceridae and absent in Sergestidae, Sicyoniidae, and Luciferidae.

Pereiopods

Dendrobranchiata typically have the first three pairs of pereiopods **chelate**, with pereiopods 4 and 5 non-chelate (fig. 63.6). **Exopods** can either be absent, as in Sicyoniidae, Sergestidae, Luciferidae, and the penaeid genus *Artemesia*, or present as in the solenoceric genera *Solenocera* and *Mesopenaeus* and in the penaeid genus *Farfantepenaeus*, or reduced as in the solenoceric genus *Hymenopenaeus*, the penaeid *Penaeopsis*, and the aristeid genus *Plesiopenaeus*.

Epipods can be absent, as in Sergestidae and Luciferidae, present on pereiopod 1 to pereiopod 3, as in Penaeidae, Sicyoniidae, and the aristeid *Pseudaristeus*, or present on pereiopod 1 to pereiopod 4 as in most of the aristeid genera (*Aristaeomorpha*, *Aristaeopsis*, *Austropenaeus*, *Hemipenaeus*, *Hepomadus*, *Parahepomadus*, and *Plesiopenaeus*) and in Benthescymidae and Solenoceridae. Epipods can have two shapes: **foliaceous** and **furcate**. Foliaceous forms are found among Aristeidae, Benthescymidae, and some Solenoceridae, and furcate forms are found among Sicyoniidae, Penaeidae and some Solenoceridae. This difference is an important feature in the phylogeny of the group.

Pereiopod 1 is without a dactyl in *Sergestes* and *Sergia*, both of which have a subchela formed by robust setae present on the flexor margin of the carpus distal margin and the

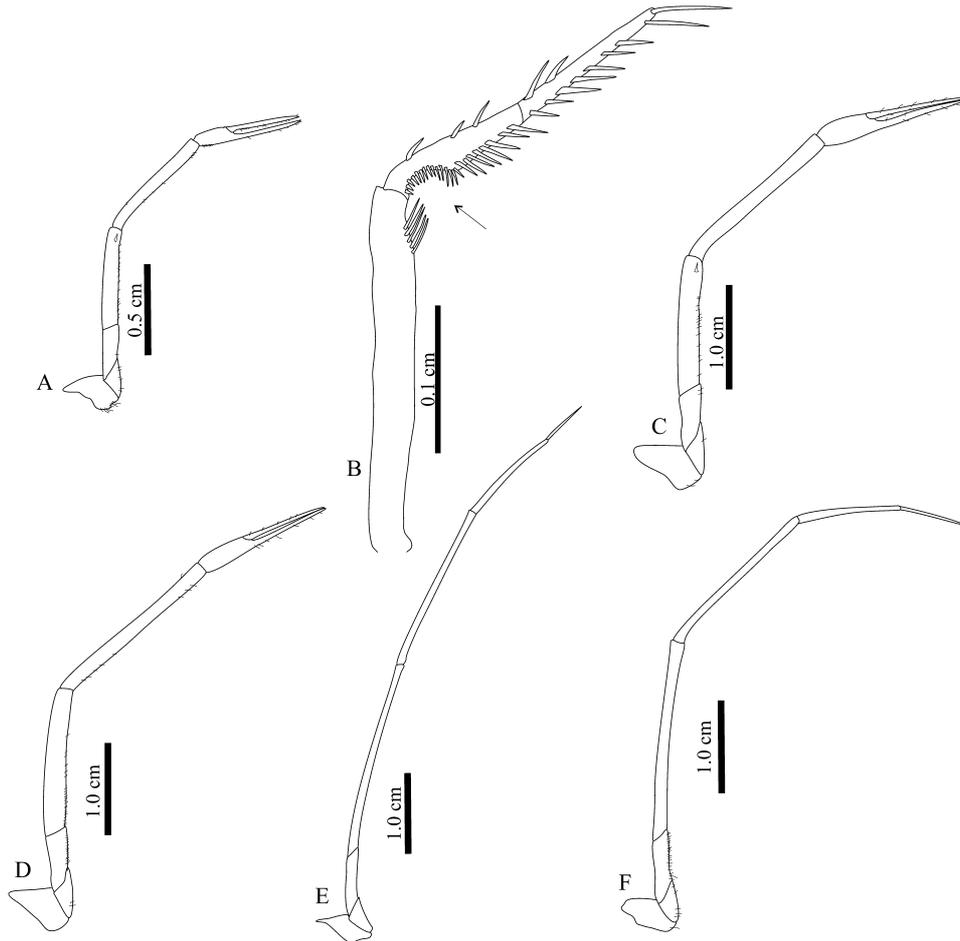


Fig. 63.6. Pereiopods. A, *Hepomadus tener*, pereiopod 1; B, *Sergestes armatus*, pereiopod 1, arrow showing the subchela; C, *Hepomadus tener*, pereiopod 2; D, *Hepomadus tener*, pereiopod 3; E, *Hepomadus tener*, pereiopod 4; F, *Hepomadus tener*, pereiopod 5. [A, C-F, modified after Tavares & Serejo, 2007.]

proximal region of the propodus (fig. 63.6B). In Luciferidae the dactyl also is absent, but there is no subchela in luciferids. The merus and ischium of all families can vary from being unarmed to being armed with 5 spines in a row.

Pereiopod 2 is chelate in most families but lacks a dactyl in Luciferidae, with no subchela formed. As in pereiopod 1, the merus and ischium of all families can vary from being unarmed to being armed with 5 spines in a row.

Pereiopod 3 has all 7 segments in all families. Although the chelate nature of pereiopod 3 is one of the diagnostic characters of Dendrobranchiata, once again Luciferidae is an exception, with no chela on pereiopod 3.

Pereiopod 4 is absent in Luciferidae and in the sergestid genus *Acetes*, and it has no dactyl in the sergestid genera *Peisos*, *Petalidium*, *Sergia*, and *Sergestes*. Most of the time, pereiopod 4 is similar in size to, or smaller than, pereiopod 3; *Hymenopenaeus* and *Xiphopenaeus* are exceptions, in which pereiopod 4 is 1.5 to 2.0 times as large as pereiopod 3.

Pereiopod 5 is absent in Luciferidae and in *Acetes* and has no dactyl in the sergestid genera *Sergestes* and *Sergia*. For the most part, pereiopod 5 is similar in size to or smaller than pereiopod 3; *Hymenopenaeus* and *Xiphopenaeus* again are exceptions, in which pereiopod 5 is 2.0 to 2.7 times as large as pereiopod 3.

PLEONAL APPENDAGES

Pleopods

The pleopods can be **uniramous** (Sicyoniidae) or **biramous** (all other families). The first two pairs of pleopods are sexually dimorphic and are modified for reproductive purposes in males as seen below.

In the first pair of pleopods, a **petasma** is developed. The petasma is a complex structure formed from the joined endopods of the first pleopods in male penaeoid shrimps (Bauer, 1991). Each half of the petasma is composed of a median lobe and a lateral lobe; median lobes are joined by small hooks, the **cincinnuli** (Bauer, 1991) (fig. 63.7C, D). The development and function of the petasma is discussed below under reproduction. Pérez Farfante & Kensley (1997) presented the following petasma classification:

- **Open:** lateral lobes quite flexible, partially or entirely extended laterally, ventral costae not or barely turned ventrally.
- **Semi-open:** lateral lobes flexible, but folded, with ventral costae distinctly turned ventromesially, delimiting relatively ample space extending from proximal to distal ends.
- **Semi-closed:** lateral lobes somewhat flexible, markedly folded, supported by strong ribs, with the ventral costae approaching rather closely, delimiting moderately large space, narrowly open distally where usually overlapped by well-developed distomedian projections.
- **Closed:** lateral lobes heavily sclerotized, sometimes making structure very rigid, with ventral costae situated ventromesially, almost abutting, and delimiting a small, sometimes extremely so, space; lateral lobe usually produced distally into spouts or horns.

An **appendix masculina** is always present on the second pair of pleopods (fig. 63.7E). It is defined as the anteriormost appendix arising from the base of the endopod, and it is quite variable in length (it can be bigger or smaller than the appendix interna) and in shape (from triangular to rounded). Some families (Aristeidae, Solenoceridae, Benthescymidae, and part of Luciferidae) also have an **appendix interna**, which is defined as the posteriormost appendix arising from the base of the endopod, i.e., between the appendix masculina and the endopod (fig. 63.7F). This appendix is also variable in length, but it has a shape that is quite digitiform most of the time; it is also covered with robust setae and is different from the appendix interna of Caridea, as in dendrobranchiates it lacks hooked setae. In Solenoceridae, in addition to these two appendices on the second pleopod of males, there

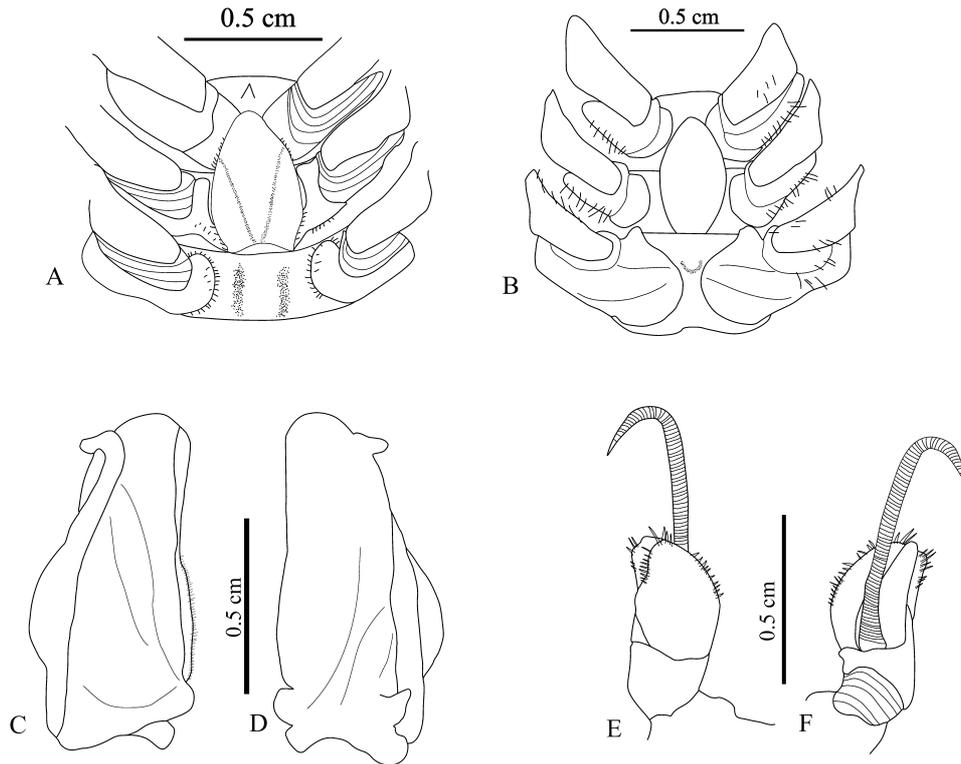


Fig. 63.7. *Hepomadus tener*. A, thelycum; B, male sternum; C, petasma, anterior view; D, petasma, posterior view; E, appendix masculina; F, appendix interna. [Modified after Tavares & Serejo, 2007.]

is a **distolateral projection** arising from the base of the endopod. The functions of the appendix interna and appendix masculina are discussed below under Reproduction.

The last pair of pleopods is enlarged and modified into **uropods**. The exopod is larger than the endopod and can have a spine on the outer margin; the endopod has no spines. Endopods and exopods both lack a **diaeresis**.

Telson

Typically, the dendrobranchiate telson has the posterior region (tip) pointed and ornamented with 4 pairs of lateral robust setae (Aristeidae, Benthescymidae) (fig. 63.8A) or 4 pairs of lateral spines (Sicyoniidae, Solenoceridae). Penaeidae, Sergestidae, and Solenoceridae also have a pointed tip, but the ornamentation is variable with spines only (as in *Parapenaeus americanus*), robust setae only (*Sergia regalis* and *Rimapenaeus constrictus*), both spines and robust setae (as in *Penaeopsis serrata* and *Artemesia longinaris*) (fig. 63.8B), or unarmed (as in *Xiphopenaeus kroyeri* and *Sergestes armatus*). In all cases, the spines and robust setae are in a lateral position. Species of the family Luciferidae have the posterior region truncate, and ornamented with lateral and terminal robust setae.

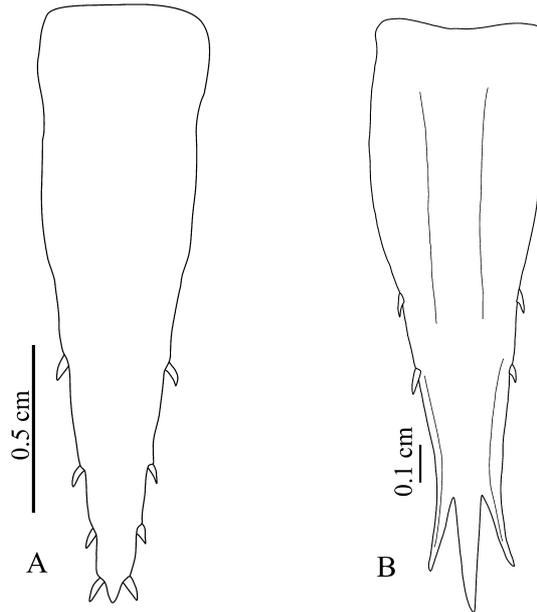


Fig. 63.8. Telson. A, *Hepomadus tener*; B, *Penaeopsis serrata*. [A, modified after Tavares & Serejo, 2007; B, modified after Tavares et al., 2009.]

INTERNAL MORPHOLOGY

Muscles

The penaeid body is quite muscular. Young (1959) (followed by Dall et al., 1990) provided a fully illustrated description of the body musculature of the white shrimp *Penaeus setiferus*, and most of our description below follows that work.

Over **twenty individual muscles** are associated with the **eye** (ocular plate, cornea, and eyestalk). The ocular plate muscles act principally to move the basal segments (forward, ventrally, raising, and rotating), resulting in movement of the entire eyestalk. All eyestalk and **optic calathus** muscles are associated with retraction and rotation of the optic calathus on the eyestalk, except for the long eyestalk abductor muscle, which when contracted swings the eyestalks horizontally to a lateral position.

The **antennules** contain **13 muscles**. Each of the three segments of the protopod has its own set of separate muscles. The muscles of the first segment move it and the distal segments laterally, toward and away from the mid-sagittal body plane. The muscles of the second segment make the same movements as those of the first, but from its point of articulation with the first antennular segment. The third segment muscles reinforce the movements of the two first antennular segments. The prosartema muscle lies upon the adductor muscle of the first antennular segment. However, instead of taking part in the adduction of the first antennular segment, it serves to stiffen the prosartema. The lateral and medial flagellum muscles act to move them laterally toward and away from the mid-sagittal body plane.

The **antennae** contain over **26 muscles** of 12 different types, including the heaviest musculature of the anterodorsal region. The five antennal segments have their own muscles that act to move the antennae laterally, toward and away from the mid-sagittal body plane. The first segment muscles are also partly responsible for the movements of the scaphocerite, raising and depressing it. The scaphocerite has muscles that swing it laterally. The muscles of the flagellum are responsible for bringing the base directly anterior to the proximal antennal segments and returning it to its normal position.

The musculature of the **maxillule** is similar to that of other Decapoda. **Ten muscles** are observed in *Penaeus*, which act to bring together, and then to separate, the spinous gnathal margins of the appendage to the midline in feeding; they are also responsible for making adjustments in the position of the gnathal parts. The **maxilla** contains **nine muscles**, the principal function of which is to operate the scaphognathite as a **gill pump**.

The musculature of the **first maxilliped** is light compared to that of the maxilla; the principal function of the **12 muscles** of the first maxilliped is in feeding, as the breathing function is mostly passive. The **second maxilliped** contains **23 muscles** of 14 different types, also involved primarily in feeding. The **third maxilliped** contains **20 muscles** of 12 different types, an arrangement that is similar to the walking legs, although this appendage acts mostly in feeding as do the other maxillipeds; the third maxillipeds grasp large food particles and pass it to pereopod 1 and also work to keep food near the mouthparts.

The musculature of the **five pereopods** is similar. Pereopod 1 contains 21 muscles of 14 different types. This limb actually does not function as a walking leg, as it is carried horizontally, directed anteriorly, and is ventral to the third maxillipeds. The arrangement of the fifth pereopod is typical of walking legs, although in dendrobranchiates these legs are lighter than their counterparts in reptantian decapods. The fifth pereopod is operated by 24 muscles of 13 types.

The **coxae** of the appendages are typically operated by a set of **four muscles** each – an adductor and abductor, and a promotor (or levator) and remoter (or depressor). Within each jointed appendage the segments are operated by pairs of opposing muscles, given names appropriate to their position in the limb and hence their functions. Additional muscles to provide an added range of movement may be present, as in the carpus for movement of the chela.

In the cephalothorax there are also large muscles associated with the **foregut**. The foregut muscles in *Penaeus* s.l. are reduced in comparison to those in the reptantians (Tazaki & Tazaki, 1997). These muscles serve different functions, acting to protract and retract the medial tooth, open and close the lateral teeth, control movements of the ventral cardiac grooves leading to the pyloric filter, and control movements of the cardiopyloric valve (Tazaki & Tazaki, 1997).

The bulk of the **body musculature** is, however, devoted to **flexion** (bending) of the **pleon**, and these muscles are extraordinarily heavy. Except for slender components of the gut, the gonads, and the nervous and circulatory systems, the space within the pleon is filled with muscles, most of them concerned with the powerful flexion of which the animal is capable. Large dorsal and ventral thoraco-pleonal muscles extend from points in the pleon to attachments deep inside the cephalothorax. There are thin, superficial dorsal and ventral

muscle layers, but the principal muscles are the dorsal extensor muscles, the oblique flexor muscles, and the transverse stator muscles.

Pleopods 3-5 are operated by more than **17 muscles each**. Muscles of the **uropods** are not similar to those of pleopods 3-5. The **16 tail fan muscles** are all related to and involved with the function of these structures in the rapid backward swimming of the shrimp (the so-called “caridoid escape response”).

Nervous system

Young (1959) provided a full description of the nervous system of the white shrimp, *Penaeus setiferus*. Some additional general information is found in Dall et al. (1990). The shrimp nervous system is composed of a **dorsal brain** connected to the ganglionated **ventral longitudinal nerve cord** below the gut by **two large tracts** (fig. 63.9).

The brain lies within the head lobe in the dorsal part of the protocephalon. The broad base of the rostrum protects the head lobe dorsally. The brain consists of three primary lobes: the **protocerebrum**, **deutocerebrum**, and **tritocerebrum**. Two of the **ganglia** of the eyestalk, the **medulla externa** and the **lamina ganglionaris**, are derived from the embryonic optic disc, while the other two, the **medulla interna** and **medulla terminalis**, are derived from the protocerebrum and should therefore be considered part of the brain. The **optic tract** rises from the anterolateral region of the brain and runs distally into the eyestalk, increasing in diameter and entering the calathus. Within the calathus, the optic tract enlarges to incorporate the various distal optic ganglia and makes contact with the nerves from the ommatidia. The protocerebrum and the deutocerebrum are joined together. The deutocerebrum is the region where the antennular, statocyst, and antennal nerve tracts end. Classically, the tritocerebrum often has been considered the first ganglion of the ventral nerve cord. This is in part because it remains ventrally located and in a primitive, divided condition, connected by a transverse commissure termed the tritocerebral or postoral commissure. The tritocerebral lobes have migrated around the mouth to join the dorsal brain in many arthropods. The tritocerebrum gives rise to the nerves of the labrum, the preoral stomatogastric system, and the postoral tritocerebral commissure (Dall et al., 1990).

The ventral nerve cord is a product of the fusion of a primitive “ladder-like” nervous system, wherein the paired ganglia of each segment have come together at the midline. Longitudinal segmented coalescence frequently has been followed by ganglionic coalescence in the ventral nerve cord with attendant obscuring of primitive metamerism.

The two **circumesophageal commissures** link the brain and the elongate subesophageal ganglionic mass in the ventral nerve cord (Dall et al., 1990). Like the brain, the subesophageal ganglion is the result of several major ganglia that have become conspicuously fused, incorporating the former ganglia of the mandibles, maxillules, and maxillae (Dall et al., 1990). Midgut gland motor neurons also have been identified in this ganglion (Dall et al., 1990). Nerves from the next region in the ventral nerve cord supply the three pairs of maxillipeds, while there is a separate ganglion for each of pereopods 1-3 (Dall et

al., 1990). **Thoracic ganglia** seven and eight are fused (Dall et al., 1990). The ventral nerve cord then narrows as it enters the pleon, where there are six segmental ganglia, the last being enlarged and sometimes called the **caudal ganglion** (Dall et al., 1990). This ganglion contains photoreceptors in some other decapods, but these have not yet been identified in Penaeidae (cf. Dall et al., 1990).

The macrurous decapod brain and optic lobes are functionally organized into a series of compact **neuropiles** and associated **cell bodies** that are connected transversely at intervals by commissures. Sandeman (1982) and Dall et al. (1990) identified some main types of neuropiles: lamina ganglionaris; medulla externa (in the eyestalk); medulla intermedia, medulla terminalis, paired anterior and posterior optic neuropiles, protocerebral bridge, central body (in the protocerebrum); medial antennular neuropile, paired lateral antennular (parolfactory) neuropiles, antennular (olfactory) lobes, accessory lobes and lateral glomeruli (in the deutocerebrum); and paired tegumentary and antennary neuropiles (in the tritocerebrum). (See also chapter 15 in vol. 3 of this series.)

In the overall structural organization of the brain areas of the penaeids, the proto- and deutocerebral neuropilar areas were fused across the midline, related to the fact that hemi-ellipsoid neuropiles and olfactory neuropiles are connected to each other by the olfactory-globular tracts (OGTs) among malacostracans. The two arms of OGTs touch each other medially forming a characteristic **chiasma** located next to the central body (Fanenbruck et al., 2004). However, the caudal-rostral organization of the median protocerebrum into the anterior median and posterior median protocerebral neuropiles is still discernible (Ammar et al., 2008). The protocerebral bridge and the central body are clearly delineated, as are the paired OLs, the lateral antennule neuropil and the median antennule neuropil (Ammar et al., 2008). The tritocerebrum in both groups is organized as two paired tegumentary neuropiles that are flanked by two lateral expansions, the antennal neuropiles (Ammar et al., 2008).

Sense organs

PHOTORECEPTORS

The most noticeable sensory structures in penaeids are the **stalked eyes**. Penaeid eyes are composed of radial units, the **ommatidia**, each corresponding with a surface facet, the **corneal lens**. The eye of a mature *Penaeus monodon* may contain over 80 000 ommatidia (Dall et al., 1990). The ommatidial surface arises from a sclerotized cup, named the optic calathus (Young, 1956). The corneal lens in adult Penaeidae is square, but in the larvae it is round (Dall et al., 1990). The cornea is a transparent component of the general body cuticle (Shaw & Stowe, 1982). Underlying the lens are four corneal cells and then four cells forming the square **crystalline lens**. All eight **retinular cells** of each ommatidium are photoreceptors. The lens is optically connected to the long, tapering crystalline tract, whose apex contacts the refractive **rhabdom**. The crystalline tract is believed to act as a light pipe under some conditions. Seven or eight light-receptive, retinular cells surround the rhabdom, each with an axon running into the underlying neuropiles (lamina ganglionaris and medulla terminalis) (Dall et al., 1990). Flanking the **crystalline cone** and

reticular cells are various pigment cells that screen the optic units of the ommatidium so that only direct oncoming light passes directly down to the rhabdom (the **apposition eye**) or they act as mirrors to reflect light from several ommatidia onto a single point in the field of rhabdoms (the **superposition eye**) (Schram, 1986). Apposition eyes are thought to be efficient detectors of movement, because of the small angles between adjacent ommatidia. Superposition eyes are perhaps less efficient detectors of movement; they are much more efficient light collectors (Dall et al., 1990). Dendrobranchiates possess either a reflecting or refracting superposition eye (reviewed by Gaten, 1998; Porter & Cronin, 2009). (See also chapter 6 in vol. 1 of this series.)

In some diurnal Crustacea, the eyes can form only apposition images, while in some deep-sea and nocturnal species only superposition images can be formed (Dall et al., 1990). In the shallow-water Penaeidae, the ommatidial pigments are capable of migration, and both types of images can be formed.

Eyes are used to locate predators and swimming prey and also to detect light intensity variations, functioning in **biorhythm control** (Dall et al., 1990). The stalked eyes cover nearly the entire visual space except for the blind spot created by the eyestalk (Shaw & Stowe, 1982).

CHEMORECEPTORS

Innervated structures (**sensilla**) on the external cuticle provide crustaceans with information about their external chemical environment. Most of these take the form of **hairlike setae**. In Decapoda, discrete clusters of chemoreceptors occur at multiple loci on the body and appendages (Ache, 1982); the entire cuticle is not chemosensitive. The first antennae, the dactyls, and the mouthparts are probably the primary chemosensory organs of decapods. The antennular flagella are traditionally regarded as special **olfactory organs** of decapods, and the large neuropiles of the deutocerebrum are often called olfactory lobes (Dall et al., 1990). Mouthparts and chelae are **taste organs**. Olfactory organs usually have complex central nervous systems connections, whereas taste receptors are relatively simple.

In addition to the eye, there is a special sensory structure, which is well developed on the median region of the eyestalks in the penaeids, called the sensory pore **X-organ** or sensory pore complex. Its function is still controversial; some authors (Chaigneau & Laubier-Bonichon, 1980; Ache, 1982) have proposed an olfactory function, but it is difficult to see what role a special olfactory sense organ in such a position would have. Dall et al. (1990) stated that this sensory structure probably functions in the reception of other kinds of stimuli.

MECHANORECEPTORS

Two types of **sensory setae** (cuticular receptors) are found in a **statocyst cavity** in *Fenneropenaeus merguensis*: central and crescent setae. Other cuticular receptors found in Penaeidae are the much-branched setae and pegs of the dactylus (Dall et al., 1990).

Other mechanoreceptors are found on the antennal flagelum of penaeids. Each segment of the antennae in *Litopenaeus setiferus* bears a pair of short dorsal setae and a much longer pair of ventral plumose setae with a pit between their bases. When the prawn is active the two antennal flagella are held dorsolaterally and parallel to the body and, at least in the genera *Sergestes* and *Funchalia*, the antennae are **vibration detectors**. The field of perception of antennae would be comparable with that of the eyes, and thus Penaeidae are well equipped for the detection of external movements, as in the case of predators.

Digestive system

The morphology of the digestive tract in Dendrobranchiata is divided into a complex **foregut** region, a compact **digestive gland** at the beginning of the **midgut** region, a long tubular simple section, and a **hindgut** region consisting principally of the **rectum** (fig. 63.10A).

The foregut of Dendrobranchiata represents the most primitive decapod foregut (Felgenhauer & Abele, 1989). It consists of a short **esophagus** (in UK English: oesophagus), an elongated **cardiac sac**, and a **pyloric chamber** (Tazaki & Tazaki, 1997). The **mouth** leads into a short vertical esophagus, surrounded by contractile muscles, which can contract and close it in a sphincter-like manner (Dall et al., 1990). The esophagus opens into the lumen of the cardiac sac, which contains the grinding part of the stomach, called the **gastric mill**. The gastric mill is centered about a large median tooth typically equipped with curved denticles along its margins and a battery of flanking lateral teeth (Schram, 1986). The **pylorus** contains a well-developed **ampulla**, but the dorsal pyloric region is not as developed as in the reptantian decapods (Tazaki & Tazaki, 1997). In the pyloric chamber, there is a **pyloric filter** that prevents the entry of particulate matter into the main collecting ducts of the **hepatopancreas** (Young, 1959).

The principal functions of the midgut are the **secretion of digestive enzymes** and the **absorption of nutrients** (Dall et al., 1990). The midgut is elongate, extending nearly the entire length of the pleon (McLaughlin, 1980). The large **digestive caeca**, or **hepatopancreas lobes**, are filled with glandular secretory cells (Schram, 1986). The hepatopancreas 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. Near the beginning of the hindgut, a small hindgut or **rectal gland** arises (McLaughlin, 1980).

In the hindgut, the muscular rectum is lined by six pad-like ridges, whose primary function appears to be grasping the fecal pellet in the peritrophic membrane and extruding it (Dall et al., 1990). One function of the **peritrophic membrane** is to protect the delicate epithelia of the midgut from ingested abrasive material (Forster, 1953; Lovett & Felder, 1990); it also plays a major role in separation of stored chyme, as well as fecal matter, from extra-peritrophic water that it is taken up by anal drinking. The **anal drinking** and

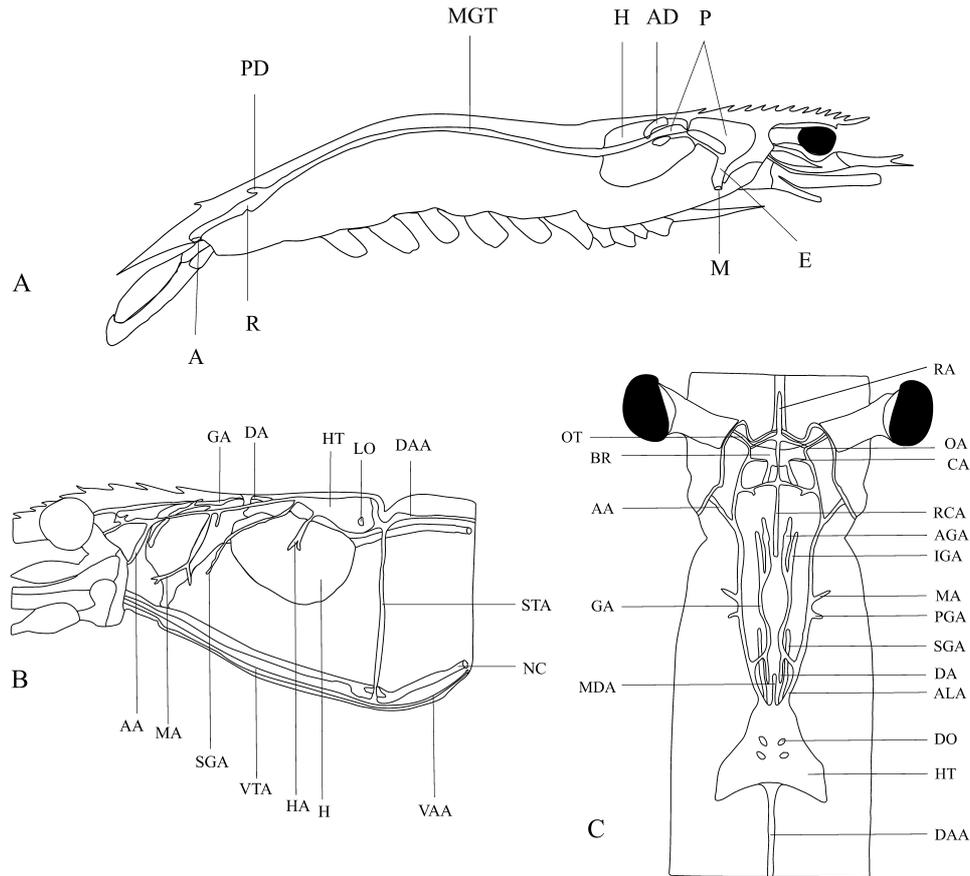


Fig. 63.10. A, digestive system; abbreviations: A, anus; AD, anterior diverticulum; E, esophagus; H, hepatopancreas; M, mouth; MGT, midgut; P, proventriculus; PD, posterior diverticulum of midgut; R, rectum. B, lateral view of circulatory system; C, dorsal view of the circulatory system; B-C abbreviations: AA, antennal artery; AGA, anterior gastric artery; ALA, anterior lateral artery; BR, brain; CA, cerebral artery; DA, artery to anterior diverticulum; DAA, dorsal pleonal artery; DO, dorsal ostium; GA, gastric artery; H, hepatopancreas; HA, hepatopancreas artery; HT, heart; IGA, inferior gastric artery; LO, lateral ostium; MA, mandibular artery; MDA, mid-dorsal artery; NC, ventral nerve cord; OA, optic artery; OT, optic tract; PGA, posterior gastric artery; RA, rostral artery; RCA, recurrent artery; SGA, subgastric artery; STA, sternal artery; VAA, ventral pleonal artery; VTA, ventral thoracic artery. [Modified after Dall et al., 1990.]

the **oral drinking** work to expand the hepatopancreas tubules. This is important because although the hepatopancreas has sets of muscles acting in its contraction, it has no muscles working in its expansion, so an extrinsic mechanism is needed. As the extra-peritrophic water is moved anteriorly to inflate the midgut, the continual pumping of water from the anus is allowed, providing uninterrupted contraction and expansion of the hepatopancreas (Lovett & Felder, 1990). The hindgut terminates in a muscular **anus**.

Circulatory system

The **heart** is compact, triangular, has three pairs of ostia, and is located in a **peri-cardium** just in front of the posterior dorsal edge of the carapace (Dall et al., 1990) (fig. 63.10B, C). Two pairs of dorsal ostia and one pair of lateral ostia drain the pericardium into the heart. The **arterial system** is rather elaborate (Schram, 1986), and the blood leaves the heart by three major arteries: a pair of anterior lateral arteries, and a single dorsal artery into the pleon (Dall et al., 1990).

Further anteriorly, the lateral anterior artery turns towards 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 proceeds to the ocular peduncles, giving off the cephalic arteries to the supra-esophageal ganglion (brain) 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 supply the cardiac stomach. Other branches of the lateral anterior arteries include the mandibular and antennal arteries that supply blood to the muscles of the mandibles, antennules, and antennae. The hepatic arteries arise from the anteroventral portion of the heart (Schram, 1986). These vessels provide the blood supply to the hepatic caecum or hepatopancreas.

Located at the posterior end of the heart, the single dorsal artery into the pleon gives off a sternal artery and then continues above the gut, sending off a pair of arteries into each somite, finally branching to the telson and uropods and joining with the extremity of the subneural artery (Dall et al., 1990). Ventrally, the sternal artery passes through the ventral nerve cord between the ganglia of the third and fourth 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 fourth and fifth pereopods and then proceeds into the pleon (McLaughlin, 1980).

Excretory system

As in other decapod groups, Dendrobranchiata eliminate most of their excretory nitrogen as ammonia. Excretion and osmoregulation are carried out by the nephridial excretory organs opening at the base of the antennae (**antennal glands**). These structures are rather large and diffuse, with a dorsal portion positioned above the supra-esophageal ganglion and a ventral portion extending up into the peduncle of the antenna (Schram, 1986). The predominant traits of antennal glands can be summarized as follows: hemolymph filtrate is delivered by an arteriole to a terminal saccule of the antennal gland, the coelomosac, which is interpreted as a remnant of the coelom. It is composed of mesodermally derived podocytes, which perform an ultrafiltration function comparable to the glomerular nephron of the vertebrates. From the coelomosac, the urine passes to a spongy labyrinth, where selective re-absorption of proteins takes place (Anger, 2001). It is then transported through a tubule of variable length, the nephridial canal, into a bladder. Eventually the urine is released through an excretory pore at the antennal base, the nephropore. However, this excretion is supplemented by other structures, especially the gill surfaces. Decapoda actually

eliminate most of their excretory nitrogen as ammonia via the gills by simple diffusion or sodium exchange mechanisms, and their antennal organs are mainly for osmotic and ionic regulation (Dall et al., 1990).

Genital apparatus

THE MALE GENITAL APPARATUS

Testes develop after the **genital apertures** have formed (Dall et al., 1990). The male testes are paired, multilobed, and lie dorsal to the digestive caeca (fig. 63.11A). Each multilobed testis connects to a long tube, the proximal **vas deferens**, leading into the U-shaped medial vas deferens (Bauer & Cash, 1991). The tubules contain only mesoderm cells and primary **spermatogonia**. Later the network disappears and a variable number of testicular lobes develop (Dall et al., 1990; Bauer & Min, 1993). The vas deferens is marked by a distal extension that forms the **ejaculatory duct** that serves to the storage of the spermatophores prior to ejaculation. In sicyoniids, **spermatophores** deposited in the seminal receptacles of the female are little more than **spermatozoa** in a seminal fluid, while in penaeids sperm is transferred in much more complex spermatophores (Bauer & Cash, 1991). The ejaculatory duct connects to an area surrounding the **gonopore** externally and is located in the ventral part of the **last cephalothoracic somite** of the male (Bauer & Cash, 1991). The **androgenic gland** becomes visible only in the pubertal animal; this gland secretes a hormone that stimulates spermatogenesis, its activity being controlled by gonad inhibitory hormone from the sinus gland (Dall et al., 1990).

THE FEMALE GENITAL APPARATUS

For Penaeidae, the **ovary** consists of an outer thin, squamous epithelium, a relatively thick layer of underlying connective tissue, and an inner layer of **germinal epithelium**. It does not contain obvious muscle fibers, and there are zones of ovarian proliferation throughout the ovary. There are two anterior lobes, 6-8 short lateral lobes, and two long posterior lobes. Two simple **oviducts** lead from the sixth lateral lobe to the genital openings (Dall et al., 1990) (fig. 63.11B). The female **gonopore** opens on the **coxa of the third pereopod** just anterior to the **thelycum** (Schram, 1986).

Reproduction

Penaeids engage in **external fertilization** and are **gonochoristic** (Campos-Ramos et al., 2006). However, two hermaphroditic specimens of *Litopenaeus vannamei* were found in a shrimp farm in Venezuela. The cause of such abnormal features is unknown but may be linked to conditions found in the shrimp farm (Pérez Farfante & Robertson, 1992). **Hermaphroditism** in other dendrobranchiate shrimps also has been suggested in several studies, but those reports are based on speculation from field data of sexual size dimorphism or skewed sex ratios (Chiba, 2007).

In dendrobranchiate males, the external genitalia are formed by the **petasma**, **appendix masculina**, and **appendix interna**. Soon after the sixth post-larval stage, the endopods

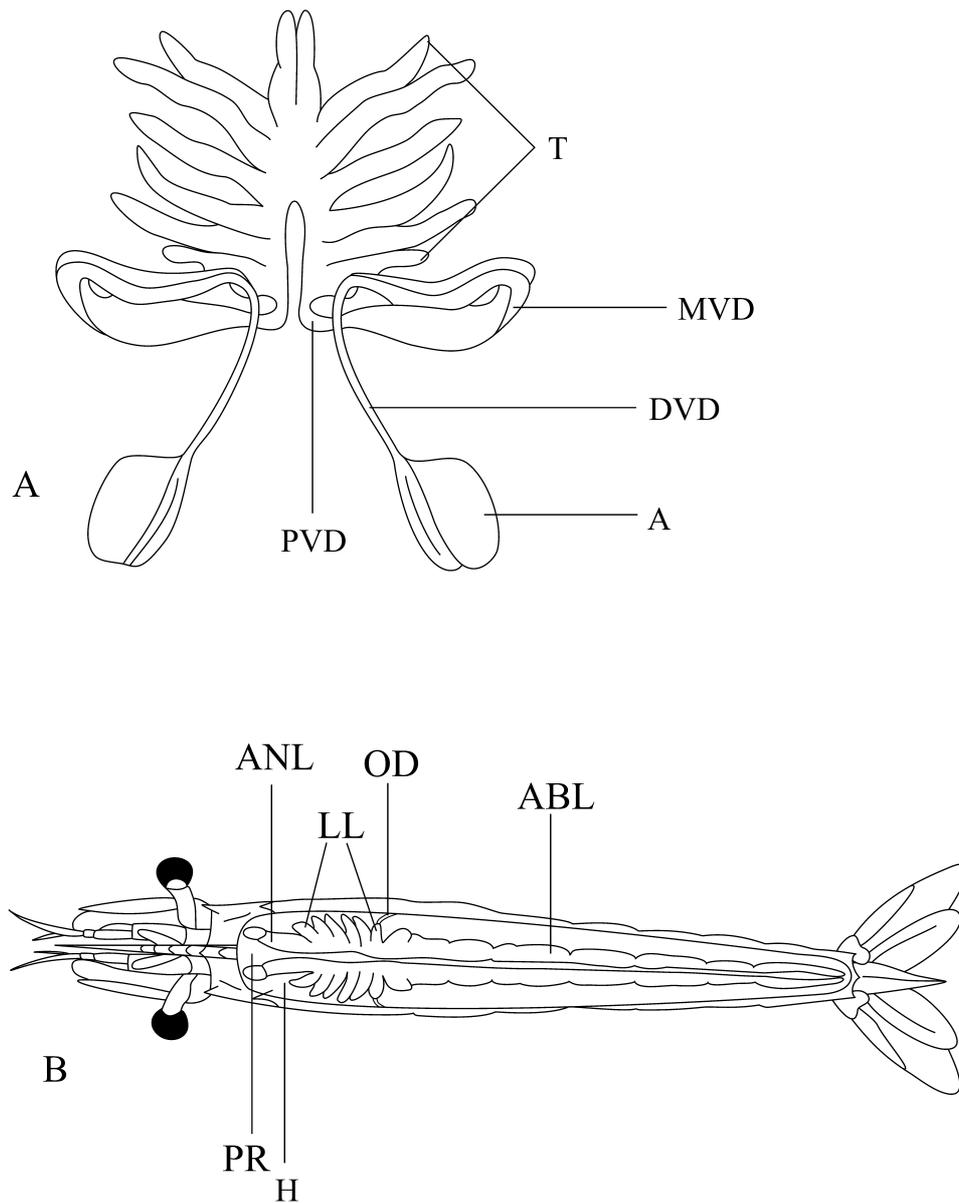


Fig. 63.11. Reproductive apparatus. A, male; B, female. Abbreviations: A, terminal ampoule; ABL, abdominal lobe of ovary; ANL, anterior lobe; DVD, distal vas deferens; H, hepatopaneceas; LL, lateral lobes; MVD, median vas deferens; OD, oviduct; PR, proventriculus; PVD, posterior vas deferens; T, lobe of testis. [Modified after Dall et al., 1990.]

begin to differentiate into the petasma, and the rudiments of the appendix masculina appear on the second pleopods, after which the genital apertures begin to develop (Dall et al., 1990).

Although presumably the **petasma** functions in **sperm injection** (aided by the appendix interna and the appendix masculina), Bauer (1991, 1992, 1996) showed that for the genus *Sicyonia* other possibilities exist. The first option deals with the **copulatory position** of males and females. As in other decapods, sicyonids copulate with the ventral surfaces opposed, but not so that the ventrally located male and female genitalia come into contact. Instead, they are diametrically opposed since the male's body is at a 90° or a somewhat oblique angle to that of the female. In this position, the male could **inseminate** only one **spermatheca** per time (the one from the side the male is mating). Also, in each insemination, the male would be able to insert only one dorsolateral projection of the petasma into the **seminal receptacle**. Consequently, the sperm mass ejected from the dorsolateral projection that is not inserted into the seminal receptacle would be lost. A comparison in copulation time is enlightening: decapods with sperm-injecting gonopods take several minutes to several hours to achieve copulation, but sicyonids take only a few to several seconds. Bauer's studies suggest that the petasma and the appendix masculina may serve to temporarily connect male and female genitalia during copulation and to adjust the position of a male genital papilla relative to the aperture of a spermatheca for injection of the sperm mass. In addition, there could be two other possible functions of the petasma and appendix masculina. First, the petasma could function as a **selective mechanism** (sexual selection by female choice) on the morphology of males, which might explain the evolution of such complex, often morphologically bizarre, male gonopods as seen in some penaeoid genera. Second, both sets of gonopods might be used only to touch and prod the female, providing key **stimulation or information**.

The **thelycum** constitutes the external genitalia of females, forming a set of modified sternal plates of the seventh and eighth thoracic sternites (sometimes of the sixth thoracic sternite too) as described above in the section on the cephalothorax. The thelycum serves to **store and transfer the sperm**, usually in spermatophores, and typically shields the seminal receptacles (Bauer, 1994; Pérez Farfante & Kensley, 1997). The seminal receptacles are also called spermatheca, and they can be defined as any enclosed space where sperm or spermatophores are deposited and stored (Bauer, 1994). In penaeids, the eighth thoracic somite of the female develops into the thelycum after the sixth post-larval stage (Dall et al., 1990).

GAMETOGENESIS

Spermatogenesis begins in the peripheral germinal layer of the testicular tubules, when spermatogonia enter into the prophase of meiosis (Dall et al., 1990).

The **spermatozoon** in the majority of dendrobranchiates (Penaeidae, Solenoceridae, and Sicyoniidae) is primarily characterized by the presence of an **acrosomal cap** that projects forward into a pointed appendage referred to as the **spike** (Medina et al., 2006). These penaeoids are also similar in that they have in the main body a **central nuclear region** and a **peri-nuclear cytoplasmic band** (Jamieson & Tudge, 2000; Medina et al.,

2006). Aristeidae, however, exhibit two lineages of spike-less spermatozoa: in one, the spermatozoon lacks an acrosome; in the other, the **acrosome vesicle** develops no projecting structure (Medina et al., 2006). The lineages without an acrosome have a central nuclear region and a peri-nuclear cytoplasmic band as in the other Penaeoidea, while the aristeid lineage with an acrosomal vesicle has an eccentric nuclear region and a subacrosomal distribution of collar cytoplasm.

Within Sergestoidea, only two species of Sergestidae have had their sperm studied, and as in aristeids they are spike-less, one with and the other without an acrosome (Medina et al., 2006). The sergestids also can be characterized either by the central nuclear region and a peri-nuclear cytoplasmic band, or by an eccentric nucleus and a subacrosomal layer of cytoplasm. Nothing is known of sperm morphology in Luciferidae.

Spermatophores are formed during the passage of spermatozoa down the vas deferens (Dall et al., 1990). The proximal and extended part of the vas deferens is lined with a secretory epithelium and is divided internally into two ducts. One duct contains clumps of spermatozoa, which are compacted into a matrix (in the **sperm duct**); the other duct secretes the wing matrix of the spermatophore, which does not contain spermatozoa (**accessory duct**) (Dall et al., 1990; Bauer & Cash, 1991). The separation of the two ducts is incomplete further down the vas deferens, but a partial septum persists to the terminal ampoule, where the spermatophore is compacted and a **hyaline layer** is secreted around the spermatophore (Dall et al., 1990).

Spermatophores can be liberated alone or as pairs, one from each side of the reproductive system (Dall et al., 1990; Bauer & Cash, 1991). When liberated in pairs, the sperm mass emerges first, followed by the wing matrix, and the two spermatophores are pressed together to form a twin spermatophore complex (Dall et al., 1990).

There is considerable variation in the form and complexity of materials transferred from the male to the female during insemination in penaeoids (Bauer, 1991). Sperm can be packaged in structurally complicated spermatophores composed of an assortment of accessory substances secreted in the male reproductive tract (Bauer & Cash, 1991). Spermatophores can be either more complex, as in some species of *Litopenaeus*, and attached externally to the thelycum, or less complex, as in Sicyoniidae, and stored in seminal receptacles of the female (Bauer & Min, 1993). There is a trend within dendrobranchiates that, as the thelycum changes from open or closed with a median spermatheca, to closed with paired spermatheca, the spermatophore is reduced from a complex, pre-formed external spermatophore to a simpler **spermatophoric mass** (Bauer, 1991). The genus *Rimapenaeus* is unusual in its packaging of sperm in numerous small spermatophores in contrast to other penaeids that present a single large mass of sperm (Bauer & Min, 1993).

During the development of **ova**, a process called multiplication, the oocyte diameter remains at about 10 nanometers. Once **pre-vitellogenesis** begins, the oocyte increases in diameter to about 70 nanometers (Dall et al., 1990). A layer of **follicle cells** develops around each oocyte towards the end of this stage and pushes the oocytes towards the periphery of the ovarian tube. During maturation, the **ovary** exhibits size and color changes that are macroscopically visible through the transparent carapace. These changes are due

to the deposition of yolk in the **oocyte**, which results in a rapid increase in oocyte diameter (Tsukimura, 2001), as well as to color changes due to carotenoids, with specific color changes related to a new maturation stage (Arculeo et al., 1995). The main constituents of **yolk** are protein and lipids, and vitellin is the major protein that accumulates within the ovary during **vitellogenesis** (Charniaux-Cotton, 1985; Chen et al., 1999).

Vitellogenesis in penaeids can rely solely on activity of the ovary (*Marsupenaeus japonicus*) or on activity of the hepatopancreas and the ovary (*Litopenaeus vannamei*, *Penaeus semisulcatus*, *Penaeus monodon*, *Parapenaeus longirostris*) (Quackenbush, 2001). **Primary vitellogenesis** is characterized by the appearance of oil globules in the cytoplasm, which later transform into vesicles (Dall et al., 1990), and is characterized by little change in overall size or diameter (Quackenbush, 2001). In **secondary vitellogenesis**, the vesicles develop into yolk granules, and cortical crypts appear and later become enclosed in well-developed, radially-arranged, club-shaped structures that are characteristic of mature oocytes (Dall et al., 1990); and the eggs actually grow in size from around 50 μm to 300 μm (Quackenbush, 2001). These inclusions appear to be the source of the jelly layer that encloses the egg after extrusion into the water. The nucleus, now much reduced in size, migrates towards the periphery of the oocyte. At maturation, the nucleus moves to the cytoplasmic membrane and undergoes its primary maturation division; the follicle cells, which remain in the ovary, separate from the oocyte, indicating that ovulation has occurred (Dall et al., 1990). The ova are now ready for liberation into the water.

This process is very important for reproduction since the yolk substances provide primary nutrition for embryogenesis and early larval development (Quackenbush, 2001; Nazari et al., 2007). Many studies with penaeids have proposed a range of three to six stages for ovarian maturation, and these stages can be determined by color as well as by morphometric, stereological, histological, and histochemical patterns (Nazari et al., 2007).

FECUNDITY

Fecundity is positively related to shrimp size and can be measured in two ways: by the number of eggs spawned, or by calculating from dissected ovaries. It is important to note that mature size varies from species to species, even within the same genus. For example, comparing *Penaeus esculentus* and *Penaeus semisulcatus*, and using as a relative measure the size at which 50% of the female population has eggs, we can determine that the former species matures at a smaller size and is less fecund (*Penaeus esculentus* mature size cl = 32 mm, 186 000 eggs; *Penaeus semisulcatus* mature size cl = 39 mm, 365 000 eggs). Comparing the maximum sizes of both species, once more *Penaeus esculentus* is less fecund than *Penaeus semisulcatus* (*Penaeus esculentus* maximum size cl = 45 mm, 479 000 eggs; *Penaeus semisulcatus* maximum size cl = 52 mm, 732 000 eggs) (Dall et al., 1990).

MATING BEHAVIOR

Mating behavior (reviewed by Dall et al., 1990) also varies depending on the species examined. There is a difference in the mating periods between **open** and **closed thelycum** species. Open thelycum species mate towards the end of the cycle, after the ovaries have

matured, while closed thelycum species mate shortly after the female has molted, while the cuticle is still soft.

Another difference between open and closed thelycum species concerns when molting occurs. Most species with a closed thelycum mate at night, as was observed for *Fenneropenaeus merguensis*, *Marsupenaeus japonicus*, and *Penaeus monodon*, although there is a daytime record for *Farfantepenaeus paulensis*. On the other hand, *Litopenaeus vannamei*, an open thelycum species, mates at sunset. Generally, in the first phase of mating, the female moves around after molting, occasionally swimming up 20-40 cm and then coming to rest on the bottom. During this period one or more males follow the female. Then the male moves to below the female, which grasps his carapace with her pereopods while continuing to swim; this is a pre-copulatory position. At least in *Penaeus monodon*, the male and female remain in position for 20-120 minutes.

Farfantepenaeus paulensis does not swim around before or during mating. If the male is dislodged from his pre-copulatory position, another male replaces him. In the second phase, the male turns upside down below the female, and they grip each other with their claws. If the successful male is dislodged from this position at that time, which is difficult, he reverts to the first phase of mating and follows the female. In *Penaeus monodon* and *Farfantepenaeus paulensis*, the third phase occurs when the male, while continuing to hold onto the female, rapidly turns perpendicular to the female's body. The male arches his body around the female, and then appears to squeeze the female and simultaneously flick his head and telson; spermatophore transfer probably takes place at this point. The male then separates from the female and swims away. In *Marsupenaeus japonicus*, the male does not rotate but remains aligned with the female. The duration of the process of **courtship** and mating varies from 30 minutes to 3 hours in *Penaeus monodon* and 10 minutes in *Marsupenaeus japonicus*. In *Farfantepenaeus paulensis*, mating takes 4-5 seconds from the time the male took a position underneath the female's body until it swims away. In open-thelycum *Litopenaeus vannamei*, mating is similar to that in *Penaeus monodon*, *Farfantepenaeus paulensis*, and *Marsupenaeus japonicus* and is even more similar to the last one because no rotation underneath the female was shown.

Among the sicyoniids the mating behavior is quite different, as shown in Bauer (1992). The **precopulatory behavior** begins when the male and female make physical contact while moving about the aquarium. If the male was behind the female when first contact was made, it immediately began to push under the female with its cephalothorax. However, if first contact was made from any other position, the male moved behind the female before pushing below it. The male then followed behind the female, and grasped or contacted the female's pleon with its long antennal flagella, which quivered or vibrated during this "following" behavior. During following behavior, the dorsal cephalic region of the male, with the rostrum, eyes, and antennules, touched and prodded the female's genital area or thelycum, where the apertures to the female's seminal receptacles are located. Next, the male pushed upwards, tilting the female's body forward so that the genital region on the posteroventral cephalothorax was lifted well off the substratum. The male assumed the copulatory position by rolling upside down below the female, with the male's body perpendicular or slightly oblique to that of the female. Median duration of the copulatory

posture varied from 3-17 s. Copulation usually terminated when the male rolled back to an upright position and backed away slightly from the female, as it happens in other penaeids, although the sicyoniid female sometimes broke off the copulation with sudden retrograde swimming by rapid abdominal flexion. After a copulation, the male frequently initiated following behavior again, although numerous and sometimes extensive bouts of following behavior often did not result in copulation.

SPAWNING

Spawning usually occurs at night (*Marsupenaeus japonicus*, *Melicertus kerathurus*, *Fenneropenaeus merguensis*, *Penaeus monodon*, and *Sicyonia ingentis*), the time of spawning varying seasonally, at least in *Marsupenaeus japonicus*. *Fenneropenaeus merguensis* spawns once per molt cycle. In captivity, but without induction, *Fenneropenaeus indicus* and *Penaeus semisulcatus* undergo multiple spawnings per molt cycle (Dall et al., 1990). It is very common to induce spawning in shrimp farms by **eyestalk ablation** to increase productivity.

Endocrine system

MORPHOLOGY

The established endocrine elements in Decapoda are the **neurosecretory system** (X-organ-sinus gland complex of the eyestalk; neurosecretory cells of the brain and the central nervous system; post-commissural organs; pericardial organs), the **Y-organ**, and the **androgenic gland** (Dall et al., 1990).

In the **X-organ-sinus gland** (XO-SG) **complex**, large groups of neurosecretory cells associated with each eyestalk ganglion transmit their neuroendocrine secretions via tracts of nerves to the sinus gland. Neurosecretory tracts from the brain also terminate in the sinus gland, which is a release site for neurohormones into the circulation. The crustacean sinus gland is a discrete, easily identified structure located between the medulla interna and medulla externa of the eyestalk (Fu et al., 2005). There are two sinus glands per animal, one per eyestalk. The neuroendocrine secretions of the XO-SG gland complex constitute a family of peptide hormones that regulate physiological activities as varied as molting, blood glucose levels, integumental color changes, eye pigment movements, and hydro-mineral balance (Fu et al., 2005). These neuropeptides include gonad-inhibiting hormone (GIH), molt-inhibiting hormone (MIH), vitellogenesis-inhibiting hormone (VIH), and crustacean hyperglycemic hormone (CHH) (Huberman, 2000; Raviv et al., 2005; Tsutsui et al., 2005; Wongprasert et al., 2006; Lee et al., 2007).

The **Y-organ** is implicated as the source of the molting hormones (ecdysones) secreted as a precursor to the hemolymph being converted into the active hormone (Huberman, 2000). The gland has been noted as a strip of tissue located in the anterior upper branchial chamber in *Metapenaeus* and in *Marsupenaeus japonicus* (cf. Dall et al., 1990).

An **androgenic gland**, a long strip of secretory tissue located along the lower vas deferens, has been studied in Penaeidae. It triggers the development of the testis and male secondary sexual characters.

Neurosecretory cells are associated with the remaining **ganglia** of the central nervous system in macrurous Decapoda, but only those of the tritocerebrum commissures have been fully described for Penaeidae (cf. Dall et al., 1990). The **post-commissure organ**, originated from the tritocerebral commissure, has a structure analogous to that of the sinus gland. Each organ sends a fine nerve to the dorsum, where it ends in a lamella containing neurosecretory droplets.

HORMONE FUNCTION

Some of the hormones important to dendrobranchiate physiology are cited above. They are critical in many processes, but here we will focus on two main functions: molting and gonadal maturation.

Crustacean **molting** (ecdysis) is controlled by at least three neuropeptides: molt-inhibiting hormone (MIH), crustacean hyperglycaemic hormone (CHH), and **crustacean cardioactive peptide** (CCAP) (Chung & Webster, 2004) and by **ecdysteroids**, secreted as the precursor **ecdysone** (Huberman, 2000). Penaeidae shrimps are characterized by a di-ecdysal molting cycle, which has a very short intermolt stage representing only 10% of the whole cycle (Carvalho & Phan, 1998). The **molt-inhibiting hormone** (MIH) is found in the XO-SG complex, located in the eyestalk. Because of this arrangement, ablation of the eyestalk results in a shortened molt cycle interval, while the implantation of the eyestalk contents restores this interval (Huberman, 2000). In some decapod groups, eyestalk ablation also results in a considerable increase in circulating ecdysteroids (Huberman, 2000), and in adult crustaceans, ecdysteroid synthesis by the Y-organ is negatively regulated by molt-inhibiting hormone (MIH) and **crustacean hyperglycaemic hormone** (CHH) (Chung & Webster, 2004). The inhibition of molting by environmental stress may be mediated by CHH (Lee et al., 2007). The CHHs are the most abundant neuropeptides in the SG, and isomorphs may have specific activities in different tissues (Huberman, 2000). Although not yet known in dendrobranchiate shrimp, in the crab *Carcinus maenas* CHH is involved in the rapid uptake of water prior to ecdysis. The CCAP hormone is apparently involved in stereotyped ecdysis behavior (Chung & Webster, 2004).

Hormones also modulate **gonadal maturation**. Two antagonistic hormones regulate development of the ovary in crustaceans, the **gonad-inhibiting hormone** (GIH) from the X-organ sinus gland complex in the eyestalk, and the **gonad-stimulating hormone** (GSH) in the brain and thoracic ganglion (Wongprasert et al., 2006). Adiyodi & Adiyodi (1970, 1985) propose that GIH and MIH actions are antagonistic: molting occurs when MIH and GSH hemolymph levels are low and those of GIH and molting hormones are high, while in gonadal maturation the situation is the opposite (Dall et al., 1990). Thus, high levels of GIH may inhibit molting during the immature stages of reproduction, while CHHs may prevent molting during the mature stages of reproduction, with the two working together to synchronize reproduction and molting during the reproductive cycle (Huberman, 2000). This model applies to females, but it has been shown that GIH also works for males (Huberman, 2000). There is evidence that in male crabs GIH acts via the androgenic gland by inhibiting its secretion; in GIH absence maturation takes place (Dall et al., 1990). As GIH is in the eyestalk, eyestalk ablation is therefore used

commercially to induce ovarian maturation, but the technique could lead to a decrease in egg quality and eventual death of the spawner (Benzie, 1998). Wongprasert et al. (2006) demonstrated that **serotonin** (5-hydroxytryptamine) operates during female gonadal maturation and spawning. In crustacean females, the late phase of gonadal maturation to form mature ova is named vitellogenesis (Huberman, 2000), which involves the production of yolk proteins that act as nutrient sources for developing embryos (Tsukimura et al., 2000). The major component of this nutritive material is the lipoprotein vitellin that is derived from a precursor called vitellogenin, which is found in the hemolymph and that can be synthesized in extra-ovarian tissues or in the ovaries (Huberman, 2000; Tsukimura et al., 2000). In this case, GIH could also be referred to as VIH. Almost nothing is known of other hormones acting in gonadal maturation in Dendrobranchiata. Among the limited data available, there is evidence for the presence of estrogens in the ovaries of *Parapenaeus fissurus* and also of the presence of prostaglandins, which would be involved in spawning and spermatophore production in penaeids (Dall et al., 1990).

DEVELOPMENT AND LARVAE

Development

Dendrobranchiata develop through **complete, early cleavage**. In *Sicyonia ingentis*, for example, cleavage occurs more or less synchronously every 25-30 minutes, **gastrulation** began at about 3.5 hours post-spawning, and nauplius larvae **hatched** in about 24 hours. The first major asynchrony in the rate of cell division in this species occurs at the 32-cell stage. At this time 30 blastomeres enter the next mitotic cycle while the other 2 remain in interphase. These 2 cells are called the mesendoderm cells and because of this pause in the mitotic cycle they are said to be arrested. Subsequent gastrulation occurs by ingression of mesendoderm cells into the blastocoel and invagination of the naupliar mesoderm. *Litopenaeus vannamei* show the same pattern of timing in cleavage (including cell arrest), in the presence of 9 initial crown cells around the blastopore, and the type of primordial endoderm cells. Some variation is reported for other groups of Dendrobranchiata. For example, *Melicertus kerathurus* mesendoderm cell arrest and subsequent ingression is at the 16-cell stage, and they have 8 initial crown cells, while *Marsupenaeus japonicus* mesendoderm cell arrest and subsequent ingression is at the 64-cell stage, and they have 9 initial crown cells (Hertzler, 2005).

Larvae

GENERAL

Dendrobranchiata typically **shed** their eggs **freely into water**, although the luciferids **brood** them for a short time on the posterior thoracopods. Larval development in Dendrobranchiata is **regular anamorphic** (Anger, 2001), although sometimes it is called by some workers (McLaughlin, 1980; Williams, 1982) **metamorphic**. An anamorphic designation is justified because during the subsequent decapodid phase, juvenile characters

are attained gradually over a variable number of molts (Anger, 2001). Thus, neither the transition between the naupliar and the zoeal phase, nor that between decapodid and early juvenile stages is truly metamorphic.

Different terms have been proposed for the various larval stages. In Penaeidae, larval morphology and behavior were first fully described by Müller (1864), who used the terms **nauplius**, **zoea**, **mysis**, and **postlarva**. Williamson (1982) and Dall et al. (1990) used the same terms and also the term **megalopa** (following Müller, 1864). Recently, Anger (2001) considered a division similar to Williamson (1982), with three different phases (nauplius, zoea, and **decapodid**) but with a change in the nomenclature of the last phase because megalopa is a term commonly used for Brachyura only. Dendrobranchiata are the only decapods with three larval phases, including several free-living naupliar stages (Anger, 2001). Within all these phases are different stages, and the number of stages can vary among the families. Penaeidae usually have **5 nauplii**, **6 zoeae (3 protozoeae + 3 mysis)**, and a **postlarva** (= decapodid) (Dall et al., 1990). All described Solenoceridae have **5-6 nauplii** and **5 zoeae (3 protozoeae + 2 mysis)** (Calazans, 2000). In Benthescymidae, the genus *Gennadas* exhibits **4 mysis stages** (Rivera & Guzmán, 2002).

Though the patterns of appendage development between the two dendrobranchiate superfamilies, the penaeoids and sergestoids, are essentially identical, the gross morphologies are rather distinctive (Schram, 1986). The sergestoid larvae tend to be more spinous and are thus sometimes referred to in the literature with the distinctive names **elaphocaris** (for the protozoea) and **acanthosoma** (for the zoea or mysis stage).

NAUPLIUS

The **nauplii** of dendrobranchiates are unique among Decapoda because they are **free-swimming** (Dall et al., 1990). The early naupliar stages are characterized by the presence of **three propulsive limbs** (antennule, antenna, and mandible) and are therefore called **orthonauplii** (Williamson, 1982). Another morphological character of these larvae is the presence of an exclusive small median eye, the **nauplius eye** (Anger, 2001). The naupliar **antennule** is always uniramous and without a flagellum. It is unsegmented at hatching, but the proximal part shows a variable number of annuli in the late nauplius (Williamson, 1982). The **antenna** is typically biramous in all naupliar stages. The appendage may be unsegmented in early nauplii, but the peduncle always consists of two segments by the end of this stage (Williamson, 1982). The endopod is unsegmented in all nauplii, and the exopod is segmented throughout its length in most nauplii (Williamson, 1982). The naupliar **mandible** endopod and exopod are unsegmented in penaeid nauplii (Williamson, 1982). The mandibular coxa (including the gnathobase) becomes the body of the mandible at the next phase; the rest of the appendage may be retained as a palp (Williamson, 1982).

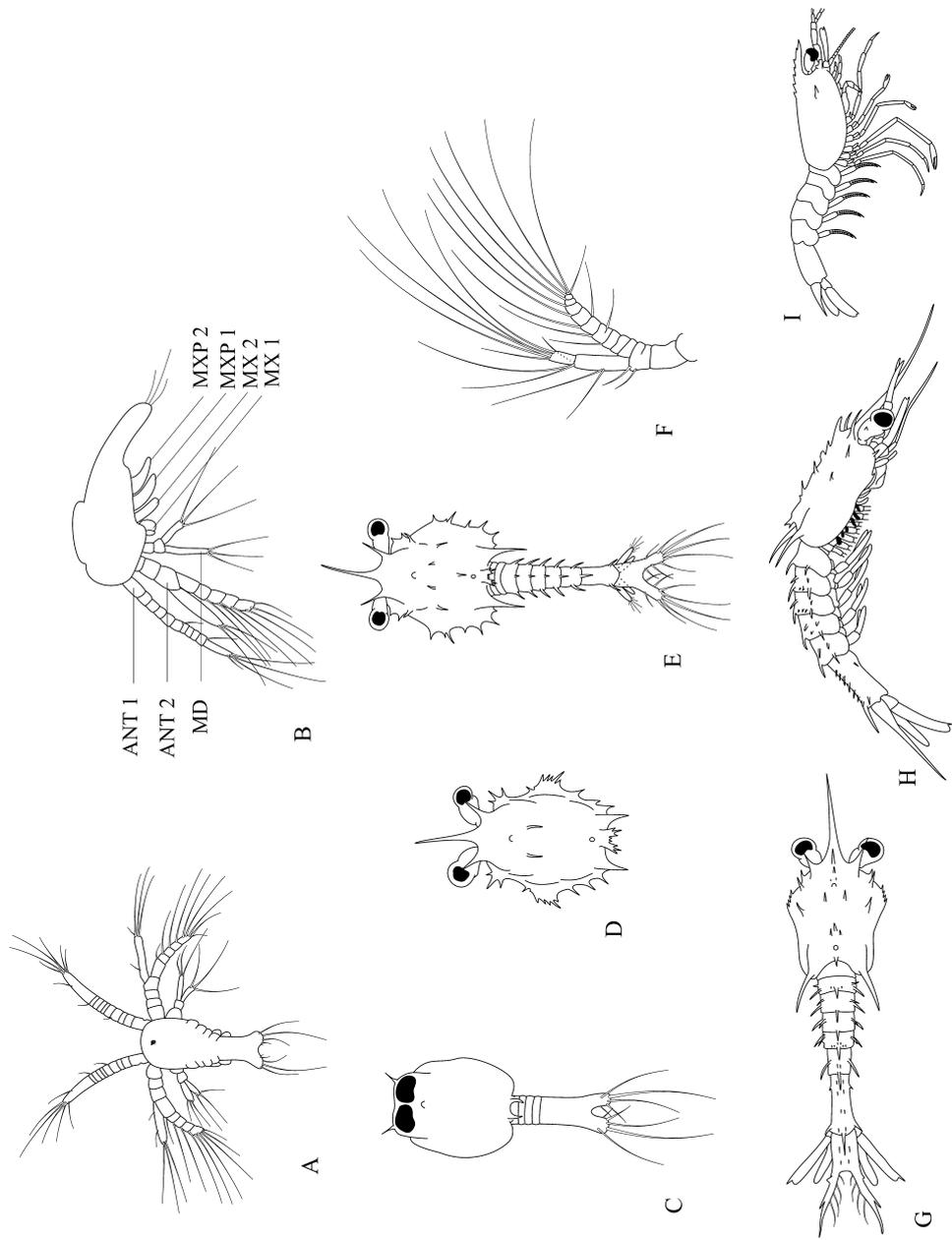
Late stages, characterized by the presence of **buds** of the maxillula, maxilla, first and second maxillipeds, as well as by masticatory swellings (**gnathobases**) on the mandible, are referred to as **metanauplii** (Dall et al., 1990) (fig. 63.12A, B). However, since the appendages that characterized the metanauplius are non-functional, Anger (2001) maintains that these belong to the naupliar phases. The naupliar phases **do not feed** and are passed through relatively quickly, within 24 to 68 hours, and a stage is reached wherein

the first two maxillipeds are developed, the telson is bifurcate, and the carapace bud is developed (Schram, 1986). This carapace, once acquired, is never lost, but it may undergo one or more metamorphoses (Williamson, 1982). A simple carapace is present in the two naupliar stages of *Lucifer* but is absent in those of *Sergestes* (cf. Williamson, 1982). Among Dendrobranchiata, the **number** of naupliar stages varies from **5 to 8**.

PROTOZOEAE

“Zoeal” development in dendrobranchiates is divided into two stages, **protozoaea** and **mysis**. The protozoaea stage of penaeids exhibits three distinct sub-stages. In the early stages of penaeoids and sergestoids (fig. 63.12C), all five pairs of head appendages are functional. The antennules and antennae maintain their ancestral natatory function, a function shared with the first two pairs of thoracopods (Williamson, 1982; Anger, 2001) (fig. 63.12F). The mandibles become feeding appendages (Anger, 2001). The endopod and exopod of the mandibles are lost, and the masticatory surface is divided into an **incisor process** and a **molar process** (Dall et al., 1990). Between the two processes are a variable number of long, movable, serrate teeth, one of which is a **lacinia mobilis** (sensu Moore & McCormick, 1969). The more posterior thoracic appendages are absent or rudimentary (Williamson, 1982). With the molt to the first protozoaea, all thoracic somites are formed. A **carapace**, attached at the somite of the maxilla, covers only part of the thorax, i.e., to about the fourth somite (Dall et al., 1990). The carapace in Penaeidae and Sergestidae is usually without a rostrum (Williamson, 1982). The carapace is unarmed in penaeids, but solenocerids possess **many spines** in all stages (Williamson, 1982). For example, the protozoaea I of *Pleoticus muelleri* has a pair of frontal spines on the anterior portion of the carapace, and in *Mesopenaeus tropicalis* a pair of frontal spines is present on the anterior portion of the carapace (Calazans, 2000). Sergestidae usually bear dorsal and lateral spines or processes on the carapace, which are often elaborately branched (Williamson, 1982). Unstalked **compound eyes**, as well as the naupliar eye, are present beneath the carapace (Dall et al., 1990). The eyes are covered in penaeid and sergestid protozoaeae in stage I only (Williamson, 1982). Frontal organs are also present in this sub-stage only. Swimming and feeding are now virtually continuous (Dall et al., 1990). At the **first protozoael stage** the pleon is still unsegmented and ends in a large bilobed telson. In this stage, the telson has either a sensory or cleaning function. Dall et al. (1990) confirmed the use of the telson for cleaning the antennae and mouthparts, and also saw that the **telson** can work as a **hydroplane**, to effectively change direction with the forward propulsion provided by the antennae.

In the **second protozoaea**, the compound eyes become stalked, the frontal organ disappears, and a rostrum, supra-orbital spines, and most leg rudiments appear (Dall et al., 1990) (fig. 63.12D). The carapace in penaeids has a rostral spine and a pair of supraorbital spines in protozoaeae II and III (Williamson, 1982). The rostral spines in solenocerids can range from smooth in *Pleoticus muelleri* to spinulate in *Solenocera necopina* and *Mesopenaeus tropicalis* (cf. Calazans, 2000). The pleon is divided into six somites, the telson not being separated from the sixth somite.



The **third protozoecal sub-stage** is referred to as a **metazoea**, because the remaining thoracopods are prominent and biramous, although still not functional (Williamson, 1982) (fig. 63.12E). In addition, the biramous setose uropods appear in the third protozoa, and the telson separates from the sixth pleomere (Dall et al., 1990). The non-functional uropods in larval sergestoids appear in the protozoa/elaphocaris stage before the pleopods, which do not develop until the mysis/acanthosoma stage.

MYSIS

With the molt to the **first mysis stage**, the larvae undergo major changes in appearance, and the body takes on a shrimplike appearance (McLaughlin, 1980) (fig. 63.12G, H). The most significant change is the development of functional pereopods with large exopods on all such limbs, which become functional locomotory appendages. However, in some Penaeoidea the posterior exopods do not become functional until mysis II (Williamson, 1982). The larvae now swim backwards, body vertical with the telson up, slowly spinning on the vertical axis; this is augmented by rapid backward thrusts from the flexion of the pleon (Dall et al., 1990). The carapace conforms more closely and covers most of the thoracic somites, and during this stage the **rostral, hepatic, and/or pterygostomial spines** appear for the first time in the penaeids. In the antennule of Penaeoidea and Sergestoidea, the peduncle divides into three segments and the inner ramus appears (Williamson, 1982). The antennae, which have lost their locomotory function, also change in appearance: the exopods of the antennae, no longer segmented, become flattened antennal scales, and the **statocyst** also appears near the base of the antennule. The mandibles again become biramous when the bud of the mandibular palp appears in the later sub-stages. The maxillae are largely unchanged; only the outer lobe grows a proximal extension and develops many marginal setae, but the setose epipod of the maxillilule disappears, while the epipod on the maxilla enlarges with each moult to form the scaphognathite in the juvenile. All three maxillipeds are now functional, rudimentary chelae appear on the first three pereopods, and gill rudiments appear on the thoracopods in the later sub-stages.

The number of mysis stages recorded in the literature is quite variable. Dall et al. (1990) defined three mysis stages on the basis of pleopod development as follows. The **first mysis** stage has no, or barely perceptible, pleopod buds on the first five pleomeres. The **second mysis** has prominent, non-articulated pleopod buds. The **third mysis** has small, two-segmented, lightly-setosed, but non-functional pleopods on the first five pleomeres.

DECAPODID

There are no dramatic changes in morphology with the molt to the decapodid phase (Dall et al., 1990) (fig. 63.12I). The postlarval or juvenile condition is achieved when

Fig. 63.12. Larval development. A-B, *Penaeus plebejus*: A, nauplius late stage (metanauplius), dorsal view; B, nauplius late stage (metanauplius), lateral view. C-I, *Pleoticus muelleri*: C, zoea (protozoa) I; D, zoea (protozoa) II; E, zoea (protozoa) III; F, zoea (protozoa) antenna; G, zoea (mysis) I; H, zoea (mysis) II; I, decapodid. [A, B, modified after Dall et al., 1990; C-I, modified after Calazans, 2000.]

all exopods are reduced or lost and the uniramous pleopods become large, setose, and functional, taking over as the sole appendages for locomotion. The larva again swims forward with rhythmic beating of the pleopods. All non-sensory cephalic appendages and the three maxillipeds assume new functions as mouthparts (Anger, 2001). The chelae on the first three pereopods are now functional, with small teeth and short bristles terminally. The supra-orbital spines disappear. The antennae change a little, with both distal rami of the first antennae becoming segmented. The mandibular palp, present since the mid-mysis stage, is usually segmented, setose, and probably functional; the lacinia mobilis is often reduced or absent (Dall et al., 1990). The endopods of both maxillae become unsegmented, degenerate, and palp-like. Both the endopod and exopod of the first maxilliped are vestigial. The endopod of the second maxilliped becomes recurved, its setation changes dramatically, and the exopod degenerates. Gills on the thoracopods are still only rudimentary. The telson continues to narrow distally and is only faintly cleft in penaeids, but in some solenocerids such as *Pleoticus muelleri* at this stage the telson is triangular in shape with a pointed tip (Calazans, 2000). Subsequently, through a gradual series of molts, the eventual adult condition is achieved.

ECOLOGY AND ETHOLOGY

Dendrobranchiate shrimp inhabit mostly marine waters, with some species of Sergestidae found in fresh water. Aristeidae, Benthescymidae, and Sergestidae are predominantly deep-water families and contain species that are either deep benthic dwellers or are members of the meso- and bathypelagic fauna (Pérez Farfante & Kensley, 1997). Most Penaeidae inhabit shallow and inshore tropical and subtropical waters (Dall et al., 1990). The majority of species of Solenoceridae occur in offshore, deeper waters. Almost all species of Sicyoniidae are found in depths of up to 200 m (Pérez Farfante, 1985). Luciferidae are planktonic.

Solenocera membranacea burrows into the mud bottom during the daytime (Heegaard, 1967). The same pattern was observed in an experimental study with *Melicertus latisulcatus*, where the specimens were active only during the dark phase; within 15 minutes of the start of the light phase, all activity ceased (Rasheed & Bull, 1992). The mud used in Heegaard's experiment contained living prey, but the shrimp did not attack them during daytime. Only when it began to darken did the shrimp rise from the mud to search for food. If there was no mud in the aquarium, the shrimp would attack and feed on prey at any time of the day when prey crossed their path. Heegaard (1967) also observed that *Solenocera membranacea* is a **voracious eater**, and when fed in the aquarium they could easily eat three or four polychaetes of 50 to 60 mm in succession, after which they often sank to the bottom and rested. This diurnal feeding is also seen in most of the penaeids (Dall et al., 1990). The **burrowing behavior** has two obvious advantages: it reduces the total energy demand, and it is an important form of defense. The burrows made in this way are not permanent, and penaeid shrimps are not considered territorial (Dall et al., 1990).

These solenocerids, when not swimming, are very sensitive to any movements or sounds, which can cause the animal to stiffen all parts of the body and **play dead** (Heegaard, 1967).

The antennae, which can be up to three times the length of the shrimp's body, also are used in the search for food. When moving along the soft bottom **searching for food**, the shrimp are reminiscent of a helicopter sweeping slowly over the ground. During this searching period, the thorax is held in a horizontal position while the pleon is kept vertically, with only the last pleomere and the tail-fan bent downward (Heegaard, 1967). In contrast, *Fenneropenaeus merguensis* searches the bottom for food by holding its first three pereopods in line at right angles to the long axis of the body and using their distal segments to make rapid probes into the substrate as it walks over the bottom; any food found is picked up and manipulated by the pereopods and mouthparts (Dall et al., 1990). Penaeids can eat small isolated particles or organisms, as well as large food items such as algal mats or large live prey. For example, *Litopenaeus setiferus* and *Farfantepenaeus aztecus* tear off a portion of algal-microbial mats and pass them to the mouthparts; then they hold it in the exhalent respiratory current and rotate it to wash most of the silt from the mat, and only when it is clean do they tear off the peripheral piece and swallow it. Another feeding behavior was observed for *Melicertus plebejus* and *Penaeus esculentus*, which, after a few days under starvation in the aquarium, attacked smaller prawns or newly molted individuals, eating first the eyes. The diet composition of *Funchalia villosa* in the eastern Gulf of Mexico revealed that over half of the food biomass was fish, with most of the balance being chaetognaths and euphausiids; olive-green debris and to a lesser extent nematocysts were also diet items (Hopkins et al., 1994). Generally, penaeids can be described as opportunistic omnivores (Dall et al., 1990).

Hopkins et al. (1994) also showed the diet composition of some species of *Gennadas*, *Sergestes*, and *Sergia*. *Gennadas* had fish and euphausiids as principal food categories, with copepods, chaetognaths, and radiolarians being important diet elements also; olive-green debris interspersed with phytoplankton and protists and nematocysts were encountered also. The Sergestidae ingested primarily euphausiids and copepods, with most of the remaining diet consisting of chaetognaths, ostracodes, and radiolarians; debris containing phytoplankton and protists and cnidarian nematocysts were also part of their diet.

Feeding is reduced around ecdysis for *Penaeus esculentus* as reported by Dall (1986), Wassenberg & Hill (1984), and other authors. For example, *Farfantepenaeus californiensis* and *Litopenaeus stylirostris* ate less for 12 to 24 hours before and 6 to 12 hours after ecdysis, and *Farfantepenaeus duorarum* stopped feeding 36 hours before ecdysis and resumed about 36 hours after ecdysis (Huner & Colvin, 1979). This is probably due to the **softness of the mouthparts** near the ecdysis period (Passano, 1960). With this reduction in feeding and the higher level of metabolic activities during the molt, the shrimp must rely on their reserves. Three nights after ecdysis, feeding rises to a level well above that during the rest of the molt cycle, and this could be explained as a need to restore the lipid reserves in the shrimp. The species, *Penaeus esculentus*, when a choice for food is given, shows a preference for molluscan over crustacean food in the nights around the ecdysis, proving to

be a **selective feeder** under laboratory as well as under natural conditions (Wassenberg & Hill, 1987; Hill & Wassenberg, 1992).

Rasheed & Bull (1992) noted, though Heegaard (1967) did not, that under high density, more time is spent in non-feeding activities and less in feeding. This confirms some reports that crowding reduces growth rate and survival in prawns.

ECONOMIC IMPORTANCE

Penaeid shrimp are an ecologically diverse group of species, and many are important resources for worldwide fisheries and aquaculture. The annual world production of shrimp, around 6 million tons (FAO, 2006), makes this market very attractive and has encouraged the development of farming of many species in several countries (Zitari-Chatti et al., 2008).

Marine shrimp farming is an important global aquaculture industry with a production greater than 1 million metric tons for the year 2000 (Barajas, 2006). A number of species belonging to the genus *Penaeus* s.l. have been produced commercially by aquaculture (Brauer et al., 2003). The contribution of farming to **global shrimp production** rose from a mere 6% in 1970 to 26% in 1990 (Primavera, 1997), and in 2006 it accounted for as much as 70 percent of shrimps and prawns (penaeids) produced worldwide.

About 80% of the production comes from Asia (Rosenberry, 1995). Three kinds of producer countries can be recognized: (1) countries that base their shrimp production mainly on their fishery yields (for example, the United States, where farmed shrimp make up only 1% of total production); (2) countries that have focused their shrimp production efforts almost exclusively on hatcheries (aquaculture) (for example, Ecuador, where farmed shrimps make up 95% of its shrimp production); and (3) countries that produce shrimp in similar percentages from both wild stocks and hatcheries (for example, Mexico, China, India, and Indonesia) (Rosa-Vélez et al., 2000).

Holthuis (1980) listed the species of Dendrobranchiata that are of interest to fisheries, grouping them into those largely used for human consumption, those constituting by-catch from fishing gear targeting another species, and those that are not commercially exploited but considered by experts to be of potential commercial value.

Aristeidae are one of the most valuable deep-water fishing resources, particularly in the Mediterranean Sea (Pezzuto et al., 2006). *Aristaeomorpha foliacea* is obtained by deep-sea trawlers in the Mediterranean off the coasts of Spain, France, Italy, Algeria, and Israel. *Aristeus antennatus* is fished by deep-sea trawlers off NW Africa and along the Mediterranean coasts of Spain, France, Italy, and Malta (Holthuis, 1980). In Brazil, the fishing potential of Aristeidae has only recently been considered; Pezzuto et al. (2006) recognized 3 species of commercial importance occurring at the southern Brazilian coast: *Aristaeomorpha foliacea*, *Aristaeopsis edwardsiana*, and *Aristeus antillensis*.

Penaeidae are by far the most important resources for both fisheries and aquaculture. Most of these penaeids are consumed locally, but some are also exported as frozen products. Currently the world market is dominated by the Chinese prawn *Fenneropenaeus chinensis* with very high landings in China. In 2005, the catch of the Chinese prawn

was of 106 329 metric tons (FAO, 2009). Some penaeid species are also reared (via aquaculture) and directly marketed from there. Important examples include the Kuruma prawn *Marsupenaeus japonicus*, the previously mentioned Chinese prawn, the giant tiger prawn, *Penaeus monodon*, and the white leg prawn *Litopenaeus vannamei* (see Debelius, 1999). *Artemesia longinaris*, because of its small size, is of minor interest to fisheries but is trawled as the by-catch of *Pleoticus muelleri* in Argentina (Holthuis, 1980).

Sicyoniidae are of minor interest to fisheries, although *Sicyonia carinata* is really quite tasty, that is hampered only by the fact that the shell is very hard (Holthuis, 1980). *Sicyonia brevirostris* has commercial importance in the western Atlantic (D’Incao, 1995).

Five genera of Solenoceridae are of interest to fisheries. *Pleoticus muelleri* is the most important crustacean to fisheries in Argentina, with annual catches of 100 metric tons or more during 1973–1976 (Holthuis, 1980) and 11 500 tons during 1981–1988 (Boschi, 1989). Only in 2005 the catch of this species was of 7510 metric tons (FAO, 2009). *Solenocera crassicornis* is commercially fished in India, Hong Kong, and Indonesia, although the two latter yields are not of great importance.

Within Sergestidae, two genera are of interest to fisheries. Some species are commercially important, e.g., *Acetes chinensis* for northeast China, Korea, and Japan, and *Sergia lucens* for Japan (Holthuis, 1980). *Sergestes similis* is very abundant in the North Pacific sei and fin whale feeding areas, with concentrations estimated at 100–4500 individuals per cubic meter. Earlier authors predicted that these stocks may have direct commercial value in the future (Butler, 1980), but that has not yet come to pass.

PHYLOGENY

The **monophyly** of Dendrobranchiata has been supported in many different studies. Felgenhauer & Abele (1983), in a paper on phylogenetic relationships among the **shrimp-like Decapoda**, recognized Dendrobranchiata as a natural group and added other characters to those of Burkenroad (1963) and Glaessner (1969), such as the presence of the petasma and eggs being shed directly into the water. Abele (1991) presented results on decapod phylogeny based on both morphological and molecular data, showing with a **total evidence analysis** that Dendrobranchiata was a natural group. Wills (1997) performed a cladistic analysis of Crustacea, including both extant and fossil groups, and also found that Dendrobranchiata emerged as a monophyletic group. In a more recent study (Dixon et al., 2003), Dendrobranchiata was considered a probable monophyletic taxon, but the authors emphasized that this clade is not recovered in all of the most parsimonious trees in their analysis with ordered characters. In several analyses (Burkenroad, 1981; Felgenhauer & Abele, 1983; Schram, 1984; Abele & Felgenhauer, 1986; Abele, 1991; Wills, 1997; Richter & Scholtz, 2001; Dixon et al., 2003), Dendrobranchiata appears as a sister group to Pleocyemata, i.e., all other Decapoda including Caridea, Stenopodidea, and Reptantia.

Hence, while there is little debate about the status of the dendrobranchiates, only two studies based on morphological characters have been performed to elucidate the relationships of all families of Dendrobranchiata (Burkenroad, 1983; and Tavares et al.,

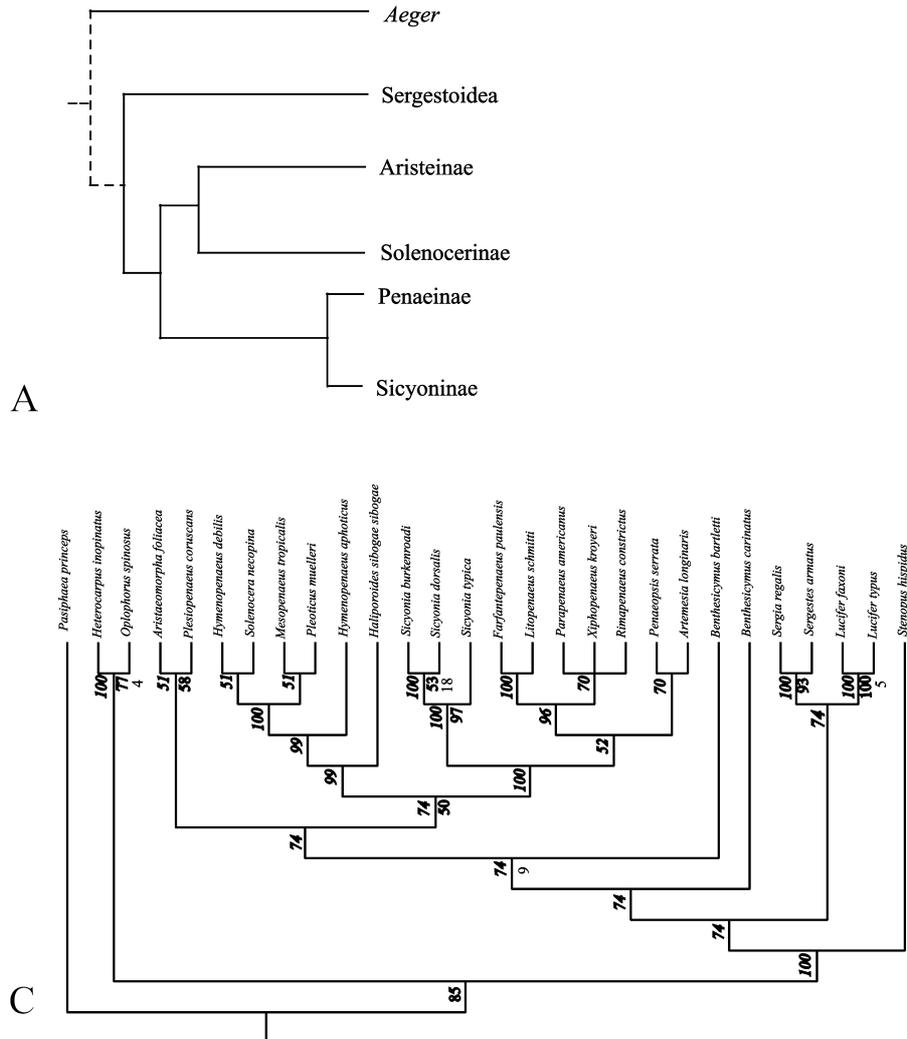
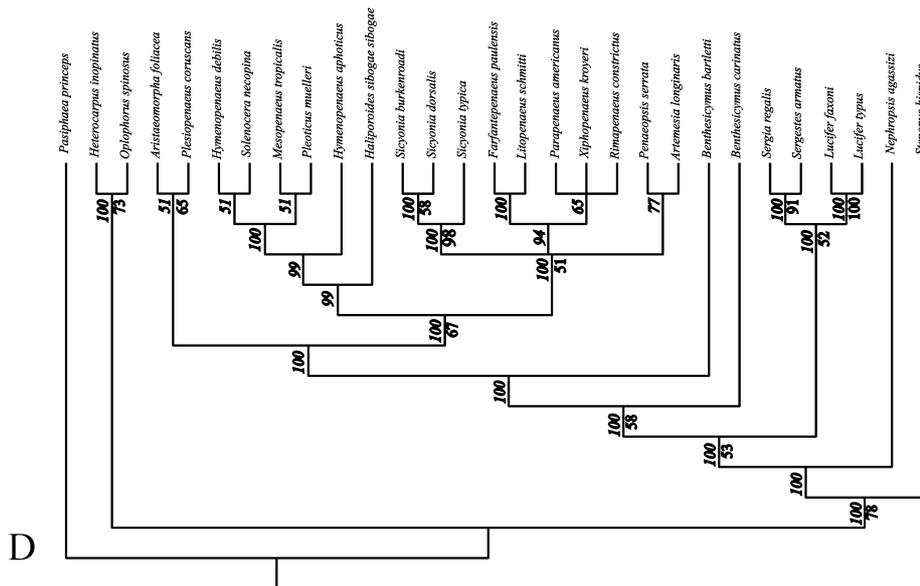
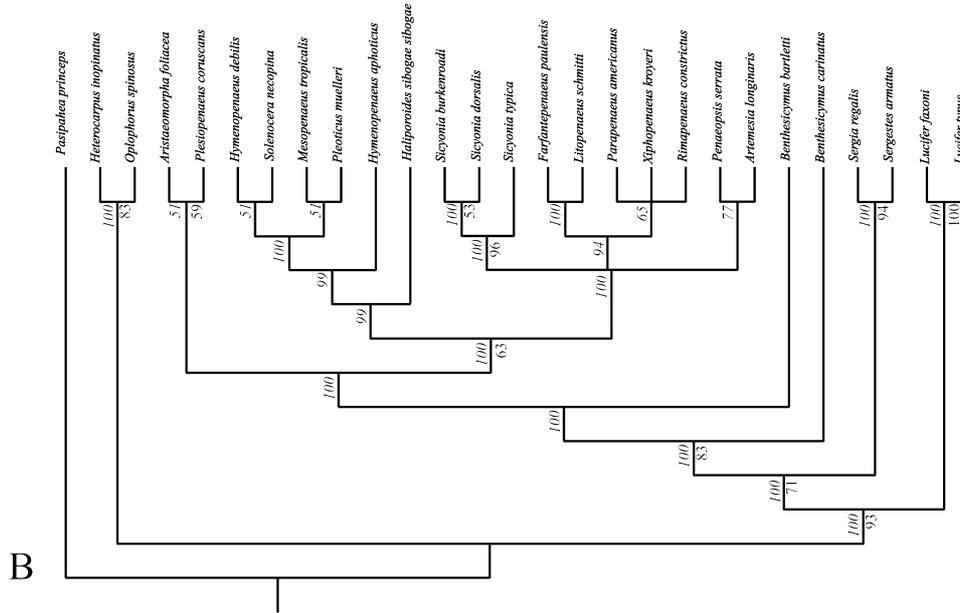


Fig. 63.13. Dendrobranchiata relationships. A, possible phylogenetic relationships with *Aeger*-like stem from which the suborder may have arisen; B, majority rule consensus tree with Caridea as an out-group; C, majority rule consensus tree with Caridea + Stenopodidea as outgroup; D, majority rule consensus tree with Caridea + Stenopodidea + Nephropidea as outgroup. B-D, with bootstrap values (>50% shown) and, in italics, the percentage of appearance of clades in the analysis. [A, modified after Burkenroad, 1983; B-D, modified after Tavares et al., 2009.]

2009). Burkenroad (1983) concluded that solenocerids are closely related to aristeids and that penaeids are closely related to sicyoniids (fig. 63.13A). Burkenroad (1983) also pointed out that among Solenoceridae *Haliporus* approaches in some aspects the form of the aristeids, while *Hymenopenaeus* and *Solenocera* approach that of penaeids. Among benthescycmids, Burkenroad (1983) believed that the genus *Benthescycmus*, when



its relationships are better understood, could justify formal separation. While Burkenroad's (1983) study is often cited, it lacked a character matrix and was **intuitively based**.

The more recent morphology-based cladistic analysis by Tavares et al. (2009) employed different out-groups and resulted in different tree topologies (fig. 63.13B-D), but all results found Dendrobranchiata as a **monophyletic group** defined by dendrobranchiate gills, prominent hinges on the pleon, larvae hatching as nauplii or protozoae, and the presence of a petasma in males. The two superfamilies Penaeoidea and Sergestoidea are also monophyletic. Penaeoidea is defined by the presence of a tubercle on the terminal article of the eyestalk and the presence of the branchiocardiac carina. Sergestoidea is defined by the absence of an exopod on the third maxilliped, the absence of a dactyl in P1, and the (related) absence of a chela in P1.

The families Luciferidae, Sergestidae, Solenoceridae, Sicyoniidae, and Aristeidae are monophyletic. Luciferidae is defined by the absence of gills, branchiocardiac carina, maxilla palp, the dactyl and chela of pereopod 2, and pereopods 4 and 5, as well as the presence of a pterygostomial spine, eggs brooded on the female pereopods, and a uniflagellate antennule.

Sergestidae is characterized by the presence of posterior spines on the sixth pleomere and the presence of a clasper organ on the antennules of the male.

Solenoceridae is characterized by the presence of a postorbital spine and a distolateral projection on the male pleopod 2.

Sicyoniidae possesses an ocular stylet, uniramous pleopods 3-5, a closed petasma, and antero-dorsal spines on pleomere 1.

No synapomorphies were found to characterize Aristeidae, and the characters used to describe the family, such as the presence of an ocular tubercle and an open petasma, are found in **more basal nodes** in the trees and are not exclusive to Aristeidae. Aristeidae also was not supported by a Bremer index in any of the three analyses of Tavares et al. (2009) and has a low bootstrap value (58%). The families Penaeidae and Benthescymidae apparently are **not monophyletic**. The characters used in the literature to define Benthescymidae (presence of an open petasma and the presence of a tubercle on the eyestalk) are in truth synapomorphies of Penaeoidea, shared by other species within the superfamily. However, only two species of a total of 40 that constitute that family were used in this study.

The characters used to diagnose Penaeidae in the literature, e.g., the presence of an ocular scale and the presence of an exopod on the second and third maxillipeds, are synapomorphies not only of Penaeidae but also appear more basally. However, as with Benthescymidae, only a few representatives of Penaeidae were used in that study.

Concerning the phylogeny of smaller groups within Dendrobranchiata, there is still much to be learned. Whether Penaeoidea is monophyletic is still contested (monophyly supported by Quan et al. (2004) based on **mDNA sequences** (fig. 63.14A-C) and by Vázquez-Bader et al. (2004) in a different molecular study (fig. 63.14D, E)), and these same authors differ on their interpretation of phylogeny within Penaeidae.

One of the most controversial points concerning the taxonomy of Dendrobranchiata is the classification of the genus *Penaeus* s.l., which initially included six subgenera:

Farfantopenaeus, *Fenneropenaeus*, *Litopenaeus*, *Marsupenaeus*, *Melicertus*, and *Penaeus* s.s. (fig. 63.15). Pérez Farfante & Kensley (1997) elevated these to full generic status, but that move triggered much debate (Baldwin, 1998; Lavery et al., 2004; Dall, 2007). Attempts to elucidate relationships in this genus have included the works of Sternberg (1996) focusing on *Litopenaeus* and based largely on genital morphology, and of Bauer (1986, 1991) and Baldwin et al. (1998) on 5 genera using **COI data**. The Baldwin et al. data did not support subdivisions of *Penaeus* s.l. based on thelycum structure made by Pérez Farfante (1969) and Tirmizi (1971) (fig. 63.16A-C). However, the molecular data do support the divisions made by Burkenroad (1934), Kubo (1949), and Burukovsky (1972).

Maggioni et al. (2000) tried to reconstruct the phylogeny of prawns of the genera *Litopenaeus* and *Farfantopenaeus* using partial sequences of the **16S mitochondrial region** (fig. 63.16D-E). Their results reinforce the hypothesis that both genera are monophyletic, but within the genera there is a lack of resolution that produces some polytomies among *Farfantopenaeus* and that do not provide enough information to resolve the relationships between Pacific and Atlantic species among representatives of *Litopenaeus*.

Lavery et al. (2004) also studied the relationship among *Penaeus* s.l. based on molecular sequences of **16S rRNA** and **COI** (fig. 63.17A-B). Their results do not support the validity of any of the six genera created from *Penaeus* s.l., nor do they support Baldwin et al.'s (1998) vision that four different groups are found among *Penaeus* s.l. However, they do provide evidence to divide this genus – but only into two groups: one with the species of *Melicertus* and *Marsupenaeus*, and the other with *Penaeus* s.s., *Fenneropenaeus*, *Farfantopenaeus*, and *Litopenaeus*.

Voloch et al. (2005) showed that *Penaeus* s.l. is monophyletic based on sequences of **16S rRNA** and **COI** (fig. 63.16C). Although *Penaeus* s.l. was shown to consist of two main clades similar to those found by Lavery et al. (2004), Voloch et al. did not discuss that similarity. The genera *Fenneropenaeus*, *Farfantopenaeus*, *Litopenaeus* also were found to be monophyletic.

Dall (2007) reviewed some of the above studies and evaluated the principal results of recent molecular research on *Penaeus* s.l., considering the monophyly of at least *Farfantopenaeus*, *Litopenaeus*, and *Fenneropenaeus* as warranted, but not at the generic level; molecular studies performed recently do not support the present division of *Penaeus* s.l. into six genera. In addition, Dall concluded that molecular biology has not provided a **useable taxonomy** of *Penaeus* s.l., and he argues for more investigations of this very important group of commercial shrimps with both molecular and morphological data. We are in agreement with Dall's (2007) opinion, although we still use the classification of Pérez Farfante & Kensley (1997), mainly because none of the studies cited above has provided a **satisfactory alternative classification** for the *Penaeus* s.l. group.

The relationships within other penaeid genera have also been investigated; these studies include the works of Tong et al. (2000) on *Metapenaeopsis* (16S rRNA and COI), which supported in general the relationships proposed earlier by Crosnier (1987, 1991, 1994a, b). One new insight gained from the Tong et al. study is that among those taxa without a stridulating organ, the deep-water inhabitants are more closely related to each other than to

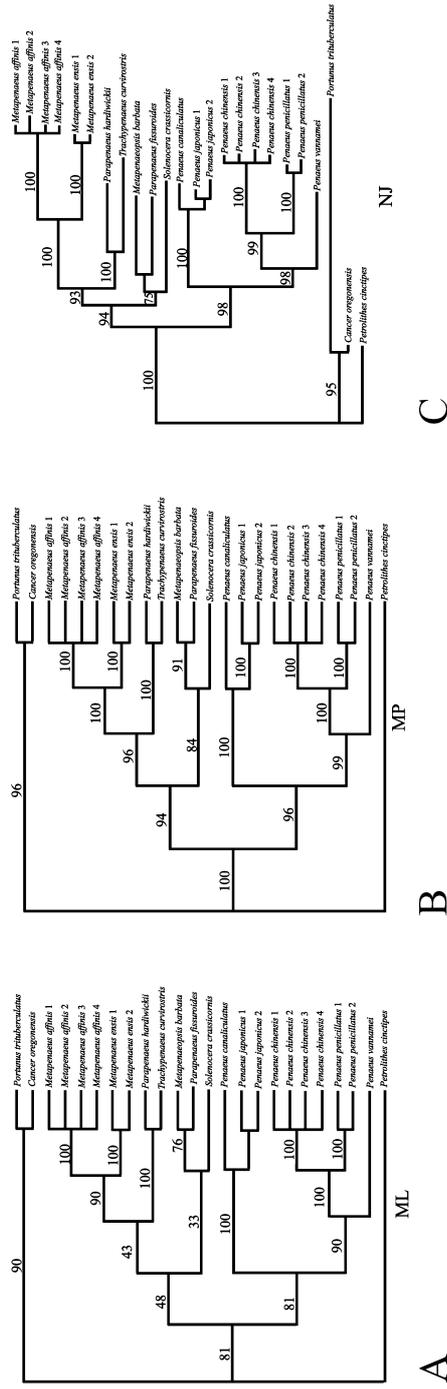
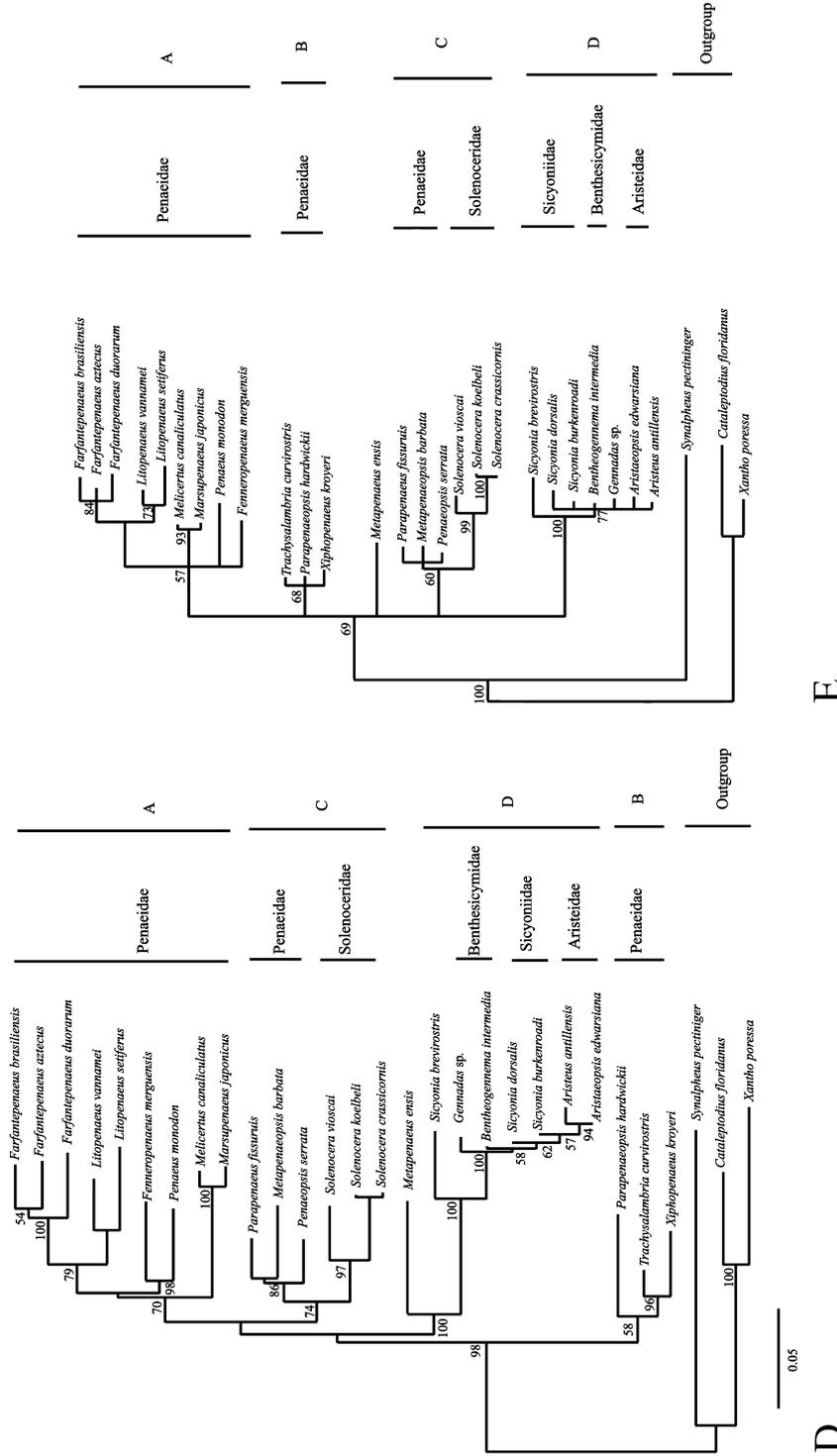
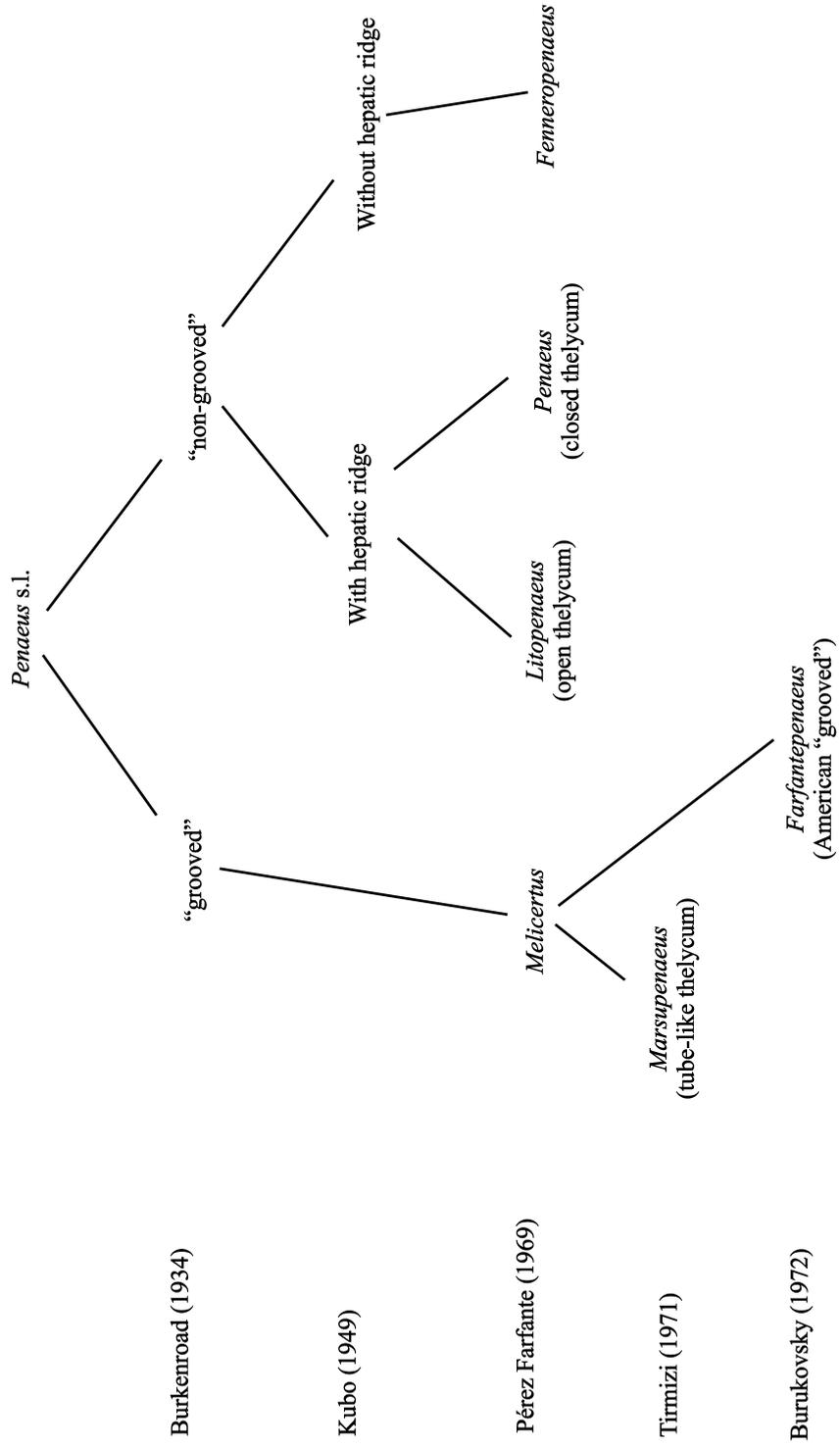


Fig. 63.14. Penaeoidea relationships. A, maximum likelihood tree; B, maximum parsimony tree; C, neighbor joining tree; D, maximum likelihood tree; E, neighbor joining tree. A-C, data obtained from 16S rRNA + COI, with bootstrap values above each branch; D-E, data obtained from 16S rRNA, with bootstrap values (>50% shown) above each branch. [A-C, modified after Quan et al., 2004; D-E, modified after Vázquez-Bader et al., 2004.]





the shallow water species, suggesting that deep-water forms diverged from shallow water species, as other members of the genus *Metapenaeopsis* inhabit shallow waters.

BIOGEOGRAPHY

Most decapod species are found in tropical and subtropical regions with a marked decrease in number towards temperate and colder regions (Boschi, 2000). This is true for Dendrobranchiata from at least along the American coasts, where the greater numbers of Penaeoidea and Sergestoidea species are found in the **Caribbean, Panamic, and Brazilian provinces**, located between the tropics, with water temperatures normally from 14° to 30°C. The Arctic, Aleutian, and Boreal provinces have fewer species of Penaeoidea, and the Arctic and Aleutian have fewer Sergestoidea; all these regions are characterized by colder waters, with temperatures ranging from 0° to 15°C.

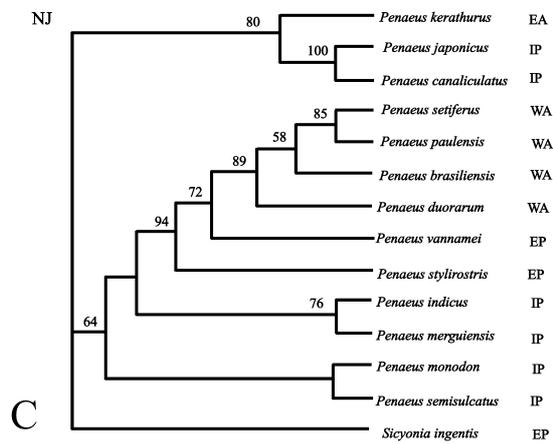
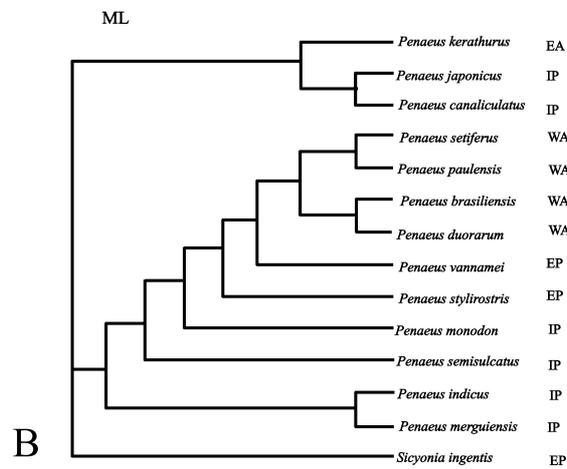
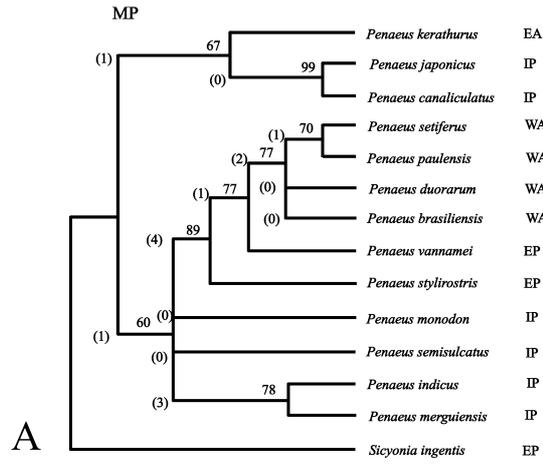
There are no similar studies in other biogeographic areas, but for the **Australian fauna**, Dall (2001) observed that the distribution of Aristeidae, Solenoceridae, and Benthescymidae seems to be restricted to a zone between 40°N and 40°S, which would agree with the lowest number of species being in provinces of high latitudes as seen in the Americas. This restriction seems to be related to the limited tolerance for low temperatures by the larvae when they are in the upper water column.

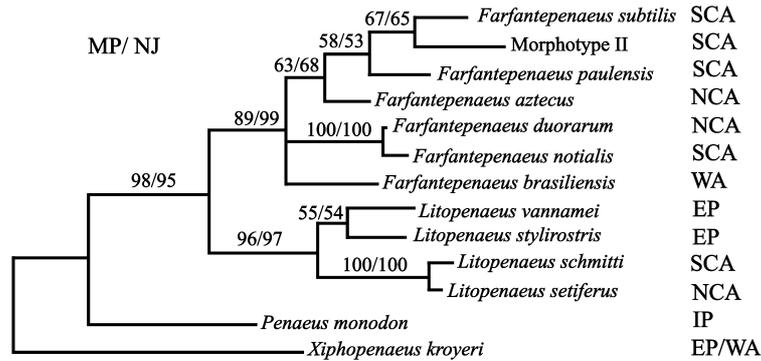
Although the **distribution of Dendrobranchiata** seems to be **generally restricted to between 40°N and 40°S**, some exceptions are found. For example, *Bentheogennema borealis* and *Bentheogennema burkenroadi* are abundant at latitudes 57°N and 52°N, respectively, in the Pacific. Similarly, in the Southern Hemisphere *Gennadas kempfi* has been collected as far south as 61°S in the Antarctic Ocean (Dall, 2001).

Aristeidae are mostly found between 200 and 2000 m depth, with a few reaching 5000 m or more. Of the 25 known species of Aristeidae, 8 have been recorded in both the Indo-West Pacific and the Atlantic Oceans. Of the remaining 17 species, 7 are from the Indo-West Pacific and appear to be more localized.

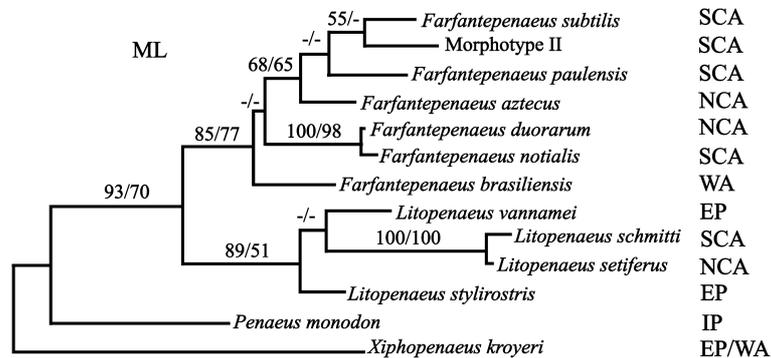
Benthescymidae are predominantly deep-water, largely pelagic shrimp (*Benthonectes*, *Gennadas*, some species of *Benthescymus*, and probably all species of *Bentheogennema*), and even those species usually thought of as benthic probably spend a large part of their time in the water column. Among the 37 species of Benthescymidae, 14 are common

Fig. 63.15. A brief history of the division of the genus *Penaeus* into subgenera. The first division into “grooved” and “non-grooved” species was made according to the presence or absence of the gastrofrontal groove or carina and the length of the adrostral carina. At first the “grooved” species formed only one group, the subgenus *Melicertus*; afterwards *Melicertus* was split into two groups. Two other groups were taken from *Melicertus*: all the American species (*Farfantepenaeus*) and the subgenus *Marsupenaeus*. The “non-grooved” species were divided into those with or without a hepatic ridge. The species with a hepatic ridge were then divided into open thelycum (*Litopenaeus*) and closed thelycum (*Penaeus* s.s.) groups. The species lacking the hepatic ridge were placed in the subgenus *Fenneropenaeus*. [Modified after Lavery et al., 2004.]





D

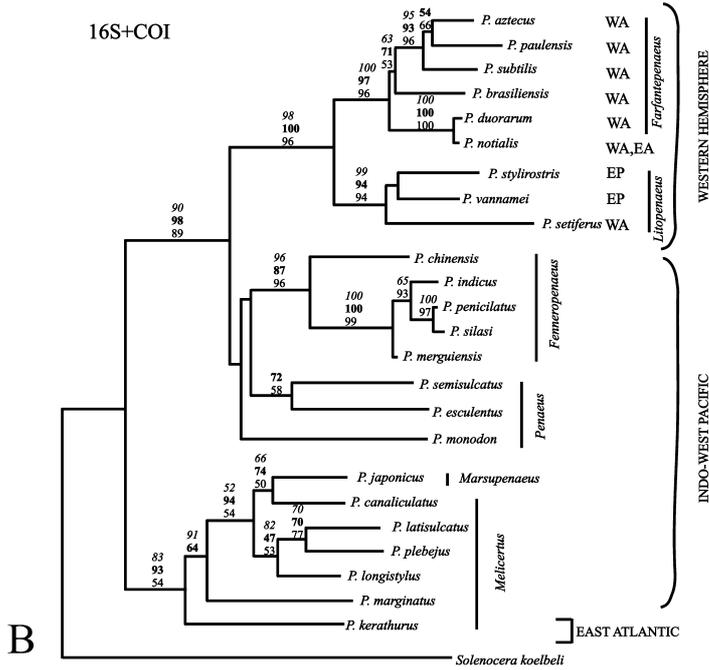


E

Fig. 63.16. *Penaeus* s.l. relationships. A, maximum parsimony tree; B, maximum likelihood tree; C, neighbor-joining tree; D, strict consensus tree; E, maximum likelihood tree. A-C, data obtained from COI, Bremer support index given in parentheses and bootstrap values >50% shown; A-C abbreviations: EA, eastern Atlantic; WA, western Atlantic; EP, eastern Atlantic; IP, Indo-Pacific. D-E, data obtained from 16S rRNA, bootstrap values shown for maximum parsimony and neighbor-joining, with branch lengths corresponding to maximum parsimony analysis; D-E abbreviations: SCA, Caribbean and/or South America; NCA, Gulf of Mexico and North America; WA, North to South America; EP, East Pacific; IP, Indo-West Pacific. [A-C, modified after Baldwin et al., 1998; D-E, modified after Maggioni et al., 2001.]

to both the Indo-West Pacific and Atlantic Oceans, with 12 of these common to the East Pacific as well; an additional 3 are found through the Indo-West Pacific, and 20 have a more restricted range (Dall, 2001).

Sicyoniidae are found mostly at depths no greater than 200 m. Species in some genera have been found from 250 to 300 m, and there are some exceptional records at 400 m depth (Pérez Farfante, 1985). Of the 43 species of Sicyoniidae, 20 occur only in the Indo-Pacific, 11 occur only in the eastern Pacific Ocean, 7 occur only in the western Atlantic Ocean, 2



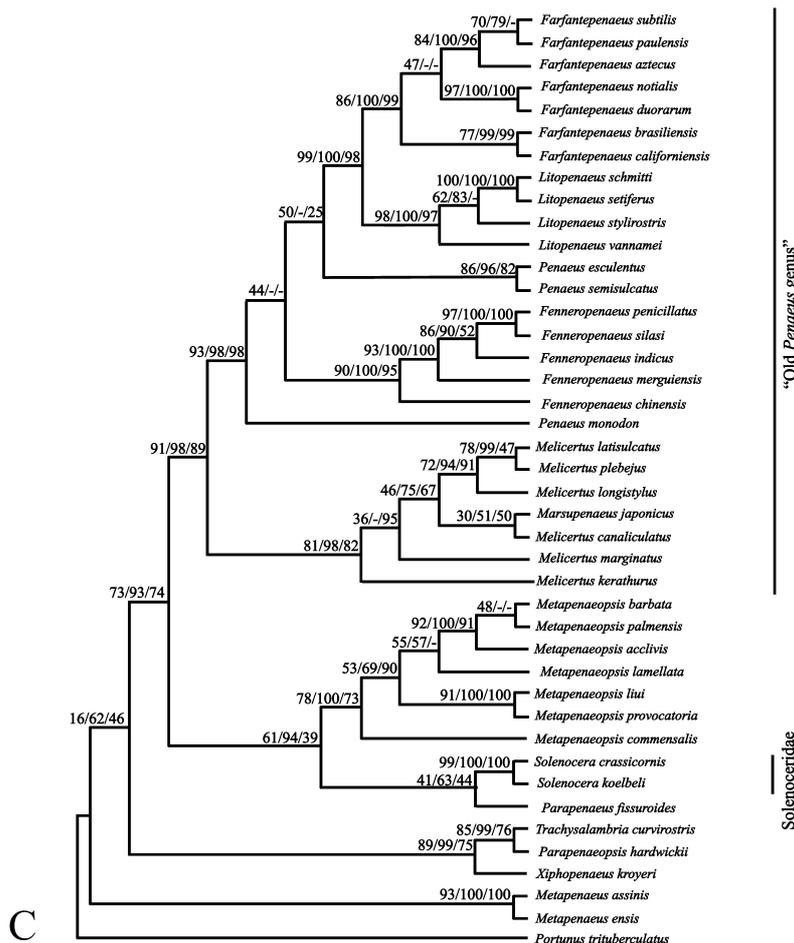


Fig. 63.17. *Penaeus* s.l. phylogenetic relationships. A-C, different maximum likelihood trees (see below); A-B, data obtained from 16S rRNA (A) and 16S rRNA + COI (B), numbers above branches indicate bootstrap values (>50% shown) from neighbor-joining analysis (in italics), parsimony analysis (in bold), and maximum likelihood analysis (normal text); A-B abbreviations: EA, eastern Atlantic; WA, western Atlantic; EP, eastern Pacific; C, data obtained from 16S rRNA + COI, numbers above branches indicate bootstrap values inferred by maximum likelihood, neighbor joining and Bayesian methods. [A-B, modified after Lavery et al., 2004; C, modified after Voloch et al., 2005.]

occur only in the eastern Atlantic Ocean, 2 occur in both the eastern Pacific and western Atlantic, and 1 occurs both in the eastern Pacific and Indo-Pacific.

Penaeidae are mostly inhabitants of shallow and inshore tropical and subtropical waters. Of the 216 known species, 166 occur only in the Indo-Pacific, 15 species occur only in the eastern Pacific Ocean, 19 occur only in the western Atlantic Ocean, 2 species occur only in the eastern Atlantic Ocean, 2 species occur on both sides of the Atlantic, 2 occur in both the eastern Pacific and western Atlantic, 2 occur in the eastern Atlantic and Indo-Pacific, 1 occurs in the Indo-Pacific and northwest Pacific, and 2 are cosmopolitan.

Solenoceridae exhibit a great bathymetric range, from shallow waters (less than 50 m) to almost 5000 m. Of the 81 known species, 55 occur only in the Indo-Pacific, 7 species occur only in the eastern Pacific Ocean, 9 occur only in the western Atlantic Ocean, 2 species occur only in the eastern Atlantic Ocean, 3 species occur on both sides of the Atlantic, 3 occur in the eastern Atlantic and Indo-Pacific, and 1 is cosmopolitan.

Luciferidae are planktonic. Of the 7 known species, 5 occur only in the Indo-Pacific, 1 occurs in both the eastern Pacific and western Atlantic, and 1 occurs in the eastern Pacific, western Atlantic, and Indo-Pacific.

Sergestidae is typically a deep-water family. Of the 90 known species, 33 occur only in the Indo-Pacific, 5 species occur only in the eastern Pacific Ocean, 7 occur only in the western Atlantic Ocean, 3 species occur only in the eastern Atlantic Ocean, 6 occur on both sides of the Atlantic, 6 occur in both the eastern Atlantic and Indo-Pacific, 2 species occur in the eastern Pacific and eastern Atlantic, 1 occurs in the eastern Atlantic and northwest Pacific, 3 occur in the Indo-Pacific, and northwest Pacific, 3 occur in the northwest Pacific and eastern Pacific, 1 occurs in the northwest Pacific and western Atlantic, 3 occur in the eastern Pacific, Indo-Pacific, and northwest Pacific, 1 occurs on both sides of the Atlantic and in the northwest Pacific, and 14 are cosmopolitan. There are also species known from Antarctic waters and in fresh water.

Little is known about the historical biogeography of Dendrobranchiata. The Indo-Pacific is probably a “**center of origin**” for the circumglobal genus *Penaeus* s.l. because, as noted above, this region contains the greatest species diversity, with about five times that found in the Atlantic (Dall et al., 1990) and with about 50% (sometimes much more) of the species of each family occurring only in the Indo-Pacific region.

A study of the biogeography of *Penaeus* s.l. conducted by Baldwin et al. (1998) supports the hypothesis of Dall et al. (1990) that the genus *Penaeus* s.l. arose in the Indo-Pacific. The genus appears to have **radiated westward** into the eastern Atlantic (because of the close relationship between eastern Atlantic and some Indo-Pacific species) and eastward into the eastern Pacific/western Atlantic (because of the close relationship between eastern Pacific/western Atlantic and some Indo-Pacific species). Western Atlantic and eastern Pacific species are currently grouped in a single clade, which suggests a radiation of the genus prior to the formation of the Isthmus of Panama. To account for the spread of *Penaeus* s.l., both vicariance (as with the Isthmus of Panama) and dispersal (during the Tertiary and Pleistocene periods) have been proposed (Baldwin et al., 1998).

Lavery et al. (2004) believed that their molecular analysis supported the idea that *Penaeus* s.l. **colonized** the Americas **relatively recently**, and only once, probably from the Indo-Pacific. As one Western Hemisphere species (*Farfantepenaeus notialis*) is also distributed in the eastern Atlantic, it seemed likely that colonization occurred via that route. This would contradict Baldwin’s (1998) hypothesis that the Americas were colonized in two different ways, from the eastern Pacific and from the western Atlantic. In addition, Lavery et al. (2004) suggested that a single lineage diverged into the closely related American subgenera, *Farfantepenaeus* and *Litopenaeus*, prior to the complete **closure of the Panamanian Isthmus**, because both genera are found on the both sides of the

Americas, and that this event was followed by vicariant speciation in both lineages since no species are found on both sides of the Americas.

Using a different, slower molecular clock from the one employed in Baldwin et al. (1998), Tong et al. (2000), studying *Metapenaeopsis*, inferred that the deep-water Indo-West Pacific species diverged from shallow waters species approximately 11-12 My. This suggests that acquisition of a deep-water habit did not occur earlier than the Miocene in the evolution of Indo-West Pacific *Metapenaeopsis*. This might accord with the fossil record where there are diverse forms known from shallow water deposits of the Mesozoic, but fewer are known from the Cenozoic (see Glaessner, 1969).

SYSTEMATICS

As stated above, the classification followed here is that proposed in the revision of Pérez Farfante & Kensley (1997) (in turn followed by Martin & Davis, 2001), despite much evidence that some families like Penaeidae and Benthesicymidae are not monophyletic. We do this because more specific studies, such as family-level revisions, are needed to establish a more effective classification for these families. The diagnoses of families below are all modified from Pérez Farfante & Kensley (1997), those for the extinct families are modified from Burkenroad (1963) and Garassino (1994).

Suborder DENDROBRANCHIATA Bate, 1888

Superfamily PENAEOIDEA Rafinesque-Schmaltz, 1815

All 5 pairs of pereopods well developed; pleurobranchs on at least somite of third maxilliped, some somites with at least 3 branchiae on each side, total number of gills at least 11 pairs.

†AEGERIDAE Burkenroad, 1963

Carapace lacking hepatic spine, but with postorbital spine. Rostrum with ventral tooth, dorsally unarmed. Third maxilliped hypertrophied. First pleomere somewhat reduced.

Aegeridae include two Mesozoic genera: *Acanthochirana* Strand, 1828 (5 species), and *Aeger* Münster, 1839 (20 species).

ARISTEIDAE Wood-Mason, 1891

Carapace lacking postorbital and pterygostomial spines; antennal and branchiostegal spines always present; postantennal spine rarely present and hepatic spines often lacking; cervical and postcervical sulci sometimes present, most often reaching dorsal midline, or almost absent and visible only laterally. Rostrum sexually dimorphic in several genera, elongate in females and juvenile males, short in adult males; usually only 3 dorsal rostral/postrostral spines; lacking ventral spines. Eye with optic calathus bearing mesial tubercle; ocular scale and styliform projection lacking. Antennule with prosartema reduced to setose boss; flagella unequal, dorsal flagellum short, flattened for most of its length, inserted

proximally on third segment; ventral flagellum sexually dimorphic in some genera. Palp of maxillule consisting of single curved article. Exopods present on all maxillipeds, present or absent on pereopods. Thelycum open; sternite XIII with deep concavity, sternite XII with variously shaped shieldlike median protuberance. Petasma open; ventral costa usually projecting free for variable fraction of its length, often extending as far as distal margin of lateral lobule. Second pleopod of male bearing appendix masculina and appendix interna, lacking distolateral projection. Third pleomere sometimes carinate, fourth to sixth pleomeres always carinate. Third through fifth pleopods biramous. Telson apically acute, bearing 3 or 4 pairs of movable lateral spines.

Aristeidae currently contain 26 species in nine genera: *Aristaeomorpha* Wood-Mason, 1891, *Aristaeopsis* Wood-Mason, 1891, *Aristeus* Duvernoy, 1840, *Austropenaeus* Pérez Farfante & Kensley, 1997, *Hemipenaeus* Bate, 1881, *Hepomadus* Bate, 1881, *Parahepomadus* Crosnier, 1978, *Plesiopenaeus* Bate, 1881, and *Pseudaristeus* Crosnier, 1978.

In addition, there is one fossil genus, *Archaeosolenocera* Carriol & Riou, 1991.

BENTHESICYMIDAE Wood-Mason, 1891

Carapace with marginal branchiostegal spine; hepatic and antennal spines present or absent; postorbital and postantennal spines lacking; cervical and postcervical sulcus reaching middorsal line, branchiocardiac and hepatic sulci usually well defined. Integument thin, soft, flexible. Rostrum short, not reaching beyond eyes, laterally compressed, dorsal rostral/postrostral teeth no more than 3, usually 2 or fewer, ventrally unarmed. Eye with optic calathus bearing mesial tubercle; ocular scale and styliform projection lacking. Antennule with prosartema usually represented by tuft of setae; with two elongate filiform flagella. Second pleopod of males with appendix masculina and appendix interna, lacking distolateral projection. Third through fifth pleopods biramous. Exopods on first to third maxillipeds, present or absent on first to fifth pereopods. Pleurobranchiae present on somites IX to XIV; one arthrobranch on somite VII, two on somites VIII to XIII; podobranchiae on second and third maxillipeds and first to third pereopods, but only on second maxilliped in *Gennadas*; epipod present on second maxilliped to fourth or fifth pereopod. Pleomeres variously carinate, occasionally ending in posterior spine. Petasma open, generally broadly lamellar, with flexible part of ventrolateral lobule attached to dorsolateral lobule for much of, or for entire, length; ventral costa entirely attached. Thelycum open or closed; if closed then having shallow seminal receptacles formed by sternal invaginations between sternites XII and XIII at base of third pereopods. Telson bearing 1 to 4 pairs of lateral movable spines; apex usually truncate, sometimes acute.

Benthescymidae currently contain 41 species in four genera: *Bentheogennema* Burkenroad, 1936, *Benthescymus* Bate, 1881, *Benthonectes* Smith, 1885, and *Gennadas* Bate, 1881.

†CARPOPENAEIDAE Garassino, 1994

Carapace subrectangular, laterally located longitudinal carina. Rostrum long with

dorsal and ventral teeth. Third maxilliped well developed. Pereiopods 2-3 with multi-articulate carpus. Uropodal exopods 2-segmented.

Two species from the Cretaceous occur in the genus *Carpopenaeus* Glaessner, 1945.

PENAEIDAE Rafinesque-Schmaltz, 1815

Body compressed, comparatively slender. Rostrum well developed, extending to or beyond distal margin of eye, sometimes surpassing antennal peduncle; armed with 5-11 dorsal and sometimes also with ventral teeth. Carapace without postorbital spine; antennal and hepatic spines usually present; cervical sulcus ending well ventral to dorsal midline. Posterior pleomeres carinate. Telson sharply pointed, armed only with lateral spines or robust setae, or with both spines and robust setae, or unarmed.

Eye with optic calathus almost always lacking mesial tubercle; basal article of eyestalk produced into moderately to slightly developed, never freely projecting, distomesial scale; ocular plate lacking styliform projection. Antennule with foliaceous prosartema, flagella of about same length, borne on apex of third segment. Exopod present on second maxilliped (except in *Artemesia*, *Macropetasma*, and *Protrachypene*), third maxilliped (absent only in *Macropetasma*), and first four pereiopods. Pleurobranchs on somites IX through XII and sometimes on XIII and XIV; rudimentary arthrobranch usually present on somite VII, two arthrobranchs on VIII through XII, and posterodorsal single arthrobranch on XIII (sometimes rudimentary anteroventral one also present on XIII); podobranchs on second maxilliped only. Epipods furcated or foliaceous, borne on first maxilliped and usually on second, missing on fourth and fifth pereiopods. Third through fifth pleopods biramous. Uropods with exopod with outer distolateral spine, or with both endopod and exopod unarmed. Petasma semi-open or semi-closed. Second pleopod of males bearing appendix masculina only, lacking appendix interna and distolateral projection. Thelycum open or closed.

Penaeidae currently contain 216 species in 26 genera: *Artemesia* Bate, 1888, *Atypopenaeus* Alcock, 1905, *Farfanteopenaeus* Burukovsky, 1997, *Fenneropenaeus* Pérez Farfante, 1969, *Funchalia* Johnson, 1867, *Heteropenaeus* De Man, 1896, *Litopenaeus* Pérez Farfante, 1969, *Macropetasma* Stebbing, 1914, *Marsupenaeus* Tirmizi, 1971, *Megokris* Pérez Farfante & Kensley, 1997, *Meliceratus* Rafinesque-Schmaltz, 1814, *Metapenaeopsis* Bouvier, 1905, *Metapenaeus* Wood-Mason, 1891, *Miyadiella* Kubo, 1949, *Parapenaeopsis* Alcock, 1901, *Parapenaeus* Smith, 1885, *Pelagopenaeus* Pérez Farfante & Kensley, 1997, *Penaeopsis* Bate, 1881, *Penaeus* Fabricius, 1798, *Protrachypene* Burkenroad, 1934, *Rimapenaeus* Pérez Farfante & Kensley, 1997, *Tanypenaeus* Pérez Farfante, 1972, *Trachypenaeopsis* Burkenroad, 1934, *Trachypenaeus* Alcock, 1901, *Trachysalambria* Burkenroad, 1934, and *Xiphopenaeus* Smith, 1869.

In addition, several extinct, mostly Mesozoic genera are known: *Albertoppelia* Schweigert & Garassino, 2004, *Ambilobeia* Garassino & Pasini, 2002, *Antrimpos* Münster, 1839, *Bombur* Münster, 1839, *Bylgia* Münster, 1839, *Carinacaris*

Garassino, 1994, *Cretapenaeus* Garassino, Pasini & Dutheil, 2006, *Drobna* Münster, 1839, *Dusa* Münster, 1839, *Hakelocaris* Garassino, 1994, *Ifasya* Garassino & Teruzzi, 1995, *Koelga* Münster, 1839, *Libanocaris* Garassino, 1994, *Longichela* Garassino & Teruzzi, 1993, *Macropenaeus* Garassino, 1994, *Microchela* Garassino, 1994, *Micropenaeus* Bravi & Garassino, 1998, *Pseudobombur* Secretan, 1975, *Pseudodusa* Schweigert & Garassino, 2004, *Rauna* Münster, 1839, *Rhodanicaris* Van Straelen, 1924, *Satyrocaris* Garassino & Teruzzi, 1993.

SICYONIIDAE Ortmann, 1898

Body thick, stout. Integument rigid, pubescent. Rostrum armed with dorsal and usually apical teeth, lacking ventral teeth, short, surpassing or at least reaching cornea but not overreaching antennular peduncle. Carapace without postorbital, branchiostegal, and pterygostomial spines, bearing or lacking antennal spine, hepatic spine present; cervical sulcus very weak or absent; hepatic carina weak, branchiocardiac strong to barely distinct. Pleon marked by transverse sulci, often tuberculate. Eye with optic calathus articulated directly to basal segment of eyestalk, intermediate segment not apparent, without mesial tubercle; basal segment without ocular scale; ocular plate bearing styliform mesial projection. Antennule with prosartema rudimentary, flagella short, cylindrical. Third through fifth pleopods uniramous, lacking endopods (unique in Penaeoidea). Exopod on first maxilliped, absent from second and third maxillipeds and all pereopods. Pleurobranchiae on somite IX only; rudimentary arthrobranch on somite VII, two arthrobranchiae on somites VIII through XIII, anteroventral one of XIII rudimentary; podobranchiae on second maxilliped; epipods on first and second maxillipeds and first three pereopods. Epipods present on pereopods 1-3, furcated or foliaceous. Petasma closed, its lateral lobes heavily sclerotized. Second pleopods in male bearing appendix masculina only. Thelycum closed. Uropod with exopod bearing distolateral spine. Telson armed with pair of lateral fixed subterminal spines.

Sicyoniidae currently contain 43 species within a single genus, *Sicyonia* H. Milne Edwards, 1830.

SOLENCERIDAE Wood-Mason, 1891

Integument thin or firm. Rostrum laterally compressed, relatively short, at least reaching cornea, sometimes surpassing the antennular peduncle, armed with 2-9 dorsal teeth, usually lacking ventral teeth. Carapace with postorbital and hepatic spines, antennal spine almost always present; orbital and pterygostomial spines present or absent; branchiostegal spine, when present, always non-marginal. Cervical sulcus well defined, reaching or almost reaching dorsal midline. Telson apically acute, usually armed with sub-apical pair of fixed spines or with pair of fixed spines and three pairs of robust setae, rarely lacking spines. Eye with optic calathus bearing small mesial tubercle; basal segment of eyestalk produced into strongly to barely developed ocular scale; ocular plate lacking styliform projection. Antennule with prosartema variable in length, usually long and foliaceous, sometimes reduced to short rigid projection; flagella usually

very long, slender, subcylindrical or flattened. Exopods on all maxillipeds and pereopods, but sometimes reduced. Epipods on pereopods 1-4, furcated or foliaceous. Pleurobranchiae on somite IX to XIV; one or two rudimentary or small arthrobranchiae on VII, two well developed arthrobranchiae on VIII through XIII; podobranchiae on second maxilliped, rarely on following appendages, never on fourth and fifth pereopods. Third through fifth pleopods biramous. Petasma open or semi-open. Second pleopod of male bearing appendix masculina and appendix interna, and with basis produced into distolateral, ventrally inclined projection or spur. Thelycum open.

Solenoceridae currently contain 81 species in nine genera: *Cryptopenaeus* De Freitas, 1979, *Gordonella* Tirmizi, 1960, *Hadropenaeus* Perez Farfante, 1977, *Haliporoides* Stebbing, 1914, *Haliporus* Bate, 1881, *Hymenopenaeus* Smith, 1882, *Mesopenaeus* Perez Farfante, 1977, *Pleoticus* Bate, 1888, and *Solenocera* Lucas, 1849.

Superfamily SERGESTOIDEA Dana, 1852

Carapace moderately to extremely compressed, rostrum shorter than eyestalk; Antennule with ventral flagellum modified or absent; pereopods 4 and 5 reduced or absent [although not in *Sicyonella*]; pleurobranchs absent, never more than 2 pairs of branchiae per somite; no more than 7-8 pairs of well-developed branchiae.

LUCIFERIDAE De Haan, 1849

Rostrum short, not reaching cornea, acute. Carapace extremely compressed, anteriorly elongate, with mandibles widely separated from antennae and eyes. Pterygostomian and antennal spines present. Eyes without mesial tubercle on optic calathus; basal segment of eyestalk not produced into ocular scale; ocular plate lacking styliform projection. Antennules lacking ventral flagellum in both sexes. Mandible lacking palp. Maxillae lacking palp, with exopod in form of a small plate. First maxilliped lacking epipod and exopod. Second maxilliped lacking epipod. Chelae lacking, or imperfect chela having no fixed finger present (only on third pereopod). Fourth and fifth pereopods absent. Branchiae absent. Genital aperture single in both sexes. Epipods and exopods absent from all pereopods. Sixth pleomere in males bearing 2 ventral processes. Petasma sessile, attached proximally to first pleopodal peduncle. Second pleopod in male with unilamellate appendix masculina. Uropod with exopod bearing distolateral spine or with both endopod and exopod unarmed. Telson truncate, armed with robust setae only, and with strong protuberance on ventral surface in males.

Luciferidae currently contain 7 species, all in the genus *Lucifer* Thompson, 1829.

SERGESTIDAE Dana, 1852

Integument thin, often very soft, bearing photophores in two genera. Rostrum shorter than eyestalks, often small to rudimentary. Carapace moderately compressed; supraorbital spine and hepatic spine present in some species of some genera; antennal, branchiostegal, and pterygostomian spines absent; cervical sulcus well marked, weak, or absent. First to fifth pleomeres dorsally rounded, sixth

somite weakly carinate. Telson acute, with no more than 3 pairs of setae, or lacking lateral robust setae. Eyes with optic calathus without tubercle; basal segment of eyestalk not produced into ocular scale; ocular plate lacking styliform projection. Ventral antennular flagellum modified in male to form clasping organ. Antennal flagellum bipartite, consisting of stiff proximal portion and more flexible distal portion. First maxilliped with exopod and epipod; second maxilliped with epipod; second and third maxillipeds and all pereopods lacking exopods. First to third pereopods (in *Peisos*) or second and third pereopods with minute chelae (*Sergestes pectinaus* lacks chelae on third pereopod). Fourth and fifth pereopods reduced (except in *Sicyonella*) or absent. Pleurobranchiae absent; one arthrobranch absent or present on second maxilliped and one or two arthrobranchiae on somites IX-XIII; podobranchiae absent, or present only on maxilliped 2. Petasma variously composed of lobus accessorius, lobus armatus, lobus connectens, lobus inermis, lobus terminalis, processus ventralis, and processus uncifer; lobes often bearing hooks. Appendix masculina unilamellate. Thelycum closed, with sternite XII and sometimes sternite XIII and coxae of third pereopod modified; seminal receptacles present, small, varying from simple shallow pockets to sac-like invaginations situated sub-mesially at base of third pereopods. Uropod with exopod bearing distolateral spine, or with both endopod and exopod unarmed.

Sergestidae currently contain 90 species in six genera: *Acetes* H. Milne Edwards, 1830, *Peisos* Burkenroad, 1945, *Petalidium* Bate, 1881, *Sergestes* H. Milne Edwards, 1830, *Sergia* Stimpson, 1860, and *Sicyonella* Borradaile, 1910 (cf. Pérez Farfante & Kensley, 1997).

In addition, two extinct genera with one species each are known: *Cretasergestes* Garassino & Schweigert, 2006a, and *Paleomattea* Maisey & De Carvalho, 1995.

APPENDIX I

Species names and genus names used in the main text of this chapter, cited with authors and dates

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- Acetes* H. Milne Edwards, 1830
Acetes chinensis Hansen, 1919
Aristaeomorpha Wood-Mason, 1891
Aristaeomorpha foliacea (Risso, 1827)
Aristaeopsis Wood Mason, 1891
Aristaeopsis edwardsiana (Johnson, 1867)
Aristeus Duvernoy, 1840
Aristeus antennatus (Risso, 1816)
Aristeus antillensis A. Milne-Edwards & Bouvier, 1909
Artemesia Bate, 1881
Artemesia longinaris Bate, 1888
Austropenaeus Pérez Farfante & Kensley, 1997
Bentheogennema burkenroadi Krygier & Wasmer, 1975
Benthesicymus Bate, 1881
Benthesicymus bartletti Smith, 1882

- Carcinus maenas* (Linnaeus, 1758)
Farfantepenaeus Burukovsky, 1997
 Farfantepenaeus aztecus (Ives, 1891)
 Farfantepenaeus californiensis (Holmes, 1900)
 Farfantepenaeus notialis (Pérez-Farfante, 1967)
 Farfantepenaeus paulensis (Pérez-Farfante, 1967)
Fenneropenaeus Pérez Farfante, 1969
 Fenneropenaeus chinensis (Osbeck, 1765)
 Fenneropenaeus indicus (H. Milne Edwards, 1837)
 Fenneropenaeus merguensis (De Man, 1888)
Funchalia villosa (Bouvier, 1905)
Gennadas Bate, 1881
 Gennadas kempii Stebbing, 1914
 Gordonella kensleyi Crosnier, 1988
 Gordonella paravillosa Crosnier, 1988
Hadropenaeus Pérez-Farfante, 1977
Haliporoides Stebbing, 1914
Halliporus Bate, 1881
 Halliporus thetis Faxon, 1893
Hemipenaeus Bate, 1881
Hepomadus Bate, 1881
 Hepomadus tener S. I. Smith, 1884
Hymenopenaeus Smith, 1882
Litopenaeus Pérez Farfante, 1969
 Litopenaeus stylirostris (Stimpson, 1874)
 Litopenaeus setiferus (Linnaeus, 1767)
 Litopenaeus vannamei (Boone, 1931)
Lucifer Thompson, 1829
 Lucifer faxoni Borradaile, 1915
 Marsupenaeus japonicus (Bate, 1888)
Melicertus Rafinesque-Schmaltz, 1814
 Melicertus kerathurus (Forskål, 1775)
 Melicertus latisulcatus (Kishinouye, 1896)
 Melicertus plebejus (Hess, 1865)
 Mesopenaeus tropicalis (Bouvier, 1905)
Metapenaeopsis Bouvier, 1905
Metapenaeus Wood-Mason, 1891
Parahepomadus Crosnier, 1978
Parapenaeus Smith, 1885
 Parapenaeus americanus Rathbun, 1901
 Parapenaeus longirostris (Lucas, 1846)
Peisos Burkenroad, 1945
Pelagopenaeus Pérez Farfante & Kensley, 1997
Penaeopsis Bate, 1881
 Penaeopsis serrata Bate, 1881
Penaeus Fabricius, 1798
 Penaeus esculentus Haswell, 1879
 Penaeus monodon Fabricius, 1798

- Penaeus semisulcatus* De Haan, 1844
Petalidium Bate, 1881
Pleoticus Bate, 1888
 Pleoticus muelleri (Bate, 1888)
Plesiopenaeus Bate, 1881
Pseudaristeus Crosnier, 1978
Rimapenaeus Pérez Farfante & Kensley, 1997
 Rimapenaeus similis (Smith, 1885)
 Rimapenaeus constrictus (Stimpson, 1874)
Sergestes H. Milne Edwards, 1830
 Sergestes armatus Krøyer, 1855
 Sergestes similis Hansen, 1903
Sergia Stimpson, 1860
 Sergia lucens (Hansen, 1922)
 Sergia regalis (Gordon, 1939)
Sicyonia H. Milne Edwards, 1830
 Sicyonia brevirostris Stimpson, 1871
 Sicyonia burkenroadi Cobb, 1971
 Sicyonia carinata (Brünnich, 1768)
 Sicyonia dorsalis Kingsley, 1878
 Sicyonia ingentis (Burkenroad, 1938)
Solenocera Lucas, 1849
 Solenocera crassicornis (H. Milne Edwards, 1837)
 Solenocera membranacea (Risso, 1816)
 Solenocera necopina Burkenroad, 1939
Xiphopenaeus Smith, 1869
 Xiphopenaeus kroyeri (Heller, 1862)
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