Chapter 17

Phylum Arthropoda: Crustacea

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Introduction

Ruppert and Barnes (1996: 682) begin their introduction to the subphylum Crustacea with the observation that ". . . crustacean diversity is so great that a description of a 'typical' form is impossible," and this is as true of the larvae as it is of the adults. Furthermore, larval development is known for only a small percentage of species in five of the six recognized classes of crustaceans, and not at all for the class Remipedia, which suggests that biologists have only begun to sample the existing diversity of crustacean larval types. Thus, the present chapter is in no way an exhaustive review of the fascinating larval forms present in the Crustacea. It is meant to be, instead, merely a glimpse of larval diversity in the world's most diverse taxon (Martin and Davis, in press).

Crustacean development can be direct, in which the egg hatches into a fully formed but miniature version of the adult (as in most of the superorder Peracarida), or entirely anamorphic, in which change between successive molts consists essentially of increasing body size, adding segments and limbs, and developing existing limbs. Usually there is some metamorphosis, and at times this can be striking.

The larval phase of marine crustaceans typically includes a pelagic phase that usually lasts several weeks. In some species, however, this planktonic larval phase may last over a year. In many other taxa, particularly those with abbreviated development, the larvae may be exclusively benthic, or spend only a very brief time in the plankton (Figures 17.2A,B) (Johnson, 1974; Serfling and Ford, 1975; Rabalais and Gore, 1985). Many crustacean larvae are initially lecithotrophic, but most are planktivorous at some point in their pelagic life. Lecithotrophy is commonly associated with abbreviated development, and in lecithotrophic species, at least some of the cephalic appendages are often reduced or absent (Figures 17.2C–E) (Rabalais and Gore, 1985).

In those taxa with planktonic larvae and benthic adults, there is usually a morphologically distinct transitional phase that settles out of the plankton and metamorphoses into the benthic post-larval phase (Figures 17.9–12). Competent larvae use a wide variety of chemical and tactical cues to evaluate potential settlement sites (Figure 17.11F), and are commonly able to delay metamorphosis in the absence of such cues (Figure 17.11H) (Crisp, 1974; Harvey, 1996; O'Connor and Judge, 1999). Curiously, in a number of taxa (such as cirripedes and pagurid hermit crabs), the settlement phase does not feed, which appears to set definite limits on the ability of these taxa to delay metamorphosis (Lucas et al., 1979; Dawirs, 1981; Harvey and Colasurdo, 1993).

The literature contains a vast number of descriptive names for crustacean larval forms. This confusing situation arose in part because taxonomic names were assigned to larval forms before it was known to which group they belonged, or often that they were even larvae (e.g., *Nauplius, Zoea, Megalopa, Glaucothoe, Cerataspis, Eryoneicus, Erichthus, Alima, Phyllosoma,* and *Amphion*). Once these organisms were recognized as the larval stages of other taxa, the now-defunct generic name often became the descriptive name of the transitional stage for that group. This practice is falling out of favor, although names for particularly distinctive or well-known larvae persist.

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Typically, crustacean larvae have been grouped broadly into three main types, which are identified by the appendages primarily responsible for swimming; a 'nauplius' swims with its cephalic appendages (Figure 17.1A), a 'zoea' with its thoracic appendages (Figure 17.1C), and a 'megalopa' with its abdominal appendages (Figure 17.1D) (Williamson, 1969; 1982a). Ecologically, the nauplius and zoea are usually dispersive phases and the megalopa is the transitional settlement phase (but see Harvey, 1993).

The 'nauplius–zoea–megalopa' series represents a generalized developmental sequence as well, although most crustaceans do not pass through all three phases. Thus, carcinologists refer to these as phases as well as types. Within a given developmental phase, successive molts in which changes are essentially anamorphic in nature are referred to as stages (e.g., Z1–Z5 in Figure 17.2A). The number of stages within a phase varies widely among taxa, and is often but not always fairly consistent within species (Williamson, 1982a; Gore, 1985). The addition and development of segments and appendages during anamorphic development within a phase usually occurs in an anterior to posterior direction (Williamson, 1982a; Schram, 1986).

A free-swimming naupliar phase is known from at least some species in all classes for which developmental information is available. Zoeae and megalopae, as they are commonly understood, are restricted to the class Malacostraca. In other classes, developmental stages that swim with thoracic appendages typically differ from adults only in anamorphic details and are thus considered to be juveniles rather than zoea larvae (e.g., copepodids in the Copepoda, although Williamson, 1982a classifies these as protozoeae). Megalopae are only found in the Malacostraca because true pleopods are only found in this taxon (Williamson, 1982a).

Nauplius

In terms of sheer numbers, the crustacean nauplius (Figures 17.1A, 17.3, 17.4) has been called "the most abundant type of multicellular animal on earth" (Fryer, 1987). The nauplius is the most primitive crustacean larval type found in extant crustaceans, and the earliest free-swimming phase in crustacean development. By far the most taxonomically widely distributed type of crustacean larva, the nauplius has been used as a key feature that unites the entire subphylum Crustacea (Cisne, 1982; Schram, 1986; Walossek and Müller, 1990). However, many crustaceans have lost this larval stage, or pass through it prior to eclosion from the egg.

Across the Crustacea, the nauplius exhibits a surprisingly conservative morphology (Figure 17.1A) (Dahms, 2000). The body is typically covered with a dorsal carapace, or cephalic shield, which is typically widest anteriorly. A carapace may be present at hatching, or may develop in later stages; its appearance and development can be either gradual or abrupt. In the orthonauplius (Figure 17.3), which is the typical form of newly hatched nauplius, there are initially only three pairs of cephalic appendages: antennules, antennae, and mandibles. The antennules are uniramous and lack a flagellum, whereas the antennae and mandibles are typically biramous. Initially, the trunk exhibits no sign of segmentation. A single median eye, visible near the anterior margin of the carapace, is typical but not universal (e.g., it is lacking in euphausiids; Mauchline and Fisher, 1969).

During subsequent molts, the trunk develops segmentation, and typically the remaining cephalic appendages and the thoracic appendages of the adults are added and developed. Once a nauplius develops appendages in addition to the three typical pairs of cephalic appendages, it is called a metanauplius (Figure 17.4). These additional appendages, not used in locomotion, may include additional head appendages, which may be rudimentary or functional, as well as rudimentary thoracic appendages. In many groups, eggs hatch as orthonauplii and become metanauplii after one to several molts; in some groups, (e.g., cephalocarids, Figure 17.4A), eggs hatch directly as metanauplii. Late naupliar stages often develop a pair of compound eyes in addition to the naupliar eye.

Swimming and feeding in the nauplius are accomplished with the cephalic appendages. Feeding behaviors seem to be triggered by chemosensory cues, at least in barnacles (Anderson, 1994). Nauplii feed on small phytoflagellates, diatoms, and other microplankton (Moyse, 1963; Barker, 1976; Stone, 1989). In a great many taxa, however, the nauplius is a non-feeding phase, especially in the early stages. All nauplii in malacostracan taxa (e.g., euphausiids and dendrobranchs) are lecithotrophic (Gurney, 1942).

There are many variations on this relatively simple theme (Figures 17.3, 17.4). The relative size and degree of setation of the cephalic appendages varies considerably across taxa, as does the shape and armature of the carapace. There are also more emphatically modified naupliar forms. The ostracod nauplius, for example, possesses a laterally compressed, bivalved carapace like that of the adult (Figure 17.3C). In fact, Cohen and Morin (1990) argue that ostracods have juveniles, not larvae, because there are no fundamental differences in the morphology, behavior, or habitat of 'larval' and adult ostracods. Hansen's (1899) 'Y-larvae' are peculiar nauplii and cyprids (see below) that have been known for more than 100 years, but their taxonomic identity is still unknown (Figure 17.3F). The well-developed carapace of a Y-nauplius is divided into a set of symmetrical plates. There are one or three large spines on the posterior margin of the carapace, and a single median spine that sits anterior to a unique structure called the dorsal caudal gland. The function of this gland, whose presence in the Y-nauplius is marked by a slightly raised oval median plate in the carapace, is unknown (Schram, 1970a, 1972).

Most nauplii are free-swimming, but some taxa have benthic naupliar stages (e.g., Mystacocarida, Cephalocarida, Ostracoda, and some harpacticoid copepods; Dahms, 2000). Many barnacles retain lecithotrophic nauplii in the parent's mantle cavity, releasing them as cyprids (Anderson, 1986).

Zoea

(Figures 17.1C, 17.5–8.) The genus *Zoea* (Bosc, 1802) was created for what turned out to be the planktonic larval stages of several species of brachyuran crabs. As biologists began to better understand the life-history patterns of crustaceans, the term zoea eventually came to refer to any crustacean larva with functional thoracic appendages, replacing numerous taxon-specific names for the same stage (see Gurney, 1942 and Williamson, 1969, 1982a for a more complete discussion of these larval names). Within this broad term lies a bewildering diversity of shapes, sizes, and ornamentation, for the zoeal body plan is most assuredly not subject to the same conservatism as that of the nauplius. Here we can do little more than summarize the general features of zoea larvae, and mention some common or striking variations.

All zoeae possess a carapace, which covers the head and the anterior portion of the thorax, and a pair of compound eyes, which are almost always sessile in the first stage and stalked in subsequent stages. A naupliar eye is also found in the early zoeal stages of the Amphionidacea, Caridea, and Palinuroidea, as well as of those malacostracans that hatch as nauplii, hereafter referred to as 'naupliar malacostracans.'

In early-stage zoeae, the antennular peduncle lacks flagellae and is unsegmented, except in stomatopods and 'naupliar malacostracans', where it has two or three segments (Figures 17.5C,D,F, 17.8C); the basal segment is annulated in protozoeal dendrobranchs (e.g., Oshiro and Omori, 1996). Later zoeal stages may subdivide the peduncle and add a dorsal flagellum, ventral flagellum, or both. The antenna is biramous except in stomatopods (Figures 17.6B,E, 17.8C). The antennal exopod is typically a flattened scale with setose margins (Figures 17.6B,E); major exceptions are found in the Brachyura, where it is normally rod-like (Figure 17.7), and the unrelated taxa Palinura, Porcellanidae, and Hippidae, where it is a simple spine (Figure 17.8D). The mandibles are usually at least slightly asymmetrical, usually lack a palp in early stages (exceptions are most likely to be seen in species with abbreviated development), and often possess incisor and molar regions that are discernible but much less developed than in adults. The maxillule and maxilla are always present in zoeae, though their degree of development varies among taxa (Figures 17.2C–E) (Williamson, 1982a).

Zoeal thoracic appendages are typically biramous. Of the eight pairs found in adults (the first three pairs correspond to maxillipeds, the last five to pereopods, or legs), stage 1 zoeae may have as few as only the first pair (e.g., in euphausiids) or as many as all eight, although this latter is usually only seen in species with abbreviated development. In most taxa, all eight pairs appear by the final zoeal stage (Figure 17.1C).

The abdomen of stage 1 zoeae typically consists of five segments plus a terminal telson (Figures 17.6C,D, 17.7D), and the last segment subdivides in the next molt or two (Figures 17.5D, 17.6A). In some groups, the abdomen is unsegmented through the first (e.g., 'naupliar malacostracans') or most (e.g., Palinuroidea; Figure 17.8D) zoeal stages; in a few cases, first-stage zoeae have all six segments, and in a few brachyurans, the last abdominal segment is fused to the telson (Lucas, 1971). The shape of the telson varies widely across the Crustacea, often following phylogenetic lines. The terminal margin of the telson possesses several pairs of 'processes', and often a single median process. These may be setae, articulated spines, or fused spines, and their number, type, and size are often surprisingly constant within a zoeal stage across crustacean families or even orders. Uropods usually appear in the third zoeal stages (Figure 17.5D), developing into fully articulated biramous structures over the next few molts (Figures 17.6B,E), although there are numerous exceptions. Their appearance and development may be accelerated in taxa with abbreviated development (Figure 17.1B); they appear more slowly in the Palinuroidea and the Stomatopoda (Figure 17.8B), and are completely absent in most brachyurans, which lack uropods as adults (Figure 17.7).

Under the general heading of zoea larvae, several distinctive names remain in active use in the literature, either for functional or historical reasons. Several of these are briefly considered below.

Protozoea and mysis

(Figures 17.5C,E,F.) In dendrobranchiate shrimps, the first three zoeal stages are sufficiently different from the subsequent zoeal stages that they have been given separate names, protozoea and mysis. Unlike the archetypal zoeae, protozoeae swim with the combined efforts of the antennae and the first two pairs of thoracic appendages; the remaining thoracic appendages are absent or relatively undeveloped. In mysis larvae, the antennae are no longer used for swimming and most to all of the thoracic appendages are well developed. Mysis larvae are not found in the Mysidacea; the name reflects the apparent similarity between late-stage dendrobranch zoeae and mysid juveniles, in the same way that the cypris larvae of barnacles are so named for their similarity to the ostracod genus *Cypris* (Williamson, 1982a).

Elaphocaris and acanthosoma

In sergestid shrimps, the protozoea and the mysis stages have a prominently spinose carapace and are called elaphocaris and acanthosoma, respectively.

Calyptopis and furcilia

(Figures 17.5A,B,D.) As in dendrobranchs, the euphausid metanauplius is followed by two distinct zoeal types, the calyptopis and the furcilia. The calyptopis is characterized by a carapace that covers the sessile eyes, an elongated trunk (compared with earlier stages), and progressive segmentation. There are normally several calyptopis stages in euphausids. In the furcilia, which likewise persists through several molts, the eyes are movable and no longer covered by the carapace, and the antennules, thoracic, and abdominal appendages develop toward the adult form. Unlike the mysis, the furcilia continues to swim with both the antennae and the thoracic appendages (Mauchline and Fisher, 1969).

Amphion

The amphion is the larva of *Amphionides reynaudi,* the sole species in the order Amphionidacea (Williamson, 1973). In most respects, the amphion is similar to a caridean zoea, differing primarily in that its telson is spatulate in early stages, pointed and possessing only two terminal spines in later stages. It has hepatic caecae, and lacks chelae at any stage.

Phyllosoma

One of the largest and most unusual decapod larval forms is the phyllosoma (Figures 17.8D,E), a unique stage shared by members of the related Palinuridae (spiny lobsters) and Scyllaridae (slipper lobsters). Some giant phyllosomas have been reported to reach 8 cm in total length (Robertson, 1968a). But this size is deceptive; they are leaflike, flattened, and nearly paper-thin, possibly an adaptation for riding on the medusae of jellyfishes (Thomas, 1963; Herrnkind et al., 1976).

MEGALOPA

(Figures 17.1D; 17.10–12.) Many crustacean groups possess an interesting and somewhat intermediate larval form that serves as a morphological and ecological transition from the planktonic zoea to the benthic adult. The terminology of this transitional form has been quite confusing. Commonly referred to as post-larvae (Gurney, 1942), this term has fallen into disfavor because they are clearly distinct from subsequent juvenile stages. Like zoea larvae, many of these transitional forms were originally described as new species or even genera before their developmental status was recognized; once these links were established, the now-defunct generic name often became the name of the transitional stage for that group. The earliest of these, *Megalopa* (Leach, 1814), is the transitional form of a brachyuran crab, and the term megalopa has become (not without controversy; see Felder et al., 1985) the general term across the Crustacea for the transitional larval stages where swimming is achieved through pleopods (Williamson, 1982a). As mentioned earlier, megalopae are only found in the Malacostraca. Another name describing this phase in decapods is 'decapodid' (Kaestner, 1970).

Megalopae are also morphologically intermediate between the zoeal and juvenile stages, often possessing features characteristic of both in addition to some characters unique to the megalopa (Rice, 1981). In 'naupliar malacostracans', there is a gradual transition from larval to adult morphology from the late mysid through the numerous megalopal stages and into the juvenile phases (Gurney, 1942; Mauchline and Fisher, 1969). Likewise, in some carideans, the transition from megalopa to juvenile is gradual enough that some authors report two or three megalopal stages while others question whether the concept of a megalopal phase is even applicable (e.g., Haynes, 1976; Rothlisberg, 1980). In most other groups, however, many morphological structures acquire the basic adult characteristic in the molt to the megalopa, which then represents a dramatic metamorphosis from the last zoeal stage. In these groups, there is normally only a single megalopal stage, although eryonids have several (see discussion under eryoneicus below).

With a variable mix of zoeal and juvenile characters, the megalopal phase shows even greater diversity than does the zoeal phase across the Malacostraca. Generally, megalopae have proportionately larger eyes (hence the name) and smaller pereopods than do adults, and the carapace is commonly narrower and smoother. In the megalopa, the abdomen projects posteriorly even when it is tucked under the thorax in adults (i.e., in 'crabs') (Figure 17.12). Megalopae typically exhibit complete bilateral symmetry, even in those taxa with pronounced asymmetries as adults (e.g., chela asymmetry in homarid lobsters, fiddler crabs, and hermit crabs; abdominal asymmetry in hermit crabs). Paguroid hermit crabs (families Paguridae, Parapaguridae, and Lithodidae) are unusual in this respect, as their megalopae often have asymmetrical claws and uropods (e.g., McLaughlin et al., 1988).

In most crustaceans, sexual maturity is not reached until post-juvenile stages. However, it appears that in the Amphionidaceae, males mature as megalopae, and females reach maturity at the next molt (Williamson, 1973), and one shrimp (*Discias atlanticus*) also apparently reaches sexual maturity as a megalopa (Williamson, 1970). Sexual characters sometimes develop even prior to the megalopal phase in a few groups (e.g., Palinura).

Several of the numerous names that have been used for megalopae at lower taxonomic levels still persist in the literature today, in part, because the organisms bear little resemblance to the archetypal brachyuran megalopa.

Cyrtopia

In the Euphausiacea, the cyrtopia differs from the preceding furcilia mainly in that swimming is now done with the pleopods. Thus, the cyrtopia fits the definition of a megalopae, but most carcinologists now consider this to be a stage in the furcilia phase (e.g., McLaughlin, 1980).

Mastigopus

These megalopae of sergestid shrimps are noteworthy mostly in that they have lost all traces of the spines that characterize the earlier zoeal phase. One unusual feature that characterizes both the megalopae and adults of this group is that the fourth and fifth pereopods are lost or greatly reduced.

Puerulus

(Figures 17.10A,B.) The unique phyllosoma larvae of Palinuroidea metamorphose into an unusual form of megalopa termed the puerulus (or nisto, or pseudibacus, in the family Scyllaridae). This phase is similar in form to the benthic adult, but is transparent, with a smooth, decalcified carapace and large, setose pleopods.

Ambiguous larval types

As Schram (1986) observes, not all known types of crustacean larvae can be easily placed in a functional 'nauplius–zoea–megalopa' classification. Most ambiguous cases involve gradual transitions between phases, or else reflect conflicts between the functional and ecological components (e.g., a larva that swims with its thoracic appendages but represents the transitional settlement stage). Several examples are described below.

Eryoneicus

Eryoneicus (Figures 17.10C,D) is the remarkable larva of an eryonid lobster (family Polychelidae). With a maximum-recorded size of over 6 cm, these crustacean larvae are exceeded in length only by some of the giant phyllosomes, but their nearly spherical carapace makes them far more massive than any paper-thin phyllosoma. Eryoneicus larvae were long considered to be the adults of a type of pelagic lobster, owing to their huge size and the common presence in larger specimens of developing male reproductive structures (Bouvier, 1905; Bernard, 1953). Early eryoneicus larvae swim with thoracic appendages, and are thus referable to zoeae; later stages have well-developed pleopods (e.g., Figures 17.10C,D) and fit the definition of megalopae in this respect (Williamson, 1982a). However, the transitional phase (i.e., megalopa in the ecological sense) has not yet been identified for any eryonid, and in fact no eryoneicus larva has been conclusively identified to species.

Antizoea and pseudozoea

(Figures 17.8A–C.) The well-developed raptorial claws of larval stomatopods (mantis shrimps) make them immediately recognizable members of the plankton; although newly hatched larvae are lecithotrophic and initially lack raptorial claws (e.g., Figure 17.8C), these typically remain in the parent's burrow (Manning and Provenzano, 1963). Like typical zoeae, early larvae of the family Lysiosquillidae lack pleopods, have uniramous antennules, as well as five pairs of biramous thoracic appendages, and are called antizoeae. Other stomatopods hatch as pseudozoeae, which initially possess only two pairs of uniramous thoracopods but do have functional pleopods. Antizoeae and pseudozoeae develop anamorphically, and later stages are called erichthus larvae in the superfamilies Lysiosquilloidea and Gonodactyloidea and alima larvae in the Squilloidea (Provenzano and Manning, 1978; Williamson, 1982a). The functional pleopods of the pelagic erichthus and alima stages technically qualify them as megalopae. However, both erichthus and alima larvae are followed by a distinct transitional form that is the ecological and morphological equivalent of the megalopal phase in other malacostracans (Schram, 1986).

The naupliar phase of the subclass Thecostraca (barnacles and their relatives) concludes with a metamorphic molt to a cyprid phase (Figures 17.1B, 17.9), which fits the broad definition of a zoea but is functionally more analogous to the megalopa. The cephalic appendages of the nauplius are lacking except for well-developed antennules, which the cyprid uses to walk on the substrate in search of a suitable attachment site. In addition, the cyprid possesses six pairs of thoracic appendages. The fusiform cephalic shield now encloses the body, but normally lacks a middorsal hinge, unlike its ostracod namesake. A pair of compound eyes accompanies the naupliar eye. The cyprid does not feed, and swims using its thoracic appendages, as do zoeae (Anderson, 1994).

However, like a megalopa, the cyprid represents a transition between the free-swimming larva and the benthic adult, and is responsible for locating suitable habitat for the sessile post-larval phase (Figure 17.9D) (Anderson, 1994). Cyprids vary widely among species in the nature and precision of the cues they use to assess potential settlement sites (Crisp and Meadows, 1963; Lewis, 1978; Chabot and Bourget, 1988; Raimondi, 1988; Young, 1991). The inability of non-feeding cyprids to replenish their energy reserves may constrain the time available to search for a suitable settlement site; in some sessile barnacles (Balanomorpha), it appears that older cyprids become less discriminating regarding settlement sites (Crisp and Meadows, 1963).

In most barnacles, a newly settled cyprid undergoes a rapid and profound metamorphosis into a sessile juvenile barnacle. During this metamorphosis, the animal changes its orientation from dorsal to head-down, the carapace and compound eyes are lost, and rudiments of the capitular plates appear. In those rhizocephalan barnacles known as kentrogonids, however, settlement of the cyprid on a suitable host leads not to a juvenile barnacle, but to one of two unique larval forms, the kentrogon and the trichogon.

Kentrogon

An individual female kentrogonid rhizocephalan can produce either small or large eggs, which develop into small or large larvae. Cyprids that develop from small eggs settle on a suitable host and develop into endoparasitic females, whereas cyprids from large eggs settle on juvenile externae as males. Once a female cyprid settles on a host, it molts into a unique attachment stage, known as a kentrogon. In some species, the kentrogon retains nearly all cypris organs except the thorax, but in others the kentrogon keeps only those structures specifically needed to perform its function. The kentrogon rapidly develops a piercing stylet through which the kentrogon injects yet another instar called the vermigon. This motile, worm-shaped stage has an exceedingly simple structure that includes only a few types of cells, primarily an epidermis, large cells that will develop into somatic tissues such as muscles, and the germline cells (Ritchie and Høeg, 1981; Høeg, 1985, Glenner et al., 2000). The vermigon is enclosed within a thin cuticle that later develops into the nutrient-absorbing cuticle of the internal parasite.

Trichogon

Male rhizocephalan cyprids take another path. Following settlement (onto immature females), they metamorphose into a trichogon, which like the vermigon is elongate and worm-shaped, and may be motile as well. The trichogon enters the aperture of the externa and migrates through the female's mantle cavity toward the seminal receptacles. The spinose cuticle of the trichogon is shed, forming a plug that prevents the entry of subsequent trichogons into the same receptacle. The trichogon eventually reaches the lumen of the receptacle where its germinative cells mature into spermatogonia (it is unclear whether male somatic tissue also survives and functions within the receptacle). The trichogon remains with the female for the remainder of her lifetime (Høeg, 1987).

A few 'Y-cyprids' have been found developing within Y-nauplii or collected from the plankton (McMurrich, 1917; Schram, 1970b; Ito, 1989). These distinctive cyprids (Figure 17.9B) have a plated carapace that does not cover the abdomen, which is also covered with plates posteriorly and possesses a pair of morphologically complex caudal rami. As in cirripedes, the Y-cypris has six pairs of biramous thoracic appendages, and the only cephalic appendages present are the antennules, although these differ considerably between the two types of cyprids (Figures 17.1B, 17.9B).

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FIGURE 17.1

Examples of primary types of crustacean larvae

A. Generalized nauplius, ventral view. (Reproduced with permission from Dahms, 2000.)
B. Cyprid of *Semibalanus balanoides* (family Archaeobalanidae), lateral view. Scale bar: 0.25 mm. (Reproduced with permission from Walley, 1969.)
C. Zoea of *Coenobita compressus* (family Coenobitidae), lateral view. Scale bar: 0.5 mm. (Reproduced with permission from Brodie and Harvey, 2001.)
D. Megalopa of *Notomithrax minor* (family Majidae), lateral view. Scale bar: 0.5 mm. (Reproduced with permission from Wear and Fielder, 1985.)

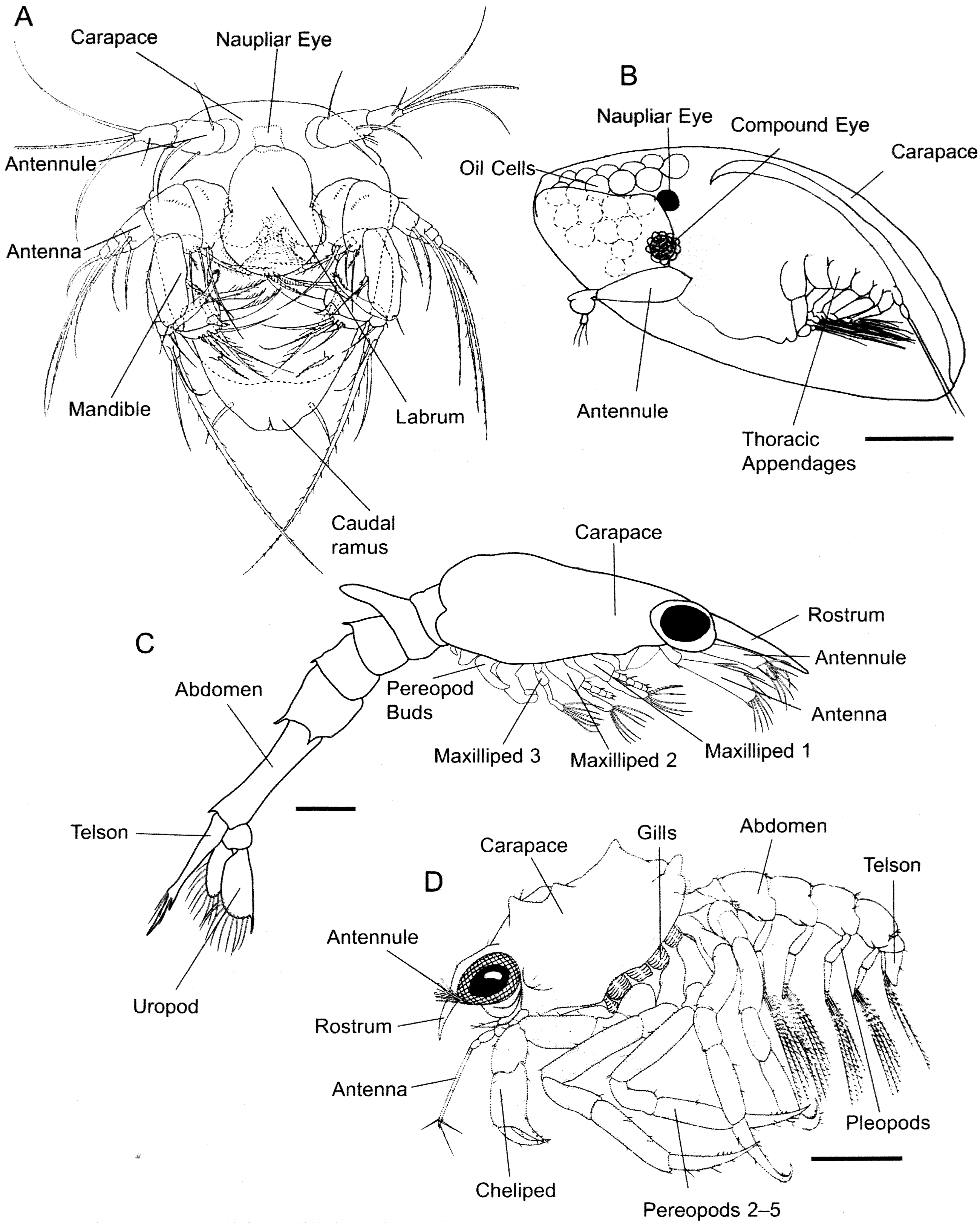

A
Carapace
Naupliar Eye
Antennule
Antenna
Mandible
Labrum
Caudal ramus
B
Naupliar Eye
Compound Eye
Carapace
Oil Cells
Antennule
Thoracic Appendages
C
Carapace
Rostrum
Antennule
Antenna
Abdomen
Pereopod Buds
Maxilliped 3
Maxilliped 2
Maxilliped 1
Telson
Uropod
D
Carapace
Gills
Abdomen
Telson
Antennule
Rostrum
Antenna
Cheliped
Pereopods 2–5
Pleopods

FIGURE 17.2

Typical and abbreviated development in congeneric crustaceans (family Coenobitidae; A,B) and examples of reduced feeding structures in lecithotrophic larvae (C–E)

A. Planktotrophic zoeal development in *Coenobita compressus*, dorsal view. Scale bar: 1.0 mm. Z1–Z5: Zoea stage 1–5. (Reproduced with permission from Brodie and Harvey, 2001.)

B. Lecithotrophic zoeal development in *Coenobita variabilis*, dorsal view. The two species are similar as megalopae (shown here) and as adults. Scale bar: 1.0 mm. (Reproduced with permission from Harvey, 1992.)

C. Maxillule in first stage zoea of *C. compressus*. Scale bar: 0.25 mm. (Reproduced with permission from Brodie and Harvey, 2001.)

D. Maxillule in fifth zoea of *C. compressus*. Scale bar: 0.25 mm. (Reproduced with permission from Brodie and Harvey, 2001.)

E. Maxillule in first stage zoea of *C. variabilis*. Scale bar: 0.25 mm. (Reproduced with permission from Harvey, 1992.)

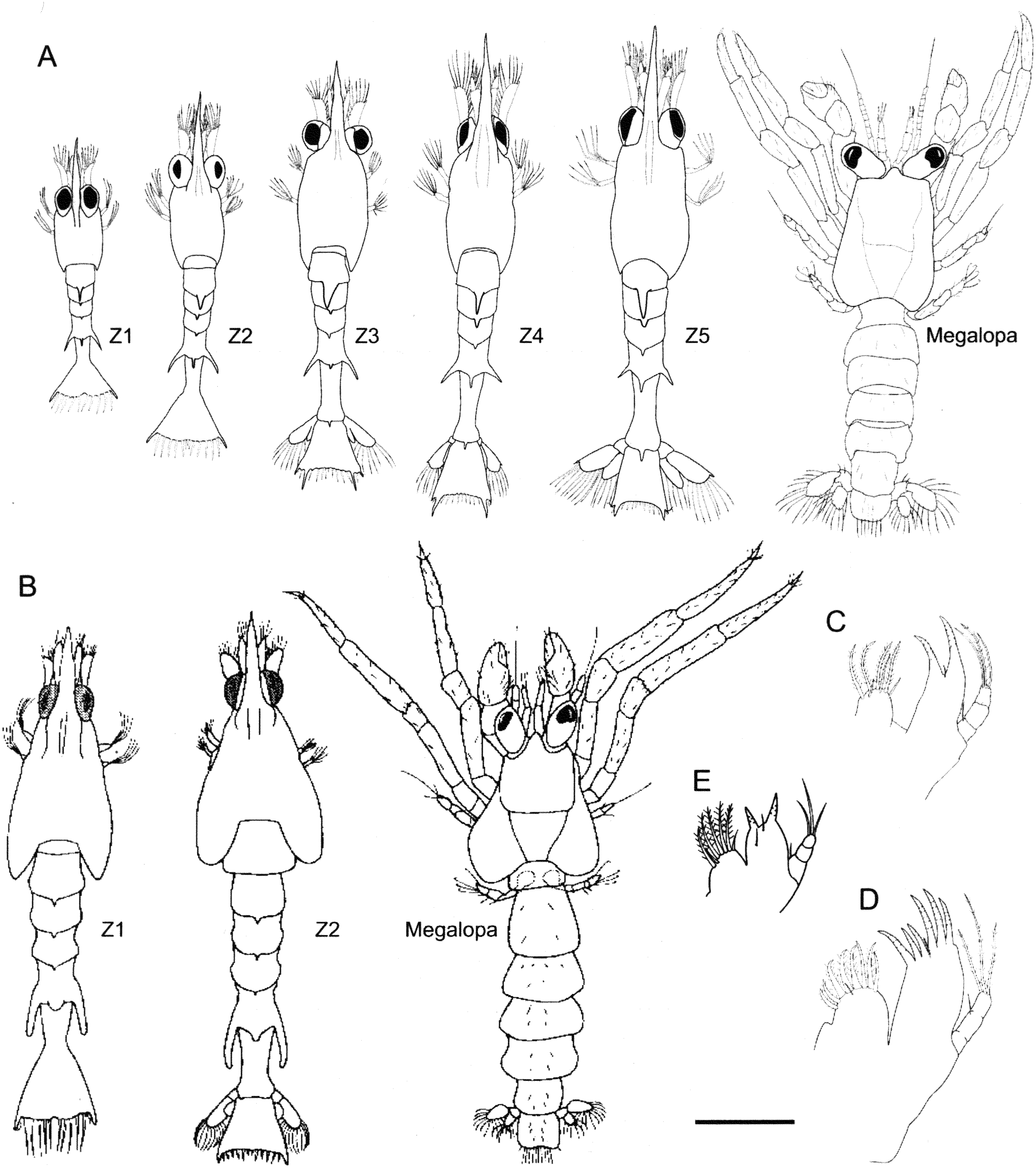

A
Z1
Z2
Z3
Z4
Z5
Megalopa
B
Z1
Z2
Megalopa
C
E
D

FIGURE 17.3

Examples of orthonauplius larvae

A. First stage nauplius of *Hemicyclops japonicus* (family Clausidiidae), ventral view. Scale bar: 30 µm. (Reproduced with permission from Itoh and Nishida, 1997.)
B. Second stage nauplius of *Paramphiascella fulvofasciata* (family Harpacticoida), ventral view. Scale bar: 30 µm. (Reproduced with permission from Dahms, 2000.)
C. First stage nauplius of *Cypris fasciata* (family Cyprididae), lateral view. Scale bar: 30 µm. (Reproduced with permission from Dahms, 2000.)
D. First stage nauplius of *Trachypenaeus* (family Penaeidae), dorsal view. Scale bar: 0.3 mm. (Reproduced with permission from Subrahmanyam, 1971.)
E. Sixth stage larva of *Baccalaureus falsiramus* (family Ascothoracidae), ventral view. Scale bar: 0.1 mm. (Reproduced with permission from Dahms, 2000.)
F. 'Type VI' Y-nauplius from Greenland (infraclass Facetotecta), dorsal (left) and ventral view. Scale bar: 0.1 mm. (Reproduced with permission from Grygier, 1987.)

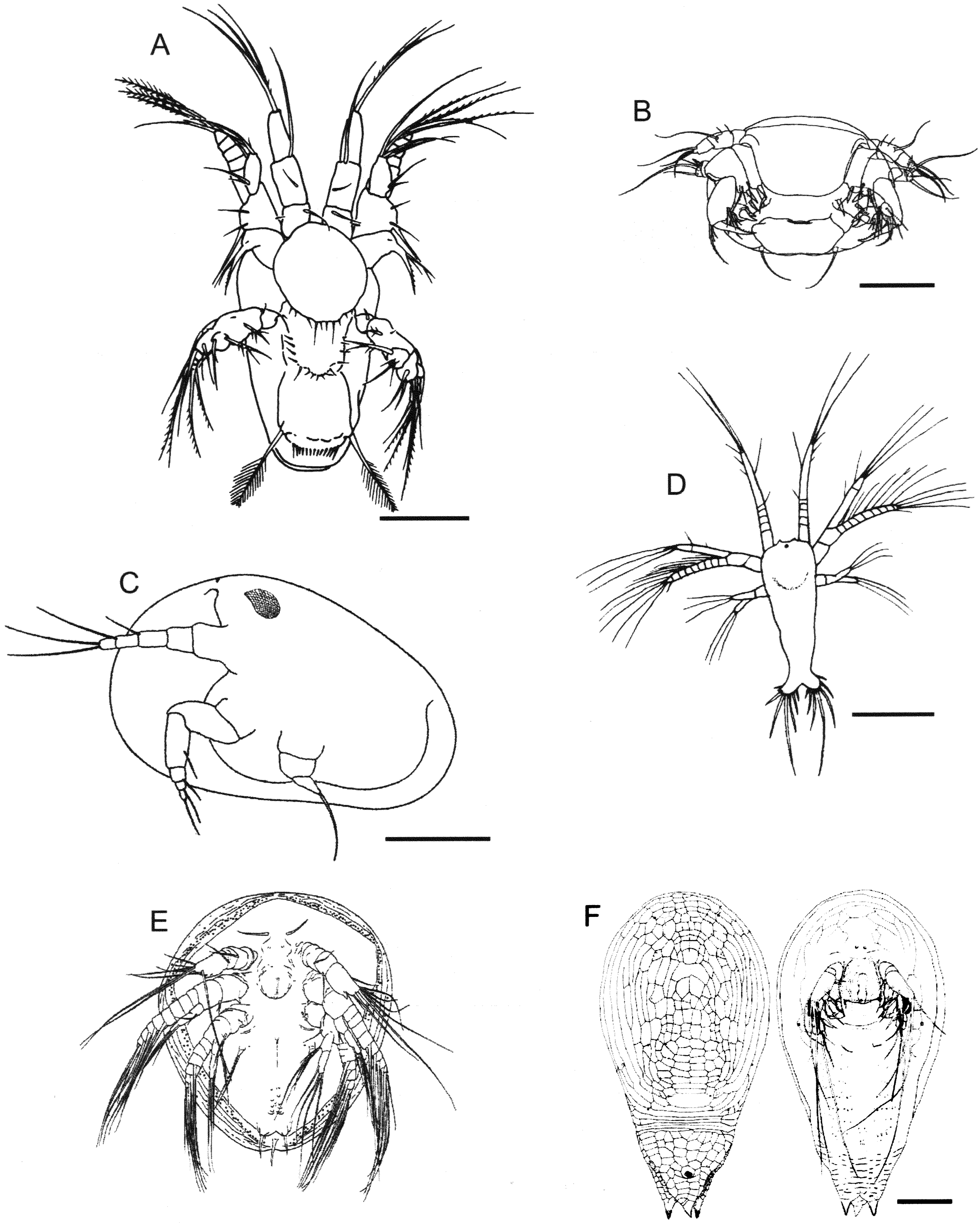

A
B
C
D
E
F

FIGURE 17.4

Examples of nauplius larvae

A. Third stage larva (metanauplius) of *Hutchinsoniella macracantha* (family Hutchinsoniellidae), ventral view. Scale bar: 0.1 mm. (Reproduced with permission from Sanders, 1963.)

B. Larva (metanauplius) of *Thysanopoda tricuspidata* (family Euphausiidae), dorsal view. Scale bar: 0.25 mm. (Reproduced with permission from Knight, 1973.)

C. Larva (metanauplius) of *Euphausia pacifica* (family Euphausiidae), dorsal view. Scale bar: 0.2 mm. (Reproduced with permission from Suh et al., 1993.)

D. First stage larva (metanauplius) of the Upper Cambrian fossil maxillopod *Bredocaris admirabilis*, ventral view. Scale bar: 50 µm. (Scanning electron micrograph courtesy of Dieter Walossek.)

E. Larva (orthonauplius) of an unidentified barnacle collected from plankton in the Bahamas, ventral view. Magnification unknown. (Photograph by C.M. Young.)

F. First stage larva (metanauplius) of *Derocheilocaris typicus* (family Derocheilocarididae), ventral view. Scale bar: 50 µm. (Reproduced with permission from Hessler and Sanders, 1966.)

G. Larva (orthonauplius) of *Pollicipes polymerus* (family Pollicipedidae) from the San Juan Islands, Washington, ventral view. Nauplii in this species range in length from approximately 0.2–0.6 mm (Lewis, 1975). (Photograph by C.M. Young.)

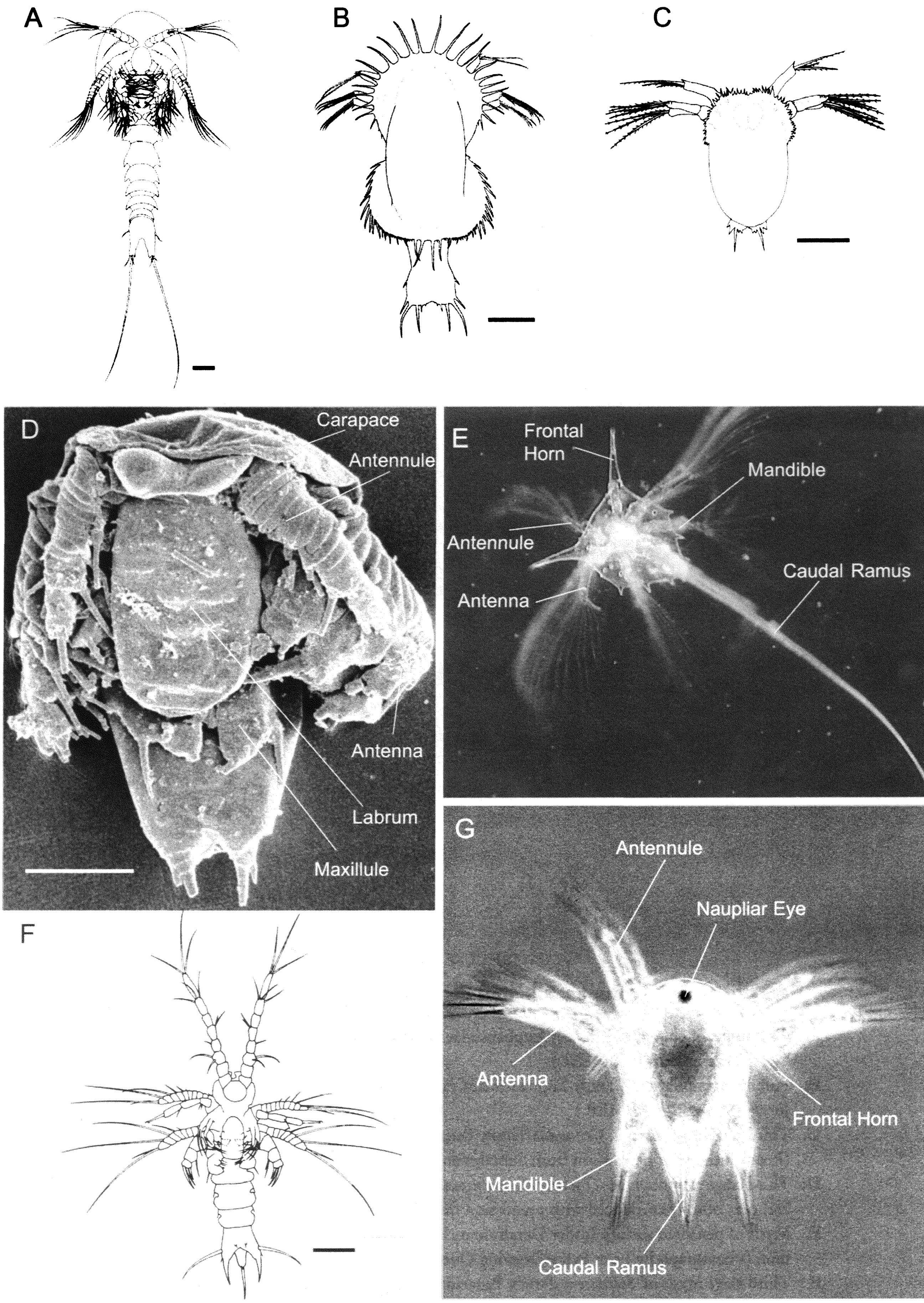

A
B
C
D
Carapace
Antennule
Antenna
Labrum
Maxillule
E
Frontal Horn
Mandible
Antennule
Antenna
Caudal Ramus
F
G
Antennule
Naupliar Eye
Antenna
Frontal Horn
Mandible
Caudal Ramus

FIGURE 17.5

Euphausiid and dendrobranch zoeae

A. Calyptopis of euphausiid (family Euphausiidae), dorsal view. Scale bar: 0.25 mm. (Photograph by Jocelyne Martin/IFREMER.)
B. Furcilia of euphausiid (family Euphausiidae), lateral view. Scale bar: 0.25 mm. (Photograph by Jocelyne Martin/IFREMER.)
C. Third stage protozoea of *Gennadas* (family Penaeidae), dorsal view. Scale bar: 0.5 mm. (Reproduced with permission from Subrahmanyam and Gunter, 1970.)
D. Third stage calyptopis of *Thysanopoda tricuspidata* (family Euphausiidae), dorsal view. Scale bar: 0.25 mm. (Reproduced with permission from Knight, 1973.)
E. Mysis of penaeoid shrimp (order Dendrobranchia), dorsal view. Body length approximately 3 mm. (Photograph by Peter Parks/Drawing Quest 3–D.)
F. Third stage mysis of *Solenocera* (family Penaeidae), dorsal view. Scale bar: 0.5 mm. (Drawing reproduced with permission after Subrahmanyam, 1971.)

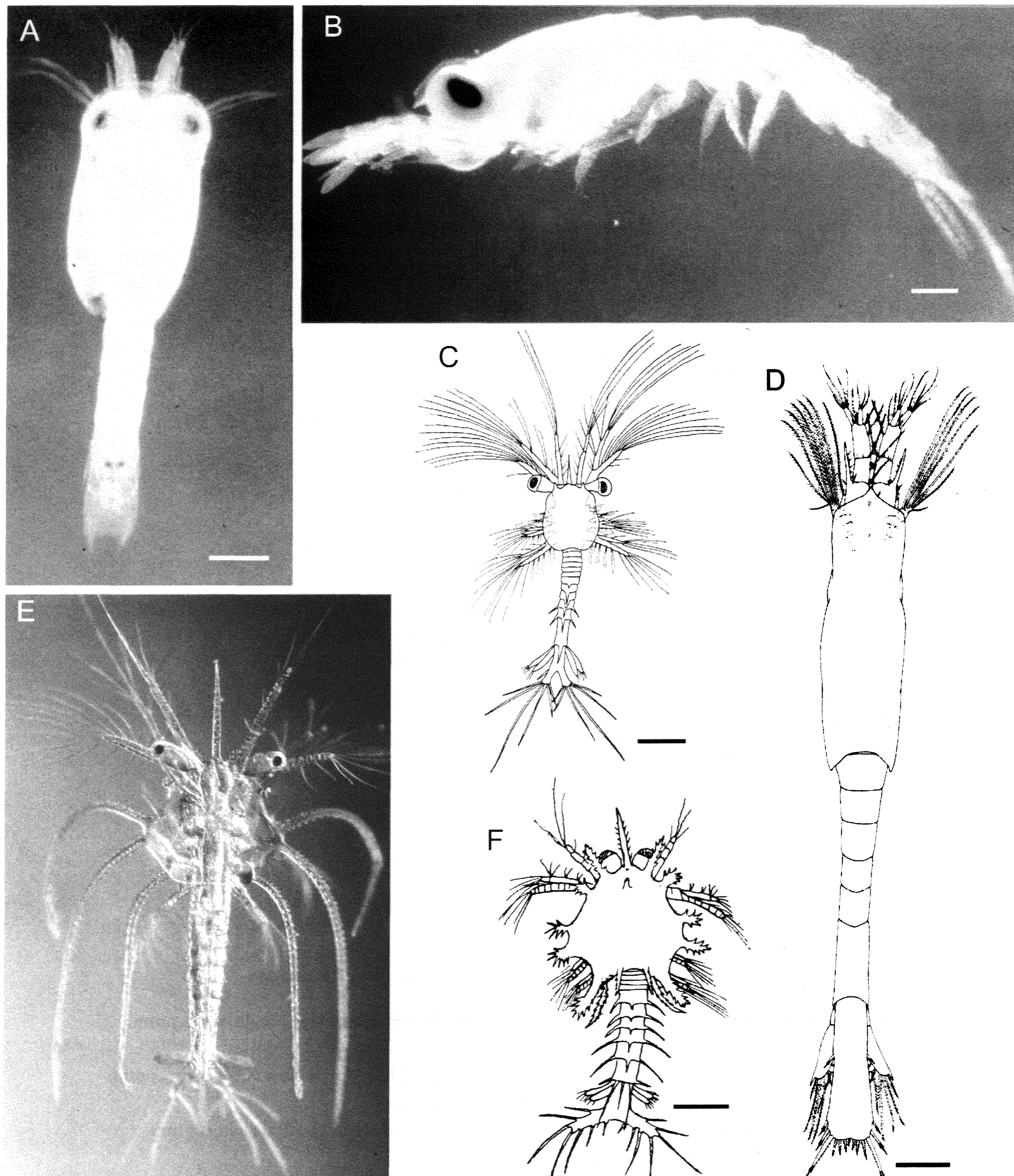

A
B
C
D
E
F

FIGURE 17.6

Zoeae of Caridea, Thalassinidea, and Anomura

A. Third stage zoea of *Crangon crangon* (family Crangonidae), lateral view. Scale bar: 0.5 mm. (Photograph by Jocelyne Martin/IFREMER.)

B. Fourth stage zoea of *Callichirus major* (family Callianassidae), dorsal view. Scale bar: 0.5 mm. (Reproduced with permission from Strasser and Felder, 1999.)

C. First stage zoea of *Galathea dispersa* (family Galatheidae), dorsal view. Scale bar: 0.5 mm. (Photograph by Jocelyne Martin/IFREMER.)

D. First stage zoea of *Albunea carabis* (family Albuneidae), dorsal view. Scale bar: 0.5 mm. (Reproduced with permission from Seridji, 1988.)

E. Ninth stage zoea of *Latreutes laminirostris* (family Hippolytidae), dorsal (upper) and lateral view. Scale bar: 0.5 mm. (Reproduced with permission from Kim and Hong, 1999.)

F. First stage zoea of *Pisidia longicornis* (family Porcellanidae), lateral view. Scale bar: 0.5 mm. (Photograph by Jocelyne Martin/IFREMER.)

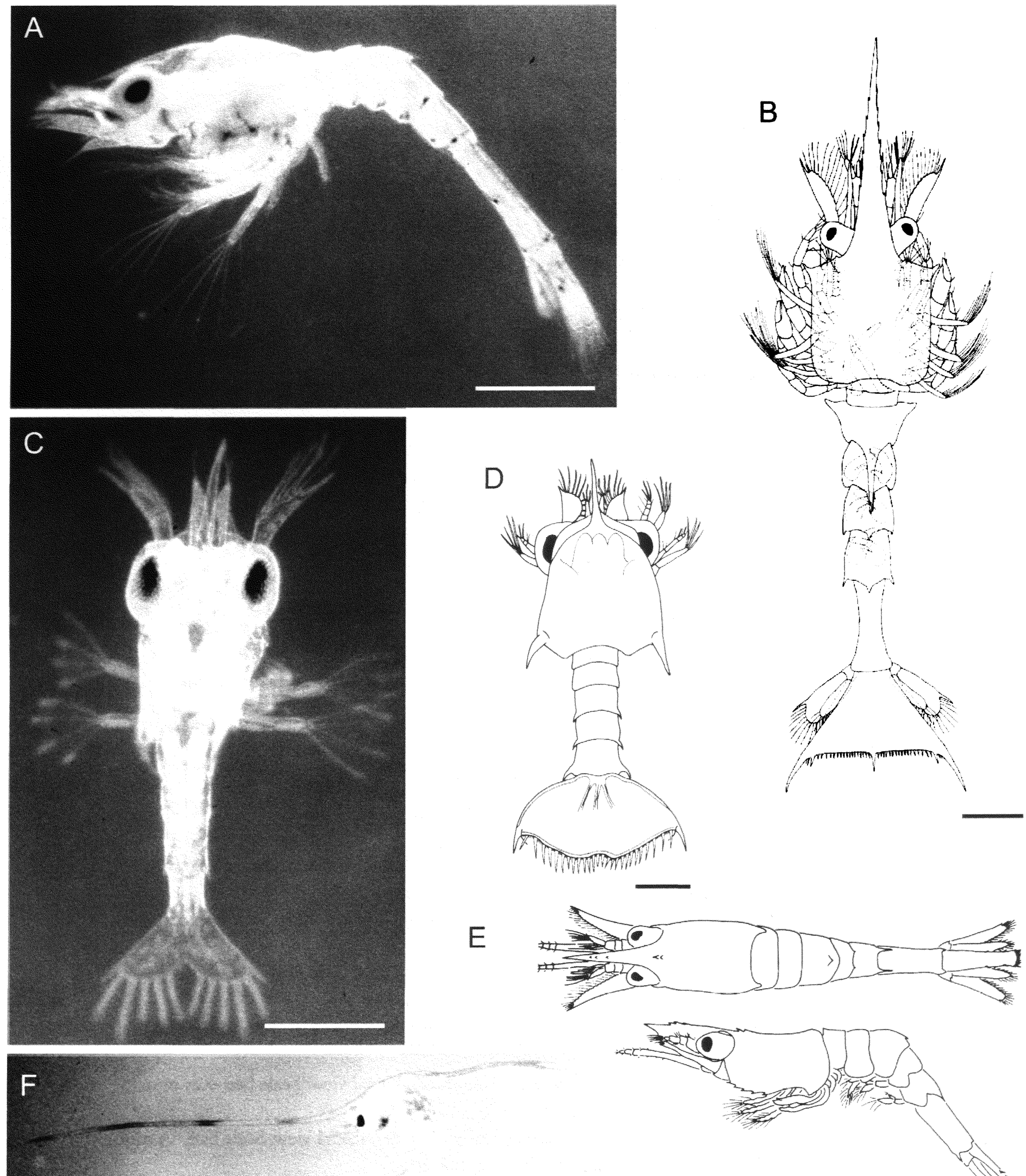

A
B
C
D
E
F

FIGURE 17.7

Zoeae of brachyuran crabs

A. First stage zoea of *Dromia wilsoni* (family Dromiidae), dorsal view. Scale bar: 0.25 mm. (Reproduced with permission from Wear and Fielder, 1985.)

B. Second stage zoea of *Philyra platychira* (family Leucosiidae), lateral view. Scale bar: 0.2 mm. (Reproduced with permission from Ko, 2000.)

C. First zoeal stage of *Notomithrax minor* (family Majidae), lateral view. Scale bar: 0.5 mm. (Reproduced with permission from Wear and Fielder, 1985.)

D. Zoea of *Tetralia* (family Xanthidae), dorsal view. Length from tip of rostrum to tip of dorsal spine: 6.4 mm (George and John, 1975).

E. First zoeal stage of *Homola barbata* (family Homolidae), lateral view. Scale bar: 0.25 mm. (Reproduced from Williamson, 1982b.)

F. Second zoeal stage of *Dorhynchus thomsoni* (family Majidae), lateral view. Scale bar: 0.5 mm. (Reproduced with permission from Williamson, 1982b.)

G. Third stage zoea of *Thia scutellata* (family Thiidae), anterolateral view. Scale bar: 0.5 mm. (Photograph by Jocelyne Martin/IFREMER.)

H and I. Unidentified brachyuran zoeae from the Bahamian plankton. Magnifications unknown. (Photographs by C.M. Young.)

J. Unidentified brachyuran zoea from the plankton at Friday Harbor, Washington, frontal view, showing carapace spines. Magnification unknown. (Photograph by C.M. Young.)

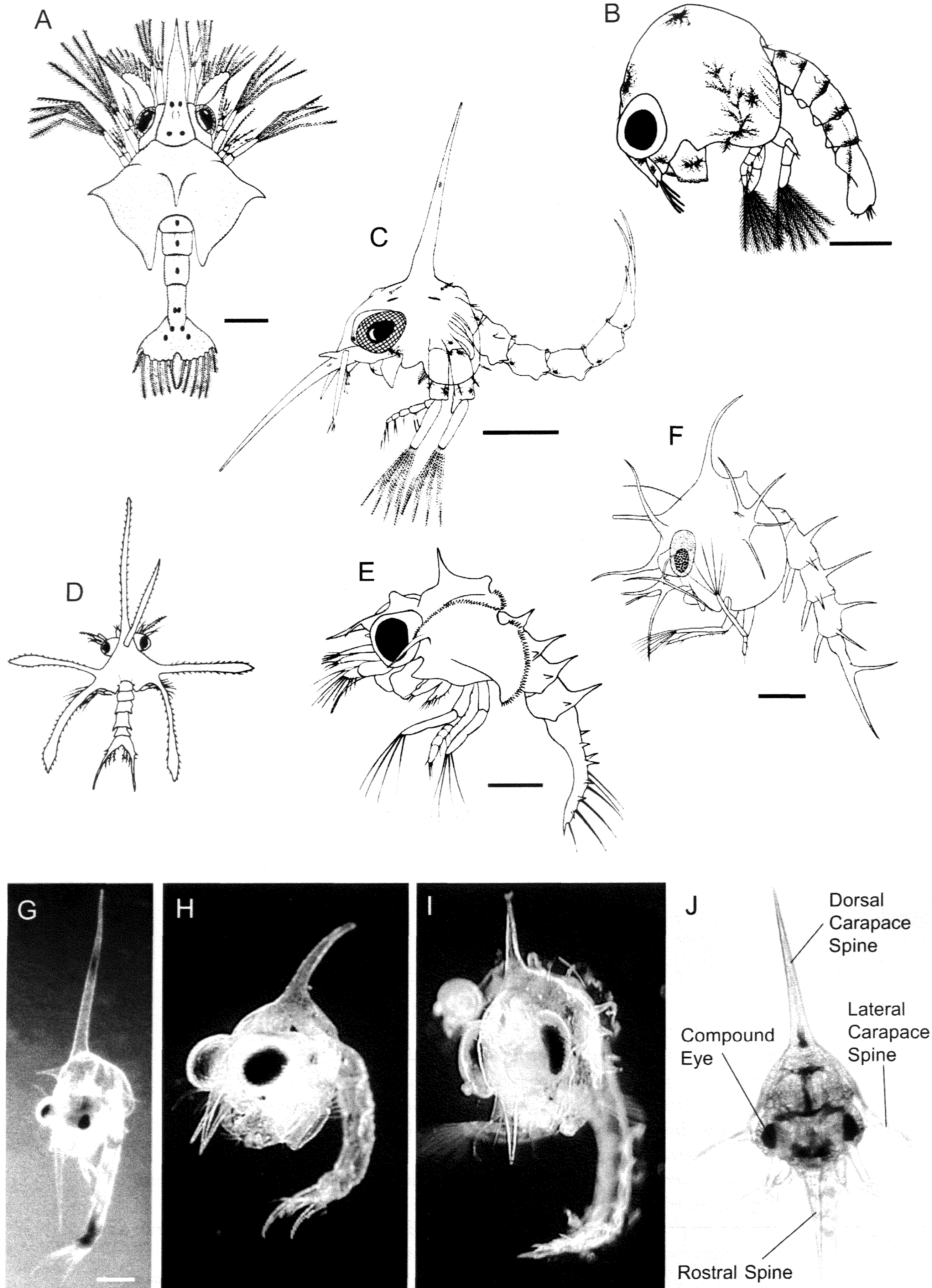

A
B
C
D
E
F
G
H
I
J
Dorsal Carapace Spine
Lateral Carapace Spine
Compound Eye
Rostral Spine

FIGURE 17.8

Atypical zoeal forms

A. Pseudozoea of a stomatopod (superfamily Squilloidea), ventral view. Body length approximately 3 mm. (Photograph by Peter Parks/Drawing Quest 3–D.)

B. Fifth pseudozoeal stage (second pelagic stage) of *Gonodactylus oerstedii* (family Gonodactylidae), lateral view. Scale bar: 1.0 mm. (Reproduced with permission from Provenzano and Manning, 1978.)

C. Antizoea of *Coronis scolopendra* (family Lysiosquillidae), lateral view. Scale bar: 0.25 mm. (Reproduced with permission from Rodrigues and Manning, 1992).

D. Fourth stage phyllosoma of *Thenus orientalis* (family Scyllaridae), ventral view. Scale bar: 0.25 mm. (Reproduced with permission from Barnett et al., 1984.)

E. Early stage phyllosoma collected from plankton in the Bahamas, probably of *Panulirus argus* (family Palinuridae), dorsal view. Body length 3mm. (Photograph by C.M. Young.)

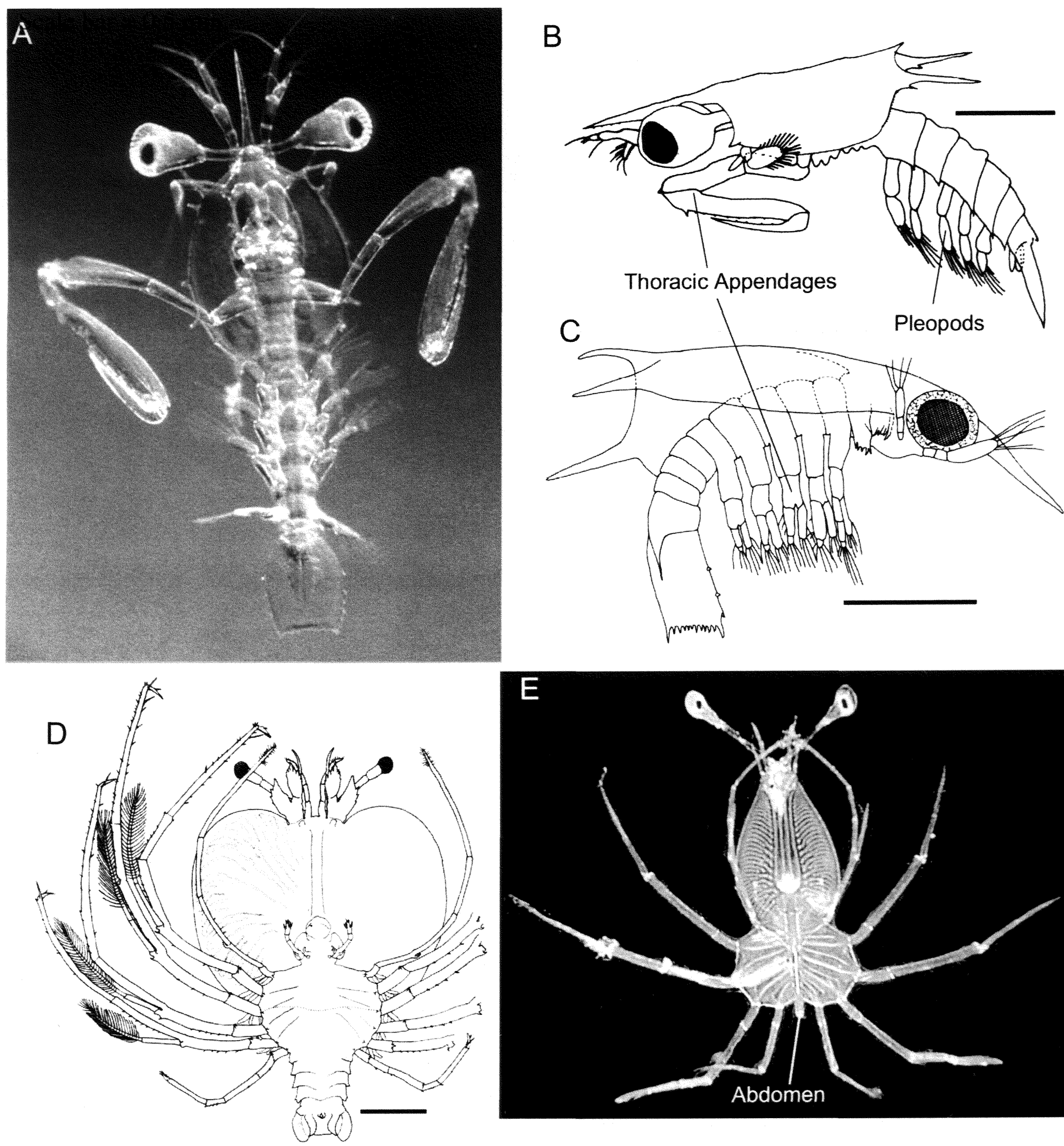
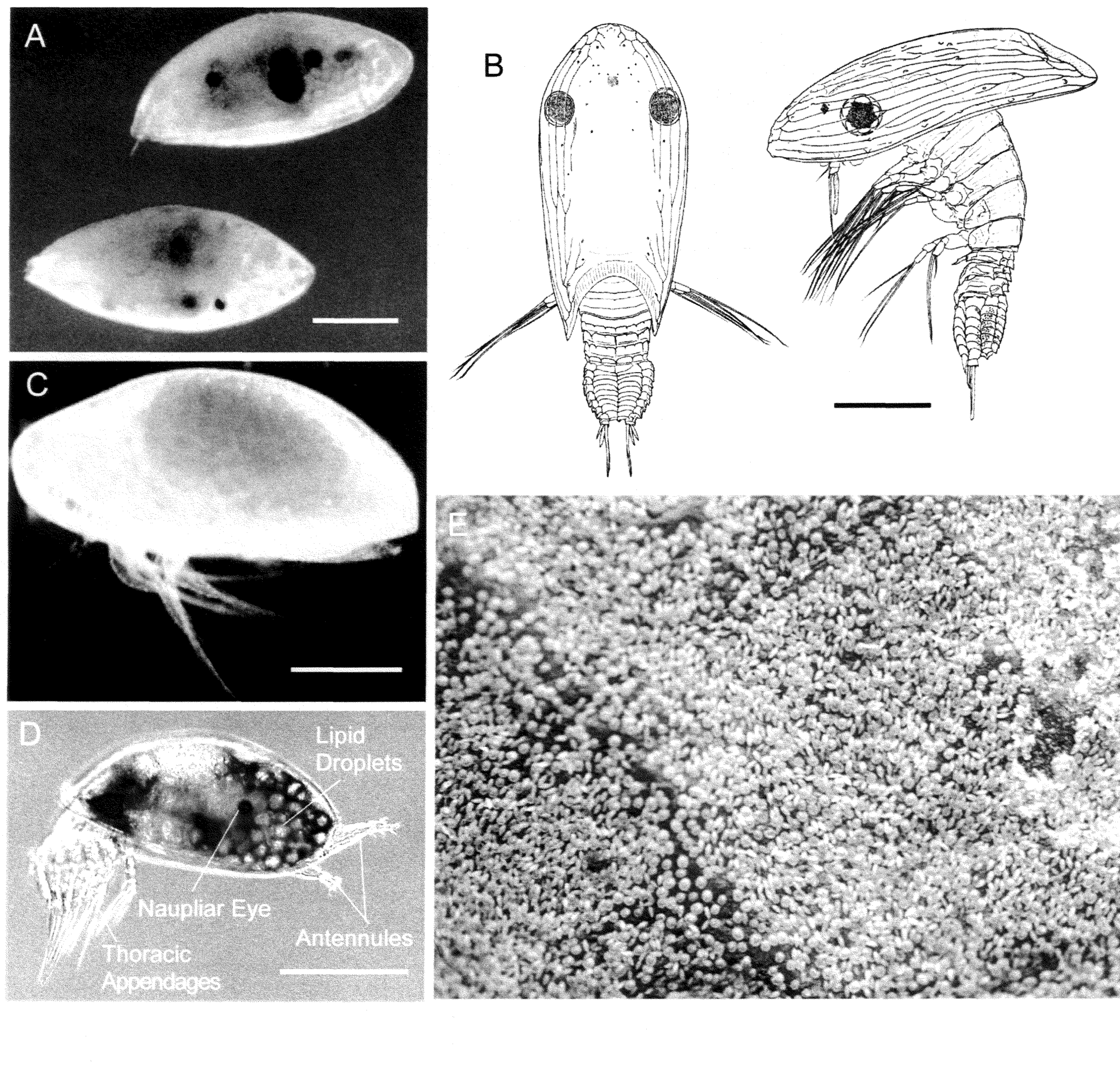

A
B
Thoracic Appendages
Pleopods
C
D
E
Abdomen

FIGURE 17.9

Cyprids

- **A.** Typical balanomorph cyprids (superorder Thoracica.) Scale bar: 0.25 mm. (Photograph by Jocelyne Martin/IFREMER.)
- **B.** Cypris Y-larva of *Hansenocaris furcifera* (infraclass Facetotecta), in dorsal (left) and lateral view. Scale bar: 0.1 mm. (Reproduced with permission from Ito, 1989.)
- **C.** *Dendrogaster deformator* (family Dendrogasteridae), lateral view. Collected from adult parasitizing the asteroid *Novodinea antillensis* at bathyal depths in the Bahamas. Scale bar: 0.25 mm. (Photograph by C.M. Young.)
- **D.** Cyprid larva of the barnacle *Balanus amphitrite*, with thoracic appendages extended. Scale bar: 0.25 mm. (Photograph by C.M. Young.)
- **E.** Dense aggregation of settling balanomorph cyprids (probably *Balanus glandula)* (family Balanidae) near Friday Harbor, Washington. Carapace length of cyprids in *B. glandula* is 0.6–0.7 mm (Brown and Roughgarden, 1985.) (Photograph by C.M. Young.)



A
B
C
D
Lipid Droplets
Naupliar Eye
Antennules
Thoracic Appendages
E

FIGURE 17.10

Megalopae of the infraorder Palinura

A. Puerulus of *Scyllarus americanus* (family Scyllaridae), lateral view. Scale bar: 1.0 mm. (Reproduced with permission from Robertson, 1968b.)

B. Puerulus of *Projasus* (family Palinuridae), lateral view. Scale bar: 10.0 mm. (Reproduced with permission from Webber and Booth, 1988.)

C. Eryoneicus larva of polychelid lobster (family Polychelidae), lateral view. Scale bar: 10.0 mm. (Photograph by R. Meier, from a specimen in the collections of the Natural History Museum of Los Angeles County.)

D. Same specimen as in C, dorsal view. Scale bar: 10.0 mm.

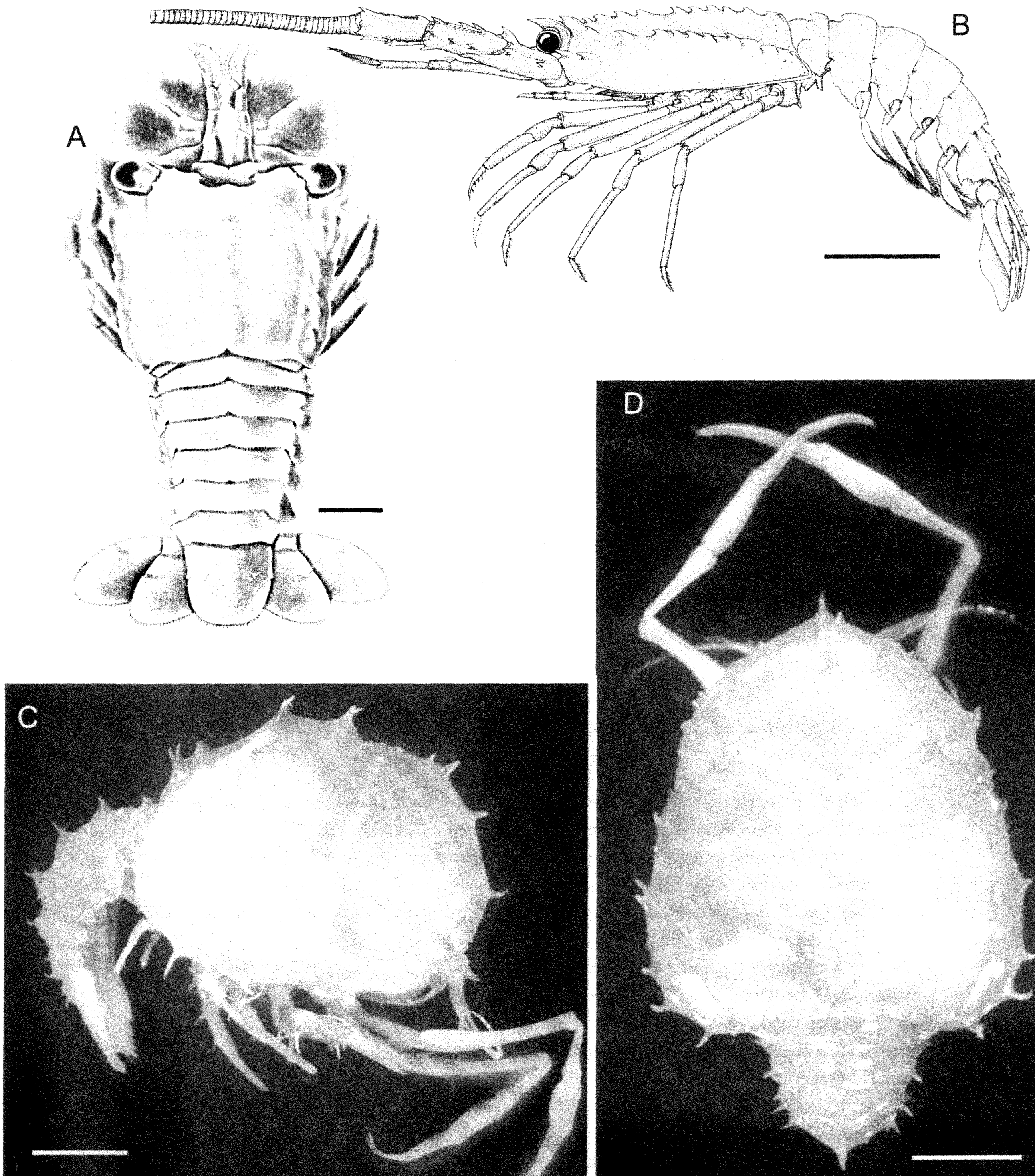

A
B
C
D

FIGURE 17.11

Megalopae of Thalassinidea and Anomura (A–C) and settlement by hermit crab megalopae (D–G)

A. *Callichirus major* (family Callianassidae), dorsal view. Scale bar: 0.5 mm. (Reproduced with permission from Strasser and Felder, 1999.)

B. *Lepidopa benedicti* (family Albuneidae), dorsal view. Scale bar: 1.0 mm. (Reproduced with permission from Stuck and Truesdale, 1986.)

C. *Allopetrolisthes angulosus* (family Porcellanidae), dorsal view. Scale bar: 0.5 mm. (Reproduced with permission from Wehrtmann et al., 1996.)

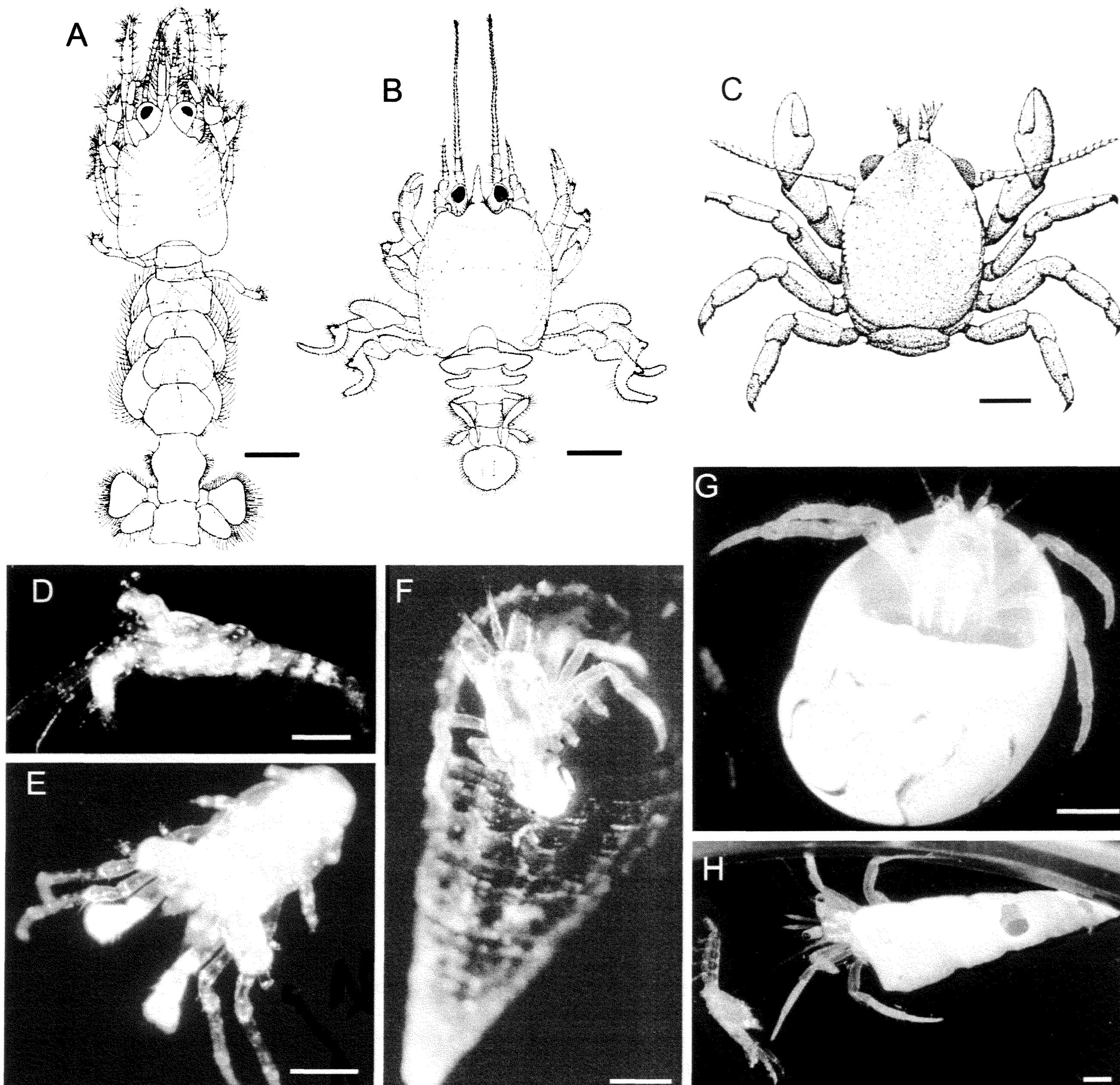
D. Swimming megalopa of *Pagurus brevidactylus* (family Paguridae), lateral view. Scale bar: 1.0 mm. (Photograph by A.W. Harvey.)

E. Megalopa *P. brevidactylus* walking on the substrate, dorsal view. Megalopae commonly make a gradual transition from being primarily pelagic to primarily benthic. Scale bar: 1.0 mm. (Photograph by A.W. Harvey.)

F. Initial investigation of a gastropod shell by a megalopa *P. brevidactylus*. Shells are essential to post-larval survival in most hermit crabs. Scale bar: 0.5 mm. (Photograph by A.W. Harvey.)

G. Megalopa of *Coenobita variabilis* (family Coenobitidae), occupying a gastropod shell. Scale bar: 1.0 mm. (Photograph by A.W. Harvey.)

H. Delayed metamorphosis of megalopae in the absence of required post-larval cues. Two same-age siblings of *Clibanarius longitarsus* (family Diogenidae), 6 weeks after becoming megalopae. The large specimen on the right received a gastropod shell 5 weeks earlier, metamorphosed a week later, and is a sixth stage juvenile. The small specimen on the left has not received a shell, and is still a swimming megalopa. Scale bar: 1.0 mm. (Photograph by A.W. Harvey.)



A
B
C
D
E
F
G
H

FIGURE 17.12

Megalopae of brachyuran crabs

A. *Dromia wilsoni* (Dromiidae), dorsal view. Scale bar: 0.25 mm. (Reproduced with permission from Wear and Fielder, 1985.)

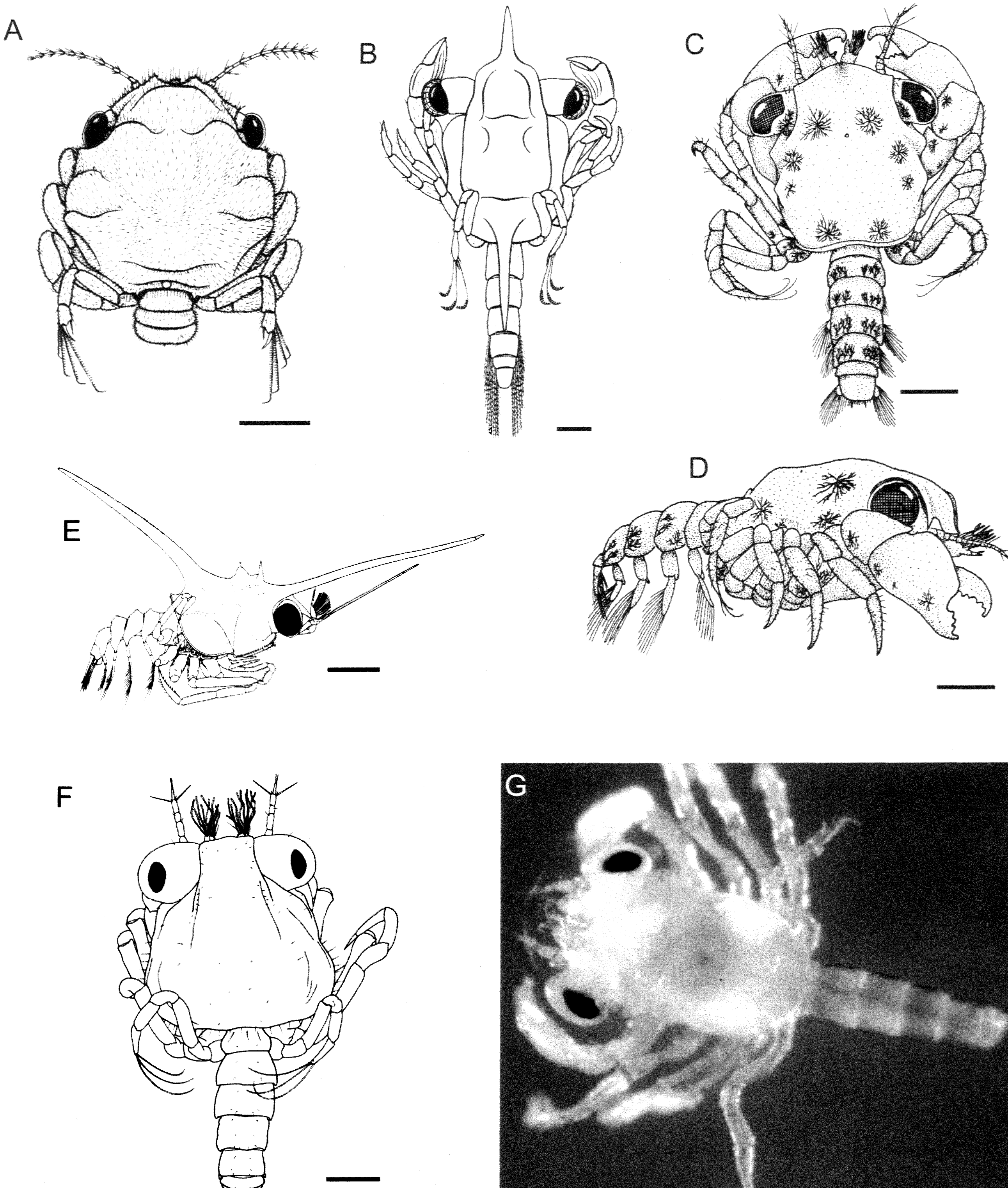
B. *Cancer novaezelandiae* (Cancridae), dorsal view. Scale bar: 0.5 mm. (Reproduced with permission from Wear and Fielder, 1985.)

C and D. *Menippe adina* (family Xanthidae), in dorsal (C) and lateral (D) view. Scale bar: 0.5 mm. (Reproduced with permission from Martin et al., 1985.)

E. *Paramola petterdi* (family Homolidae), lateral view. Scale bar: 2.0 mm. (Reproduced with permission from Wear and Fielder, 1985.)

F. *Sesarma guttatum* (family Grapsidae.) Scale bar: 0.2 mm. (Reproduced with permission from Pereyra Lago, 1993.)

G. *Pisa* sp. (family Majidae.) Scale bar: 0.5 mm. (Photograph by Jocelyne Martin/IFREMER.)


A
B
C
D
E
F
G