

Phylum Nemertea

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INTRODUCTION

Although most zoologists have had little direct experience with the phylum Nemertea, many are acquainted with the striking image of a fully formed nemertean pilidium larva. Many embryologists know about the pilidium larva, thanks to the works of Metschnikoff (1869), Salensky (1886) and Wilson (1900). However, the other planktonic larvae of nemerteans, the so-called direct developers, are very poorly known, although Jägersten (1972) gave them prominent attention in his widely cited monograph.

During the last 150 years, various observations about nemertean planktonic larvae have been made; many of these have been compiled in Friedrich's (1979) monograph on nemertean morphogenesis, and they have also been summarized in a review by Cantell (1989). More recently, the use of modern experimental embryological techniques has resulted in significant advances in our understanding of aspects of larval morphogenesis, especially with regard to the early development (Henry and Martindale, 1997a, and references therein). However, knowledge of nemertean larvae remains relatively rudimentary when compared with what is known about larvae in many other groups.

A comprehensive and widely accepted phylogeny of nemerteans is not currently available. However, strong evidence is emerging that the two most speciose groups of nemerteans, the orders Hoplonemertea and Heteronemertea, are monophyletic (Sundberg and Saur, 1998; JLN, unpublished observations). A smaller, third order, the Palaeonemertea (including the Cephalothricidae), is traditionally recognized. However,

it appears to be at least paraphyletic, with one or more of its included taxa comprising the most basal clades in a nemertean phylogeny (JLN, unpublished observations). Thus, the term 'palaeonemerteans', from here onward, refers to a presumed paraphyletic assemblage, rather than a monophyletic taxon. Hoplo- and palaeonemerteans traditionally are regarded as direct developers, whereas all heteronemerteans whose life cycles have been studied produce a pilidium larva or a larva that appears to be derived from a pilidium. Consequently, based on phylogenetic evidence to date, the pilidium is most likely to be an apomorphic larval form unique to the Nemertea. Although non-pilidial larvae of nemerteans are not known to undergo a radical metamorphosis, scattered observations (Maslakova and Malakhov, 1999) provide cause to question the assertion that all non-heteronemerteans are direct developers.

REPRODUCTIVE BIOLOGY

Most nemerteans are dioecious, and almost all of the hermaphroditic species occur within the suborder Monostilifera of the Hoplonemertea (Friedrich, 1979). Spermatogenesis and oogenesis in nemerteans have been addressed recently by Stricker et al. (unpublished observations) and Stricker and Folsom (1998), respectively. Mature oocytes range from 50 μm to 2.5 mm in diameter (Friedrich, 1979), with approximately commensurate differences in yolk content (Stricker et al., unpublished observations). Ovaries may possess from one to more than 100 mature oocytes, which are usually arrested at prophase I of meiosis; the number of oocytes varies

within a species-specific range (Friedrich, 1979; Stricker et al., unpublished observations). Yolk production appears to be mostly by an 'autosynthetic' mode, but several exceptions are suspected, for example, *Carcinonemertes epialti* (Stricker and Reed, 1981), *Tubulanus polymorphus* (Stricker et al., unpublished observations), and most pelagic nemerteans (Norenburg and Roe, 1998a) exhibit some exogenous contribution to yolk synthesis. Both elongate and compact-headed sperm are produced in the phylum, but fertilization mode is not clearly correlated with sperm type (Stricker and Folsom, 1998).

Most species of nemerteans are oviparous. The mode of spawning is known for relatively few nemerteans, mostly those from littoral habitats. Among littoral forms, spawning ranges from broadcast release of gametes into the surrounding sea, to pseudocopulation with eggs attached in a gelatinous matrix to a benthic substratum (Riser, 1974; Stricker, 1987). Heteronemerteans known to have planktonic pilidium larvae are broadcast spawners. Conversely, the heteronemerteans *Lineus ruber* and *L. viridis* pseudocopulate while depositing their eggs in a gelatinous cocoon (Riser, 1974), producing pilidium-like encapsulated larvae, known as Schmidt's and Desor's larvae, respectively (Friedrich, 1979). A few nemerteans bear living young, and some of these can be considered to obtain extraembryonic nutrition by viviparity (Norenburg, 1986). In contrast to popular belief, vegetative reproduction by fission is a significant mechanism of propagation for only a few species in the genus *Myoisophagos* (including the former *Lineus sanguineus*, *L. socialis*, and *L. vegetus*) (Riser, 1974, 1994).

EMBRYOGENESIS

Early embryogenesis and recent experimental studies are reviewed by Henry and Martindale (1997a). Cleavage is spiral, as in other protostomes. However, the blastomeres of the 4-cell stage are of equal size and lie in a single plane. Thus, a well-defined cross-furrow does not separate opposite blastomeres of the animal and vegetal poles as in annelids and mollusks (Henry and Martindale, 1997a). Apparently unique to nemerteans, 4-cell embryos of *Cerebratulus lacteus* that are bisected along the second cleavage plane, thereby disrupting established animal-vegetal and dorsoventral axes, erect novel sets of axial relationships that can, but do not always, generate normal-appearing pilidia (Henry and Martindale, 1997b). The blastula is usually a hollow coeloblastula, but may be a solid stereoblastula (Friedrich, 1979). During gastrulation, the archenteron is established by invagination or polar ingression of cells at the vegetal pole. The fate of the blastopore is seldom

described, although it is thought to close permanently in hoplonemerteans, and it usually moves inward with formation of the stomodeum in palaeo- and heteronemerteans (Iwata, 1960a; Friedrich, 1979). The stomodeum becomes a more anteriorly located invagination on the ventral surface of the larva, posterior to the brain (Friedrich, 1979; Iwata, 1985). In most hoplonemerteans, the stomodeum fuses with the rhynchodeum (proboscis aperture) and comes to lie in front of the brain (Friedrich, 1979). The origin of mesoderm in nemerteans and whether this varies by species has been in dispute (Henry and Martindale, 1997a). However, Henry and Martindale (1996) demonstrated that larval mesoderm in the pilidium of the heteronemertean *C. lacteus* is generated both as ectomesoderm from the 3a and 3b micromeres, and as endomesoderm derived from the 4d micromere. Henry and Martindale (1997a) speculated that adult mesoderm might arise from dormant endomesodermal cells.

LARVAL DEVELOPMENT

Nemertean larval development is usually characterized as direct or indirect, with the latter being synonymized with a pilidium-forming life cycle (cf. Friedrich, 1979). Direct development in nemerteans has been defined as "a path of development that leads to the establishment of the adult body plan (bauplan) without the formation of an intermediate feeding larval stage that possesses a distinct body plan" (Henry and Martindale, 1997a). With the exception of the two presumably derived forms, noted earlier for *L. ruber* and *L. viridis*, all known species with pilidia hatch at, or shortly after, the gastrula stage. Depending on the species, direct developing nemerteans may hatch from the egg capsule beginning at the gastrula stage or at stages up to a fully functional, non-sexual juvenile (Iwata, 1960a; Riser, 1974; Friedrich, 1979; unpublished observations). Among those hatching as pre-crawling juvenile forms, some remain within a cocoon, as in some supralittoral hoplonemerteans (e.g., *Pantionemertes*, cf. Norenburg, 1986). The planktonic larval phase of palaeonemerteans appears to be limited by both yolk reserves and capacity for planktotrophic feeding, whereas planktonic hoplonemertean larvae appear not to feed and are limited by yolk reserves (JLN, unpublished observations). At the risk of introducing new confusion, the elongate planktonic pre-adult phase of such 'direct-developing' palaeo- and hoplonemerteans will herein be referred to as a 'planuliform' larva. Dieck (1874) also referred to a 'cephalothricid' larva of this type as a planula.

If one expands the view of indirect development to include non-pilidial forms, there have been several reports, starting with Dieck (1874), of 'direct developers'

that appear to shed or resorb their larval ectoderm. Maslakova and Malakhov (1999) describe this phenomenon as development of a 'hidden' larva. These hidden larvae, as well as pilidia, may in turn correspond with the concept of maximal indirect development proposed by Davidson et al. (1995).

A fact that is clearly under appreciated in the secondary literature is that planuliform larvae are actually quite common among palaeonemerteans (Figures 7.1A–C), an observation also made by Jägersten (1972). To this list can be added four species from the Indian River Lagoon (Florida, USA): *Carinoma* cf. *tremaphoros* (Figure 7.1A), *Tubulanus pellucidus*, an undescribed *Tubulanus*, and an undescribed cephalothricid (JLN, unpublished observations). The latter four originate from small eggs with little yolk reserves and they are planktotrophic for as long as a week in captivity (JLN, unpublished observations). Based on the typical egg sizes of palaeonemerteans, planktotrophy is likely to be the rule in this group, as was noted by Iwata (1960b) and Jägersten (1972). This is also the case for heteronemerteans (Cantell, 1989). In contrast, hoplonemerteans usually have significantly larger eggs (e.g., Friedrich, 1979) and produce planuliform larvae that generally have a short planktonic phase (Friedrich, 1979; Stricker, 1987). Such larvae undergo little or no elongation in the plankton (JLN, unpublished observations), and appear to be lecithotrophic while in the plankton (Stricker, 1987; JLN, unpublished observations).

Elongate planktonic larval forms apparently belonging to two species of monostiliferan hoplonemerteans were collected in the Gulf Stream off southern Florida (Figures 7.1D,E). The specimens were 3–4 mm long and most adult structures were moderately well-defined. However, the gut was still occluded by copious amounts of presumptive yolk bodies. One of these forms resembled a planuliform larva collected by Jägersten (1972: figure 20D) off the west coast of Sweden. Jägersten (1972:91) also described finding a planuliform palaeonemertean larva with a fully differentiated proboscis, albeit, perhaps, non-functional. Another such larva, about 2 mm long, was collected 5 km off southern Florida (Figure 7.1C; JLN, unpublished observations). However, no palaeonemertean larvae with a recognizable proboscis were caught in plankton of the Indian River Lagoon in weekly sampling following the first appearance of planuliform larvae in the Indian River Lagoon (JLN, unpublished observations). Palaeonemertean planuliform larvae and pilidium larvae feed on a range of planktonic organisms, usually microplankton in the dinoflagellate size range (Cantell, 1969; JLN, unpublished observations), but Jägersten (1972) observed a palaeonemertean larva feeding on a pilidium its equal in size. In contrast, hoplonemerteans apparently do not

begin feeding until the proboscis is functional, as was noted by Iwata (1960b), and they may never be planktotrophic.

LARVAL ANATOMY

By about the time of gastrulation, most nemertean larvae are fully ciliated. Each cell generally possesses multiple cilia, but the cilia may be sparsely distributed, especially in pilidium larvae (Cantell et al., 1982). All known free-swimming larvae of nemerteans develop an apical tuft of elongate cilia, associated with an apical plate of ectodermal cells (Iwata, 1960a; Stricker and Reed, 1981; Cantell et al., 1982; Lacalli and West, 1985; Henry and Martindale, 1994; unpublished observations). The planuliform larvae of palaeo- and hoplonemerteans usually also have a posterior tuft of elongate cilia (Iwata, 1960a; Stricker and Reed, 1981; Henry and Martindale, 1994; unpublished observations). An anterior tuft is present in the planktonic and lecithotrophic, pilidium-like larva of *Micrura akkeshiensis* (Iwata, 1958). It is not present in the encapsulated Desor's and Schmidt's larvae.

Based on ultrastructural studies, these elongate tufts of cilia, or cirri, may consist of mono- or multiciliated cells (Stricker and Reed, 1981; Cantell et al., 1982; Lacalli and West, 1985). The anterior cirrus of the planuliform larva of *Carcinonemertes epialti* (Figure 7.1F) contains multiciliated cells with non-striated ciliary rootlets and is associated with nerve fibers (Stricker and Reed, 1981). Alternatively, either multiciliated or monociliated cells with striated rootlets constitute the apical cirri in two different pilidia examined by Cantell et al. (1982). The apical plates of two types of pilidia examined by Lacalli and West (1985) were associated with muscle fibers, but not nerve bundles. The apical and posterior cirral cells of *C. epialti* also bear elongate microvilli (Stricker and Reed, 1981), which are similar to those found on collar cells in pilidium larvae (Cantell et al., 1982).

All known palaeonemertean larvae have one or more pairs of lateral cirri anterior to the mouth (Figure 7.1B) (Iwata, 1960a; Jägersten, 1972; JLN, unpublished observations). In *Carinoma* cf. *tremaphoros* (from the Indian River, Florida), there may also be up to three pairs of cirri lateral to the mouth (JLN, unpublished observations). Although the apical cirrus of pilidium larvae is shed with the rest of the larval body at the time of metamorphosis, the fates of the anterior and posterior cirri of planuliform larvae is rarely addressed. Stricker and Reed (1981) reported that these cirri are absent in juveniles of the monostiliferan hoplonemertean *C. epialti*, and they are also absent in the encapsulated larva of *Tetrastemma candidum* (Maslakova and Malakhov, 1999). However, an apical (frontal) and posterior cirrus develop in the

hatched juvenile (Maslakova and Malakhov, 1999). Contrary to the report for *C. epialti*, most other juvenile and adult monostiliferans have apical and caudal cirri, corresponding positionally to the larval cirri (JLN, unpublished observations). These cirri are increasingly difficult to observe as animals increase in size (JLN, unpublished observations). The apical plate of many hoplonemertean larvae becomes the adult frontal organ (Friedrich, 1979), the site of the frontal cirrus. In contrast, while most palaeonemertean adults have scattered cirri, these are seldom apical (JLN, unpublished observations). Some palaeonemertean adults have a distinct apical brush of stiff cilia, as also occurs in the planuliform larva of *Carinoma* cf. *tremaphoros*, along with the apical cirrus.

Based on light microscopic studies, the larval ectoderm of palaeonemertean species such as *Procephalothrix simulus* and *P. filiformis*, *Tubulanus punctatus* (Iwata, 1960a), *Callinera* sp. (Jägersten, 1972), and *Procephalothrix spiralis* (JLN, unpublished observations) is apparently syncytial. In some cases, this ectoderm appears to include large vacuolar or fissure-like spaces (Iwata, 1960a). Five species of hoplonemerteans have been reported to shed their larval epidermis: *Carcinonemertes carcinophila* (van Beneden, 1861), *Emplectonema gracile* (Delsman, 1915), *Prostoma graecense* (Reinhardt, 1941), and *Argonemertes* (= *Geonemertes*) *australiensis* (Hickman, 1963). In addition, Dieck (1874) described a 'cephalothricid' larva (probably a *Carcinonemertes*, cf. Coe, 1943; a hoplonemertean, rather than the presumed palaeonemertean), being observed under a coverslip, as shedding bits of a thin ciliated larval epidermis, revealing fully ciliated epidermis. Maslakova and Malakhov (1999) reported that in the hoplonemertean *Tetrastemma candidum*, the larval ectoderm is resorbed and replaced by intercalation of mesodermally derived epidermis, relatively late in embryogenesis (i.e., the proboscis and its sheath, nervous system, and gut rudiments are already differentiated). The authors termed this a 'hidden larva' and viewed the putative loss of the apical plate and larval ectoderm as a form of metamorphosis (Maslakova and Malakhov, 1999). Maslakova (personal communication) notes that Lebedinsky (1989: figures 94–96, p. 103) illustrated essentially the same process for a polystiliferan hoplonemertean, *Drepanophorus spectabilis*. Although the other authors mentioned above described shedding of epidermis, Maslakova and Malakhov (1999) inferred that these several instances may be homologous and concluded that a hidden larva may be the rule in hoplonemerteans. No evidence was found for a secondary larval epidermis in either the Japanese worm referred to as *Emplectonema gracile* (Iwata, 1960a) or in ultrastructural studies of *Carcinonemertes epialti*

(Stricker and Reed, 1981). However, the latter studies focused on hatched larvae, which may already have passed the critical stage of ectoderm reorganization. Thus, further analyses of the larval ectoderm in both palaeo- and hoplonemerteans are required. In any event, a definitive epidermis develops in planuliform larvae and differentiates progressively more glandular cells as the larvae age.

Ocelli are common in palaeo- and hoplonemertean larvae (Figure 7.1A,B,D,E, even in species whose adult lacks evident ocelli (Iwata, 1960a; Jägersten, 1972; JLN, unpublished observations). The ocelli of palaeonemertean larvae are intra- or subepidermal (Iwata, 1960a; JLN, unpublished observations), as they are in the adults. The ocelli of hoplonemertean larvae and adults are submuscular (Stricker and Reed, 1981; JLN, unpublished observations), and when present in larvae, they rarely are lost in adults. *Ototyphlonemertes*, a group of mesopsammic species characterized by the presence of statocysts, lack ocelli as adults, but at least some species have a planktonic larva with ocelli and statocysts (cf. Jägersten, 1972; Chernyshev, 2000). Ocelli are usually present as an anterolateral pair in palaeo- and hoplonemertean planktonic larvae. A single darkly pigmented group of cells, interpreted as an ocellus, also occurs medially at the anterior margin of the mouth in larvae of the palaeonemertean *Carinoma* cf. *tremaphoros* (Figure 7.1A), which lacks adult ocelli (JLN, unpublished observations). In pilidia, ocelli occur only in the developing juveniles of species that have ocelli as adults (Cantell, 1969).

Pilidia and related larvae lack nephridia until these are formed in the juvenile, as reported for *Micrura akkeshiensis* (Iwata, 1958). It is not known when the nephridia of palaeo- and hoplonemertean larvae develop.

Although all adult nemerteans have an anus, and its presence has been of central importance in discussions of nemertean evolution, little is known about timing of anus formation in planuliform larvae (Jägersten, 1972) or pilidial juveniles (Cantell, 1969). An anus is not evident in planuliform larvae until the other adult structures such as cerebral ganglia and proboscis are clearly differentiated (Jägersten, 1972; JLN, unpublished observations).

Pilidium

The helmet-shaped pilidium (Figures 7.2–4) has a domed cap, or episphere, with a dorsal apical plate and a ventral mouth surrounded by a broad oral field (Figure 7.2B). The cirrus-bearing apical plate of the pilidium can be partially retracted into the episphere by a well-developed strand of larval musculature (Cantell, 1989). The cavity within the episphere is the remnant of the blastocoel and is filled with a viscous, fluid-like extracellular matrix (JLN, unpublished observations) that

contains mesenchymal cells, muscles, and nerve fibers (Lacalli and West, 1985).

The larval gut is a blind-ended sac that projects dorsally from the stomodeum and resides within the episphere. In well-developed larvae, the anterior and posterior poles of the episphere, which are situated perpendicular to the animal-vegetal axis of the embryo, extend slightly to form an anterior and a posterior lobe. In addition, the lateral margins of the episphere descend below the level of the mouth as a pair of distinct lateral lobes. The larva is bilaterally symmetric, so that the lateral lobes are mirror images. However, the shapes of the anterior and posterior lobes are more or less independent of each other. Variation in the shape of the episphere and the four lobes creates a wide range of morphological diversity in pilidium larvae (Figures 7.2-4). These have been grouped or classified into varieties, such as *gyrans*, *magnum*, *pyramidale*, *recurvatum* (Figure 7.4), each of which represented a species according to Bürger (1895). Schmidt (1931) and Dawydoff (1940) recognized these as morphotypes that could encompass groups of species. Several varieties of pilidia and their juvenile forms were extensively studied by Cantell (1969), who viewed some morphotype groupings as lumping together species from different families. However, the current taxonomy of heteronemerteans, which is based on adult structures, appears to be highly artificial and an unreliable guide to species relationships, so that species presently allocated to different genera or families may actually belong together (Norenburg, 1993; unpublished observations). Ultimately, it is synapomorphies among the pilidial structures, not overall appearance, that must determine the phylogenetic informativeness of pilidial anatomy. Despite these caveats, the list of pilidial types and associated species presented by Friedrich (1979) appears to reflect phylogenetic relationships as well as many traditional morphological characters are able to do (JLN, unpublished observations).

The larval ectoderm of pilidia forms the covering of the distinctively inflated episphere, within which the juvenile worm with its definitive adult epidermis eventually develops. In addition to the apical plate cells (Figure 7.3J), the larval ectoderm is regionally differentiated into thin, plate-like, multiciliated and glandular cells throughout the surface of the episphere (Cantell et al., 1982; Lacalli and West, 1985). The four lobes, on the other hand, have a margin that is thicker and of more complex composition. This margin bears a distinctive band of elongate cilia arising from multiciliated cells and innervated monociliated cells that are interspersed among the multiciliated cells (Lacalli and West, 1985). Nielsen (1987) showed that in at least two forms of pilidium, this ciliary band consists of an outer band of very long compound cilia lining the entire margin of the oral field (= ventral

margin of episphere) and an inner band of smaller cilia restricted to the lateral lobes (Figure 7.2B). The inner band is U-shaped and lies just medial to the marginal cilia of the lateral lobes while traversing the oral field behind the mouth (Figure 7.2B) (Nielsen, 1987). Nielsen (1987) speculated that pilidium larvae may be 'downstream' feeders that capture particles on the ciliary side opposite the source of flow, but he noted that unequivocal evidence for this view was lacking. The epidermis may also contain distinctive, more or less species-specific pigmented cells or chromatophores (e.g., Cantell, 1969), but these have yet to be studied in any detail. There seems to be no distinctive basal lamina underlying the larval epidermis of pilidia (Lacalli and West, 1985; JLN, unpublished observations). In fact, some of the glandular cells appear to secrete basally, presumably contributing to the viscous extracellular matrix that fills the blastocoel (JLN, unpublished observations). At least one pilidium has larval muscle fibers that are clearly cross-striated (Norenburg and Roe, 1998b), a feature known from palaeonemertean and polystiliferan hoplonemertean adult worms, but not from heteronemertean adults (Turbeville, 1991; Norenburg and Roe, 1998b).

The hallmark feature of pilidium larvae is development of the juvenile worm from a set of ectodermally derived invaginations surrounding the larval stomodeum, called the imaginal disks (Metschnikoff, 1869). There are usually seven disks: three bilaterally paired disks (cephalic, cerebral organ, and trunk disks) and one unpaired, posterior dorsal disk (Friedrich, 1979). The disks are primarily invaginations of the larval ectoderm into the blastocoel, and give rise to ectodermally derived adult structures (Henry and Martindale, 1997a). The portion of the disk that differentiates as adult epidermis becomes separated from the blastocoel lining (larval ectoderm) by a cavity, termed the amnion (Henry and Martindale, 1997a). The left and right cephalic disks meet medially as they enlarge (Figures 7.2A, 7.3B,D,F), and the proboscis begins to develop from that contact region. The proboscis, which is one of the first recognizable structures (Figures 7.2A, 7.3D,F), extends as a cord of tissue across the dorsal side of the larval gut, from the cephalic disks to the dorsal disk (JLN, unpublished observations). As the left and right trunk disks grow, they fuse with the developing dorsal disk. The cerebral organ disks of pilidia differentiate primarily as cerebral organs, whereas in the modified larva of *Micrura akkeshiensis*, the cerebral organ disks are attached to the stomodeum until the cephalic disks come in contact with them (Iwata, 1960a). In pilidium larvae, the fused cephalic and trunk + posterior disks gradually enclose the cerebral organ disks and the proboscis, together with the larval gut and some of the adjacent blastocoel (Friedrich, 1979). The amniotic spaces fuse when the epidermal tissues of adjacent disks come into

contact, eventually forming a single cavity, with the stomodeum becoming the only point of attachment between larval body and juvenile. The larval gut gives rise to the juvenile digestive system, with the blastopore becoming the boundary between foregut (= stomach) and intestine (Iwata, 1960a). The anterior-posterior axis of the juvenile worm is usually at 90° to the larval anterior-posterior axis. The pilidium may continue to feed in the plankton for some considerable time after the juvenile has formed (Cantell, 1989). Metamorphosis consists of the juvenile breaking out of the larval body and often includes ingestion of the larval body (Cantell, 1969), which may be the most effective means of severing the tissue connection at the stomodeum.

Heteronemerteans also produce three types of pilidium-like larvae. Each has recognizable imaginal disks, although these differ in details of number and development (Friedrich, 1979). These are Desor's, Schmidt's, and Iwata's larva, from *L. viridis*, *L. ruber*, and *M. akkeshiensis*, respectively. The first two larvae are encapsulated and lack a planktonic phase, whereas the third is planktonic. Desor's and Iwata's larva are clearly lecithotrophic, although their respective egg sizes, 300–400 µm and 170 µm, differ substantially (Henry and Martindale, 1997a). Schmidt's larva has been considered a variant of Desor's larva (Jägersten, 1972), but the egg of *L. ruber* egg is 250 µm and the larvae consume neighboring abortive eggs (Friedrich, 1979). It seems almost self-evident that all three are modified pilidium larvae (see also Friedrich, 1979; Cantell, 1989) of species that are primarily littoral. Parallel larval modification occurs in a variety of littoral invertebrates, and although encapsulation may be interpreted as an adaptation to environmental extremes (Cantell, 1989 and references therein), adverse conditions are only a concern once the larva is non-planktonic. For example, avoidance of dispersal to adverse habitats seems a more likely proximate selective pressure for the Desor's and Schmidt's larvae. The typical pilidium is an obvious dispersal mechanism and is recognized as such by most authors. Iwata (1958) implicitly argued for an evolutionary progression from a Desor larva stage, through an Iwata larva stage, to a planktotrophic pilidium. Jägersten (1972) argued that the reverse is more plausible, while recognizing that these extant larvae are only representative of ancestral forms.

Although pilidium larvae are characteristic of the order Heteronemertea, Cantell (1969) noted that an *auriculatum* type of pilidium was produced by *Hubrechtella dubia*, a supposed palaeonemertean. In fact, Hylbom (1957) had proposed that some morphological traits of adult *H. dubia* placed this species in an intermediate grade between some palaeo- and heteronemerteans. Cantell (1969) recognized two possible interpretations of the available information: (1) the pilidium is primitive

for the phylum, or (2) *H. dubia* is a heteronemertean that has lost a key heteronemertean character, the outer longitudinal body-wall musculature. Morphology-based cladistic analysis of the phylum provides little support for the first hypothesis. However, it strongly supports a sister-group relationship between the Heteronemertea (*sensu lato*) and *Hubrechtella*, without necessarily requiring loss of an outer longitudinal musculature (JLN, unpublished observations). *Hubrechtella dubia* provides an additional interesting anecdote in this context. Eight of the approximately 10 described species of *Hubrechtella* have been found only in tropical or sub-tropical waters, whereas *H. dubia* and *H. typica* occur in the decidedly non-tropical waters off Scandinavia. One of the most common palaeonemerteans off southern Florida and in the Caribbean Sea is a species that is morphologically indistinguishable from *H. dubia* (JLN, unpublished observations). The coincidence of an apparently anomalous Scandinavian distribution of *H. dubia* and proximity of the Gulf Stream give cause to contemplate potential phylogeographical connections.

CONCLUDING COMMENTS

The nature of the pilidium and the diversity of its morphology make it one of the outstanding examples of evolution in the biphasic, pelago-benthic life cycle as envisioned by Jägersten (1972). However, where the pilidium fits into evolution of nemerteans remains speculative or controversial. Jägersten (1972) concluded that the pelago-benthic life cycle is plesiomorphic for the phylum and has been retained as the plesiomorphic condition in all three major nemertean groups, with the pelagic phase of heteronemerteans having diverged most dramatically from the ancestral state. No strong evidence exists at present for or against this proposition. There is now ample evidence that palaeonemerteans constitute a paraphyletic assemblage encompassing both the hoplo- and heteronemerteans, although the exact branching patterns are not necessarily stable or consistent (JLN, unpublished observations). For the pilidium to be plesiomorphic for the phylum, loss of a pilidium would have to occur several times, resulting in a convergent planuliform larva each time. Although there is compelling evidence that nemerteans may share a most recent common ancestor with mollusks and annelids (Turbeville et al., 1992; Winnepeninckx et al., 1995), there are no definitive homologies and no clearly recognized synapomorphies between pilidia and the planktonic larvae of other protostome groups. Pilidium development is fascinating in its own right, and clearly invites exploration of barely illuminated major avenues of research. However, there is no compelling evidence to view pilidia or their development as an ancestral model for nemerteans. Rather, palaeone-

merteran planuliform larvae seem to be the preferred candidates for addressing questions pertaining to direct versus indirect development in protostome evolution and for understanding evolution of nemertean larvae.

Anecdotal observations on feeding by the planuliform larva of *Carinoma* cf. *tremaphoros* from southern Florida are worth reporting in this context (JLN, unpublished observations). The larva has a broadly rounded anterior end and tapers to a narrow posterior. The oral surface tends toward concave, with an oral furrow evident along the middle one-third of the anteroposterior midline of the ventral surface of the body (Figure. 7.1A). When the larva feeds on moving microplankton it sometimes flattens and extends the body margin on each side of the mouth to a sufficient degree to form what might be called pseudo-lappets. If this slight change in the oral field affords increased capture efficiency, one can envision rapid selection for larger lappets; i.e., this may be a key innovation permitting a new level of exploiting the pelagic life style. Increasing feeding efficiency permits or promotes an increasing duration of the planktotrophic phase via selection for an inflated larval morphotype, much as is found in other groups with long planktotrophic phases. Inflating the body can be achieved by: (1) more or less expanding the whole body, which then gets mostly incorporated into the adult morphology, as in most annelids and mollusks; or (2) hypertrophy of small populations of cells, in this case those surrounding the apical plate and perhaps the oral region. Option (2) could result in the differentiating tissues of the prospective adult becoming gradually pulled apart as the larva increases in size. Concurrently, various cell-cell and tissue-specific pathways of developmental 'communication' stay intact, albeit somewhat stretched in places, so that everything comes together properly as the imaginal disks meet. Clearly, in the absence of real data, there still is room for much speculation and further investigations in nemertean development.

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FIGURE 7.1

Planuliform larvae of palaeonemerteans and hoplonemerteans

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- B.** Dorsal view of *Cephalothrix* sp. (Palaeonemertea.) Planuliform larva from shallow plankton off Fort Pierce, Florida, November, 1982. Scale bar: 20 μ m.
- C.** Palaeonemertean, almost fully formed juvenile worm (with lateral sensory organs masked by pigment band.) Found in shallow plankton, December, 1982. Scale bar: 100 μ m.
- D.** Monostiliferan 1 (Hoplonemertea.) Swimming larva/juvenile, gut filled with yolk, all adult structures except gonads differentiated; from shallow plankton off Fort Pierce, Florida, March, 1983. Scale bar: 100 μ m.
- E.** Monostiliferan 2 (Hoplonemertea.) Swimming larva/juvenile, gut partially filled with yolk, all adult structures except gonads differentiated; from shallow plankton off Fort Pierce, Florida, March, 1983. Scale bar: 100 μ m.
- F.** *Carcinonemertes epialti* (Hoplonemertea.) Scanning electron micrograph (SEM) of newly hatched larva. Scale bar: 50 μ m (Scanning electron micrograph reproduced with permission from Stricker and Reed, 1981.)

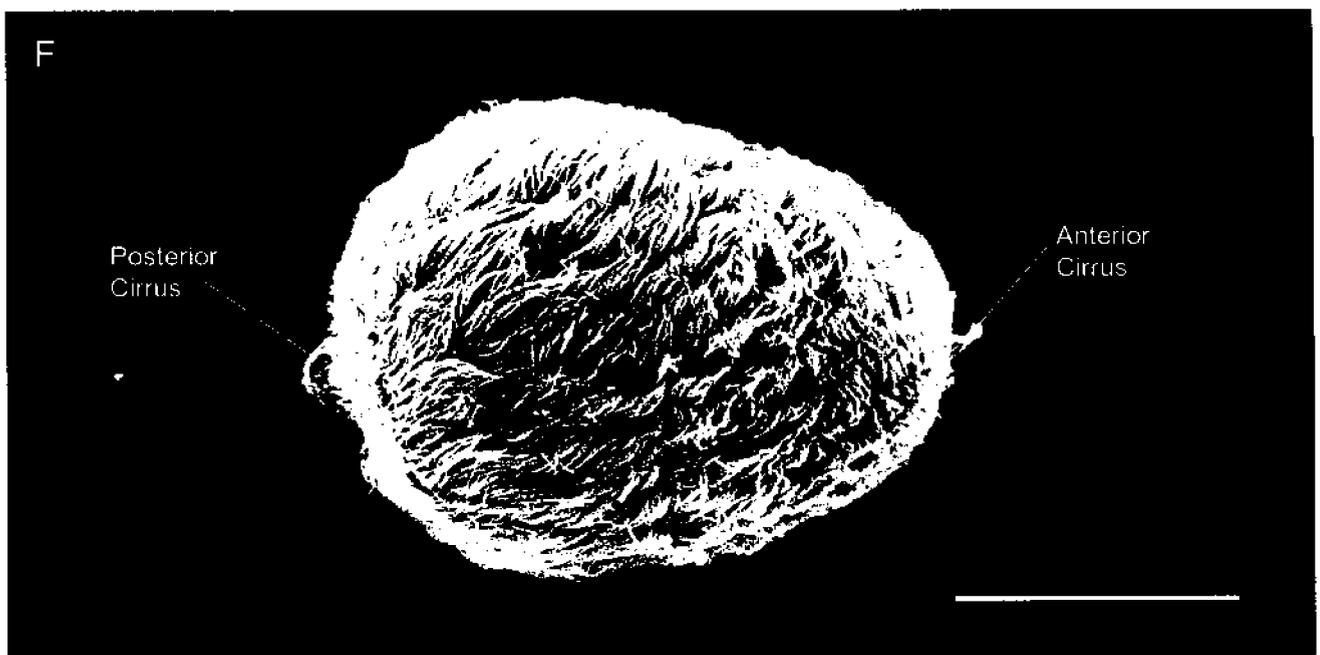
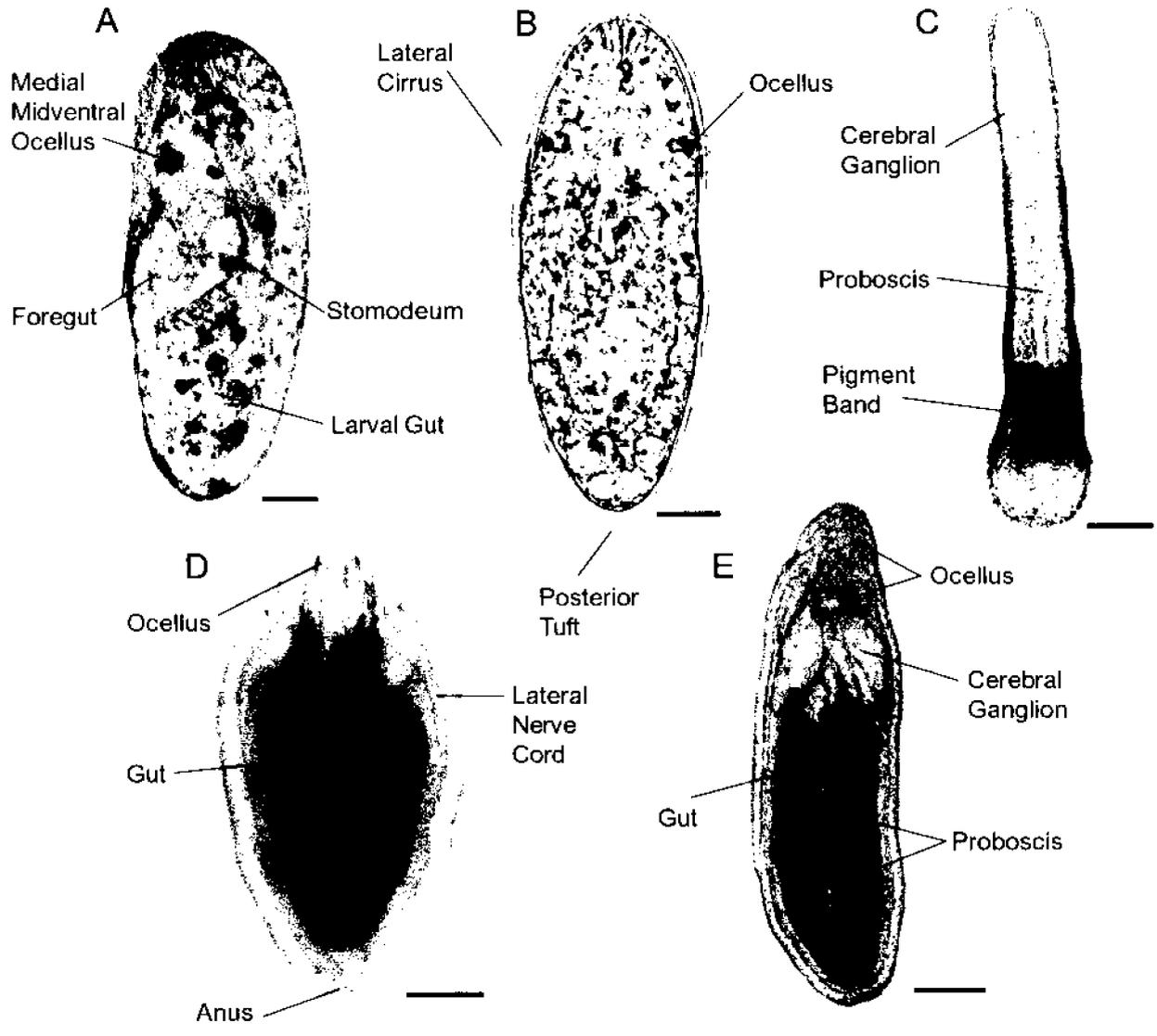
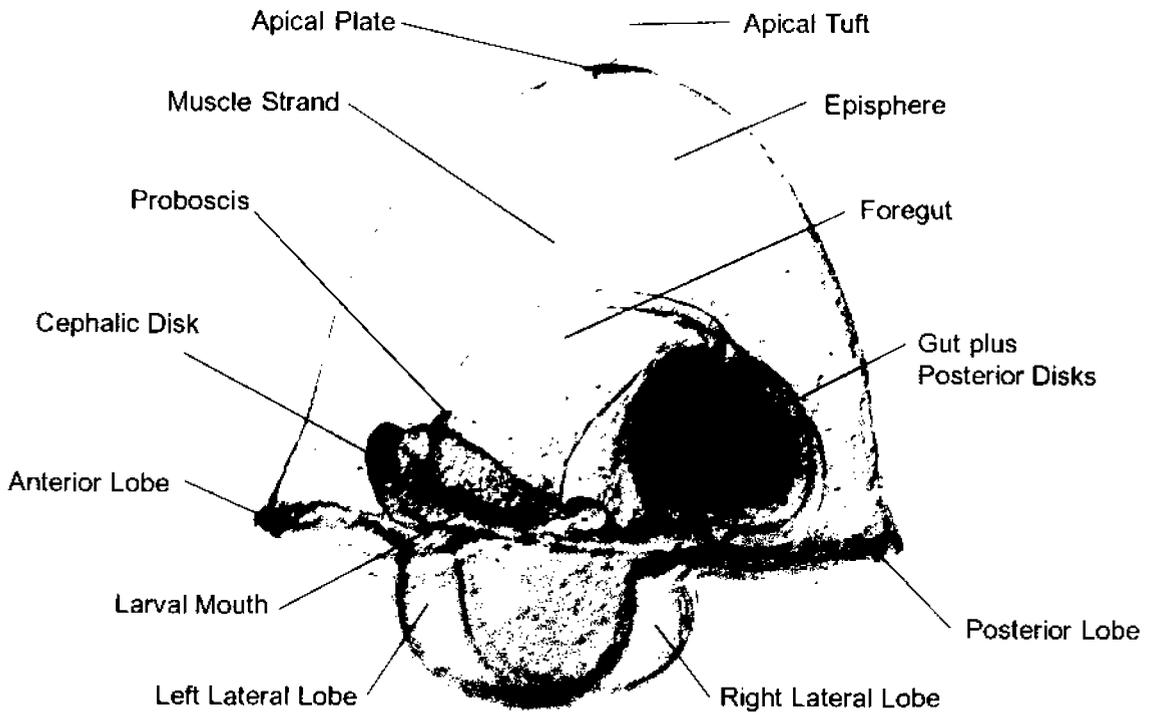


FIGURE 7.2

Anatomy of pilidium larvae (Heteronemertea)

- A. Unidentified heteronemertean larva from the plankton in the Northeast Pacific. Scale bar approximately 50 μm . (Photograph by Russel L. Zimmer.)
- B. Ventral surface of a pilidium larva. Scale bar: 50 μm . (Scanning electron micrograph by Claus Nielsen.)

A



B

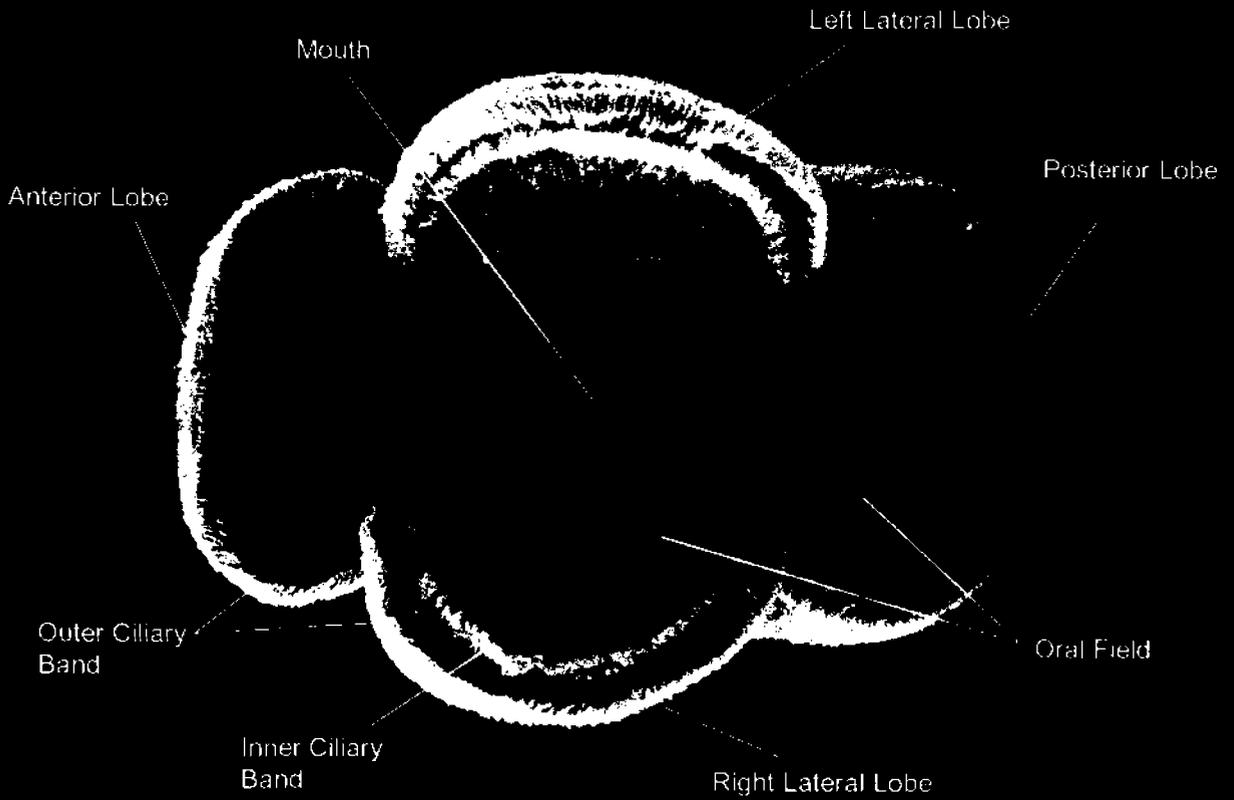
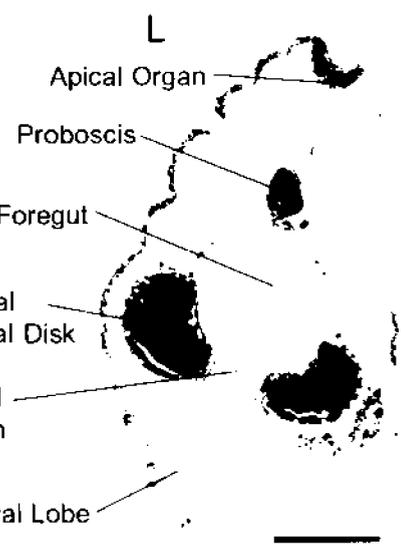
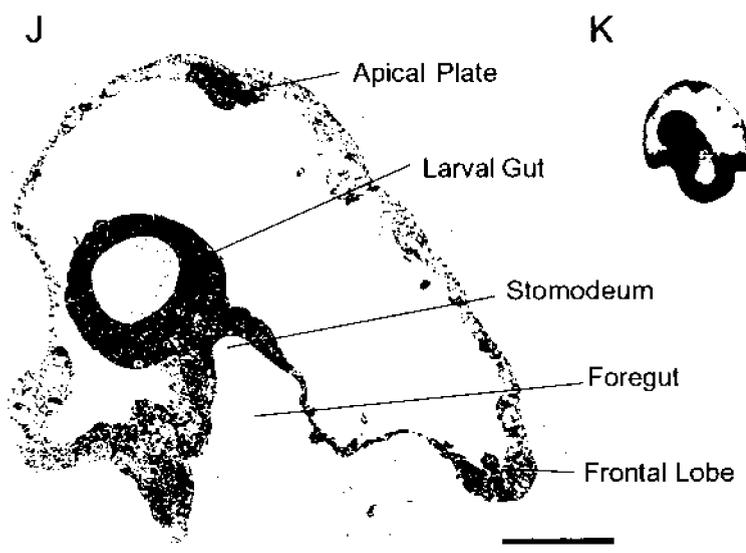
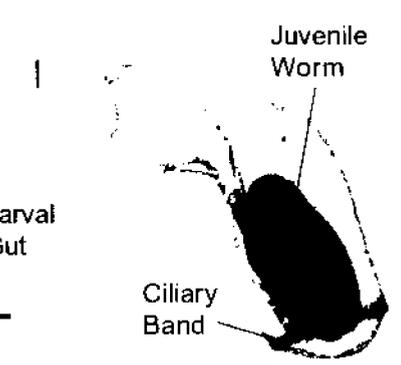
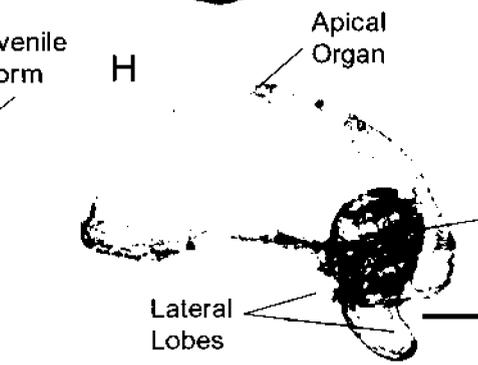
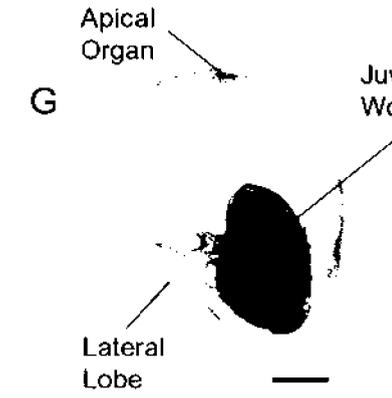
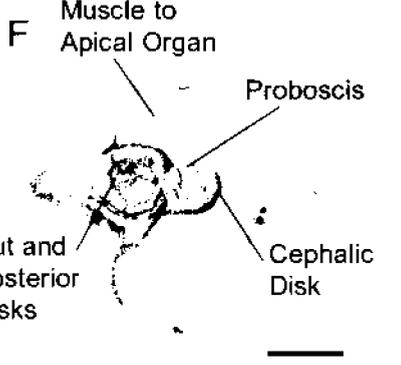
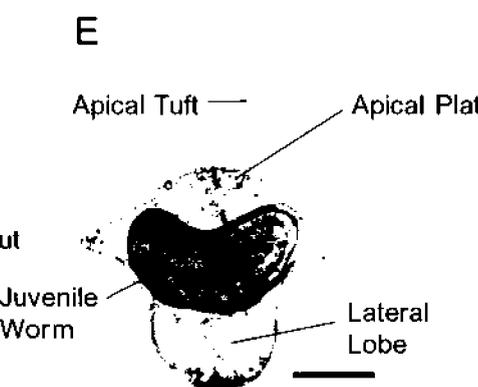
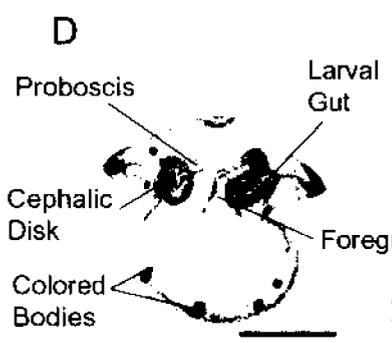
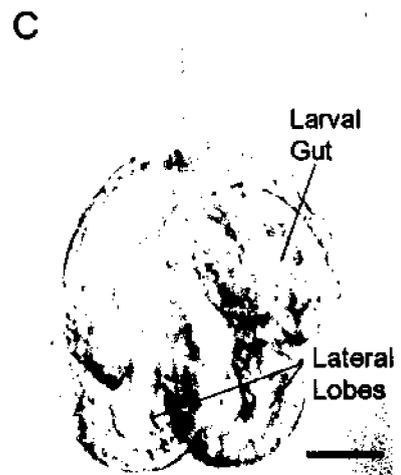
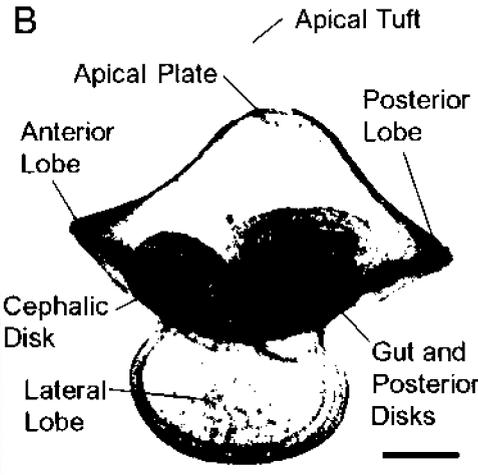
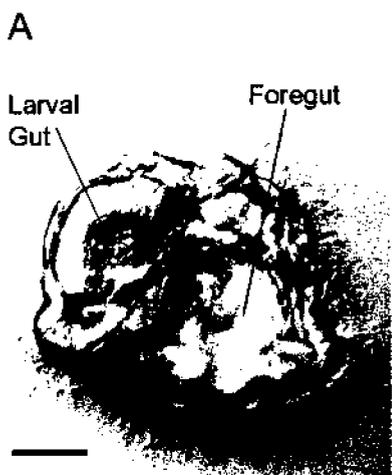


FIGURE 7.3

Diversity of pilidia

- A. Four-day-old pilidium larva of *Cerebratulus lacteus* (Heteronemertea.) Scale bar: approximately 25 μm . (Photograph by S.A. Stricker.)
- B. Unidentified pilidium from the plankton at Friday Harbor, Washington. Scale bar: 100 μm . (Photograph by Craig M. Young.)
- C. Five-day-old pilidium of *Micrura alaskensis* (Heteronemertea.) Scale bar: approximately 25 μm . (Photograph by S.A. Stricker.)
- D. Unidentified heteronemertean pilidium. Note that posterior disks are not distinguishable from the larval gut. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- E. Heteronemertean pilidium. Note large juvenile and elongate cilia along the margin of lateral lobe. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- F. Heteronemertean pilidium. Scale bar: 100 μm . (Photograph by Russel L. Zimmer.)
- G. Pilidium larva (Palaeonemertea), probably member of *Hubrechtella* sp. collected from Gulf Stream plankton off Fort Pierce, Florida. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- H. Pilidium (Heteronemertea.) Note outlines of large, flat epithelial cells. From shallow plankton off Fort Pierce, Florida. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- I. Pilidium larva of recurvatum type (Heteronemertea.) Scale bar: 100 μm . (Reproduced with permission from Cantell, 1966.)
- J. Mid-sagittal section of a pilidium larva, approximately along the larval dorsoventral axis. Scale bar: 50 μm . (Photograph by Thurston Lacalli.)
- K. Pilidium larva sectioned in J. (Photograph by Thurston Lacalli.)
- L. One-micrometer plastic section through a pilidium larva. Mid-frontal section approximately along larval dorsoventral axis. Scale bar: 60 μm . (Photograph by J.L. Norenburg.)



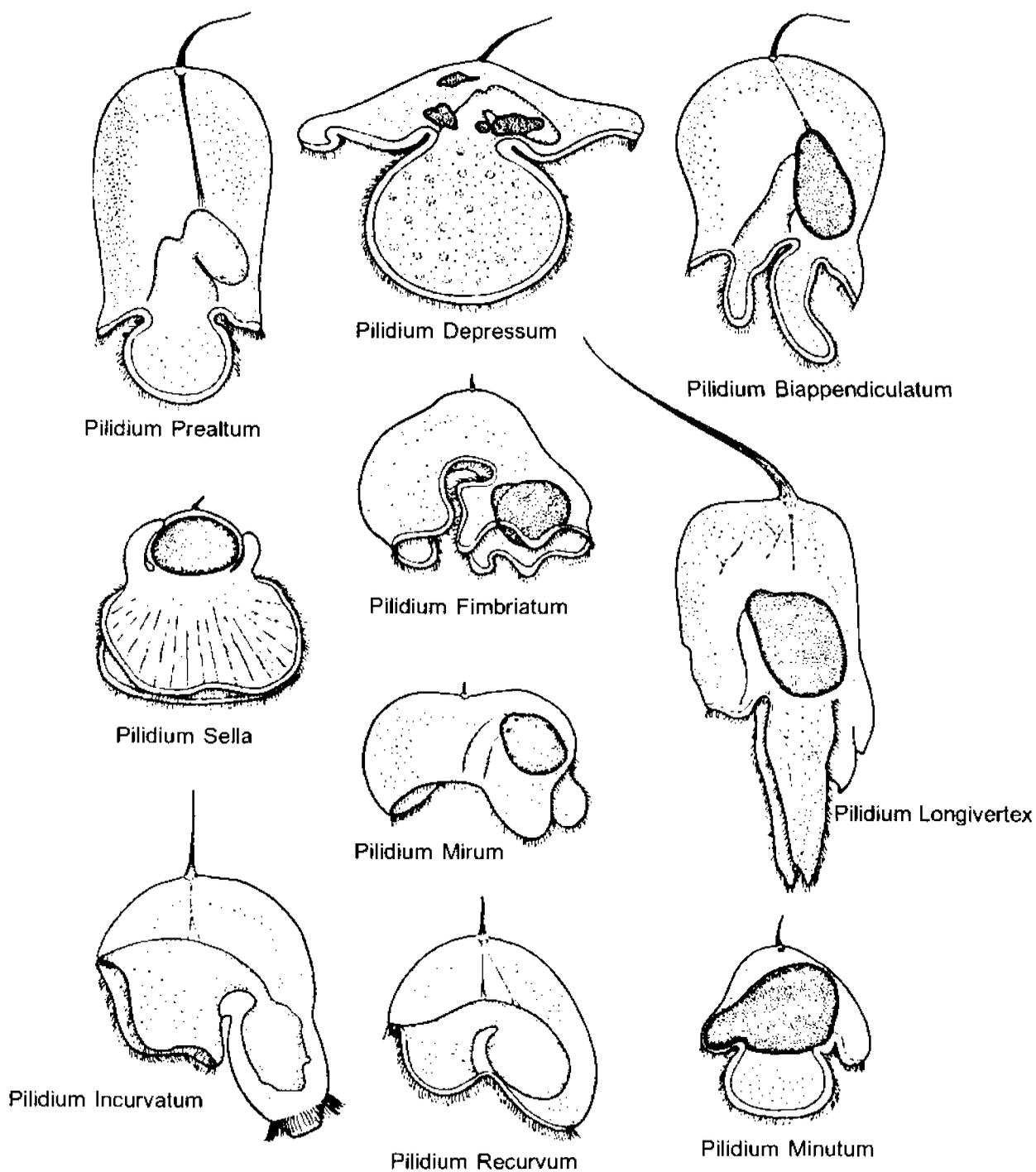


FIGURE 7.4

Classification scheme for various forms of pilidium larvae

Note that the names are not species, but refer to the forms of the larvae only. (Reproduced with permission from Jägersten, 1972.)

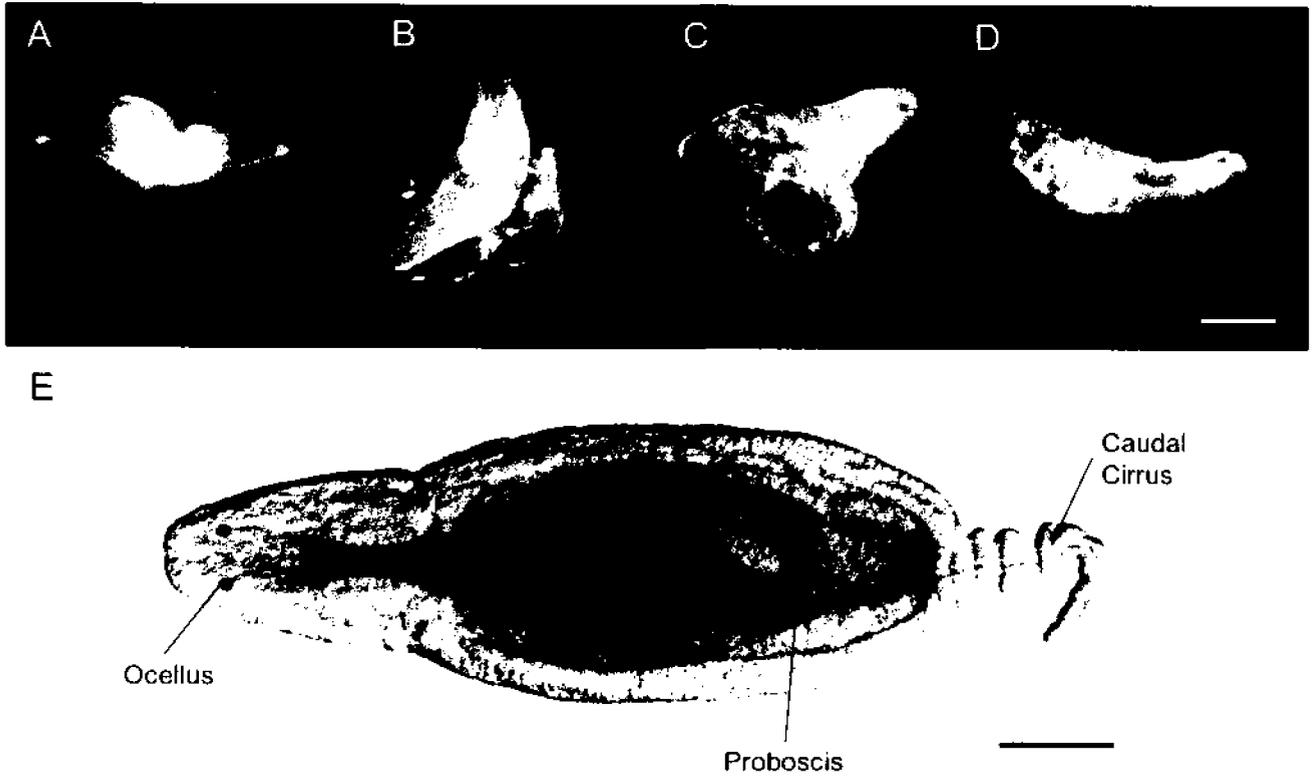


FIGURE 7.5

Pilidium larva (Heteronemertea) showing 'metamorphosis' and juvenile

A–D. Sequence showing metamorphosis of a pilidium larva. Scale bar: approximately 100 μm .
(Copyrighted photographs by Thurston Lacalli.)

E. Juvenile heteronemertean with caudal cirrus, immediately after metamorphosis. Scale bar:
approximately 30 μm . (Photograph by Russel L. Zimmer.)

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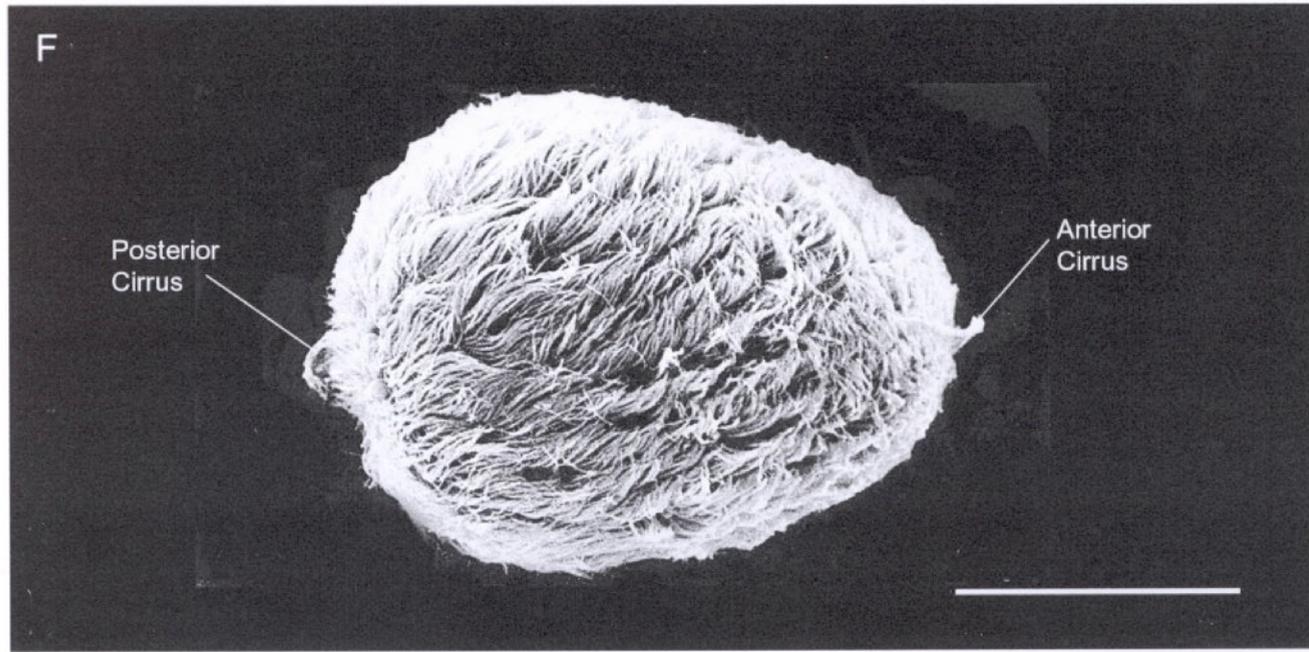
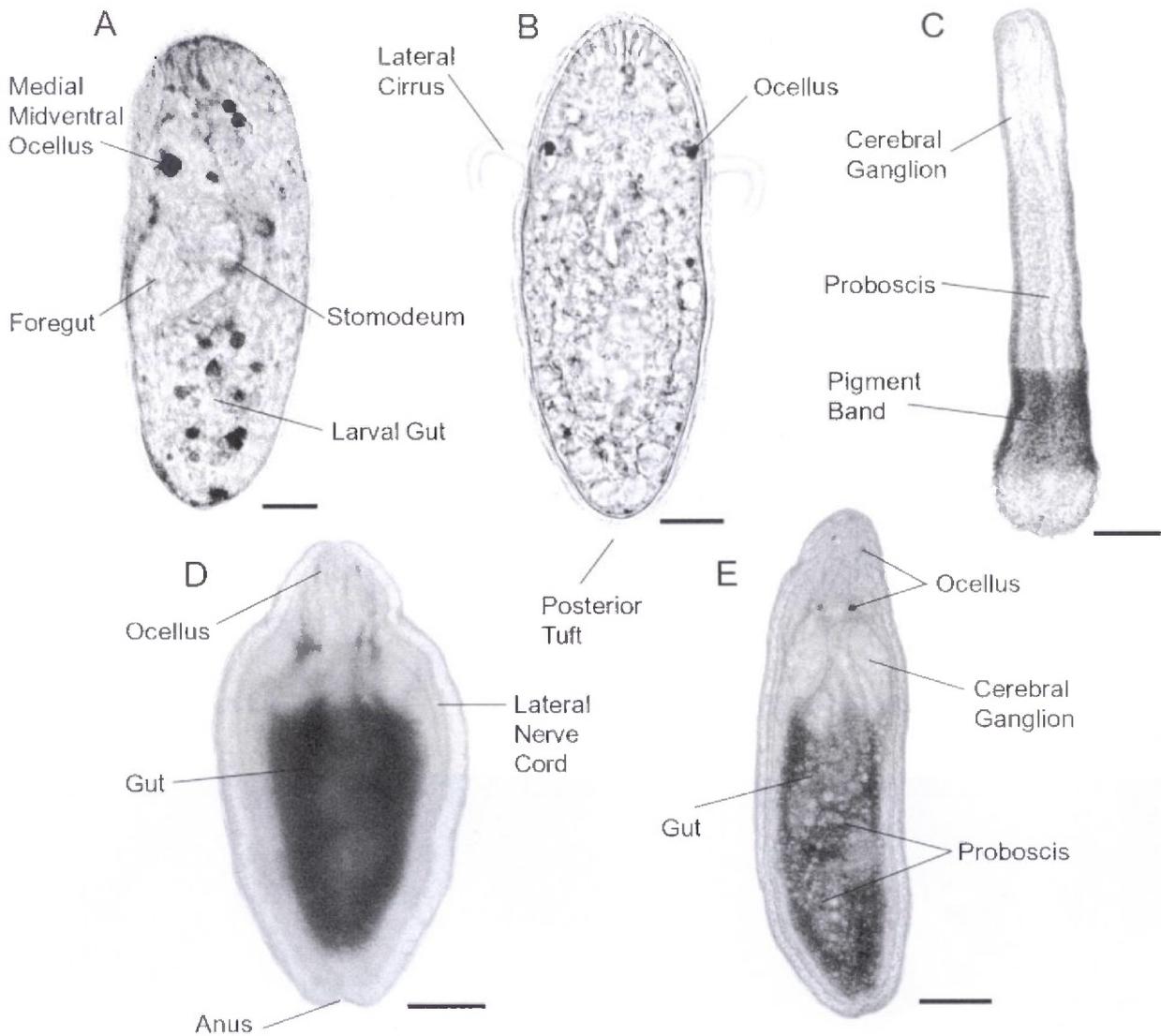
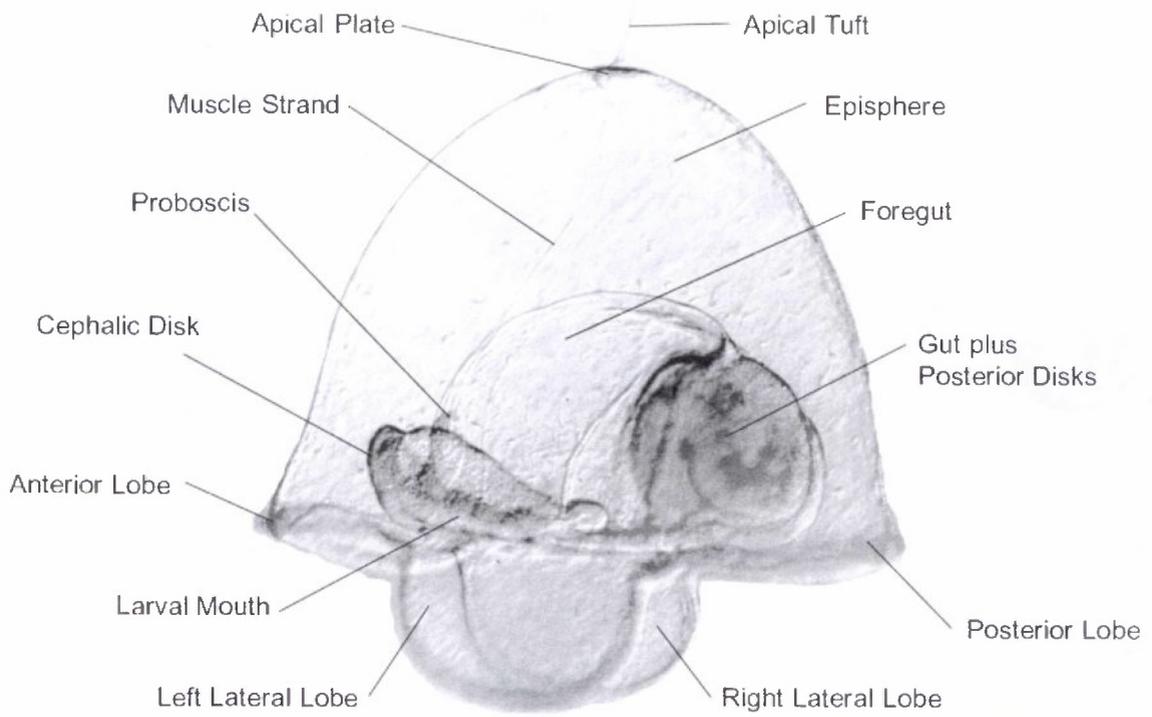


FIGURE 7.2

Anatomy of pilidium larvae (Heteronemertea)

- A. Unidentified heteronemertean larva from the plankton in the Northeast Pacific. Scale bar approximately 50 μm . (Photograph by Russel L. Zimmer.)
- B. Ventral surface of a pilidium larva. Scale bar: 50 μm . (Scanning electron micrograph by Claus Nielsen.)

A



B

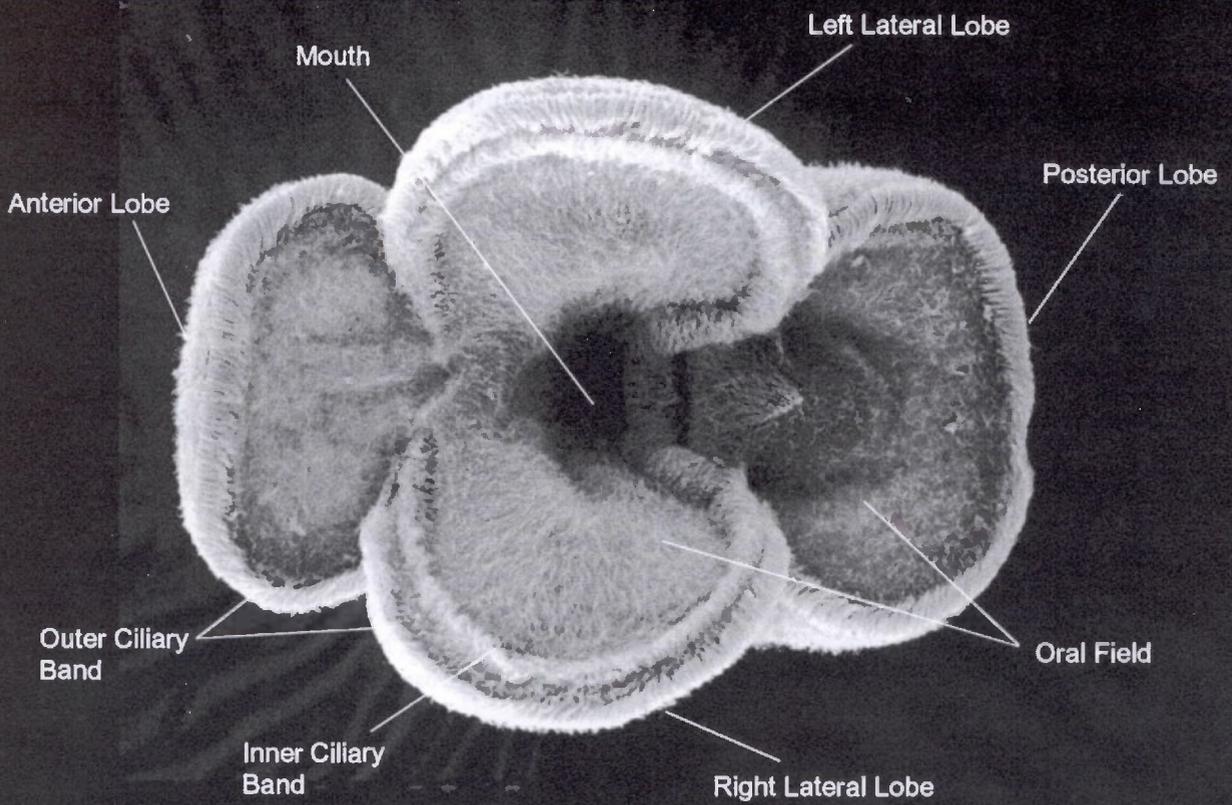
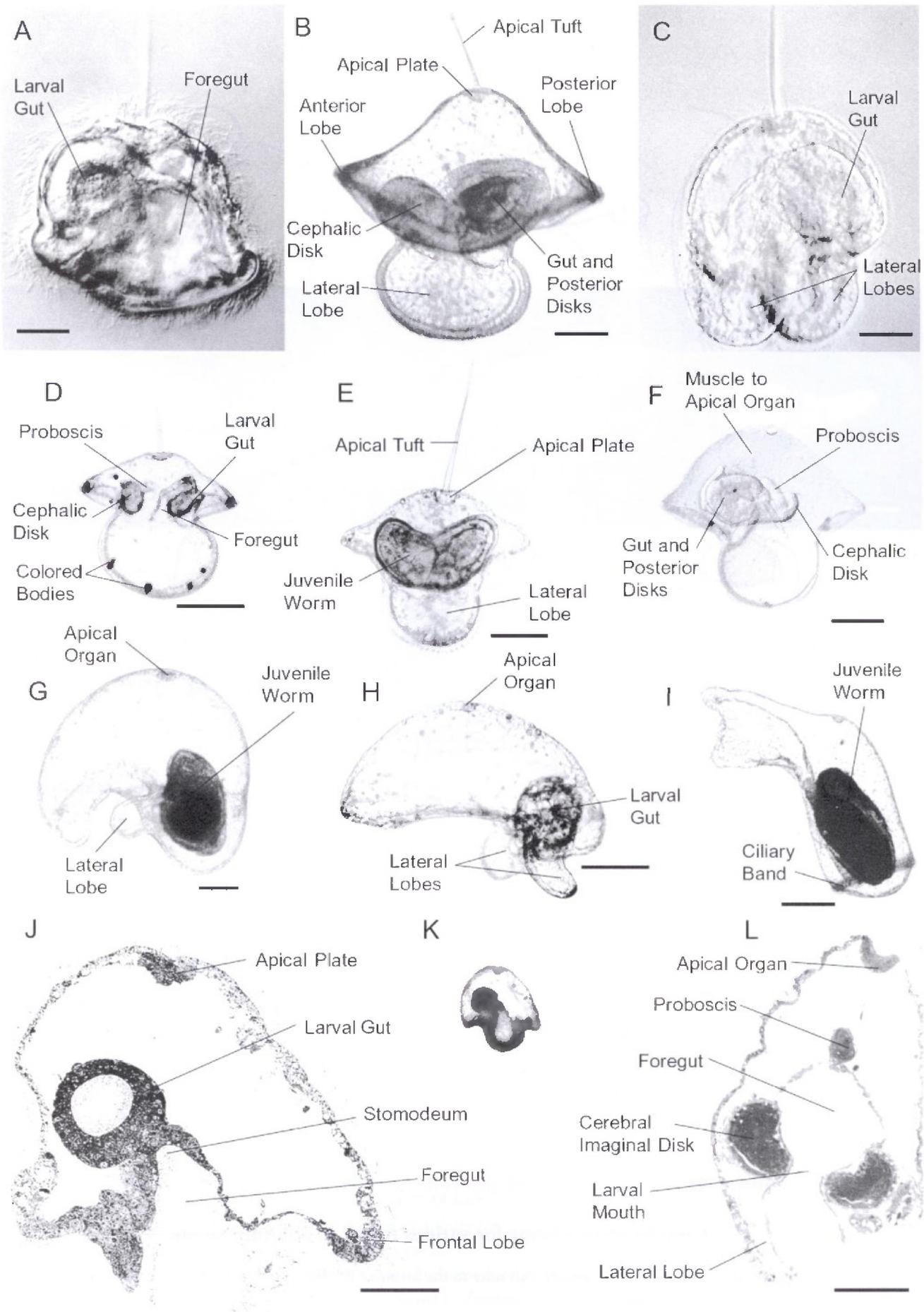


FIGURE 7.3

Diversity of pilidia

- A. Four-day-old pilidium larva of *Cerebratulus lacteus* (Heteronemertea.) Scale bar: approximately 25 μm . (Photograph by S.A. Stricker.)
- B. Unidentified pilidium from the plankton at Friday Harbor, Washington. Scale bar: 100 μm . (Photograph by Craig M. Young.)
- C. Five-day-old pilidium of *Micrura alaskensis* (Heteronemertea.) Scale bar: approximately 25 μm . (Photograph by S.A. Stricker.)
- D. Unidentified heteronemertean pilidium. Note that posterior disks are not distinguishable from the larval gut. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- E. Heteronemertean pilidium. Note large juvenile and elongate cilia along the margin of lateral lobe. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- F. Heteronemertean pilidium. Scale bar: 100 μm . (Photograph by Russel L. Zimmer.)
- G. Pilidium larva (Palaeonemertea), probably member of *Hubrechtella* sp. collected from Gulf Stream plankton off Fort Pierce, Florida. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- H. Pilidium (Heteronemertea.) Note outlines of large, flat epithelial cells. From shallow plankton off Fort Pierce, Florida. Scale bar: 100 μm . (Photograph by J.L. Norenburg.)
- I. Pilidium larva of recurvatum type (Heteronemertea.) Scale bar: 100 μm . (Reproduced with permission from Cantell, 1966.)
- J. Mid-sagittal section of a pilidium larva, approximately along the larval dorsoventral axis. Scale bar: 50 μm . (Photograph by Thurston Lacalli.)
- K. Pilidium larva sectioned in J. (Photograph by Thurston Lacalli.)
- L. One-micrometer plastic section through a pilidium larva. Mid-frontal section approximately along larval dorsoventral axis. Scale bar: 60 μm . (Photograph by J.L. Norenburg.)



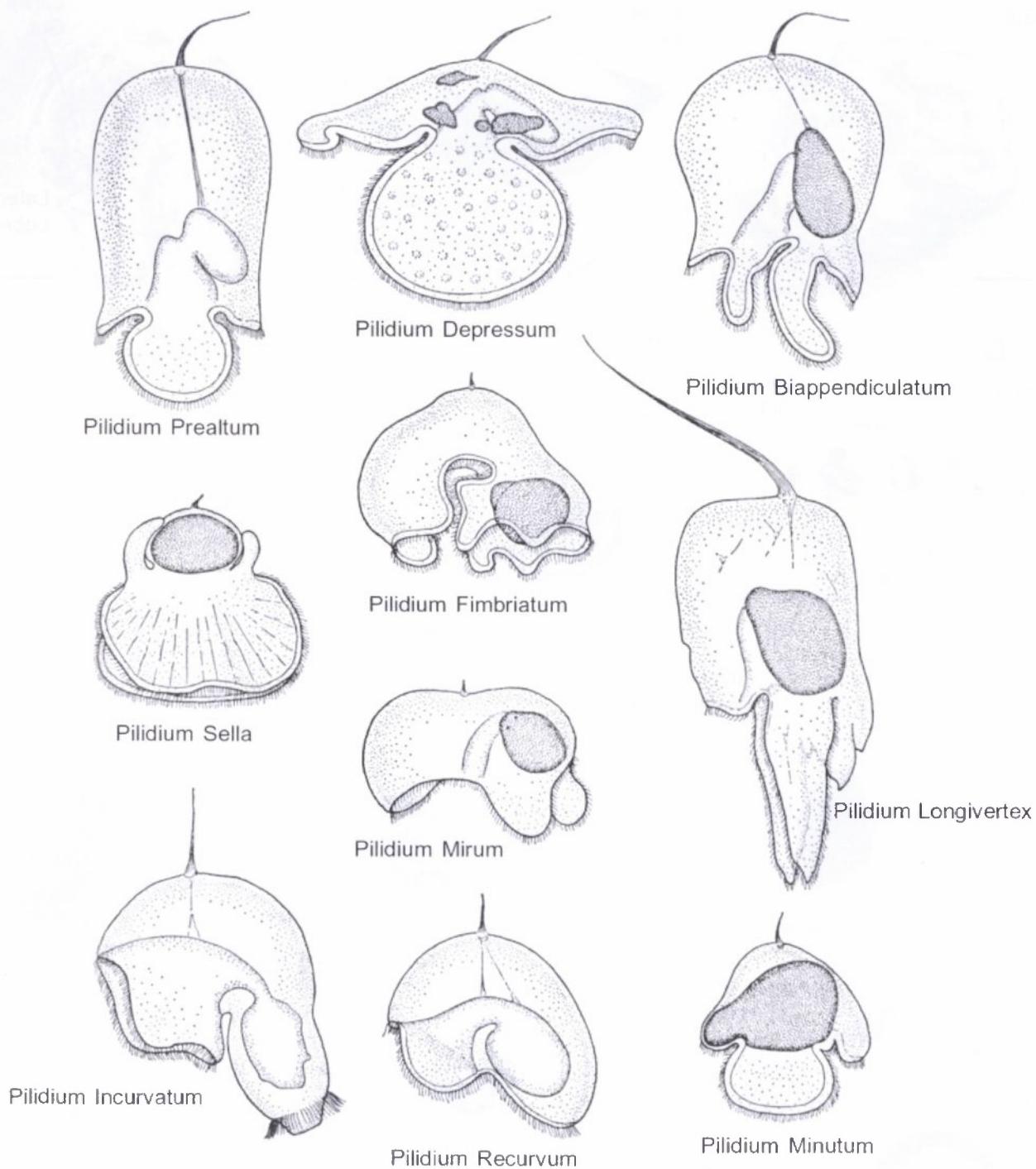


FIGURE 7.4

Classification scheme for various forms of pilidium larvae

Note that the names are not species, but refer to the forms of the larvae only. (Reproduced with permission from Jägersten, 1972.)

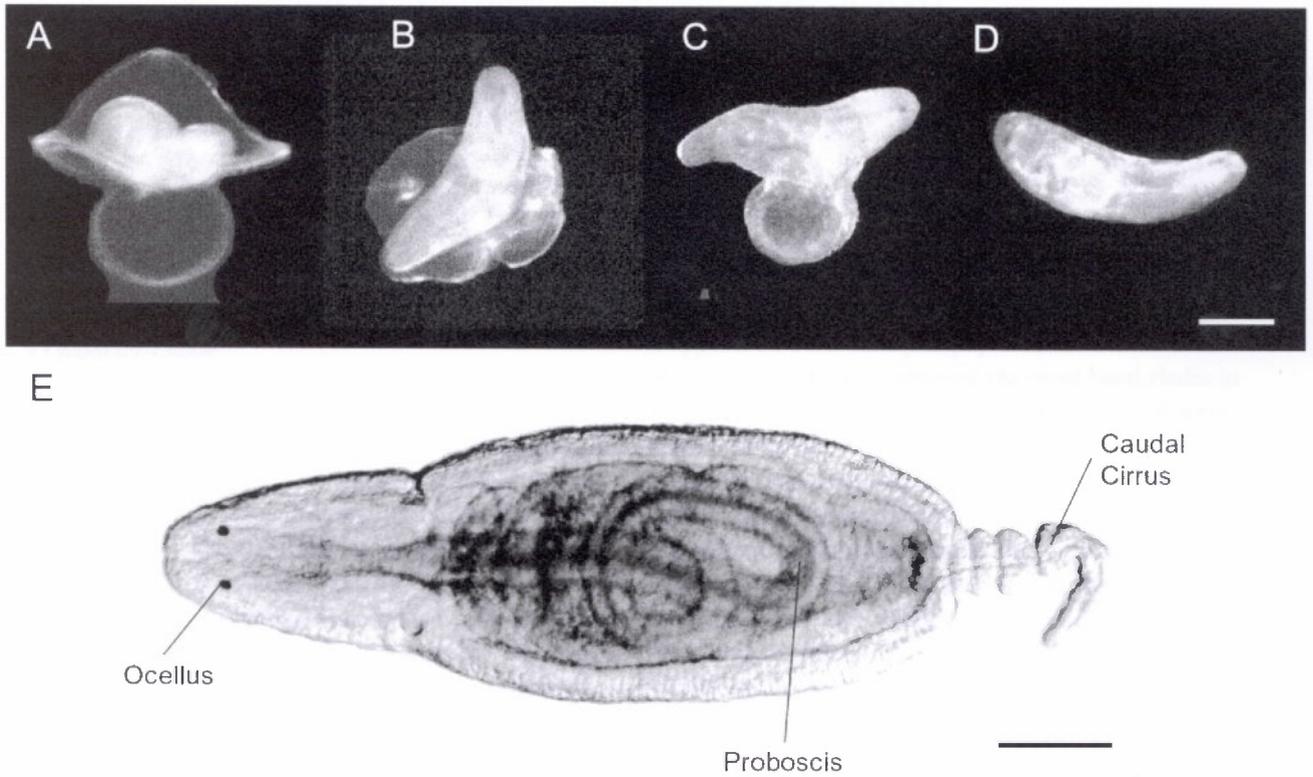


FIGURE 7.5

Pilidium larva (Heteronemertea) showing 'metamorphosis' and juvenile

- A–D. Sequence showing metamorphosis of a pilidium larva. Scale bar: approximately 100 μm . (Copyrighted photographs by Thurston Lacalli.)
- E. Juvenile heteronemertean with caudal cirrus, immediately after metamorphosis. Scale bar: approximately 30 μm . (Photograph by Russel L. Zimmer.)