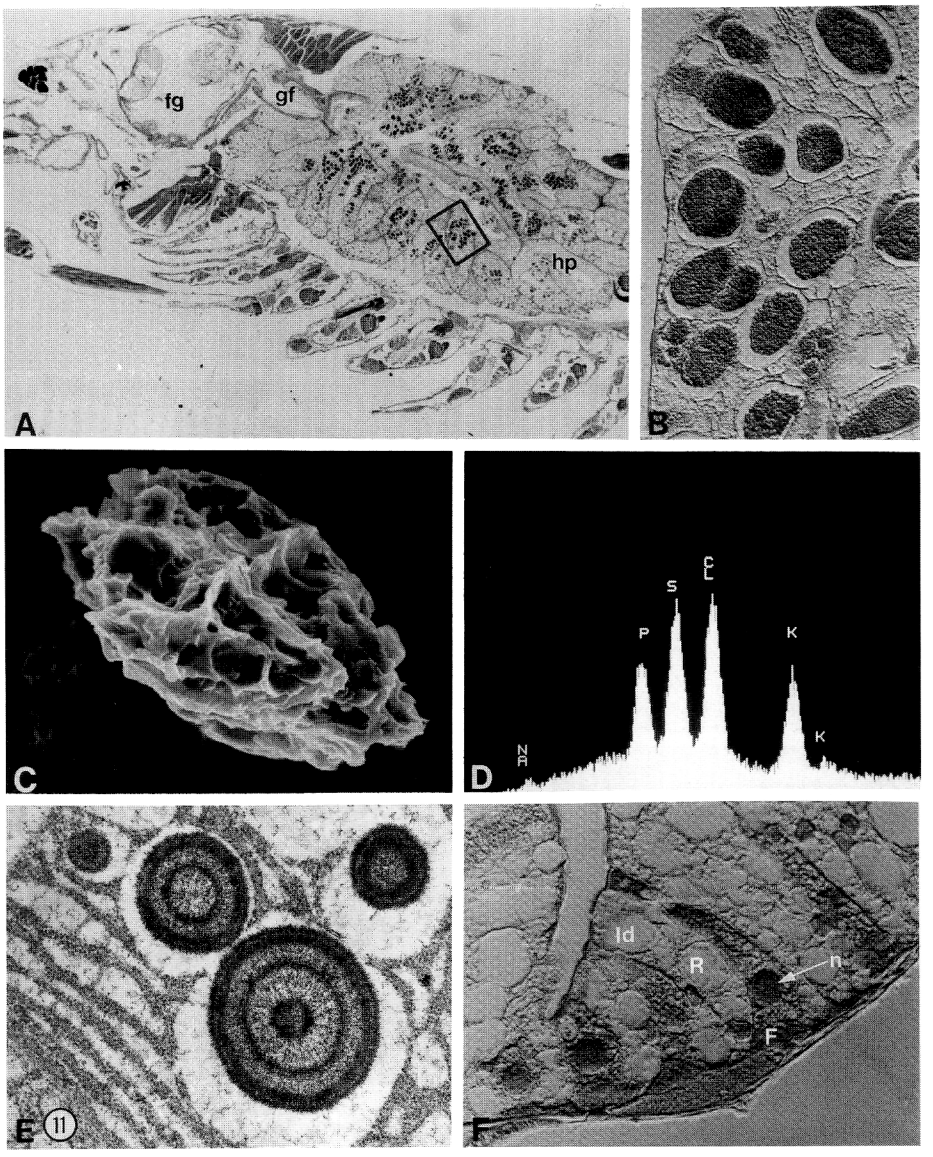

Fig. 11. Mineral inclusions of the decapod hepatopancreas. **A:** Sagittal histological section through the cephalothorax of *Procaris ascensionis;* black box indicates region of gland that harbors mineral inclusions. ×50. **B:** Close-up histological section of mineral inclusions within the R-cells (Nomarski image). ×500. **C:** Individual inclusion from R-cell; note rugous morphology. SEM. ×1,600. **D:** X-ray elemental analysis of inclusion shown in C. **E:** Calcium concretions from hepatopancreas of *Procambarus leonensis.* ×16,000. **F:** Histological section of hepatopancreas of *Procaris ascensionis;* note R- and F-cells. ×700. F, fibrillar cell; fg, foregut; gf, gland filter; hp, hepatopancreas; ld, lipid droplet; n, nucleus; R, reserve cell.

Al-Mohanna et al. (1985) described M-cells, or midget cells, from the dendrobranchiate shrimp *Penaeus semisulcatus,* adding a new cell type for the decapod hepatopancreas. M-cells are round in section and always are in direct contact with the basement membrane. These cells may produce cytoplasmic extensions which ramify among

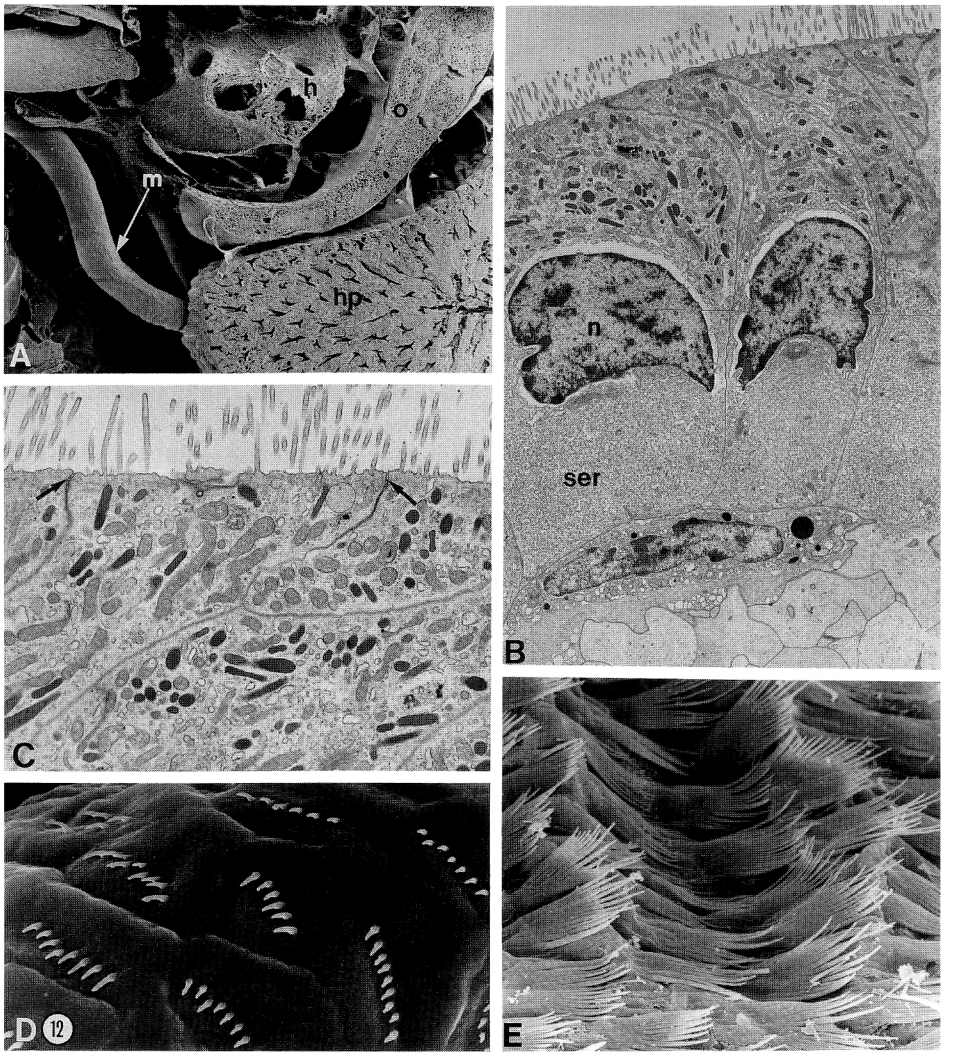

Fig. 12. Ultrastructural features of the midgut and hindgut. **A:** Close-up in region where the midgut exits the posterior portion of the hepatopancreas of *Systellaspis* (by paraffin-carving, SEM). ×650. **B:** Longitudinal section of columnar midgut cells of *Procaris ascensionis;* note prominent fields of SER located below the level of the nucleus. TEM. ×2,800. **C:** Close-up of apical portion of midgut cells shown in B; arrows indicate cell junctions; note cellular inclusions and numerous mitochondria. TEM. ×5,000. **D:** Hindgut of *Procambarus leonensis;* note posteriorly directed clusters of spines. SEM. ×1,500. **E:** Armature of the hindgut of *Lepidophthalmus louisianensis*. SEM. ×2,000. h, heart; hp, hepatopancreas; m, midgut; n, nucleus; o, ovary; ser, smooth endoplasmic reticulum.

neighboring cells (see Icely and Nott, chapter 6, this volume). One of the more distinctive features of this cell is the presence of spheres, rods, and other membrane-bound cytoplasmic inclusions that may occupy the entire cell volume. The function of M-cells is probably storage of some organic reserve (Al-Mohanna et al., 1985).

The Midgut

The endodermally derived midgut may vary greatly in its length from quite short, as in many reptant decapods (e.g., *Galathea,* Pike [1947]; *Astacus,* Huxley [1877]; brachyuran crabs; Smith [1978]), to elongate, as in many caridean shrimps (e.g., *Systellaspis,* Figs. 3, 12A). The length of the midgut is not

uniform within taxonomic divisions (Smith, 1978). The midgut extends from the foregut, through the posterior portion of the hepatopancreas, into the abdominal somites (Figs. 3, 12A) before joining the hindgut. The low to tall columnar cells of the midgut sit on a variously developed basement membrane (Factor, 1981) and usually exhibit a prominent microvillous border (Fig. 12B,C) that in many species exhibits a glycocalyx (e.g., *Penaeus;* Talbot et al., 1972; Lovett and Felder, 1990). The apical cell surfaces are connected by prominent junctional complexes (Fig. 12C; see also Talbot et al., 1972). The nucleus may be basally or centrally located. Rough and smooth endoplasmic reticulum are present (Fig. 12B,C). The RER is usually found in the apical portion of the cell, whereas the smooth endoplasmic reticulum (SER) is basal and rarely occurs above the level of the nucleus (Fig. 12B). Mitochondria, Golgi complexes, and large numbers of round to rod-shaped inclusions and secretory granules are also found in the apical cytoplasm of the cell (Fig. 12C). The function(s) of the midgut are not entirely clear, but osmoregulation, nutrient absorption, and the production of the peritrophic membrane that wraps the fecal material of most decapods have been attributed to this region of the gut (Forster, 1953; Vonk, 1960; Talbot et al., 1972; Gibson and Barker, 1979; Felder, 1979; Hopkin and Nott, 1980, and many others).

The Midgut Ceca. In many decapod crustaceans, the midgut gives rise to blindly ended ceca in a variety of locations and patterns (see Mykles, 1977; Smith, 1978, for review). Anterior (at the foregut juncture) and posterior midgut ceca (PMGC, arising from the midgut–hindgut juncture) have been described from many decapods (Smith, 1978). As an example of this common but little known gut appendage, the posterior midgut cecum of the thalassinoid mudshrimp *Lepidophthalmus louisianensis* will be described.

The PMGC extends dorsally from the juncture of the midgut and hindgut (Figs. 4, 13A,B) and lies freely in the hemocoel. A large acinar tegumental gland complex surrounds the gut at the midgut–hindgut junction at the level where the PMGC arises from the gut proper (Figs. 4, 13A,B; Felgenhauer, chapter 2, External Anatomy and Integumentary Structures, this volume). The gland cells empty their contents via ducts that exit at the anterior region of the hindgut. The PMGC is composed of tall columnar cells exhibiting a microvillous border lacking a glycocalyx (Fig. 13C). The nuclei are basally located, with most of the common cell organelles such as Golgi complexes, mitochondria, RER, and extensive fields of basally located SER (Fig. 13C). Electrondense cellular inclusions are also commonly found throughout the cytoplasm (Fig. 13C). A presumably unique feature of the PMGC is the presence of cells within the connective tissue on the hemocoel side of the PMGC. These cells contain large numbers of myelinlike figures or multilamellar bodies similar to those found within the surfactant-producing type II alveolar cells of vertebrate lung (Fig. 13D–F; see Williams, 1977).

The Hindgut

The hindgut of decapods is, like the foregut, ectodermally derived and lined with chitin (Figs. 4, 12D,E). As is seen in the midgut, the length of the hindgut is variable throughout the Decapoda (see Smith, 1978, for discussion). The most striking feature of the decapod hindgut is the presence of cuticular scales (Fig. 12E) or groups of spines (Fig. 12D). These cuticular modifications always direct their spines in the direction of the anus and presumably aid in movement of the fecal mass toward the anus.

RESPIRATORY SYSTEM

Branchiae (Gills)

All decapod crustaceans possess branchiae (gills), with the exception of the aberrant dendrobranchiate shrimp *Lucifer* (Sergestoidea). The number and arrangement of gills varies depending on the species, but typically four gills are attached to some or all of the thoracic somites. One gill blanket, the pleurobranch

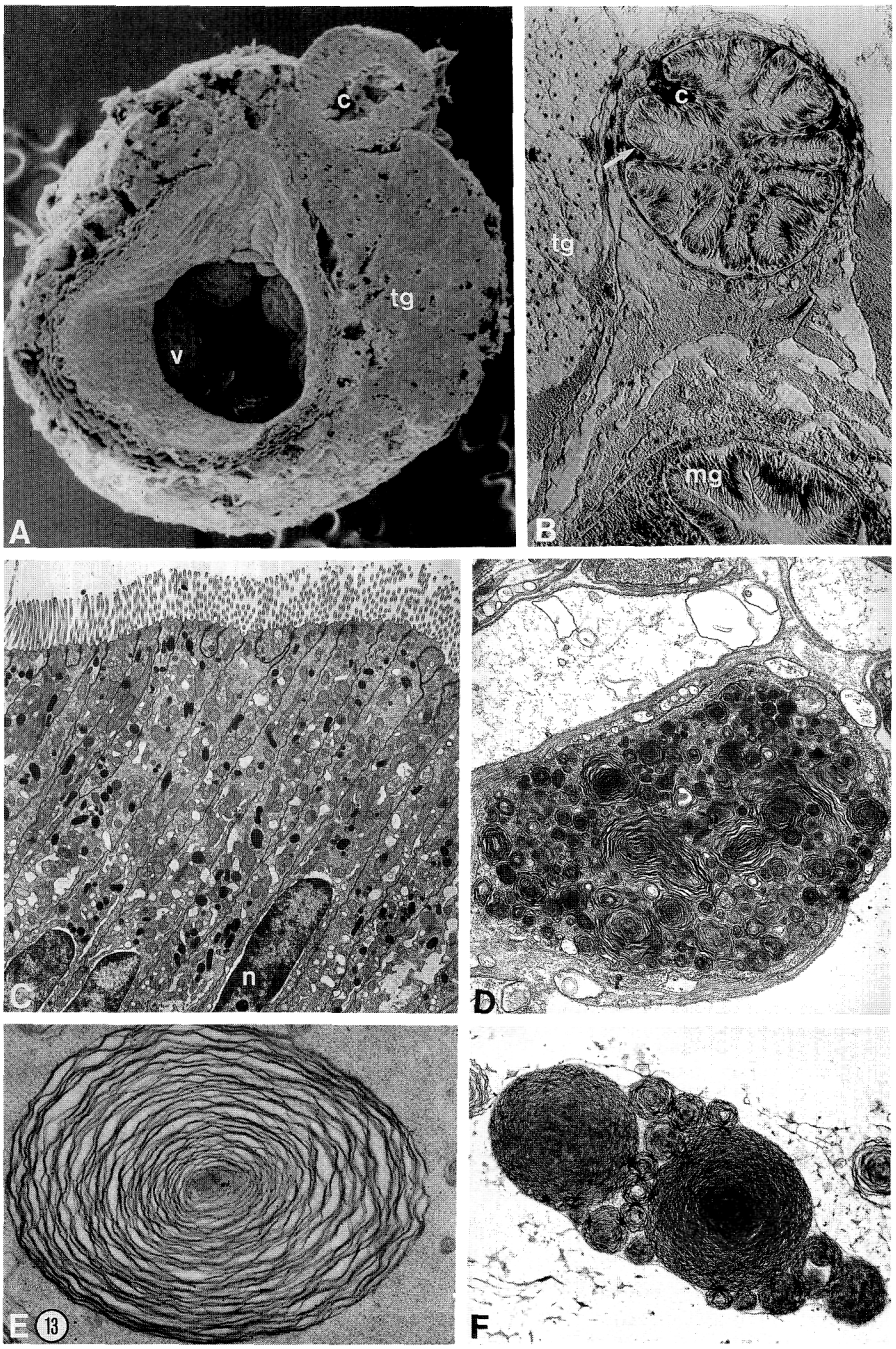

Fig. 13. Posterior midgut cecum (PMGC) of *Lepidophthalmus louisianensis*. **A:** Paraffin-carved cross section through the midgut–hindgut juncture; note the dorsal cecum (c), tegumental gland mass (tg) surrounding the juncture, and the internal valves (v). SEM. ×150. **B:** Histological cross section through the anterior midgut and PMGC; arrow indicates basement membrane of the PMGC. ×600. **C:** Ultrastructure of columnar cells making up the PMGC. TEM. ×2,900. **D:** Surfactant cell of PMGC; note fields of myelin-like multilamellar bodies. TEM. ×8,500. **E:** Close-up of multilamellar body. TEM. ×25,000. **F:** Freeze-substitution of multilamellar bodies. TEM. ×12,000.

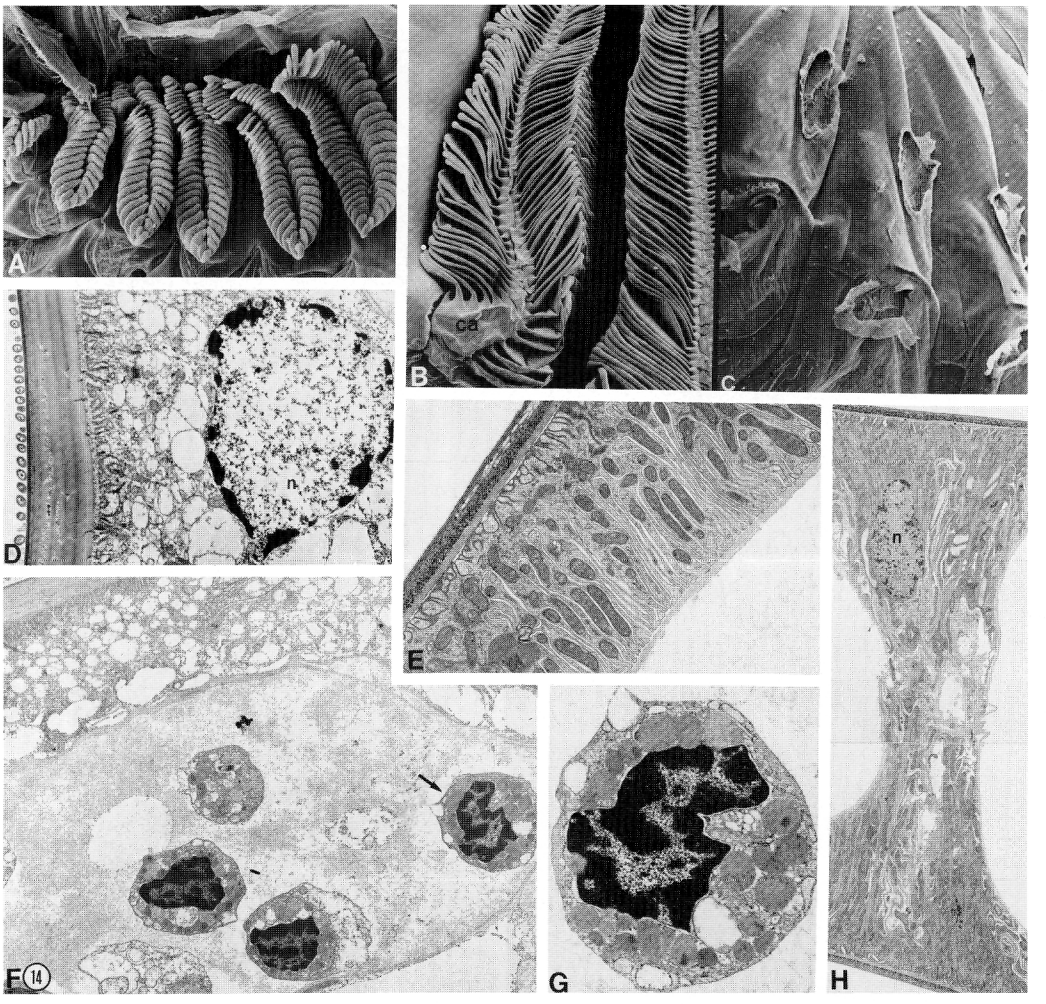

Fig. 14. Ultrastructure of decapod gills. **A:** Lateral view of phyllobranch gills of *Palaemonetes kadiakensis*. SEM. ×30. **B:** Phyllobranch gill of *Ranilia* sp.; note central axis (ca). **C:** Attachment sites of phyllobranch gills of *Systellaspis* (gills removed by sonication). SEM. ×100. **D:** Ultrastructure of phyllobranch gill cuticle from *Sesarma reticulatum;* note row of bacteria on outer surface. TEM. ×10,000. **E:** Ion regulatory region of the phyllobranch gill of *Callinectes sapidus* sp.; note mitochondria in elaborate basal infoldings. TEM. ×18,000. **F:** Low-magnification view of the hemocoel below the gill cuticle of *Sesarma reticulatum;* note circulating hemocytes (arrow) within hemocoel. TEM. ×10,000. **G:** Close-up of hemocyte pictured in f. TEM. ×20,000. **H:** Pillar cell of *Callinectes sapidus*. TEM. ×18,000. n, nucleus.

(Fig. 14C), is usually attached to the lateral wall of the somite dorsal to the articulation of the walking leg. Two gills, the arthrobranchs (Fig. 14C), are usually attached to the arthrodial membrane between the coxa and the body wall. The remaining gill, the podobranch, is attached to the coxa of the walking leg (pereiopod) (Calman, 1909).

The arrangement of the gills on the thoracic somites, walking legs, and mouthparts is termed the branchial formula (Fig. 14A) and is commonly used in most modern species descriptions of decapods.

Gill Types. Three distinct gill morphologies, dendrobranchiate, trichobranchiate, and phyllobranchiate (Fig. 15A–F), are found among the members of the Decapoda. The dendrobranchiate gill (Fig. 15A,B) is unique

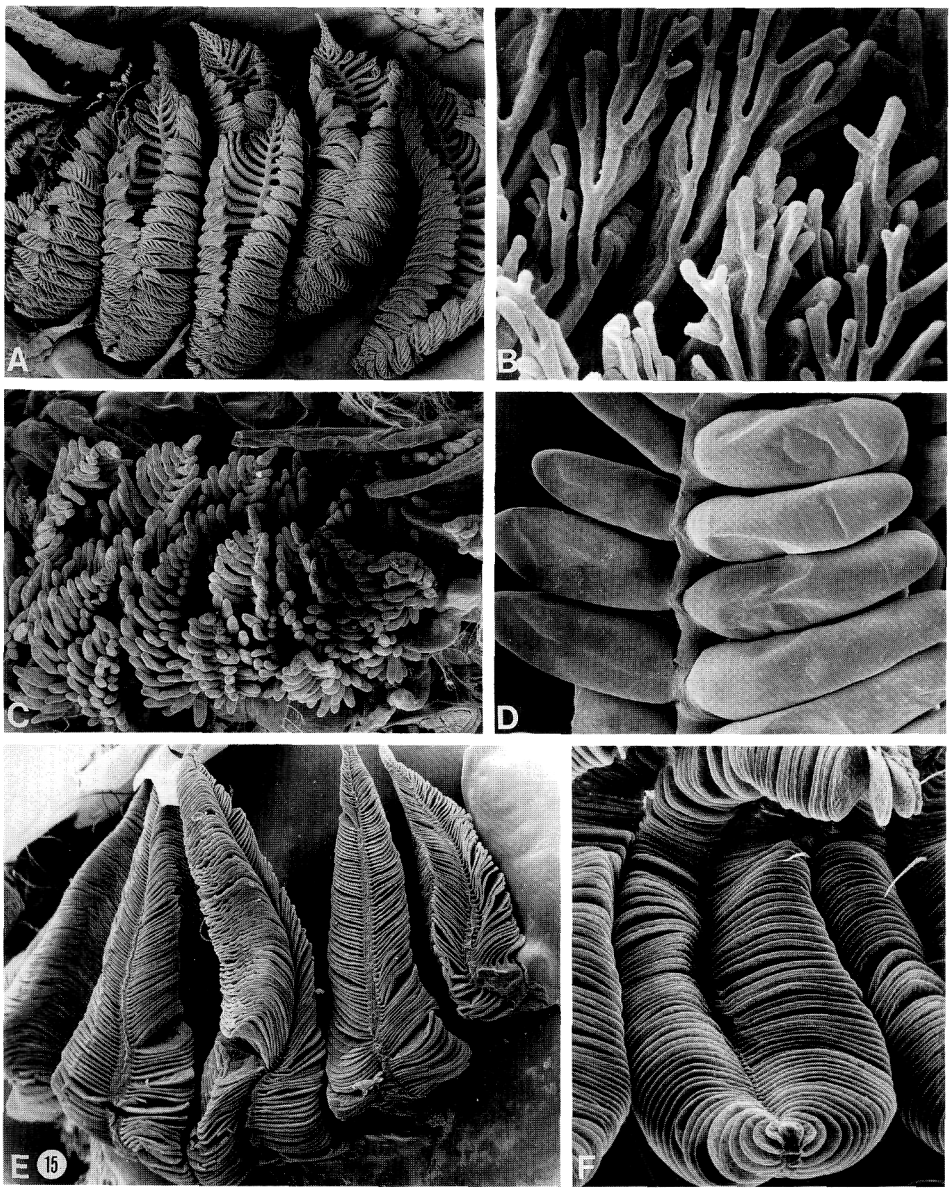

Fig. 15. Gill types of the Decapoda. SEM. **A:** Dendrobranchiate gills of *Penaeus setiferus*. ×50. **B:** Close-up of dendrobranchiate gill lamellae of *Penaeus setiferus*. ×125. **C:** Trichobranchiate gills of *Stenopus hispidus*. ×50. **D:** Close-up of trichobranchiate gill lamellae of *Nephrops* sp. ×220. **E:** Phyllobranchiate gills of *Ranilia* sp. ×15. **F:** Close-up of phyllobranchiate gills of *Lysmata wurdemanni*. ×200.

to the suborder Dendrobranchiata (penaeoid and sergestoid shrimps). The trichobranchiate (Fig. 15B,C) and phyllobranchiate gills (Figs. 14A,B, 15E,F) are widely distributed in apparently unrelated taxa throughout the suborder Pleocyemata (Felgenhauer and Abele, 1983). It must be noted, however, that intermediate forms of the above types are not uncommon throughout the Decapoda (Calman, 1909; Felgenhauer and Abele, 1983).

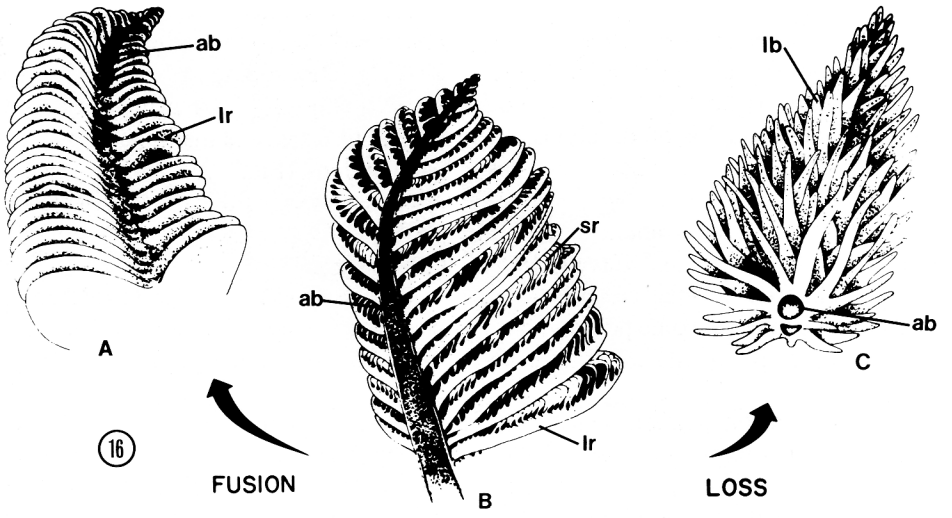

Fig. 16. Hypothesis suggested by Boas (1880) and Burkenroad (1981) for the evolution of gill types among the Decapoda. **B:** Typical dendrobranchiate gill, consisting of lateral branches (lb,lr) extending from the main branchial axis (ab) with a series of subdivided secondary rami (sr) from each lateral branch. Expansion of the lateral branches of the dendrobranchiate type would result in **A,** phyllobranchiate gill. Loss of secondary rami (sr) and/or reduction of the lateral branches would give rise to **C,** trichobranchiate gill. (From Felgenhauer and Abele, 1983.)

The dendrobranchiate gill (Fig. 15A,B) has paired lateral branches arising from the central branchial axis, with a series of subdivided secondary rami coming off each lateral branch (Fig. 15B). Variation does occur and the secondary rami may be rather complex, as in some species of sergestid shrimp. The trichobranch gill is characterized by serial, tubular rami arising from the central branchial axis (Fig. 15C,D). No secondary rami are ever present as in dendrobranch gills. The phyllobranch gill exhibits flat paired lamellar branches extending from the branchial axis (Fig. 15E,F). The lamellar branches are much more flattened and leaflike than those of the trichobranch gill (Fig. 14B).

Huxley (1878) and Bate (1888) suggested that the trichobranchiate gill type gave rise to the dendrobranchiate and phyllobranchiate types. Boas (1880) and Burkenroad (1981) both suggested that the dendrobranchiate gill could have given rise to the trichobranchiate and phyllobranchiate gills. Whichever suggestion is correct, there is little doubt that the phyllobranchiate condition represents the derived state (Fig. 16; Felgenhauer and Abele, 1983).

Branchial Ultrastructure. The branchiae are the primary sites of respiration in decapods. Additionally, these structures have been found to play a role in ion regulation and excretion (Gilles and Pequeux, 1985, and references therein). The branchial cuticle may vary greatly in its thickness, depending on whether the gills are anterior or posterior in the branchial chamber. Morphological differences may be seen in anterior gills, which may have a respiratory function versus the posterior lamellae that serve as ion regulators (Copeland, 1968; Barra et al., 1983; Towle and Kays, 1986; Goodman and Cavey, 1990). Thicker epithelial conditions are seen in areas involved with ion regulation (Fig. 14E) versus those that have a purely respiratory function (Fig. 14D). Those areas of the gill that function in ion regulation characteristically show extensive infoldings of the basal–lateral membranes and abundant mitochondria (Fig. 14E). Other regions of decapods (e.g., branchiostegites; see Talbot et al., 1972; Felder

et al., 1986; Taylor and Taylor, chapter 7, this volume) have also been determined to have ion regulatory and respiratory abilities.

At least six cell types have been reported within branchial epithelia of decapods: the chief cells, pillar cells (= trabecular or pilaster cells), striated cells, glycocytes, nephrocytes (= podocytes), and granular cells (see Johnson, 1980; Goodman and Cavey, 1990, for review). Chief cells, pillar cells, and striated cells make contact at some point with the endocuticle of the gill lamella, whereas nephrocytes, glycocytes, and granular cells are not associated with the endocuticle (Foster and Howse, 1978; Goodman and Cavey, 1990). Chief cells make up the majority of the branchial epithelia (Goodman and Cavey, 1990). Pillar cells (Fig. 14H) are supportive cells that are thought to provide the structural framework facilitating efficient blood flow (Johnson, 1980; Ciofi, 1984, and others). Striated cells are usually restricted to areas near the excurrent hemolymph channel and presumably function in ion regulation (Goodman and Cavey, 1990). Nephrocytes are usually fixed phagocytic cells exhibiting interdigitating foot processes that attach by desmosomes to branchial membranes. Nephrocytes filter hemolymph via pedicel pore diaphragms and the basal lamina. Sequestered substances are enclosed within vacuoles in these cells (Fontaine and Lightner, 1974; Foster and Howse, 1978; Johnson, 1980; Goodman and Cavey, 1990). Glycocytes and granulocytes are packed with glycogen granules and complex fibrillar aggregates (Foster and Howse, 1978; Goodman and Cavey, 1990). Little is known concerning the function of these cells other than storage.

REPRODUCTIVE SYSTEM

Male System

The Testes. In general, the testes lie dorsally in the posterior third of the thoracic cavity and may, in some groups (e.g., most reptant decapods), extend diverticula into the abdominal somites. In dendrobranchiate shrimps, the testes are lobular in form. The testes of caridean shrimps are simple tubes connected to one another anteriorly (Fig. 17A,B). Developing spermatids (= spermatocytes) (Fig. 17C) are usually round to oval within the testes and mature as they transit the vas deferens (Fig. 17F) to the gonopore. A good discussion of this process in the caridean shrimp *Crangon* is found in Arsenault et al. (1979).

The Vas Deferens. The vas deferentia are paired structures that conduct spermatozoa from the testes to the genital apertures (gonopores) at the base of the fifth walking legs (Fig. 17F). In addition to acting as a conduit for spermatozoa, the vas deferens is also responsible for "packaging" the spermatozoa into a spermatophore (Fig. 17E). Within the dendrobranchiate and caridean shrimp, the spermatophore is a simple cordlike mass. The spermatophore of most brachyuran and anomuran crabs are singular units of spermatozoa or "sperm balls" (Fig. 17G). However, in some species of the lower brachyuran crabs (e.g., *Dromidia, Ranilia*) and some anomuran crabs (e.g., *Clibanarius*), spermatophores are linked to one another in a chainlike fashion via a thin membranous sheath.

The Spermatozoa. Decapod spermatozoa are rather unusual among invertebrates in being aflagellate and nonmotile. The spermatozoa of decapods can be divided into those that exhibit a single spike, unistellate spermatozoa (Fig. 18A–E), to those with a variable number of spikes that surround the cell body, multistellate spermatozoa (Fig. 18F). Natant decapods typically exhibit the unistellate condition, whereas many reptant decapods are multistellate in form. Below I describe briefly the basic ultrastructural features of each morphological type.

Unistellate Spermatozoa. This spermatozoan type is frequently referred to as "thumbtack" or "button" type, owing to the spermatozoans' resemblance to tacks (Fig. 18A–E). Three distinct regions can be discerned at the ultrastructural level: the cell body, cap, and spike (Fig. 18A–D). The cell body contains the typically uncondensed nucleus, which is

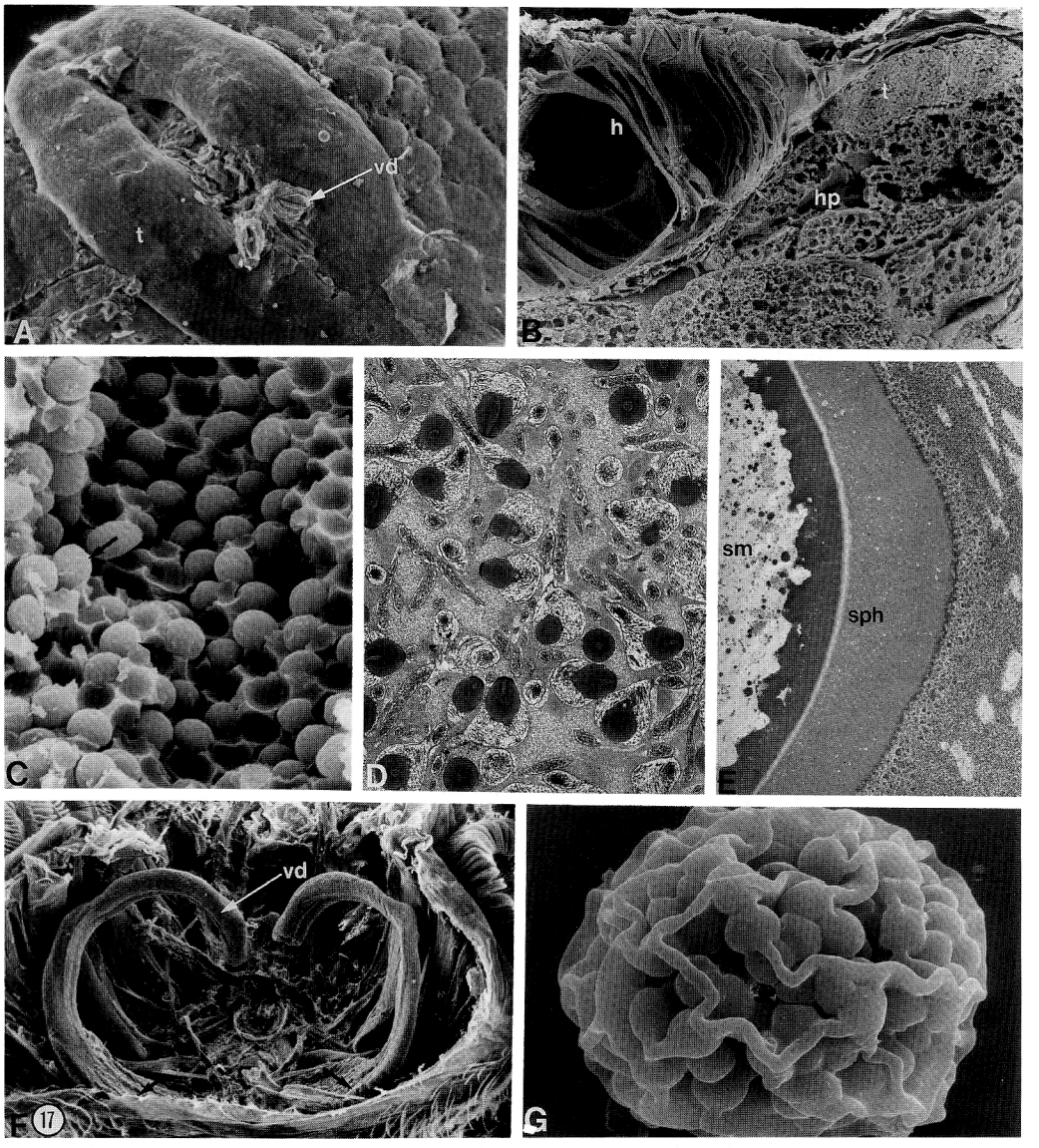

Fig. 17. Features of the male reproductive system. **A:** Bilobed testis of *Lysmata wurdemanni;* note the vas deferentia that exit each lobe of the testis. SEM. ×125. **B:** Sagittal paraffin-carved section (SEM) through the male thorax of *Procaris ascensionis;* note the lobe of the testis lying dorsal to the hepatopancreas. ×100. **C:** Spermatids (arrows) within the testis of *Penaeus setiferus*. SEM. ×900. **D:** Multistellate spermatozoa of *Iliacantha* sp. within the testis. TEM. ×3,800. **E:** Spermatophore wall and internal sperm mass of *Palaemonetes kadiakensis*. TEM. ×8,000. **F:** Vas deferens of *Lysmata wurdemanni;* note they exit at the base of the fifth pereiopod (black arrows). SEM. ×45. **G:** Spermatophore (sperm ball) of *Parthenope* sp. SEM. ×200. h, heart; hp, hepatopancreas; sm, sperm mass; sph, spermatophore wall; t, testis; vd, vas deferens.

not bounded by a nuclear envelope (Fig. 18C). In addition to the nucleus, mitochondria may be present (sometimes only present in spermatids in some species; see Koehler, 1979).

The cap region contains electron-dense fibrils of varying diameters and accompanying centrioles (one or two) in the central portion just above the spike. These fibrils usually exhibit a characteristic cross-striated pattern