

Fig. 18. Spermatozoan types of the Decapoda. **A:** Unistellate spermatozoan of *Palaemonetes kadiakensis*. SEM. $\times 4,000$. **B:** Ventral view of spike region of spermatozoan pictured in A; note that the three basic divisions (spike, cap, and cell body) of the spermatozoan can be easily recognized. SEM. $\times 10,000$. **C:** Transverse section through unistellate spermatozoan shown in

A. TEM. $\times 4,200$. **D:** Unistellate spermatozoa of *Penaeus setiferus*. SEM. $\times 4,000$. **E:** Transverse section of unistellate spermatozoan pictured in D. TEM. $\times 4,500$. **F:** Multistellate spermatozoa of *Callinectes sapidus*; note multiple arms (a) extending from the cell body. SEM $\times 4,100$. s, spike; cp, cap; cb, cell body; n, nucleus.

in many species (Koehler, 1979; Lynn and Clark, 1983b; Felgenhauer and Abele, 1988). The fibrils may anastomose and extend down into the spike (Fig. 18C). An organized acrosomal complex has been described for the dendrobranchiate shrimp *Sicyonia ingentis* by Kleve et al. (1980), but for most species, especially caridean shrimp, no distinct acrosome has been demonstrated. Shigekawa and Clark (1986) provide an excellent discussion of what is known concerning the acrosomal reaction.

The spike may be elongate in some species (Fig. 18A–C) to quite short in others (e.g., *Crangon*; see Arsenault et al., 1979; Boddeke et al., 1991). Two basic types of spike association with the egg surface have been described: either a spike-first contact with the egg (Kleve et al., 1980; Barros et al., 1986) or a cap-first egg interaction (Lynn and Clark, 1983a,b).

Multistellate Spermatozoa. This spermatozoan type is a multistellate cell with radiating arms (= spikes of some authors) extending from the cell body (Fig. 18F). These appendages are not homologous to the unistellate spike (Talbot and Summers, 1978; Hirsch, 1986). The most striking feature of this gamete is its highly structured acrosome (Fig. 19A,B). The nucleus surrounds the large electron-dense acrosomal complex that is composed of several distinct ultrastructural features. The acrosomal vesicle is bilayered in most brachyuran crabs, consisting of an inner and outer region (Fig. 19A,B,D). The acrosomal vesicle may be flanked by a prominent lamellar region (Fig. 19A,B). The acrosomal tubule is presumably supported by a battery of microfilaments or microtubules (Fig. 19A–D), depending on the species. The anterior portion of the acrosomal tubule is covered by a distinct electron-dense acrosomal cap (Fig. 19A,B). At the base of the acrosomal tubule is a thickened ring that evidently aids in the support of the tubule (Fig. 19A). The nucleus may or may not extend into the usually stellate arms. The brachyuran crab *Iliacantha* sp. exemplifies nuclear pene-

tration into the arms (Fig. 19E,F). Other species of reptant decapods may have a microtubular component within the radiating arms, as in the crayfish *Procambarus leonensis* (Fig. 20A–C,E). The acrosomal reaction is essentially an eversion of the cell, turning the acrosome “inside out” with subsequent injection of the nucleus (Brown, 1966, Talbot and Chanmanon, 1980; Goudeau, 1982, and others; Fig. 19G).

The spermatozoan of astacoid reptant decapods (e.g., crayfish) is different in its organization from that described above. The prominent acrosomal vesicle is horseshoe-shaped and is not bilayered, but is crystalline in nature (Fig. 20A,D). The acrosomal tubule is much reduced and distinct microtubules are not easily discerned (Fig. 20D,F). The radiating arms are greater in number (up to 20 or more in some species) and are supported by microtubular arrays (Fig. 20A,B,E). The cell membrane of this gamete is much thicker than that of most decapod spermatozoa and has been termed the cell capsule (Fig. 20A,E). Mechanics of the acrosomal “reaction” and egg interactions have not been described.

Female System

The ovary is located in the dorsal portion of the cephalothorax in the same relative position as the male testis (Fig. 3), e.g., lying dorsal to the hepatopancreas (Fig. 12A). As in the testis, the ovary is paired and its size depends on the age and reproductive condition of the individual. Unlike the testis, the ovary commonly extends into the abdominal somites, and in some groups, such as many of the anomuran crabs, the ovary is restricted to this position (Kaestner, 1970; McLaughlin, 1983). Details concerning the maturation process and ultrastructural features of the ovary and follicles can be found in Johnson (1980) and Talbot (1981a,b). In macrurous forms, the ova pass from the ovary down the oviducts and exit via the gonopore on the third walking legs (pereopods). In brachyurous forms, the short oviducts lead to a saclike spermatheca within the musculature of the second walking

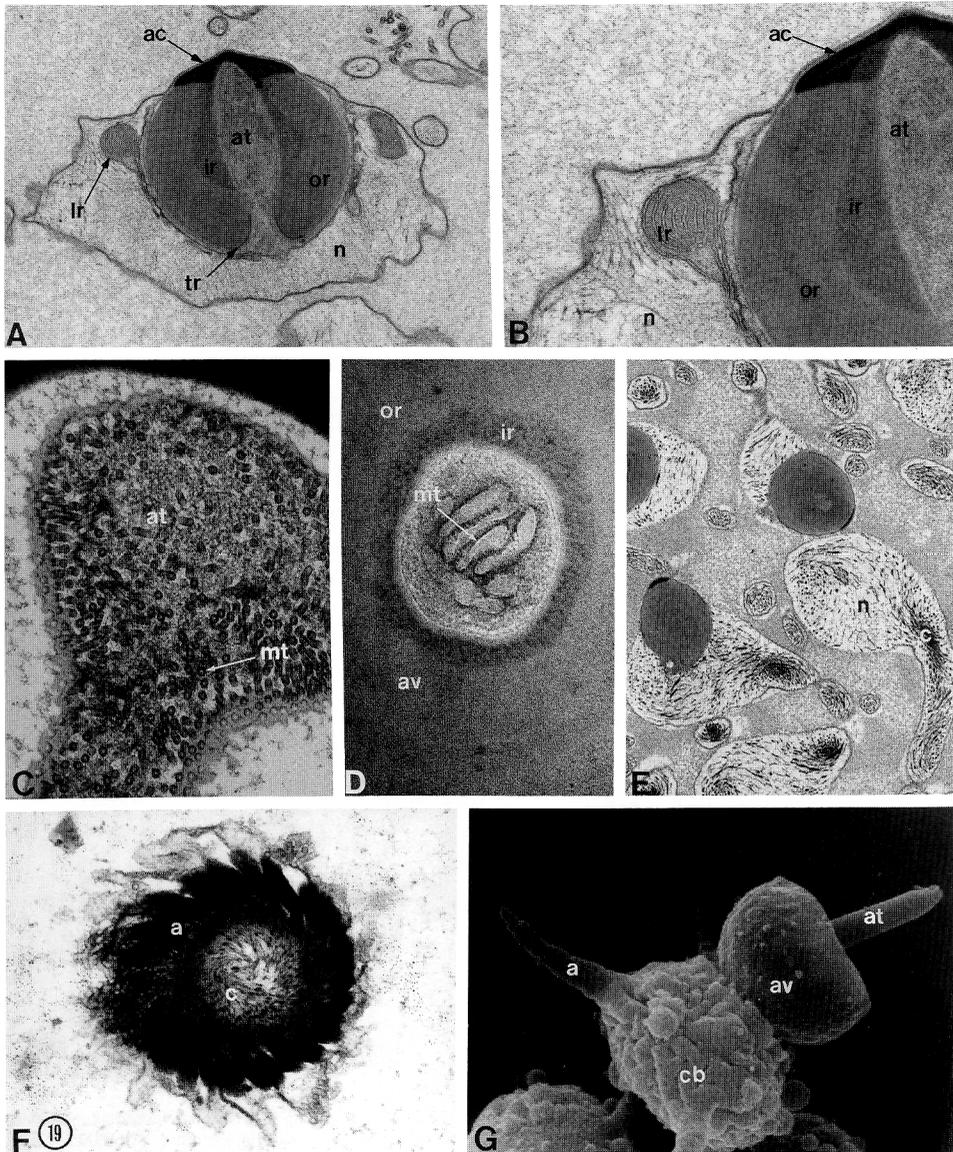


Fig. 19. Ultrastructural details of decapod multistellate spermatozoa. A-F by TEM. **A:** Multistellate spermatozoan of *Callinectes sapidus*. $\times 3,000$. **B:** Close-up of acrosomal region of *Callinectes sapidus*. $\times 10,000$. **C:** Oblique section through acrosomal tubule from the spermatozoan of *Parthenope* sp.; note numerous microtubules (arrow). $\times 22,000$. **D:** Cross section through the acrosomal tubule of *Iliacantha* sp. Note the microtubules within the tubule and the bilayered condition of the acrosomal vesicle. $\times 80,000$. **E:** Multistellate spermatozoan of *Ili-*

cantha sp. $\times 9,000$. **F:** Cross-section through the arms of the spermatozoan pictured in E; note chromatin extending into the arms from the nucleus. $\times 35,000$. **G:** Artificially induced acrosomal reaction of the multistellate spermatozoan of *Eurydium* sp. SEM. $\times 8,500$. a, arm; ac, acrosomal cap; at, acrosomal tubule; av, acrosomal vesicle; cb, cell body; ir, inner region; lr, lamellar region; mt, microtubules; n, nucleus; or, outer region; tr, thickened ring.

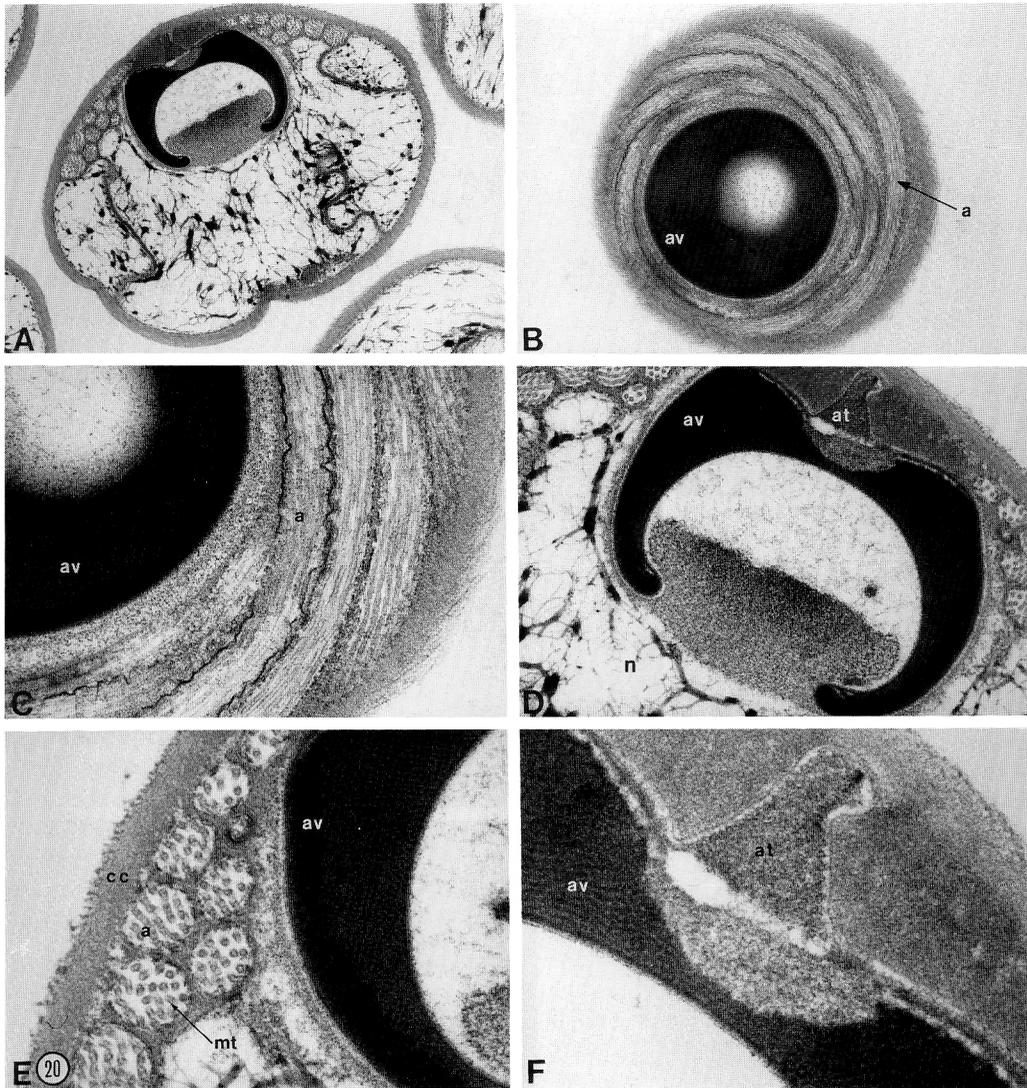


Fig. 20. Ultrastructural features of crayfish spermatozoa. TEM. **A:** Ultrastructural aspects of the spermatozoon of *Procambarus leonensis*. $\times 3,000$. **B:** Oblique section through anterior region showing arms supported by microtubules. $\times 22,000$. **C:** Close-up of acrosomal vesicle and microtubules within the arms. $\times 40,000$. **D:** Ultrastructural details of acrosome.

$\times 36,000$. **E:** Close-up of acrosomal vesicle; note thick cell coat and microtubules supporting the arms. $\times 36,000$. **F:** High magnification of acrosome and presumed acrosomal tubule. $\times 50,000$. a, arm; av, acrosomal vesicle; at, acrosomal tubule; cc, cell coat; mt, microtubules; n, nucleus.

legs (pereiopods). Unlike most macrurous decapods, internal fertilization is practiced by this large group of crabs and spermatozoa are stored within the spermatheca following copulation. The eggs are fertilized as they pass onto the abdominal pleopods for brooding

(Warner, 1977). The method by which decapods incubate their eggs varies depending upon the group. Dendrobranchiate decapods release eggs into the water (although *Lucifer* carries them briefly on the pereiopods; Burkenroad, 1981), while all other decapods

for which data are available carry the eggs on the pleopodal setae (Felgenhauer and Abele, 1983).

THE EXCRETORY-OSMOREGULATORY SYSTEMS

The antennal, urinary or green glands are paired excretory organs located at the base of the second antennae. The excretory pore exits on the coxa of the antenna (Fig. 21A, arrow) and its location is a constant feature among decapods. Antennal glands are generally composed of four components: the coelomosac (= end sac), labyrinth, proximal and distal tubules (= nephridial canal), and bladder (Fig. 22). The description below is of the green gland of the crayfish *Procambarus leonensis*.

The mesodermally derived coelomosac is composed of podocytes that perform an ultrafiltration function similar to that of the vertebrate glomerular nephron (Kummel, 1964; Schmidt-Nielsen et al., 1968; Tyson, 1968; Peterson and Loizzi, 1974; Johnson, 1980). The labyrinth is composed of an extensive network of coiled cuboidal cells in the inactive state and columnar cells in the active secretory condition. The labyrinth cells typically have a centrally located nucleus (Fig. 21E) with numerous mitochondria packed within the extensive infoldings of the basal lamina (Fig. 21F,G) characteristic of transport tissue (e.g., gills, branchiostegite; Mantel and Farmer, 1983). The apical portion of these cells has an extensive brush border (Fig. 21E,F). The labyrinth is a transport system involved in the movement of ions and reabsorption of proteins (Peterson and Loizzi, 1974). The nephridial canal (= proximal-distal tubules) acts as the conduit between the labyrinth and bladder. The length of the nephridial canal varies greatly depending upon species. The bladder is usually a large reservoir for urine storage and may play a role in final urine modification (Riegel, 1972).

CIRCULATORY SYSTEM

The circulatory system of decapods is centered around a bulbous, dorsal heart, located

in the posterior region of the cephalothorax. The heart receives blood through a series of ostia (Figs. 3, 23). It is surrounded by a pericardial sac that is penetrated by passageways where venous blood returns to the pericardial chamber. The number of ostia of the heart may vary depending on the species, but three pairs is the most commonly reported number (McLaughlin, 1983; Schram, 1986). The location of the ostia varies also from paired arrangements in the dorsal, lateral, and ventral positions around the heart (Figs. 12A, 23).

Figure 23 illustrates the general layout of the major arteries comprising the circulatory pattern of most decapods (Burnett, 1984). Several major arteries exit the anterior aorta (Fig. 23) servicing the rest of the body. The anterior aorta (= dorsal artery) may be equipped with an enlargement termed the cor frontale, first described by Baumann (1917). The basic anatomy of this modification is remarkably similar among the decapods studied by Steinacker (1978), who considered the cor frontale to function as an "auxiliary heart" (= accessory heart of Maynard, 1960).

The hemocytes of decapod crustaceans are circulating cells (Fig. 14F,G) of the hemolymph that perform a diversity of physiological and pathological functions (see Ravindranath, 1980; Bauchau, 1981; Hose et al., 1987), from wound repair (Fontaine and Lightner, 1973), to clotting of the hemolymph (Stutman and Dolliver, 1968), to hardening of the cuticle (Vacca and Fingerman, 1983), to name but a few. Classification of these cells has been attempted for many years, but owing to the different criteria used to determine types by many investigators, much confusion still remains and has prevented comparative inferences to be made on form and function (Martin and Graves, 1985); however, see Vascular Elements and Blood (Hemolymph) chapter 5, by Martin and Hose, this volume. Most of the investigations on these cells have been cytochemical in nature and were focused on devising a means of classifying these difficult cell lines (for discussion see Martin et al., 1987).

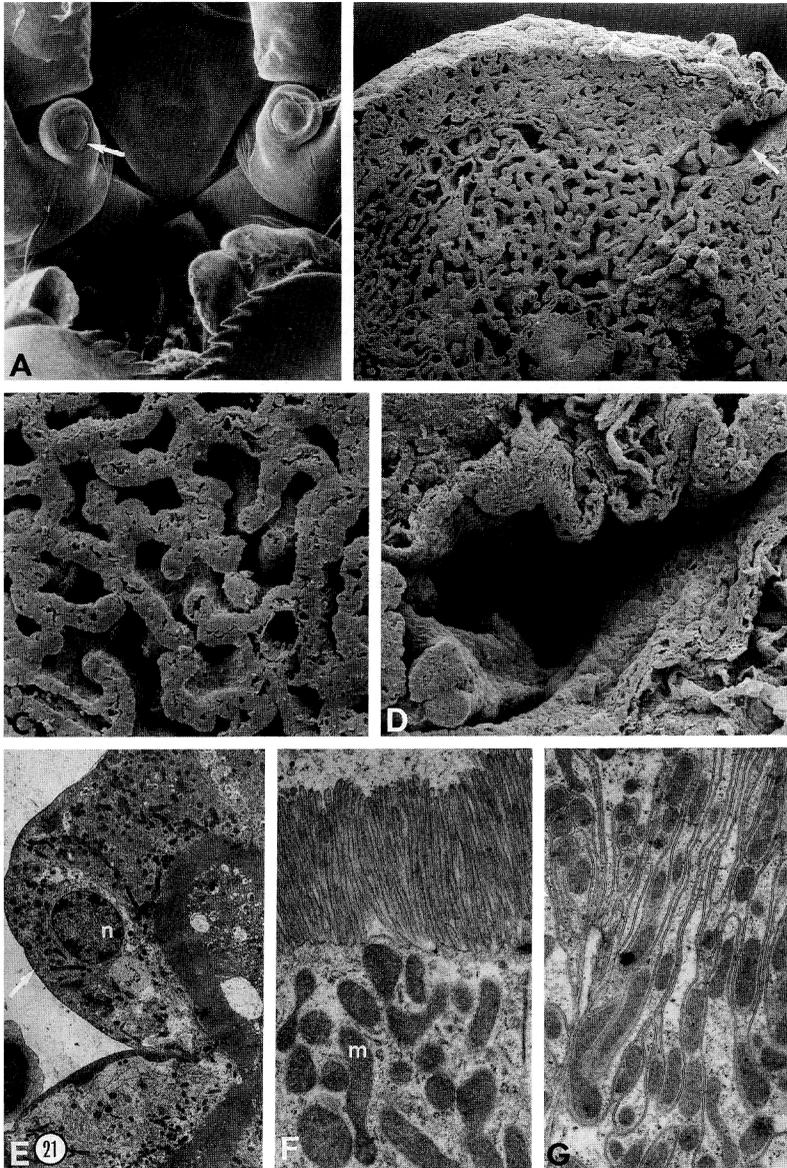


Fig. 21. Ultrastructural features of the decapod urinary and osmoregulatory systems. (A, from *Systellaspis* sp.; B-G are from *Procambarus leonensis*). **A:** Urinary pore (arrow) at base of antennal peduncle. SEM. $\times 50$. **B:** Paraffin-carved section through the labyrinth region of the green gland; arrow indicates region that exits to the proximal tubule. SEM. $\times 50$. **C:** Close-up of the convoluted cell layers of the labyrinth shown in

B. SEM. $\times 450$. **D:** Region of labyrinth that leads to the proximal tubule. SEM. $\times 200$. **E:** Ultrastructure of the labyrinth cells; note centrally located nucleus (n). TEM. $\times 3,000$. **F:** Close-up of brush border of labyrinth cells; note mitochondria (m) and long microvilli. TEM. $\times 18,000$. **G:** Close-up of mitochondria packed within the basal lamina indicated by arrow in E. TEM. $\times 20,000$.

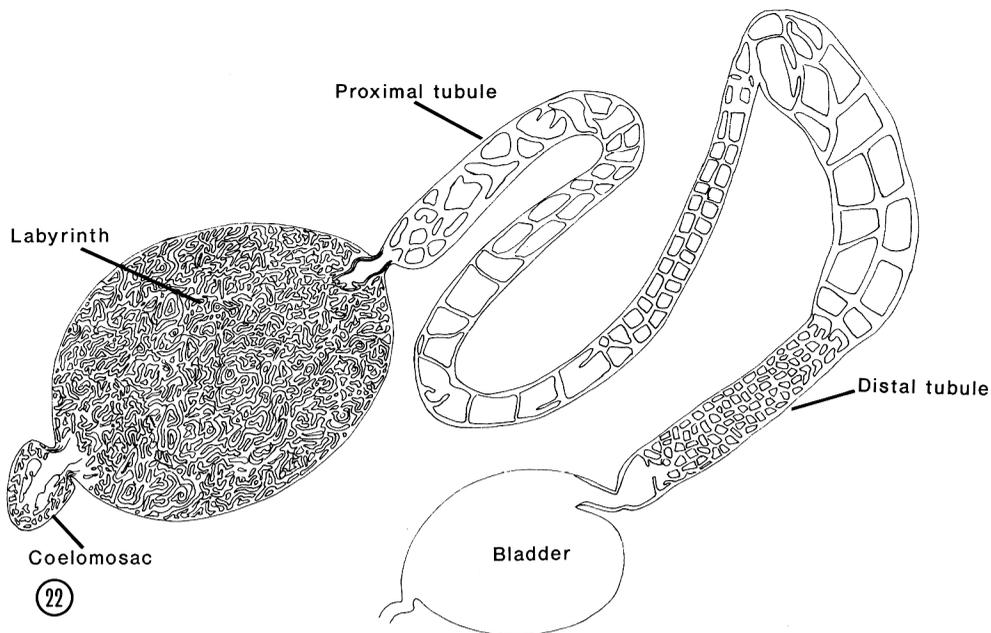


Fig. 22. Schematic drawing of the antennal green gland of the crayfish indicating the major regions of the gland. (After Riegel, 1972.)

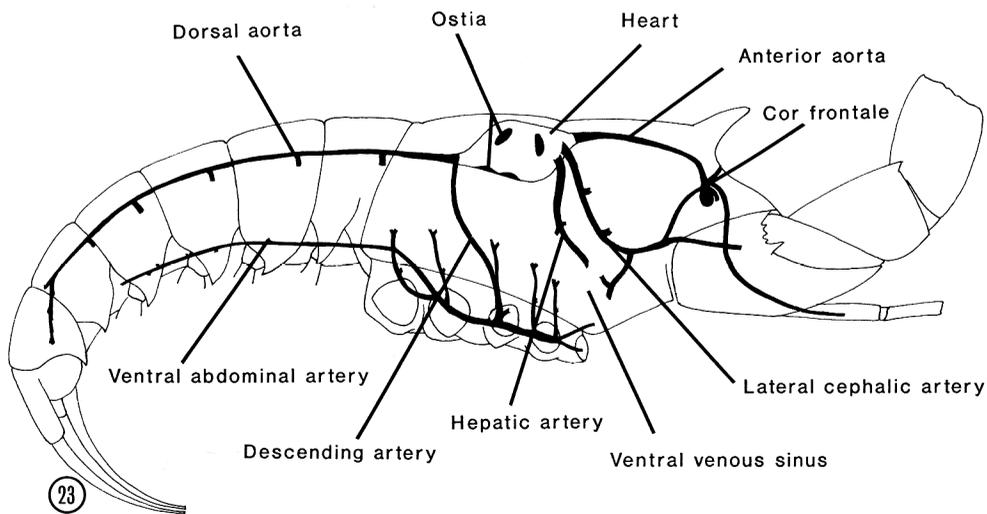


Fig. 23. Schematic drawing of the circulatory system of a typical decapod. (After Burnett, 1984.)

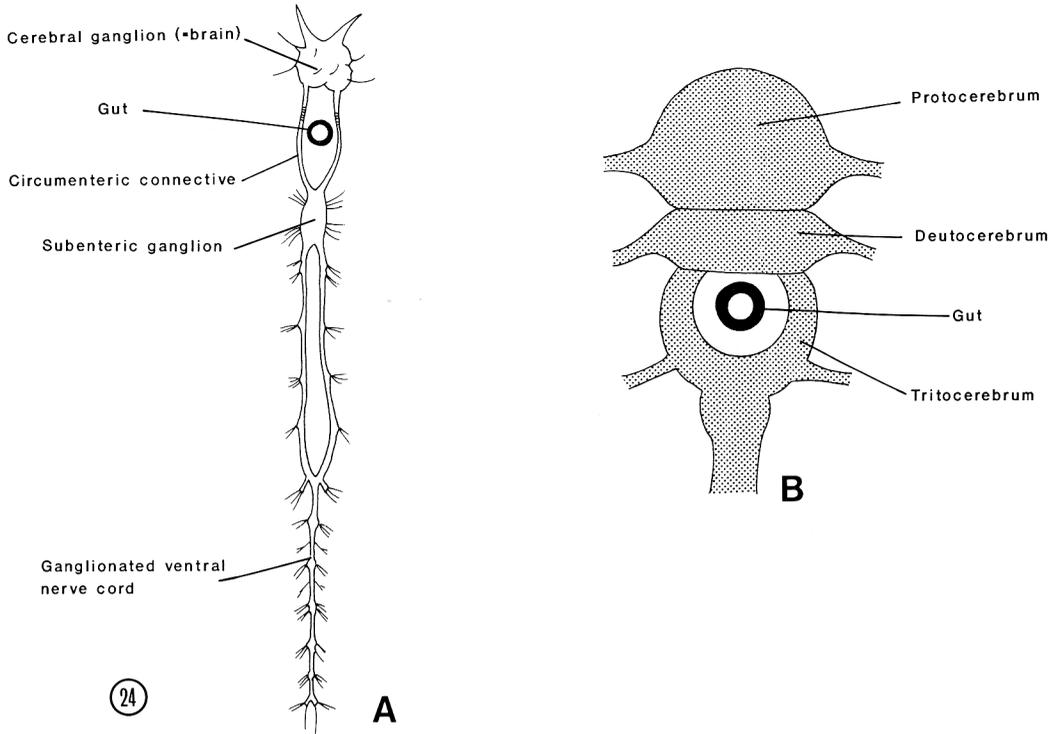


Fig. 24. **A:** The central nervous system of the crayfish, showing the basic ladderlike arrangement of the ventral nerve cord. **B:** Schematic drawing of the regions of the brain. (After Brusca and Brusca, 1990.)

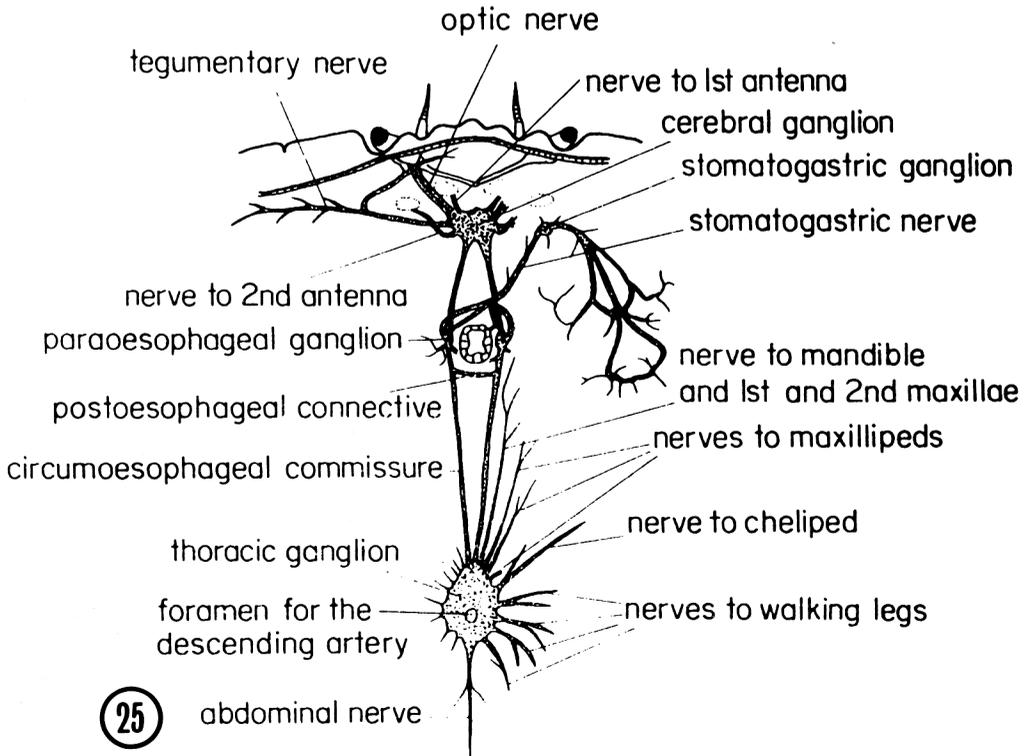


Fig. 25. The nervous system of a typical brachyuran crab. Note fusion of abdominal ganglia. (After Pearson, 1908.)

NERVOUS SYSTEM

The central nervous system is composed of a dorsal brain connected to a ventral longitudinal nerve cord located below the alimentary canal (Fig. 24). The brain is composed of three regions: the protocerebrum, deutocerebrum, and tritocerebrum. The ventral nerve cord is typically a "ladderlike" system wherein fused paired ganglia occur in each of the abdominal somites of macrurous forms and are reduced to a single postesophageal ganglion in brachyurous forms (Fig. 25).

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