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Reprinted from Turtox News, Vol. 34, No. 4, Vol. 34, No. 5 and Vol. 34, No. 6, April, May and June, 1956

The Ostracod

A Neglected Little Crustacean

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• Textbooks on invertebrate zoology say very little about ostracods, if indeed they mention them at all. Most texts state that the carapace is bivalved, the body lacks segmentation, and crustacean characteristics are evident in the jointed appendages. With rare exceptions, the illustrations are of dismembered parts of ostracods, and show little or nothing on the organization of the animal. Several statements that have appeared in literature are erroneous, and the figure in at least two textbooks has the mouth above the upper lip instead of behind it.

For one reason or another, most zoologists have avoided studying ostracods. Perhaps some have been discouraged by the small size of the animals. Adults of many species are less than 1 millimeter long. A more serious hinderance to study, however, is the ostracod's general body plan. The diagnostic structures are enclosed in a bivalved carapace. It is absolutely necessary to remove the valves from around the body and appendages to classify an ostracod. But as we shall see presently, the dissection is not as great an obstacle as many people believe, and the difficulties are rewarded by acquaintance with the biology and morphology of this not-very-well-known crustacean.

Ostracods live in many environments. They are found in open oceans, bays, swamps, lakes, streams, ponds, temporary pools, and springs. Some are pumped out of wells from underground waters. One species has even been reported in the damp leaf mold of a tropical forest. Some ostracods live in the Arctic and Antarctic regions, whereas others abound in very warm springs. Most ostracods are benthonic, but some swim free nearly all of their lives. Only a few species are commensal on other crustaceans and fish, and none is known to be parasitic. Many fresh-water species occur both in Europe and in North America because of a peculiarity in their life cycle. Their eggs can withstand desiccation for long periods of time; it was discovered that some eggs remain viable after drying for many years. Eggs blown by the wind or carried in mud on the feet of birds have only to settle in fresh water to hatch and start the species in a new locality.

Some species reproduce by syngamy and others by parthenogenesis; none is hermaphroditic. One species is known to be syngamic in one environment and parthenogenetic in another, but, insofar as indicated by meager reports, all other species have only one method of reproduction. Many syngamic species show dimorphism in the form of the carapace. One of the unusual features of ostracods is the size of the spermatozoa: in males of some species, they are several times as long as the carapace. These spermatozoa are absolutely, as well as relatively, the largest in the animal kingdom.

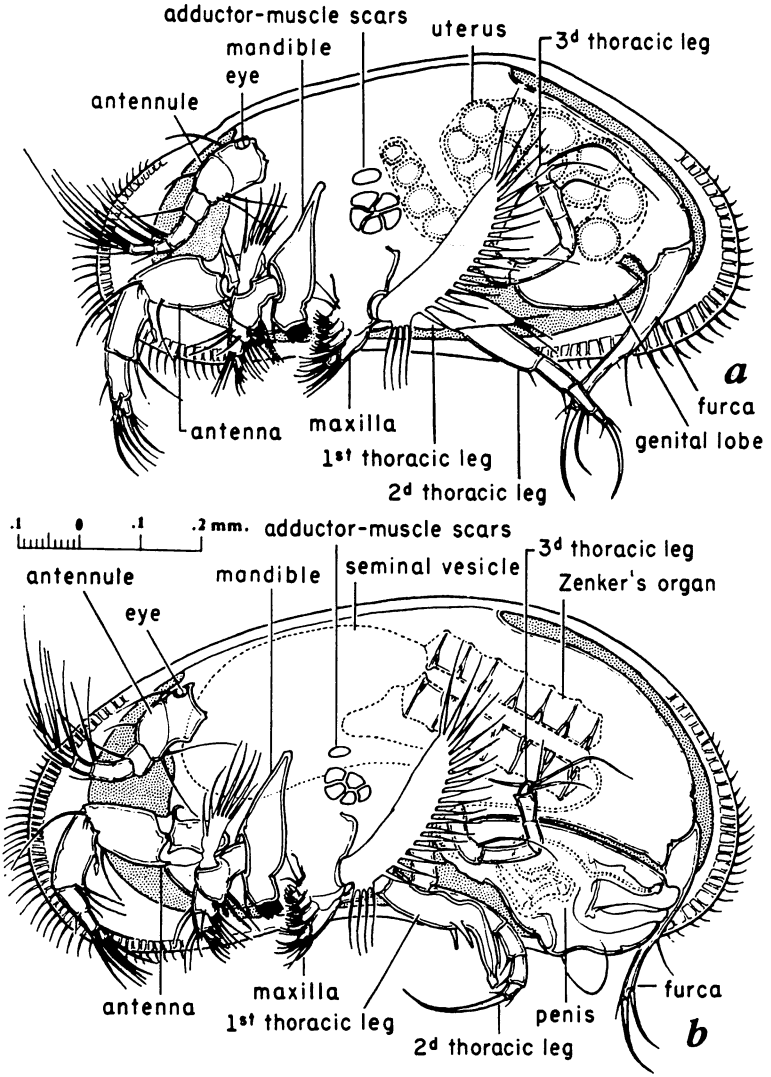

Fig. 1. *Candona suburbana* Hoff. *a*. Female with left valve removed. *b*. Male with left valve removed. In each figure the maxilla is turned to show the endites, which normally lie medial to the palp. Both figures to scale at the left.

The Genus *Candona*

Candona is ideal for laboratory study. Ostracods of this genus live in quiet bodies of water in temperate latitudes. They are bottom dwellers, crawling on or burrowing in the detritus on the floor of ponds and lakes. Some are living within a few miles of nearly every reader of this page. *Candona* can be separated from nearly all other

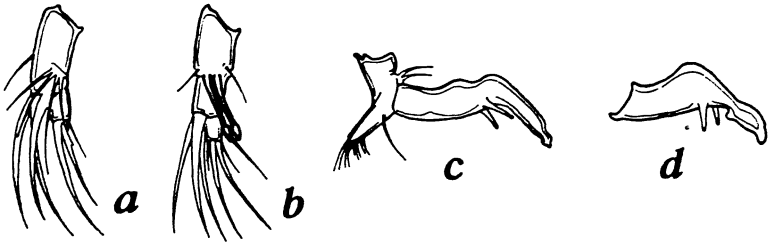

Fig. 2. *Candona suburbana*. *a, b*. Inner faces of distal podomeres of female and male antenna. *c*. Outer face of male left 1st thoracic leg. *d*. Inner face of endopod of male right 1st thoracic leg.

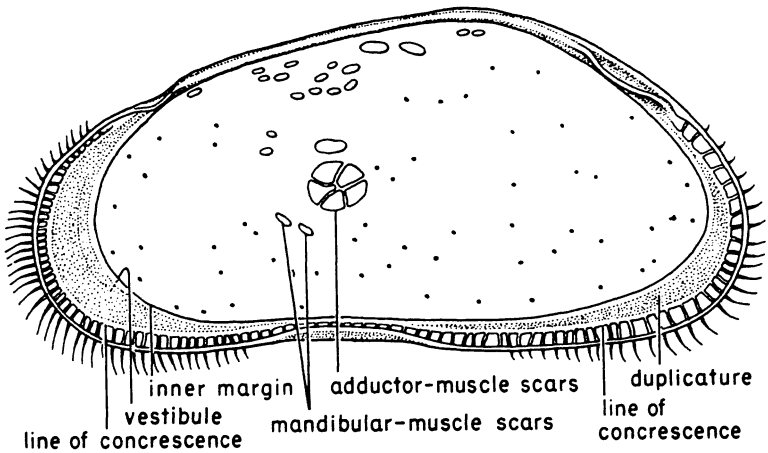

Fig. 3. *Candona suburbana*. Inner face of female right valve.

fresh-water genera by its white or very pale golden carapace, the shape of the valves (Figs 1, 3), and by its inability to swim. The approximately 100 species of the genus have only slight differences in details of the appendages and in the shape and size of the valves. Males are known in only about half of the species, and the rest are assumed to be parthenogenetic.

Candona species are easily maintained in aquaria and multiply rapidly. They thrive best on diatoms and algae, but most do well on dead leaves. The aquarium should be aerated; it can be stocked with water plants if an air hose is not available Very young specimens can be isolated in individual vials and their ontogeny followed. They mature in about one month.

Observing the Living Animal

Certain features are best observed in living specimens. A few adults can be removed from the aquarium to shallow dishes by means of a pipette. As can be seen with a binocular microscope at about 36 diameters magnification, the two valves of each ostracod are hinged only along their dorsal borders, and have free edges around the rest of their periphery. The hinge is covered by a thin ligament, which by contraction opens the carapace. If the animal is disturbed by gentle poking with a needle, it will close the valves quickly, hermetically sealing itself inside. Although the valves are composed of

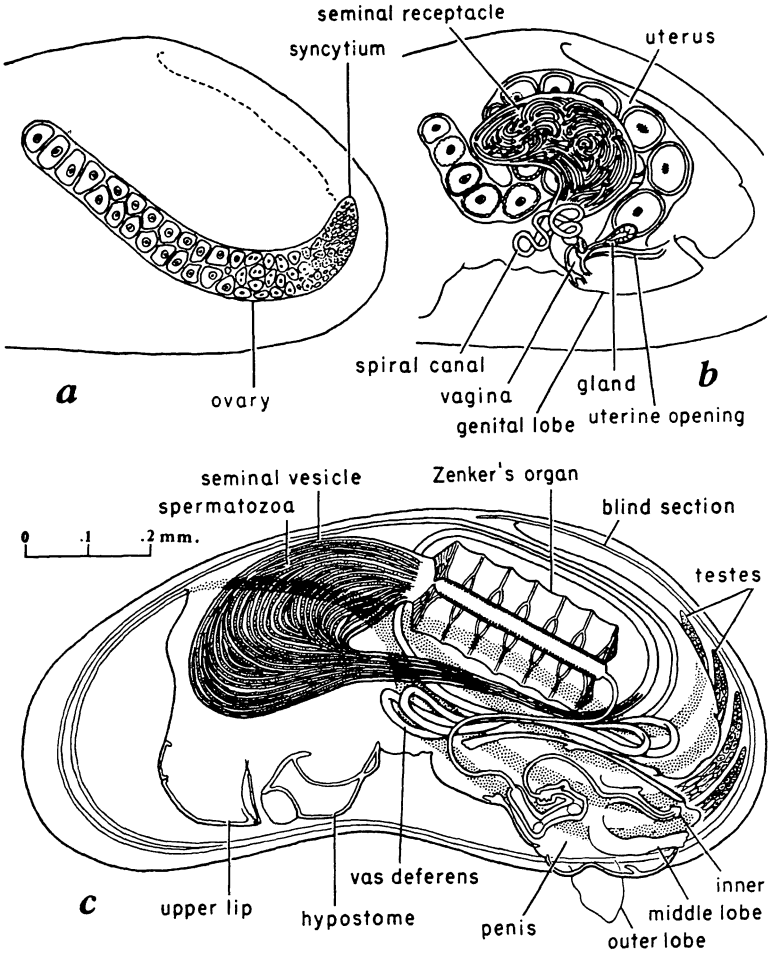

Fig. 4. *Candona suburbana*. Sex systems. *a*. Female gonad in the hypodermis. *b*. Right half of female system in the body. *c*. Right half of male system.

a layer of calcite between layers of chitin, they are thin enough to reveal faintly some structures of the animal within. The animal can be held on its side by a thin cover glass.

The body shows up as a pouchlike mass suspended from the dorsal region of the carapace. In the anterodorsal region, just below the front end of the hinge, there is a dark spot that now and then brilliantly reflects light. This is the single median eye. Near the center of the valve, slightly anterior, several spots can be discerned through the valve, arranged with one above and the others closely spaced and forming a rosette. They are the adductor muscles, which extend through the body from one valve to the other and close the carapace by their contraction (Fig. 3). Posteroventral to the adductor muscles, a rapid rhythmic motion can be observed; this is the beating of a long exopod plate on the maxilla. Anteroventral to the adductors there is a very dark area, which includes the teeth and setae of the oral region, stained with juices of algae on which the animal feeds.

If the specimen happens to be a female, several eggs can be seen in the posterior half of the body. If it is a male, seven

short parallel bars show through the posterodorsal area of the valve; these are wreaths of chitin spines inside the ejaculatory apparati, or Zenker's organs (Figs. 1*b*, 4*c*). In the posteroventral region of the valve the gonads can be recognized. They lie in the hypodermis, a thin flap of tissue extending from the body and lining the inner suface of the valve. The female has a wide band, the ovary, in each valve, whereas the male has four narrow parallel bands, the testes, in each valve (Figs. 4*a*, *c*). The long hairs on the surface of the valve are setae, which lead through the shell to nerves in the underlying hypodermis and warn the ostracod of contact with other objects.

If undisturbed for a minute or two, the ostracod will open the valves and thrust out two pairs of appendages along the ventral border, the antennae near the front and the second thoracic legs near the rear. These are the walking appendages. When the animal rights itself, two thin appendages are swung out from the anterodorsal region, equipped with long delicate filaments, and used to "feel" the area in front of the animal. They are the antennules, which probably serve as tactile and balancing organs.

Needle Dissection

A very instructive dissection can be made of the ostracod "on the half shell". Remove an adult by a small pipette and place it on a blotter. The animal, finding itself out of water, will close the valves, and the outside of the carapace can be thoroughly dried. The ostracod can be handled easily by a small sable-hair brush moistened slightly. In the field of a binocular microscope, put a small quantity of Duco or other quick-drying, water-insoluble cement on a small glass slide and immediately place the ostracod in the cement on its side. Be certain the cement attaches the ostracod by only one valve. Submerge slide and ostracod in a shallow dish containing a chloretone solution. If a few small bubbles adhere to the carapace, they can be dislodged with the brush. After several minutes, the animal will relax its adductor muscles and gradually open the valves. When the specimen is completely anesthetized run it through alcohol to xylol, being careful not to expose the upper valve. If any part of the specimen dries during the procedure, air bubbles will adhere and cause difficulty in the dissection.

When the ostracod is in xylol, slip the tip of a bent needle under the edge of the upper valve and break the adductor muscles. The upper valve can then be removed entire and placed to one side for further examination. This kind of preparation shows many features of the body plan that "smear" preparations do not. A little practice will enable one to make "half shell" dissections accurately and efficiently.

General Body Plan

As can now be readily determined, the body of the ostracod has no distinct boundary between head and thorax. It lacks an abdomen. The body narrows abruptly behind the head, and the thorax tapers to the posterior end of the body. The anterodorsal part of the head is the forehead, the anteroventral part the upper lip, the ventral part the mouth, and the posteroventral the hypostome (Fig. 4*c*). The forehead and upper lip are joined and rigid, with a framework of chitin rods. The upper lip is thick and serrate on the rear edge, which forms the anterior border of the mouth. The hypostome is a movable sternum-shaped structure behind the mouth. The long uniramous antennules are attached to the forehead. The antennae are joined to the sides of the head near the junction of the forehead and upper lip. The mandibles are equipped with teeth that meet in the mouth and are used in mastication. The maxillae lie along the sides of the hypostome, which they more or less hide. There are three pairs of thoracic legs, each of different shape, and a terminal pair of furcae in the rear half of the ostracod. The genitalia lie between the 3d thoracic legs and the furcae.

Appendages and Furcae

The antennule (Figs. 1*a*, *b*) has seven podomeres, which are interpreted as coxa, basis, and five podomeres of the endopod. The four distal podomeres are provided with long setae used to explore the area in front

of the animal. The antenna is a walking leg, equipped with strong claws at the end. It has a short, strong coxa, a long basis, and an endopod of three podomeres. The long seta at the end of the basis may be a vestigial exopod. The antennae are dimorphic (Figs. 2*a, b*). In the male the penultimate podomere is nearly divided in half and bears, on its inner face, two heavy club-shaped setae thought to be sensory and used in copulation. On the rear edge of the first podomere of the endopod there is a sense club, a special sensory seta said to be a chemoreceptor.

The mandible is a powerful appendage. The long coxa is strongly chitinized and provided with masticating teeth at its ventral end. The palp, which extends forward and includes the basis and the three-podomere endopod, has small terminal claws; it sweeps food particles backward to the mouth. A thin, delicate, setiferous plate on the top of the basis is the exopod. It is said to be respiratory, but this may be questioned (probably all the surface of the body takes part in respiration).

The maxilla is difficult to study unless removed from the rest of the animal. Its voluminous base, hanging down over the side of the hypostome, consists of an undivided protopod. The endopod is a palp of two podomeres, which extends forward to the rear edge of the mouth. Medial to the palp, in a horizontal row, there are three endites, often called the "masticatory processes," although they do not masticate. The palp and endites have numerous setae at their ends, which convey food particles to the mouth. The exopod is a long, delicate, setiferous plate; it moves rapidly, several times a second, and creates currents along the side of the body that aid respiration and carry food particles into the carapace.

The 1st thoracic leg is pivoted to a lateral process on the posterodorsal end of the hypostome. The protopod is large, with the proximal part vertical and the distal part directed forward; the terminal setae convey food particles forward towards the mouth. The exopod is an inconspicuous little process with a few setae. The endopod is dimorphic. In the female (Fig. 1*a*) it is a long lobe on the rear part of the leg, provided with a few terminal setae. In the male (Figs. 2*c, d*) the left and right endopods differ slightly in size and shape; each is a clasping organ used to hold fast to the edge of the female valve during copulation. The flexible terminal part is called the finger.

The 2d thoracic leg (Figs. 1*a, b*) is long and uniramous. It is used in walking. The endopod is long, tapering, directed backward, and ends in a strong, curved claw. This appendage in some species of *Candona* is slightly dimorphic in the lengths of the podomeres and claw.

The 3d thoracic leg is modified as a cleaning organ. The undivided protopod hangs vertical, the first podomere of the endopod is directed backward, and the rest of the leg is directed dorsally. The protopod is extremely flexible; it can pivot and enroll on its axis to bring the leg to many positions. The very small terminal podomere has three long setae, which are used to sweep out foreign particles from inside the carapace.

Each furca has a long rodlike ramus and two terminal claws. The width of the ramus and the size and curvature of the claws differ slightly in male and female. The furca is used to clear foreign objects from the posterior part of the carapace. It does not appear to be locomotor.

The Valves

Each valve contains two calcareous parts. The distal part is the outer lamella; it is the only part seen when the carapace is closed. The proximal part, a narrow flange just inside the free edge, is the duplicature (Fig. 3), so-called because it duplicates the chitin-calcite-chitin structure of the outer lamella. The two parts are joined together by a thin layer of chitin, the adhesive strip.

The open channel between the duplicature and the outer lamella is called the vestibule (Fig. 3). It extends from the line of concrescence (the inner border of the adhesive strip) to the inner margin (the inner edge of the duplicature). The duplicature has thin chitin ridges on the medial face, which fit into grooves of the opposite duplicature and hermetically seal the valves when drawn together.

The valves are attached to the adductor muscles, which draw them together and to muscles that operate several anterior appendages, lead to the endoskeleton, and adjust the body. The muscles leave permanent

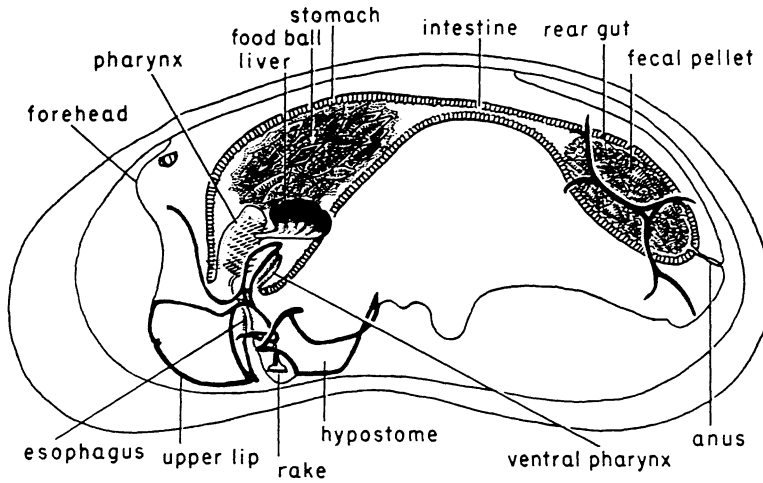

Fig. 5. *Candona suburbana.* Digestive system. Right half of the system in the male. The body framework of the left side is added in solid black.

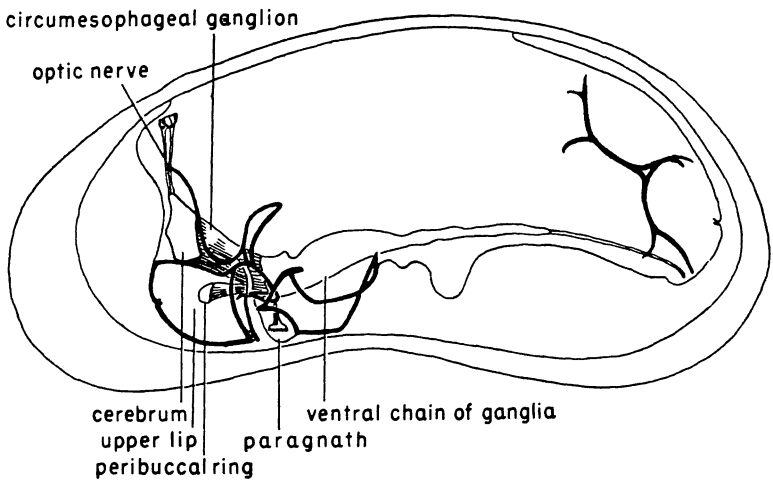

Fig. 6. *Candona suburbana.* Nervous system. Right half of the system in the male; the body framework of the left side is added as in Figure 5.

scars at their points of attachment.

New valves are formed after each ecdysis. They are secreted by the hypodermis. Nerves in the hypodermis are connected to setae on the outside of the valve by pore canals. The small round pores through the outer lamella are known as normal pore canals, and those through the adhesive strip as radial pore canals.

The male (Fig. 1*b*) has much greater volume in the posterior half of its carapace than the female (Fig. 1*a*). The additional space accommodates the large penes and the Zenker's organs.

Sex Systems

In both female and male, the sex system is paired, and the left half is not connected to the right. The female system (Figs. 4*a*, *b*) includes ovaries, uteri, uterine openings, vaginae, and seminal receptacles. The external parts are a pair of genital lobes between the 3d thoracic legs and the furcae. Each lobe is pointed at the rear in *Candona,* and the shape of the tip is regarded as a specific character. Each genital lobe contains two openings, a uterine opening and a vagina.

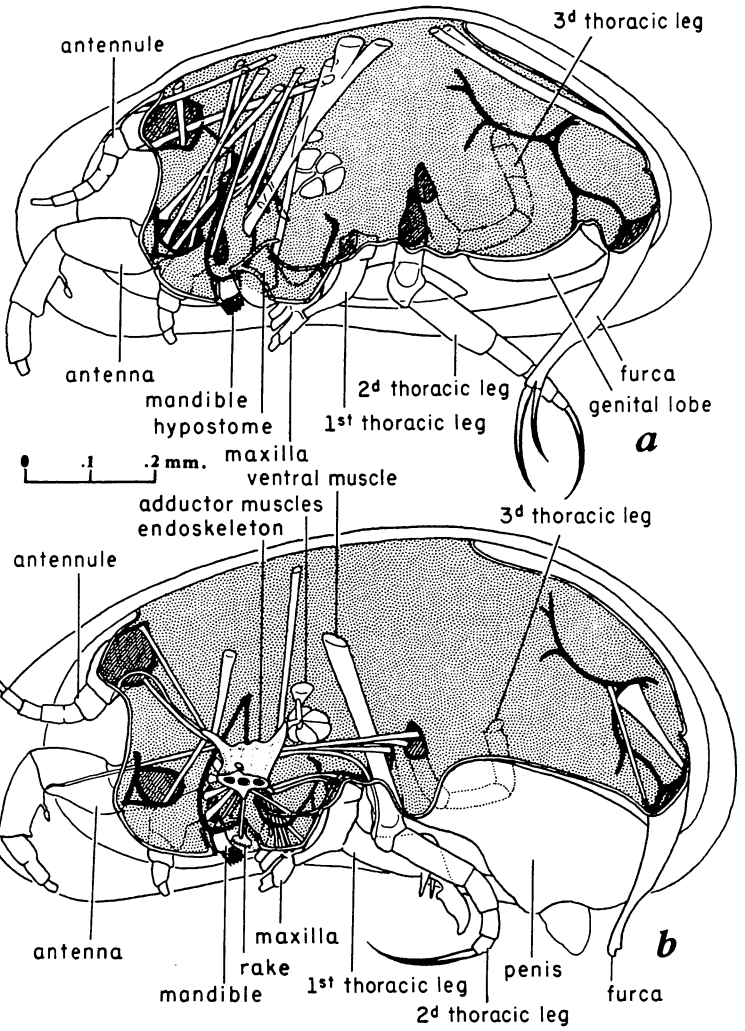

Fig. 7. *Candona suburbana*. Musculature. *a*. Female with muscles attached to dorsal part of right valve. *b*. Male with muscles attached to the endoskeleton, adductor muscles, dimorphic ventral muscle, and furcal muscles in the right half of the body.

To study details of the internal female organs it is necessary to make serial sections. The specimen must be decalcified before embedding. Sections show clear differentiation of tissues with Ehrlich's haematoxylin and eosin.

The ovary (Fig. 4*a*) is often left in the hypodermis when the valve is removed. If not, it can be found in a smear of the body contents or identified in serial sections. The posterior end is the syncytium. Eggs are formed and push forward with growth. The ostracod ovary is particularly good for study of oogenesis, because stages of differentiation are present in positional, as well as chronological, sequence. The ovary starts in the posterior part of the hypodermis, curves down, forward, and up, and enters the body as the uterus without a demarcation.

The uterus (Fig. 4*b*) is distended with eggs in every adult female. In the front section of the uterus, the shell is added to the eggs, first as small granules and finally as a strongly chitinized coating. The eggs are laid through the uterine openings on

the inner edge of the genital lobe.

The vagina is both the adit and exit for spermatozoa. The vagina leads into a spiral canal, which can be seen through the body wall, and thereby into the seminal receptacle. Seminal receptacles in bred females are distended with scores of spermatozoa. (In syngamic species, unbred adult females are hard to find.) The seminal receptacles are not connected to the uteri. The genital lobe contains numerous muscles that draw the vagina and uterine opening together, and spermatozoa are thought to pass into the uterus by this route.

The male penis is strongly modified in the ostracod by the carapace. It must be long enough to reach out from the carapace of the male into that of the female, but it must also be retracted when the male closes his valves. It is very complex, and not completely understood. Each of the paired penes has lateral chitinous shields and three lobes inside (Figs. 1*b*, 4*c*). Only the front end is joined to the body.

The four testes in each half of the hypodermis are curved and parallel; they lie in about the same position as the ovary in the female. They enter the body and unite to form a vas deferens. Each vas deferens has a devious circuit before it reaches the penis. It re-enters the hypodermis in the anterodorsal region, curves parallel to the free edge, and extends to the posterodorsal region as a blind section. This part of the vas deferens is sometimes confused with the testes, and some accounts list five testes in the hypodermis. Spermatozoa reaching the blind end reverse their direction. In the ventral region the vas deferens divides, with the second branch running parallel to the first and entering the body in the anterodorsal region (Fig. 4*c*). Thence, the vas deferens extends to the posterior half of the body, loops back and forth a few times, encircles the Zenker's organ, and enlarges to form a seminal receptacle. In smear preparations, the seminal receptacles are usually broken open, releasing the mass of long spermatozoa.

In back of the seminal receptacles are the Zenker's organs. Each Zenker's organ surrounds a narrow part of the vas deferens. It consists of seven wreaths of chitin spines and an enclosing membrane. Hundreds of tiny muscles connect the spines in such a way that the organ can rhythmically contract to pump spermatozoa out by a narrow tube and through the inner lobe of the penis.

Digestive System

The ostracod has an elaborate set of food-gathering devices. The upper lip is fixed, except for a median movable process in its posterior region, but the oral edge is serrate. The hypostome, however, is swung back and forth by muscles and serves to concentrate particles in the mouth (Fig. 5). Along its front edges the hypostome has a pair of soft setiferous lobes, the paragnaths (Fig. 6), which move food forward. The rakes (Fig. 5), two chitinous serrate structures embedded in the front part of the hypostome, lift particles upward.

Food is swept backward to the mouth by the mandibular palp and forward to the mouth by the palp and endites of the maxilla and by the protopod of the 1st thoracic leg.

The only masticatory organs are the mandibles, which have strong teeth at the ventral ends of the coxae. The teeth meet in the center of the mouth.

The mouth, esophagus, pharynx, and ventral pharynx are covered with chitin and form the stomadaeum. A pair of glands in the upper lip, called the salivary glands, empty into the mouth and are supposed to secrete digestive fluid. Food is moved upward in the esophagus by muscular action and pitched into the stomach by setae on the movable pharynx and ventral pharynx.

A liver or hepatopancreas empties into each side of the stomach. The food forms a food ball in the stomach, surrounded by digestive fluid, presumably supplied entirely by the livers. Later it passes through a narrow intestine into the rear gut and becomes a fecal pellet. Most, if not all, digestion takes place in the stomach. There is little proctodaeum, and the anus is a simple unmuscled opening.

Nervous System

The nervous system resembles that of other crustaceans. The cerebrum is located in the lower part of the forehead. It can be subdivided only by the nerves leading into it. The circumesophageal ganglia join the cerebrum to the ventral chain of ganglia (Fig. 6). From the front end of the ventral chain there is a peribuccal ring of nerves extending into the upper lip. The ventral chain tapers posteriorly and ends at the furcae.

In addition to the central nervous system, there are ganglia in the basal parts of the appendages. Sensory nerves lead from the appendages, furcae, digestive system, and hypodermis to the central system.

Musculature

Muscles in the ostracod are attached to the valves, the framework of the body, and the endoskeleton. Their arrangement can be worked out from serial sections. From the dorsal part of the valve (Fig. 7*a*) muscles extend to the antennules, antennae, mandibles, hypostome, and rear part of the body. Other muscles attached to the valve (Fig. 7*b*) are those to the endoskeleton, the adductor muscles, and (in the male only) ventral muscles. The ventral muscles are used in copulation; by contraction they strongly compress the body, turn the Zenker's organs about 90 degrees, and swing the penes out of the body and forward. They also unfold the complicated penes, which contain no muscles.

The endoskeleton is an elaborate chitin structure behind the esophagus and below the stomach. It is embedded within the body, and suspended from the dorsal part of the carapace. It has muscles leading to the appendages, the hypostome, the rakes, and the adductor muscles. The muscles to the mandibles are exceptionally well developed.

The furcae are operated by muscles attached to the chitin framework on the rear part of the body (Fig. 7*b*).

Ontogeny

The ostracod grows by ecdysis, like other arthropods. It meticulously sheds the chitin covering of the appendages and body as well as the valves. *Candona* has nine instars, of which only the last is mature. Space precludes a detailed account of the succession of appendages. In general, the animal hatches with antennules, antennae, and mandibles, and other appendages are added in later instars. Appendages first appear as anlagen and later add podomeres and setae to assume the definitive form. Sex organs appear in the eighth instar, but are neither clearly differentiated nor functional until the final, or adult, instar.

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