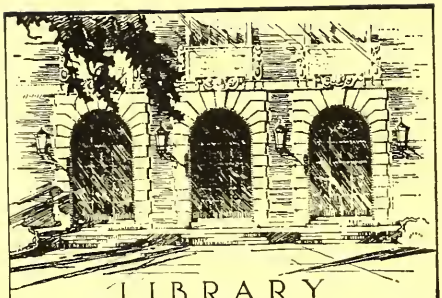

The Morphology of Ostracod Molt Stages

BY ROBERT V. KESLING

ILLINOIS BIOLOGICAL MONOGRAPHS: *Volume* XXI, *Nos. 1-3*

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Contents

Introduction

Recent oil explorations have increased the importance of micropaleontology, which can be used to determine the stratigraphic sequence in many cases. Ostracods are now being used as stratigraphic markers, and their use will be increased if greater taxonomic accuracy can be obtained. The small size of the animal, less than one millimeter in length in most species, permits whole faunas to be secured from well cuttings and well cores. Ostracods are also prolific in many formations, so that relatively small amounts of material are necessary to obtain abundant specimens. The hard parts are well preserved, even in many highly indurated and folded strata.

The ostracods have a long geologic range, so that additional information on the zoology, biology, and ecology of the animal can be applied to a large number of genera occurring in many formations. Further, the value of the ostracod is increased by its adaptation to fresh-water environments as well as marine.

Much of the taxonomic work on fossil species has been done by paleontologists who understood very little about the nature of the living animal. Conversely, much of the classification of living species has been done by zoologists with little or no knowledge of fossil forms or the geologic history of the order. The result has been two systems of classification, the one based on the size, shape, and ornamentation of the shell and the other on the finer details of the appendages. This impasse has even reached a point where a single specimen is classed as one genus by the paleontologists and another genus by the zoologists.

Although much taxonomic work on fossil and living ostracods is being done in the United States, there is not an adequate description of an ostracod in the English language. One of the best available descriptions is given by Hoff (1942, pp. 41-49), who found it imperative to devote a section of his taxonomic work to the morphology of fresh-water ostracods so that his systematic work could be more fully understood. Most of the morphological work on ostracods was done by German workers between 1854 and 1926. A recent monograph by Dom Remacle Rome (1947), a French worker, gives some additional facts about ostracod structures.

The incomplete knowledge of the ostracod has caused some important paleontological questions to remain unanswered. Many structures, such as the so-called brood pouch, are found on fossil forms and not on living ones, and there is no adequate explanation of their function or signifi-

cance. Indeed, there is even a question in many fossil species as to which end of the shell is anterior and which posterior, and it is quite possible that the dorsal and ventral orientation has been reversed in some instances. Where the specimens are scarce in a formation and vary in size, it is problematical whether the small specimens are adults of a small species or only instars of a larger species. At the present time there is no way of determining from a single specimen what instar is represented. Another problem arises from the differences in shell shape and size due to sex differences. It is known from living species that there are greater differences between the male and the female of one species than between females of different species, and the determination of sex in fossil forms is largely conjecture. These are only a few of many unanswered problems in micropaleontology.

The writer chose *Cypridopsis vidua* O. F. Müller as a living species for investigation because it has several characteristics advantageous to a complete study. It belongs to the family Cypridae, which has both freshwater and marine species. The genus *Cypridopsis* is reported back as far as the Pennsylvanian period by Scott (1944, p. 144). The species *vidua* is geographically widespread and has been reported from North America, Paraguay, northern Africa, Europe, western Russia, and the Azores. Furthermore, it is adapted to a variety of environments, including mountain lakes, brackish water, streams, lakes, and ponds. It is abundant in many locations. This common ostracod is easily cultured for laboratory observations. *Cypridopsis vidua* reproduces parthenogenetically, and the lack of any males insures that all immature instars are of the same sex.

The study of this species has been designed to give a full description of a typical living ostracod, some pertinent biological information, and a comparison of the valves of the various instars.

The writer wishes to acknowledge the kind assistance and guidance of Dr. Harold W. Scott of the geology department and Dr. Harley J. Van Cleave of the zoology department of the University of Illinois. The microtome sections were prepared by Miss Marion Birkner under the direction of Dr. Van Cleave. The X-ray pattern of the shell material was made by Mr. Karl Koenig. The work was done while the writer held fellowships from the Shell Oil Company (1947-48) and the California Company (1948-49).

I. Taxonomy

Order OSTRACODA Latreille

Latreille (1802, p. 17) was the first to use the term Ostracoda, which he originally spelled "Ostrachoda." However, he included genera of both Ostracoda and Cladocera under this designation.

Straus (1821, p. 58) was the first to set up a group to include the genera which we now consider ostracods. He termed this group *Ostrapodes,* as set aside from the Cladocera also included in Latreille's Ostracoda. Since this is the first term applied to this group of organisms, they should by rules of nomenclature be called *Ostrapodes.* Since the term Ostracoda has been accepted for such a long time, it is doubtful if it will ever be replaced by the rightful designation.

The common German name for the ostracods is *Muschelkrebse,* and Johansen (1921, p. 88) suggested the English equivalent "mussel-shrimps," but the usage has never been widely followed.

The ostracods are characterized by having a dorsally hinged bivalved shell and at most only five pairs of post-oral appendages: maxillae; first, second, and third thoracic legs; and the furcae (which are often not classed as appendages). The shell has no growth lines, which distinguishes it from the shells of certain phyllopods (Conchostraca) and certain small mollusks (Sphaeriidae).

Family CYPRIDAE Zenker

In this family of ostracods all the thoracic legs are different, the exopodite of the antenna is greatly reduced, and the teeth of the hinge are greatly reduced. The surface of the shell is usually smooth. The antennules and the antennae are usually equipped with long natatory setae. The first thoracic leg is modified as an auxiliary feeding structure.

Subfamily CYPRIDOPSINAE

Shell high and short, 1 mm. or less in length. Antenna of five podomeres. Outer "masticatory" process of the maxilla with two strong setae. Third thoracic leg with distal pincers arrangement. Furca reduced to a base ending in a long seta or "flagellum."

Genus CYPRIDOPSIS Brady 1867

Shell tumid; valves approximately the same size. Natatory setae of the antennules and antennae well developed. Terminal podomere of the maxillary palp longer than wide.

Brady and Norman (1896, p. 725) proposed the genus *Pionocypris* for ostracods of this description having the left valve overlapping the right anteriorly and posteriorly, and restricted the genus *Cypridopsis* to those species having the right valve overlapping the left. The genus *Pionocypris* has not been generally accepted. The writer has not examined other species of *Cypridopsis* (as used here), many of which are limited to Europe; so he does not offer an opinion on the validity of Brady and Norman's genus and follows the generally accepted use of the genus *Cypridopsis*.

CYPRIDOPSIS VIDUA (O. F. Müller 1776) Brady 1867

Cypris vidua O. F. Müller 1776. O. F. Müller, 1776, p. 199; Müller, 1785, p. 55; Zaddach, 1844, p. 35; Baird, 1849, pp. 152-53; pl. 19, figs. 10-11; Zenker, 1854, p. 79; Chyzer, 1858, p. 512; Claus, 1868, p. 151, pl. 1, figs. 6-8; Frič, 1872, p. 227, also called *Gestreifter Muschelkrebse, Lasturnatka žíhovaná;* Chambers, 1877, p. 155; Underwood, 1886, p. 337.

Monoculus vidua (O. F. Müller 1776) Jurine 1820. Jurine 1820, p. 175.

Cypridopsis vidua (O. F. Müller 1776) Brady 1867. Brady, 1867; Herrick, 1887, p. 31; Sars, 1890, p. 17; Vávra, 1891, pp. 75-77, fig. 23; Richard, 1896, p. 173; Turner, 1896, pl. 5, fig. 13; Kaufmann, 1900 a, p. 107; G. W. Müller, 1900, pp. 80-81; Sharpe, 1903, pp. 990-91; Daday, 1905, p. 252; Cushman, 1907, pp. 37-38; Kofoid, 1908, p. 258; Vávra, 1909, pp. 114-15; Fowler, 1912, pp. 72-73; Weckel, 1914, p. 179; Wohlgemuth, 1914, p. 16; Sharpe, 1918, p. 807, fig. 1253; Wolf, 1919, p. 44; Korschelt, 1920, p. 73; Herr, 1921, p. 15; Klugh, 1921, p. 73; Schreiber, 1922, p. 493; Bronnstein, 1924, p. 82; Reed and Klugh, 1924, p. 274; Bronnstein, 1925, pp. 3, 6, 16; Holmes, 1937, p. 492; Graf, 1940, p. 486; Klie, 1940, p. 61; Redeke and Dulk, 1940, p. 143; Hoff, 1942, p. 151; Hoff, 1943a, p. 53; Hoff, 1943b, p. 117.

Cypriodopsis [*sic*] *vidua* (O. F. Müller 1776) Ferguson 1944. Ferguson, 1944, p. 719.

Cypridopsis vidua vidua G. W. Müller 1912. G. W. Müller, 1912, p. 210; Furtos, 1936, p. 491, Dobbin, 1941, pp. 230-31.

Cypridopsis vidua obesa Towle 1900. Towle, 1900, p. 347; G. W. Müller, 1912, p. 210; Furtos, 1933, p. 431.

non Cypridopsis obesa Brady and Robertson 1870. Brady and Robertson, 1870, p. 15.

Cypridopsis vidua helvitica G. W. Müller, 1912. G. W. Müller, 1912, p. 210.

non Cypridopsis helvitica Kaufmann 1900. Kaufmann, 1900b, p. 310.

Cypridopsis pustulosa Furtos 1933. Furtos, 1933, pp. 431-32.

? Cypridopsis crassipes Masi 1909. Masi, 1909, pp. 372-74, pl. 12, fig. 8.
Pionocypris vidua (O. F. Müller 1776) Brady and Norman 1896. Brady and Norman, 1896, p. 726; Norman and Scott, 1906, p. 113; Sawaya, 1942.
Pionocypris vidua vidua (G. W. Müller 1912) Gauthier 1939. Gauthier, 1939, pp. 225-26.

Type Locality: Europe.

Description of the Adult Female: Shell smooth, ovoid. Greatest height approximately two-thirds of the length, and located slightly anterior to the middle of the shell. Shell tumid when viewed from above. The greatest width a little more than the height, and located slightly posterior to the middle of the shell. The ventral margin slightly sinuate in lateral views. The surface marked by very minute depressions. Shell hairy, particularly near the borders of the valves. The left valve slightly overlaps the right anteriorly, posteriorly, and ventrally; very little overlap in the region of the hinge. The anterior margin of the right valve equipped with fifteen to twenty tubercles, varying in size with individuals. The color of the shell pale green, yellowish green, yellowish white, or pale yellowish brown. The shell marked by four bands of color varying from light green to deep green, and even black in some individuals. The color bands located in general: one anterior, one immediately behind the eye, one slightly posterior to the middle, and one near the posterior end.

The bands extend from the dorsal margin down the sides of the valves, and the location and size of these markings are variable. Some individuals have bands so pale they can be seen only by transmitted light. Individuals collected from the same locality show wide variations in color and markings.

The natatory setae of the antenna extend beyond the terminal claws. The exopodite of the first thoracic leg bears five setae. The outer "masticatory" process of the maxilla has two sharp, blade-like setae without notched borders.

Length of the adult shell is approximately 0.65 mm.

II. General Description

Body Segmentation

The structure of the ostracod has been profoundly influenced by the development of an enclosing shell in the very early history of the order. Apart from the appendages, the various structures of the animal do not show close affinities with those of the higher Crustacea.

The compact, shortened body can be seen only after removal of one of the valves of the shell. It has no true segmentation, although there is a slight constriction of the body near the middle to mark the boundary between the two regions of head and thorax. There is no abdomen. The body tapers bluntly at the posterior end and terminates in a pair of preanal furcae. There are seven pairs of appendages: the antennules, the antennae, the mandibles, the maxillae, and three pairs of thoracic legs. The first four pairs are attached to the head and are used chiefly for swimming, walking, and feeding. The three pairs of thoracic legs are part of the thoracic region and are adapted for feeding, creeping, and cleaning of the shell. The thorax also contains the genital regions.

The body of the ostracod occupies the middle two-thirds of the length and is suspended from the dorsal region as an elongate chitinous pouch. It is very deep and rather blunt at the anterior end, tapers slightly throughout its length, and ends rather abruptly at the posterior end, where the paired whip-like furcae are attached.

Head Region

The head portion of the body has, in addition to the appendages, three prominent features which are intimately connected with the arrangement and operation of the appendages: the forehead, the upper lip, and the hypostome.

The forehead and upper lip are closely connected. Both are formed of a framework of chitinous rods with a continuous flexible chitin cover. The forehead protects the median eye and provides sockets for the antennules and antennae. It is narrowly rounded and forms the dorsal anterior termination of the body.

The antennules, sometimes referred to as the first antennae, are the first pair of cephalic appendages. They are long and tapering uniramous structures, formed of the endopodite only. The strong broad bases are inserted in the forehead somewhat below the level of the median eye and very close together. The seven podomeres of each antennule taper to very

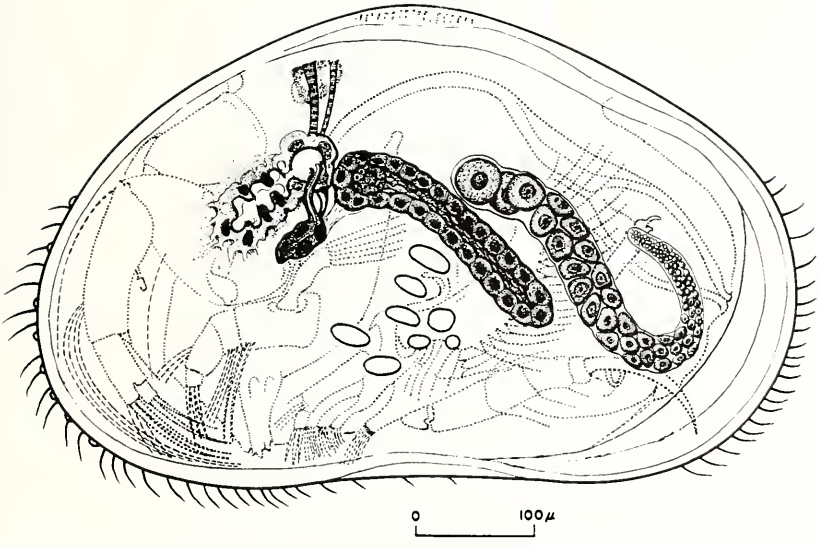


FIG. 1. Left valve of *Cypridopsis vidua* with the outer chitin and the calcareous layers removed to show the organs in the epidermis.

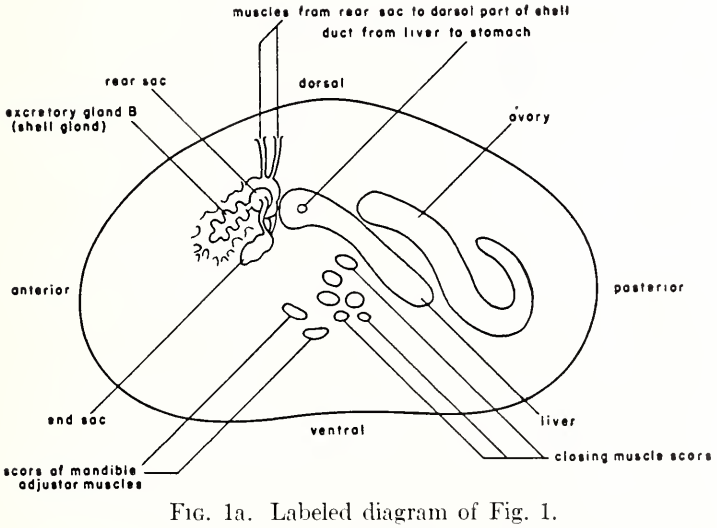


FIG. 1a. Labeled diagram of Fig. 1.

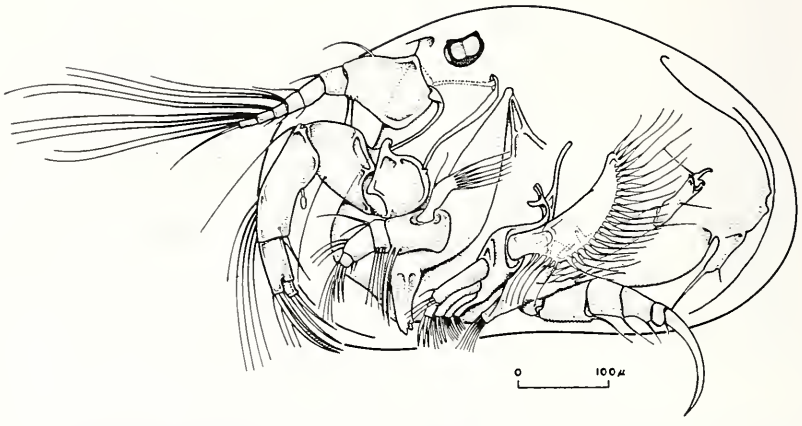


FIG. 2. *Cypridopsis vidua* with the left valve removed to show the appendages.

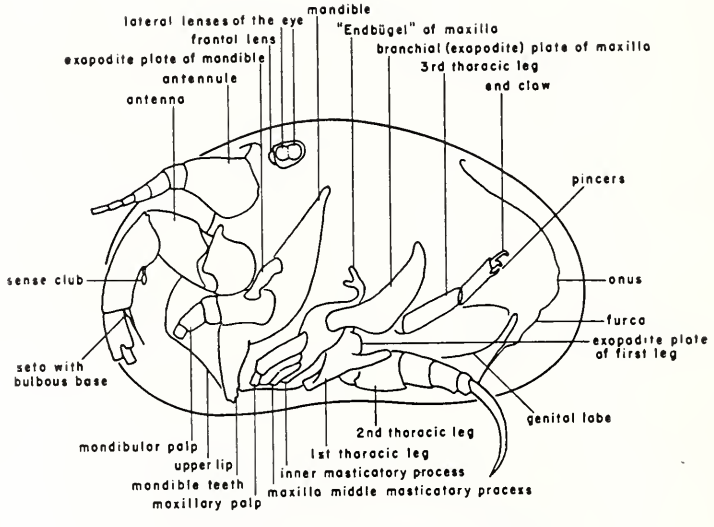


FIG. 2a. Labeled diagram of Fig. 2.

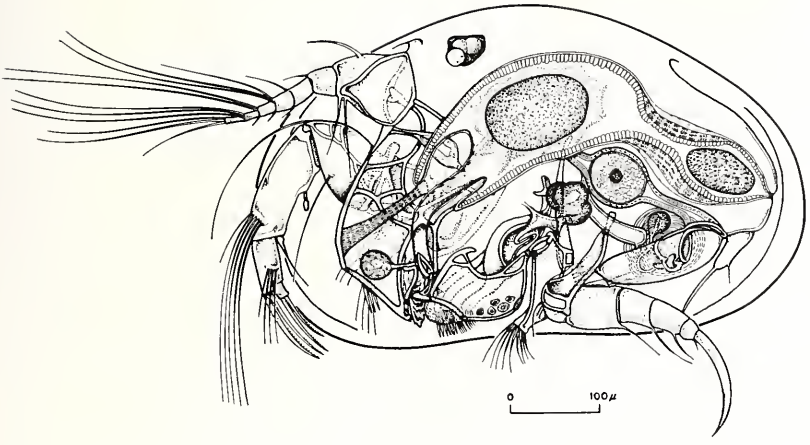


FIG. 3. *Cypridopsis vidua* cut along the median sagittal plane, and with the left half removed.

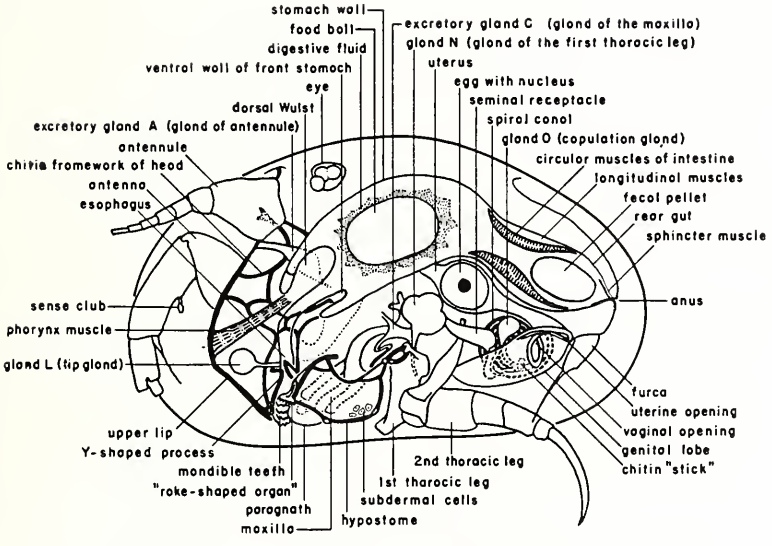


FIG. 3a. Labeled diagram of Fig. 3.

small diameter at the distal end. The four distal podomeres are equipped with very long, feathered setae which are used for swimming and for balance. The two antennules curve forward and downward and diverge somewhat at the ends. The long setae spread out forward in a horizontal plane like two fans. When the animal is walking or climbing, these long setae are constantly feeling the area in front of it.

The antennae, also known as the second antennae (when the antennules are referred to as the first antennae), are the second pair of cephalic appendages. They are attached at the side of the forehead below the antennules, very near the junction with the upper lip. The antennae are more strongly constructed than the antennules and bear long claws at the end. The five podomeres may be classed as two of the protopodite and three of the endopodite. The exopodite is either absent entirely or represented by a thin seta. The antennae are directed forward, then down, and distally posterior and ventral. The first podomere of the endopodite bears two essential features: the swimming or natatory setae and a sense organ. The five long, feathered setae are attached to a scale on the distal inner margin, and extend beyond the terminal claws. The sensory organ is club-shaped and suspended from the ventral posterior margin near the middle of the podomere. In swimming, the ostracod uses the antennae and the very flexible antennules simultaneously to row itself through the water. The antennules are flexed upward and back, while the antennae are forced downward and back.

The helmet-shaped upper lip lies immediately below the forehead and forms the anterior ventral termination of the body. The rear ventral rim of the upper lip is the forward edge of the mouth opening. There are no appendages attached to the upper lip and it can be seen clearly in a side view of the dissected animal.

From the chitinous framework of the upper lip there are two triangular chitinous processes projecting into the mouth cavity.

The heavily toothed mandibles lie on either side of the mouth in indentations between the upper lip and the hypostome. The first podomere of the mandibles is elongate and lies almost vertical along the sides of the body, its dorsal tip reaching nearly to the level of the antennules. About one-third of the distance from the teeth toward the dorsal tip, a palp projects anteriorly from the elongate podomere. This palp is strongly developed and consists of a second podomere of the protopodite and three additional podomeres representing the endopodite. From the second podomere of the protopodite (basal member of the palp) a delicate, hand-shaped branchial plate extends dorsally from a chitinous socket. This is the exopodite. It terminates in long, tapering hairs. The endopodite has many long setae extending downward and forward from the two proximal podomeres, which curve downward. The third podomere is shortened and

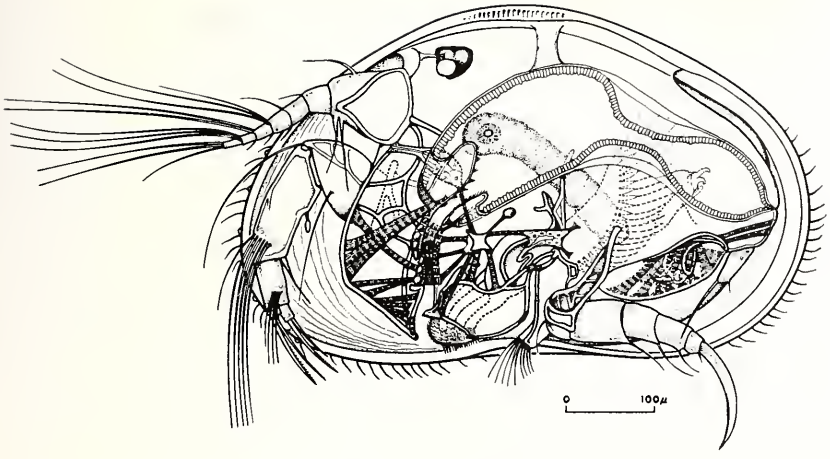


FIG. 4. Right half of *Cypridopsis vidua*. Gland L, gland N, and the genital organs have been removed to show the musculature.

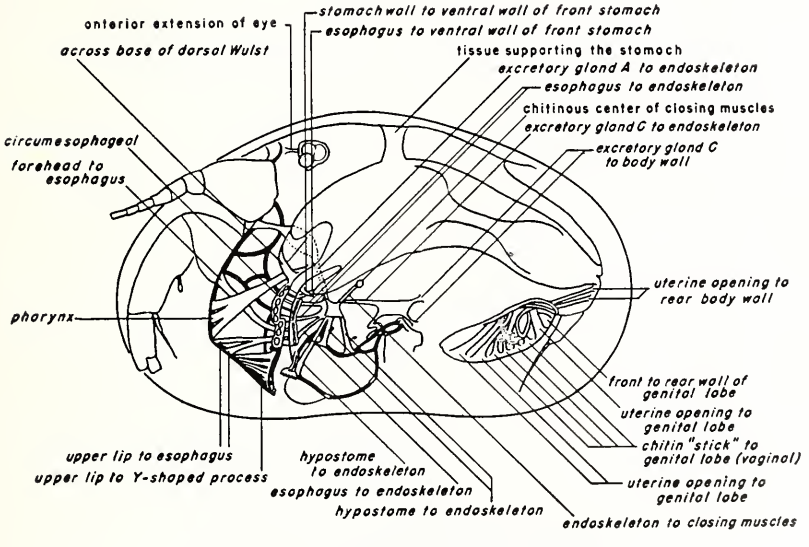


FIG. 4a. Labeled diagram of Fig. 4.

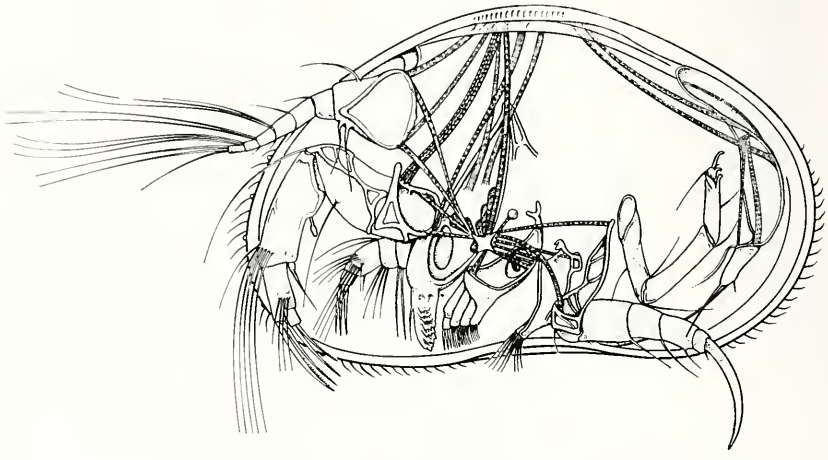


FIG. 5. Right half of *Cypridopsis vidua*. Forehead, upper lip, hypostome, digestive system, and the genital organs have been removed.

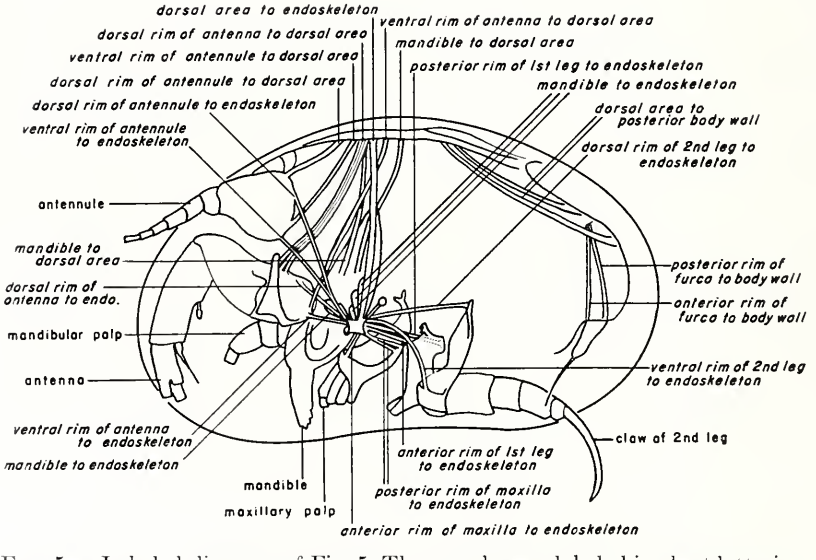


FIG. 5a. Labeled diagram of Fig. 5. The muscles are labeled in slant lettering.

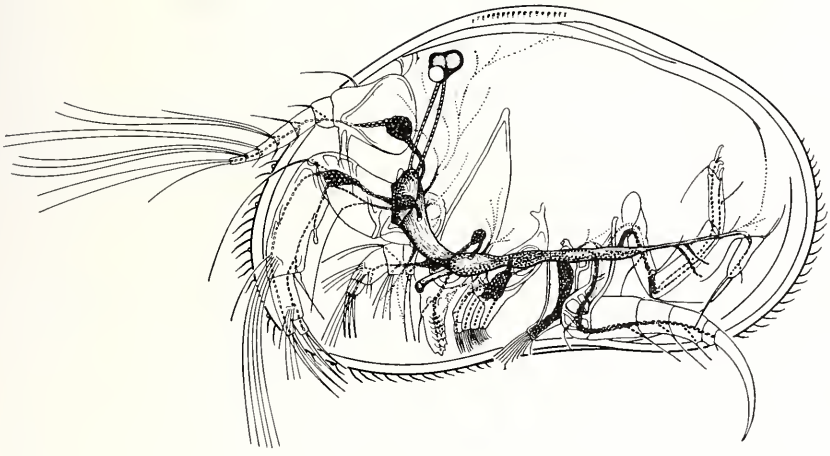


FIG. 6. Right half of *Cypridopsis vidua* showing the nervous system.

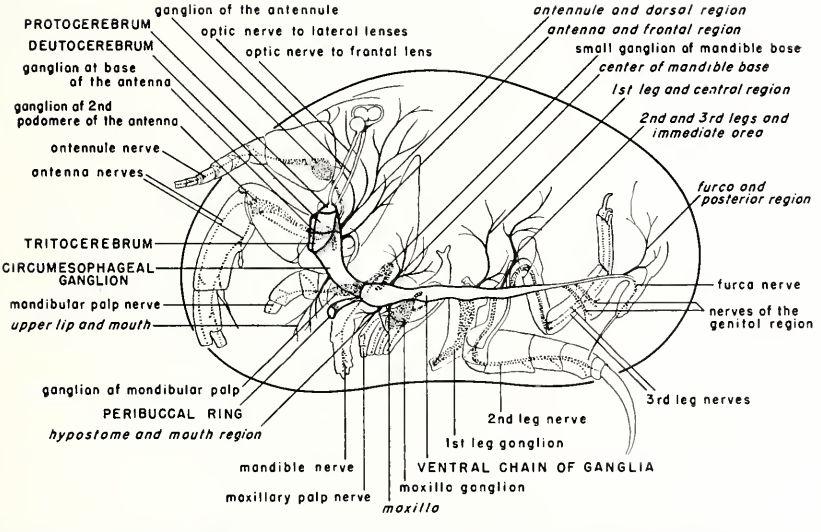


FIG. 6a. Labeled diagram of Fig. 6. Sensory nerves are indicated by vertical lettering, and the motor nerves are indicated by slant lettering.

armed with three strong claws at the end. The palp is used as a feeding and feeling organ.

The hypostome is the ventral posterior portion of the head. It is a keeled structure, shaped like the sternum of a bird. The forward end widens to make the posterior portion of the mouth. The pointed posterior end of the hypostome curves upward and terminates in a chitin girdle-shaped loop. At the rear of the mouth is a pair of chitin shafts with toothed structures on the ends. These are frequently ignored or misinterpreted in ostracod descriptions. They are called *rechenformig* or rake-shaped organs by Claus, and that descriptive term will be used in this paper. The rake-shaped organs are straining and feeding structures.

The fourth pair of cephalic appendages, the maxillae, lie behind the mandibles and on the sides of the hypostome. The basal podomere is strongly developed and ends distally in three short, cylindrical masticatory processes, which are scarcely movable, and a palp of two podomeres bearing fine claws and setae, which can move independently of the basal member. The exopodite is especially well developed in the maxilla as a branchial plate bearing numerous feathered setae on the posterior rim. This plate is respiratory in function and in seventh and eighth molt stages, where the calcium carbonate and coloring of the shell are not as dense as in the adult, it can be clearly seen in the living animal continuously sweeping forward and back on its basal pivot. The palp and three distal masticatory processes lie more or less in a transverse plane, so that a side view usually shows only the outermost member, the palp. The maxilla slants forward and down in the animal, and in the lower portion is strongly curved around the hypostome. This brings the masticatory processes of the two maxillae to the median plane immediately posterior to the teeth of the mandibles. Although the small processes themselves have very little independent motion, the whole maxilla is in rapid motion in the feeding processes, passing small particles toward the mouth.

It has been noted that the boundary between the head and thorax is not sharply set off. This is particularly true in the Cypridae. The hypostome at the posterior end slants upward and converges in a prow structure. At the dorsal posterior tip of this prow, a chitin girdle is formed of processes which extend laterally on the sides and then recurve and join to form a loop. From the outside tips of this girdle, the first thoracic legs are suspended.

Thoracic Region

The first pair of thoracic legs is modified in the Cypridae for feeding. It was their position and function which led early German workers to refer to this pair of legs by other terms. Zenker called them the *zweites*

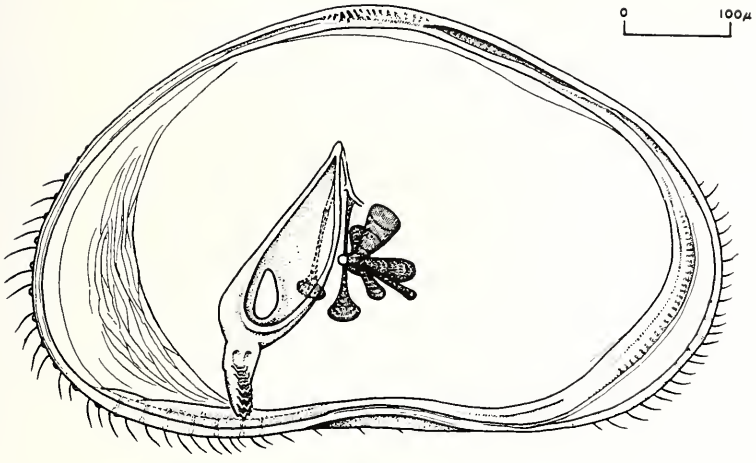


Fig. 7. Right valve and mandible of *Cypridopsis vidua*. The closing muscles and the mandible adjustor muscles are also shown.

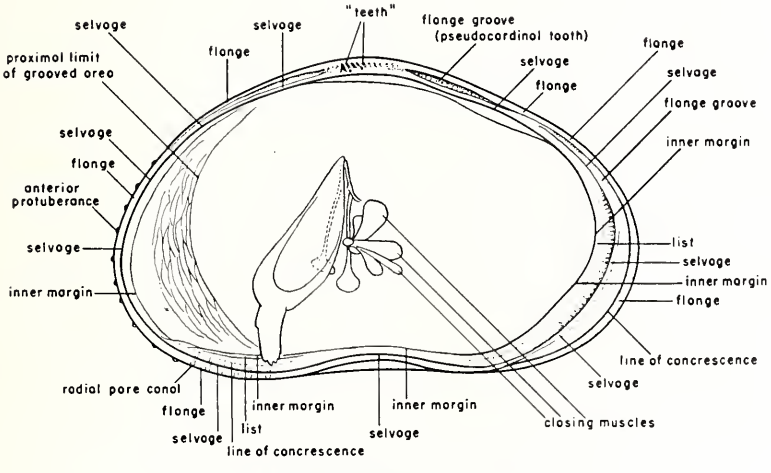


Fig. 7a. Labeled diagram of Fig. 7.

Maxillenpaar (second pair of maxillae), and Claus referred to each of them as a *Kieferfuss* (jaw-foot). However, a morphological comparison with the Cytheridae, where the thoracic legs are all very similar, shows these legs to be modified thoracic legs, and they are discussed here as appendages of the thorax.

The leg is small, and because of its position behind and under the maxilla, it is difficult to see in a side view. It has the shape of an inverted T; the protopodite makes the stem and anterior half of the crossbar, and the palp (endopodite) makes the posterior half. The distal end of the protopodite is provided with rather long setae which are used in feeding. This portion of the leg normally lies almost horizontal, pointing toward the mouth, and partially obscured by the masticatory processes of the maxilla. The palp extends posterior and outward, and bears three long setae on the distal end. There is also an exopodite, a delicate semicircular branchial plate, which extends posteriorly from the vertical stem. This bears five tapering hairs on the posterior rim which are transparent and difficult to see in unstained material.

The second pair of thoracic legs is strongly developed for use in walking, climbing, and clinging to inclined surfaces. Each is composed of five podomeres and terminates in a strong, curved claw. The basal podomere of this uniramous appendage is often incompletely described in literature. It lies almost vertical, behind the first thoracic leg and the hypostome. It is covered by a strong, complex chitin framework, and is strongly joined to the body on the dorsal and inner margins. The other four podomeres are directed backward horizontally. The first three are well developed, and the fourth is short and tapered, like a truncated cone. This distal podomere is strongly attached to the strong claw, but has great freedom of movement at its junction with the penultimate podomere. In walking and clinging, the two strong claws of the second thoracic legs act in a forward direction in opposition to the backward action of the terminal claws of the antennae.

The third pair of thoracic legs is modified for cleaning the inside of the shell. Each of the legs is directed downward, then backward, and then dorsally, so that the shape is that of a modified U. The first podomere of this uniramous appendage is the most flexible and complexly muscled podomere of the whole animal. The chitin forming the cylindrical wall is delicate and highly flexible, enabling the leg to turn a full 180° on itself. Thus the range of the cleansing action of this appendage covers almost the entire interior of the shell. Of the three other podomeres, the first two are long and the terminal is very much shortened. The penultimate podomere is notched inward at its distal end. Around the dorsal border of this notch it bears a semicircular fringe of hairs. The ventral border of the notch is modified as a small chitin plate. This plate is the ventral face of

a curious set of pincers at the end of the leg. The dorsal face of the pincers is a projection of the ultimate podomere. In addition, the short ultimate podomere also bears an elongate, toothed claw which can be used for dislodging foreign, irritating materials from between the body and the shell. The pincers are a very efficient organ, and can be observed to seize small foreign particles and remove them from the shell.

The genital regions lie behind the third thoracic legs, on the ventral surface of the thorax. They are seen externally as two lobes, elongate between the thoracic legs and the furcae. Near the middle of the lobes, on the sides nearest the medial plane, are the paired vaginal openings, framed with thick chitin. The paired uterine openings lie behind and inside the vaginal openings.

The furcae are much reduced in this species, and appear as short bases with tapering "flagella" at the distal ends.

Digestive System and Glands

The digestive system consists of the mouth, esophagus, stomach, intestine, rear gut, and anus. The mouth is a large atrium with the distal ends of the mandibles at the two sides, the upper lip at the front, and the hypostome at the rear. The esophagus is very muscular and leads upward into the large stomach. The movement of food from the esophagus into the stomach is aided by a large tongue-shaped organ at the front of the stomach, called the dorsal *wulst*. The stomach is separated from the large rear gut by a narrow, heavily muscled passageway, here termed the intestine. Most of the digestion takes place in the stomach. The food is formed into balls which pass from the stomach into the rear gut, and finally are expelled as fecal pellets.

The livers lie in the epidermal layers of the two valves and pour their secretion into the anterior part of the stomach through two lateral ducts. This secretion acts as a digestive fluid.

Excretion is accomplished by three pairs of glands, here called excretory glands A, B, and C. The first pair is located on the sides of the esophagus and empty below the antennules through ducts. The second pair is located in the epidermis of the valves, opening between the valves and the antennae by short ducts. The third pair is found near the middle of the body, and empty behind the maxillae through S-shaped ducts.

There are also glands producing secretions, which are here called glands L, N, and O. The first pair is located in the upper lip and pour their secretion into the mouth. They appear to be salivary glands. The second pair is found near the middle of the body, to the inside of the two excretory C glands. Their secretion is emptied through the posterior borders of the first thoracic legs. The third pair is found in the genital lobes, and connect to the vaginal atria. They may be vestigial copulatory glands.

III. Detailed Description

Antennules

The long, tapering antennules are very important organs to the ostracod, serving as swimming and feeling structures. In swimming, the animal propels itself forward by strokes of the antennules and antennae.

In walking and climbing, the setae of the antennules are spread out in front of the animal, their tips lying in a horizontal plane. They are constantly in motion, exploring the area ahead. If one of the antennules be damaged, the motion of the animal in walking becomes erratic, although the appendages used for walking are not impaired at all. This strongly substantiates the writer's theory that the antennules serve as balancing organs.

When the animal closes the shell, the antennules are strongly curved downward by contraction of the flexor muscles. The long natatory setae are then directed backward between the antennae and along the ventral margin inside the shell.

In addition to the remarkable flexibility of these appendages, there is another motion which has been observed. The animal is able to shorten the length of the antennules by as much as 10μ by simultaneous contraction of the flexor and extensor muscles. It is not known what use the animal makes of this ability. When an ostracod was placed in a chlorotone solution, it slowly shortened and lengthened the antennules several times before completely relaxing under the influence of the narcotic.

The two antennules are joined to the forehead at a position in the anterior one-third of the animal about 40μ below the dorsal border. The basal podomeres are set very close together; the forehead narrows to 25μ between them.

The basal podomere of each antennule has a large triangular opening on the inner face (Fig. 8). The podomere is not joined to the forehead directly along the entire perimeter of this opening. The outer border is attached directly, but the inner borders have a triangular inset of flexible chitin. This inset is joined to the basal podomere along the two distal sides, and to the forehead along the proximal side (Fig. 14). In a needle dissection, the inset frequently remains attached to the forehead.

There are two structures which give strength to the attachment of antennule and forehead. The first is a chitin rod with a forked end which lies embedded in the surface of the forehead (Fig. 13, delta). The short fork at the end is directed anteriorly, and fits into a small notch on the

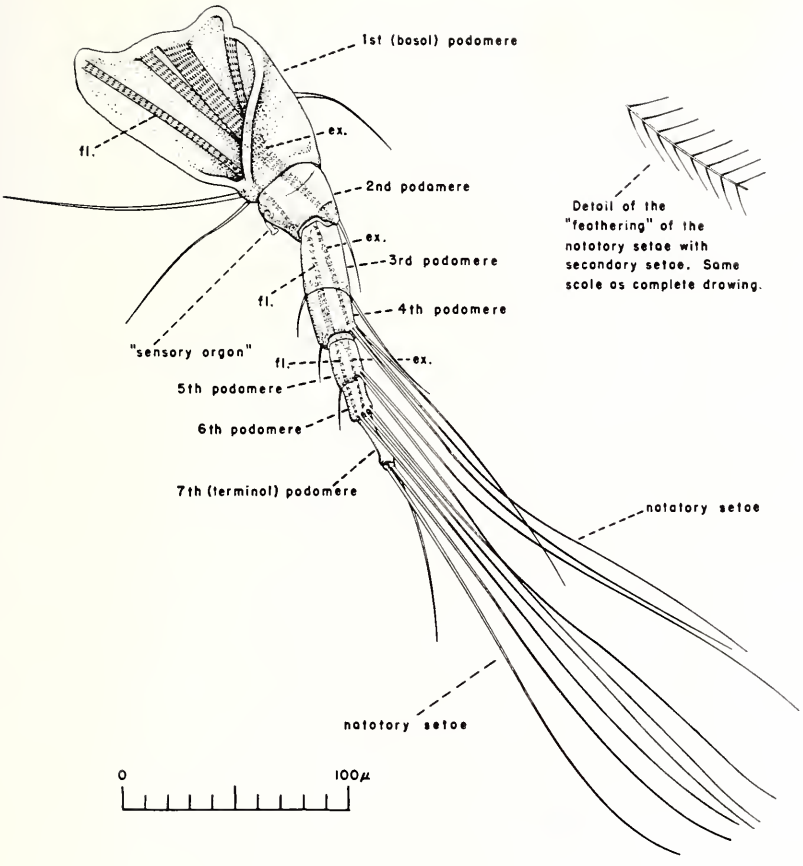


FIG. 8. Inner face of left antennule.

outside proximal border of the basal podomere. The second structure is another chitin rod which fits against the base of the triangular inset. This rod lies horizontal (Fig. 14, alpha) and its posterior end meets with another rod (Fig. 14, beta) which terminates anteriorly at the base of the antenna. These two rods, which together link the inset of the antennule to the base of the antenna, have no free motion; therefore, they must be considered as strengthening and supporting structures rather than as mechanisms for transmitting motions between antennule and antenna.

The length of each antennule is approximately 230μ, and the natatory setae extend an additional 220μ. The antennule is composed of seven podomeres, of which the proximal two probably represent the protopodite and the distal five the endopodite. (Claus 1893, p. 22: "Von diesem besitzt das basale den bei weitem grössten Umfang und ist mit dem kurzen und beträchtlich verschmälerten zweiten Gliede als Stamm oder

Schaft der Gliedmasse zu betrachten.") There is no development of the exopodite, unless it be the short seta on the dorsal distal border of the second podomere.

The basal podomere is by far the largest. It measures 100μ in length, and tapers from a height of 70μ at its proximal end to slightly over 30μ at its distal. The large opening and the junction with the forehead have already been described. There are three well-developed setae on this podomere, all with large bases. The first is about 50μ long, attached on the dorsal border. The second and third are attached closely together near the ventral distal end; the proximal seta is over 100μ long, and the distal about 80μ.

The second podomere of the antennule is short, but strongly chitinized (Plate 54, No. 254). It is about 30μ long, and tapers from 30 to 25μ in diameter. There is only one seta, about 30μ long, attached to the dorsal distal end. This small seta may represent the vestige of the exopodite.

There is also a very delicate sensory structure located on the outside face near the ventral border. It is only 10μ long, and consists of a narrow tubular shaft directed forward and a short, flared, bell-shaped end. This structure has been described by Rome (1947, p. 90), who termed it *l'organe chemocepteur*. Its definite use is unknown.

The third and fourth podomeres are partially fused. Although the junction between them is well defined, there is no movement possible. They appear to act as a single unit in all motions of the antennule. The third podomere is 30μ long and 20μ in diameter. It bears two setae near its distal end; both are attached on the outer side, the dorsal one about 60μ long and the ventral one about 25. The fourth podomere fits against the third with no constriction at the fused junction. It is 20μ long and 20μ in diameter. There are four distal setae; the ventral one is only 25μ long, but the three dorsal are well developed and serve as natatory setae. Two of these are 220μ long, and the other is 150μ.

The distal one-half of all the natatory setae are "feathered" with very delicate secondary setae (Fig. 8). These small secondary setae are seen with difficulty in water; and when the antennules are embedded in balsam or diaphane, the indices of refraction of the chitin and the mounting medium are so close that the secondary setae become invisible. The secondaries are spaced approximately every 10μ in the "feathered" portion, with each dorsal seta paired with a corresponding ventral one. Each one is about 20μ long.

The fifth podomere is 20μ long and 15μ in diameter. At its distal end it bears dorsally two natatory setae 230μ long, and ventrally one seta 20μ long.

The sixth podomere is 20μ long and 10μ in diameter. Distally it bears

three natatory setae on the inner dorsal side. These are the longest of all the setae, measuring 250μ.

The terminal podomere is 25μ long and 5μ in diameter. The distal end is enlarged somewhat, and the three setae are joined to the end. Two of these are 220μ long, and the third is about 80μ.

The basal podomere is capable of movement itself. Muscles connect the outer proximal rim to the dorsal region of the shell and to the endoskeleton. The dorsal edge of the base of the antenna has one extensor to the dorsal region of the shell and a second extensor to the endoskeleton (Fig. 5). The ventral edge has one flexor to the dorsal region and another to the endoskeleton. (Plate 1, Nos. 193, 194; Plate 33, No. 201).

Several muscles extend from the proximal rim of the basal podomere to the dorsal proximal tip of the third podomere. These strong extensors are used in the powerful swimming stroke. There is a small muscle connecting the ventral proximal tips of the first and third podomeres, serving as a flexor. The movement between the basal and second podomere is not independent of the rest of the antennule, and is somewhat restricted.

Additional extensor muscles connect the distal ends of the third and fifth, and of the fifth and terminal podomeres. There are corresponding flexor muscles in the ventral positions (Fig. 8).

The nerve system of the antennule is connected with the central portion of the cerebrum known as the deutocerebrum. The nerve bundle leads to the spherical ganglion in the basal podomere of the antennule (Plate 62, No. 284). This ganglion is well developed. There is a large nerve bundle from the dorsal part of this ganglion, which tapers to a small diameter at the end of the protopodite (Plate 9, No. 45; Plate 10, No. 49; Plate 30, No. 188). The nerve cord extends through the antennule to the terminal end. The small motor nerves operating the muscles of the antennule also originate in the deutocerebrum.

The ganglia of the two antennules may be the centers of the sense of balance. This is suggested by the erratic movement of the ostracod in walking, after one antennule is amputated. The small size of *Cypridopsis vidua* prevents the severing of the sensory nerves between the ganglia and the deutocerebrum without damaging the structure of the head and antennules and killing the ostracod. Therefore, the writer's interpretation of the antennule ganglion as a "balance center" is incompletely substantiated.

Antennae

The two antennae are essential locomotor appendages of the ostracod. They are used in conjunction with the antennules for swimming, and with the second thoracic legs for walking and climbing. Many early

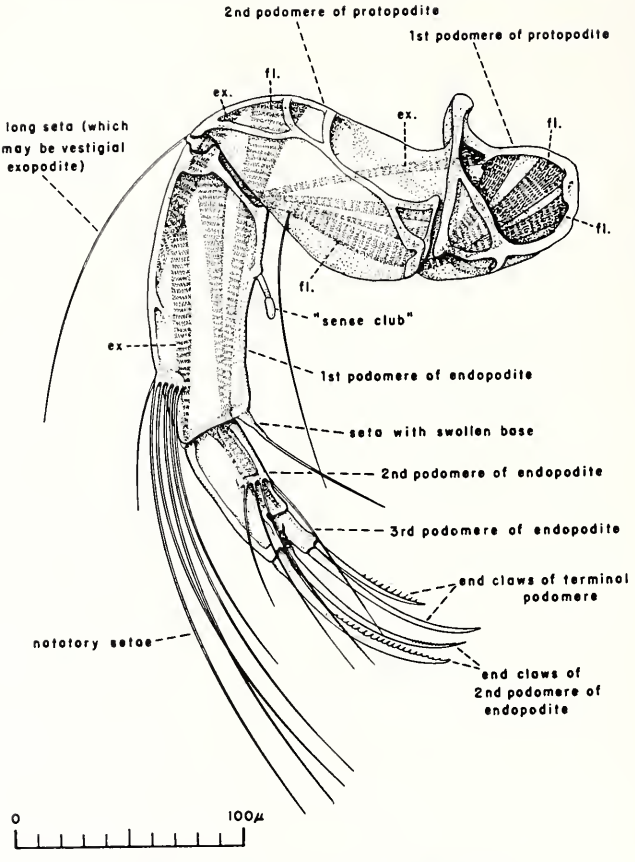


FIG. 9. Inner face of right antenna.

writers regarded the antennae as the first pair of feet (Hoeven 1856, p. 633). Because of their close coordination with the antennules in swimming, other workers on ostracods, including Claus (1893, p. 24), designated the antennules as the "first antennae" and the antennae as the "second antennae."

The motion of the antennae in swimming is downward and back. The long natatory setae provide sufficient surface for powerful propulsion. The end claws are used in walking, climbing, and clinging to inclined surfaces. The antennae can be bent to a position close to the forehead and upper lip, and are entirely encased within the shell when it is fully closed.

The antennae are joined to the forehead near its junction with the upper lip (Fig. 14). They are set onto the sides of the head with the bases 80μ apart (Plate 4, No. 15). A chitin rod, lying embedded in the wall of the head (Fig. 13, beta), fits into a small cavity in the chitin rim

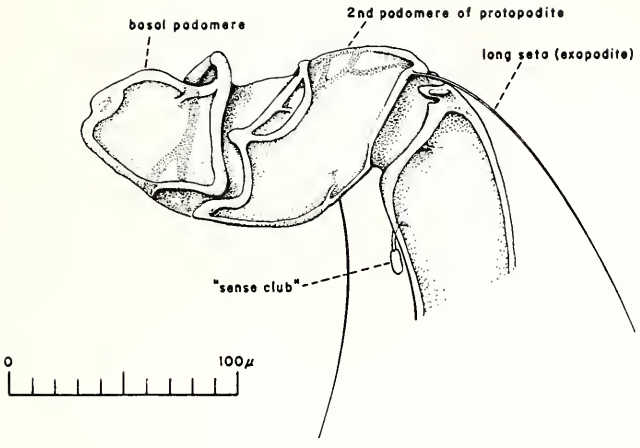


FIG. 10. Outer face of right antenna.

of the basal podomere of each antenna. Posteriorly, this rod joins another rod connected to the antennule (Fig. 9). Neither of the two rods is capable of movement, and they only strengthen the wall of the head structurally to withstand the strong reaction from the powerful antennae and antennules.

The total length of the antenna is 360μ, and the end claws extend an additional 80μ. The natatory setae extend slightly beyond the distal ends of the claws. The five podomeres of this uniramous appendage may be divided logically into two of the protopodite and three of the endopodite (Fig. 9). The exopodite is absent, or reduced to a long, narrow seta.

The basal podomere is powerfully reinforced by a chitin framework. It is shaped very much like an elbow joint used in plumbing — one opening fits against the head, and the other joins onto the second podomere. This basal member of the protopodite is practically incapable of movement, being lightly fused to the head. It is 60μ long and 80μ high at the anterior rim.

The second podomere of the protopodite is slightly over 100μ long. The cross-section of this podomere is elliptical, and it is about 60μ high and 45μ thick. The chitin framework differs from that of any other podomere of the body, and controls the movement of the podomere to a great degree. At the proximal end, the ventral perimeter is reinforced by a U-shaped chitin structure. The two tips of this structure lie on the sides of the podomere (Figs. 4 and 5) and act as fulcra to control mechanically dorsal and ventral movement of the antenna. The remainder of the proximal rim is connected to the basal podomere by thin, highly flexible chitin. Distally from the U-shaped piece, chitin rods extend along the sides to a dorsal

reinforcement at the distal end of the podomere. There are two setae near the distal end. The ventral one is a delicate seta 120μ long attached to the inside. The dorsal seta measures 150μ long; it may be the vestige of the exopodite.

The first podomere of the endopodite is 120μ long. It is also elliptical in cross-section, measuring 45μ high and 35μ thick. At the proximal end there is a broad notch of strong chitin on the dorsal side, which fits around the chitin prominence on the end of the second podomere. There are two curious sensory structures on this podomere, both of them on the ventral border. The first, an unusual club-shaped appendage, is 30μ from the proximal rim; the second, a seta with a large, swollen base, is at the distal tip. The club-shaped structure has a shaft 10μ long and about 3μ in diameter, and an enlarged tip of the same length and about 5μ in diameter. It has been called the "sense club" by Sharpe (1918, p. 798), and *Spürborsten oder Spürfäden* by Claus (1893, p. 26), who originally described it. Claus believed it to be sensitive to chemical and physical changes in the water. Hoff (1942a, p. 48), states that it has been considered an olfactory organ. The shaft of the club contains nerve fibers, so it would appear that the structure is sensory. However, the specific use or the specific sensitivity of the organ has never been proved. The terminal seta with the enlarged base may also be sensory. It would be a very exacting project to prove the particular sensitivity of these two structures. About 30μ from the distal end of the podomere, a chitin scale is attached to the inside dorsal edge. To this scale the natatory setae are attached like the teeth of a comb. Five of these setae are about 200μ long, and the sixth is only a little over 50μ. All of them are "feathered" with secondary setae in the distal one-half of their length. The longest project slightly beyond the ends of the terminal claws.

The second podomere of the endopodite is dorsally about 60μ long, but ventrally it is only 40μ. The terminal podomere is set into this ventral indentation. Near the middle of the inner side there is a small ventral comb structure bearing four setae slightly less than 100μ long. At the dorsal termination there are two long claws bearing teeth. The claws are 90μ long. The dorsal one of the two is heavier and equipped with longer, stronger teeth than the ventral (Fig. 9).

The terminal podomere is very small. The length is only 20μ, and the diameter 10μ. It extends less than 10μ beyond the dorsal tip of the second podomere of the endopodite, since it is set into a ventral niche. Distally this ultimate podomere terminates at the bases of two claws. The dorsal claw is over 80μ, and the ventral one is less than 60μ long. Both bear small teeth in their distal portions, those of the dorsal claw being very fine. (Plate 56, Fig. 263).

The musculature of the antenna is marked by the unusual develop-

ment of the flexor muscles. These are more numerous and much larger than the extensors. This is entirely in accord with the observed movement of the antenna in swimming and walking.

Although the basal podomere is joined directly to the side of the forehead and is capable of only limited movement, it has extensor and flexor muscles attached to the outer rim connecting it both to the dorsal region of the shell and to the endoskeleton (Plate 2, No. 5). A group of three small flexors extends from the dorsal rim to the median dorsal region (Plate 28, No. 181; Plate 31, Nos. 193-95). One small extensor connects the outer ventral rim with the dorsal region. The muscles to the dorsal region do not move the basal podomere to a great extent, and they may serve to raise the anterior portion of the body by their contraction. The muscles to the endoskeleton consist of one flexor attached to the dorsal rim and one extensor attached to the ventral (Plate 9, No. 46; Plate 33, No. 203).

The second podomere is lowered by three large flexor muscles which extend from its proximal ventral tip to the outer proximal rim of the basal podomere. It is raised by a single small extensor which is attached at the distal ventral tip and terminates posteriorly at the rim of the basal podomere. It has been pointed out above that the tips of the proximal U-shaped chitin structure act as fulcra. Movement of the podomere hinges on these two lateral points.

The third podomere (first podomere of the endopodite) joins the second at almost a right angle. The muscles which operate this podomere are modified from the usual arrangement by this factor. The extensor muscle is attached at the middle of the dorsal border, connecting it with the distal dorsal tip of the second podomere. The three flexor muscles are attached in the normal manner, linking the proximal ventral rim of the third podomere back to the corresponding position of the second.

The second podomere of the endopodite is operated by an extensor of the usual arrangement. There are, however, two flexors. The first flexor connects back to the proximal dorsal rim of the first podomere of the endopodite. The second flexor extends all the way back to the distal dorsal area of the second podomere of the protopodite.

The terminal podomere possesses independent movement. It has small extensor and flexor muscles connecting back to the proximal rim of the preceding podomere in the usual manner.

The end claws do not appear to possess independent action, but move only with their corresponding podomere.

The nervous system of the antenna is not complex, but it is incompletely described in literature. The sensory bundle of nerves leads to the portion of the cerebrum which has been designated the "tritocerebrum." The antenna itself houses two ganglia, one in the basal podomere (Plate

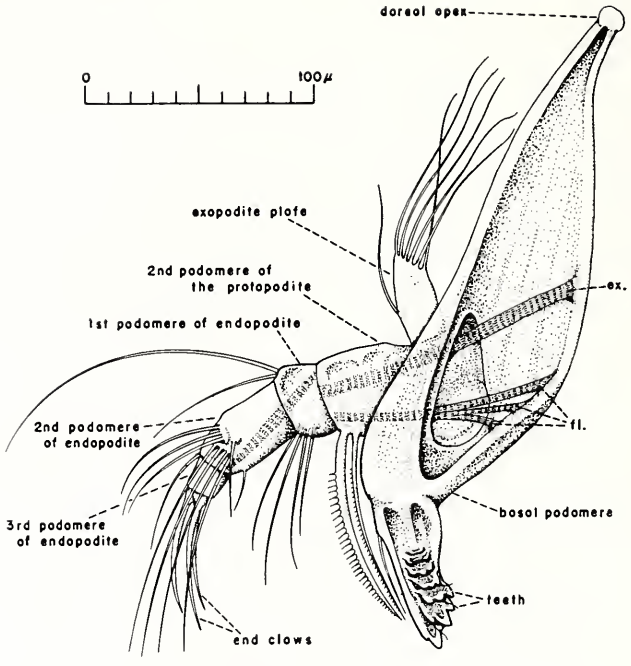


Fig. 11. Inner face of right mandible.

69, No. 303) and one in the second podomere (Plate 9, No. 46; Plate 31, No. 195). The proximal ganglion is small and globular, about 10μ in diameter. It is connected to the tritocerebrum by a small nerve bundle about 10μ long. There are two nerve bundles connecting the two ganglia, the dorsal one being the larger. The distal ganglion is laterally much compressed, and somewhat triangular in side view. One dorsal and one ventral nerve bundle extend distally to the end of the antenna, with side branches to the sense club, various setae, and the bases of the claws. The motor nerves operating the muscles of the antenna also originate in the tritocerebrum. They are difficult to trace in *Cypridopsis vidua,* but in larger species, such as *Candona crogmaniana,* they are much more distinct.

Mandibles

The mandibles are the only true masticatory appendages of the ostracod. They lie at the sides of the atrium, and the distal teeth can meet in the center. They retain the full character of crustacean appendages, having both endopodite and exopodite parts in addition to the protopodite. The endopodite is developed as a palp, and the exopodite is a plate bearing setae. The palp functions as an accessory feeding organ, passing particles of food backward to the mouth.

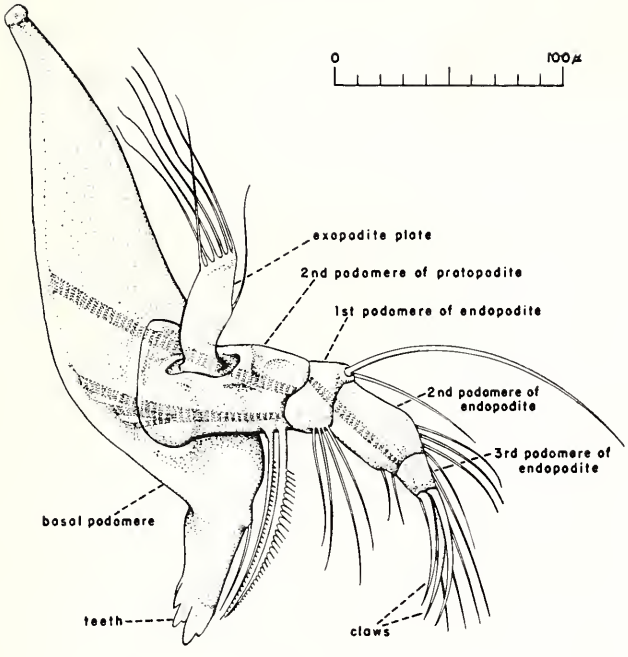


FIG. 12. Outer face of right mandible.

The basal podomere is the largest of all podomeres of the ostracod, and is heavily chitinized. It is 300μ long and over 60μ wide near the center. It joins onto the body wall around the subcuneate inner flange, which is over 200μ long. The distal 60μ of this podomere is set off by a slight constriction, and bears the seven rows of teeth (Fig. 11). The rows of teeth are best developed at the distal end, and become shorter and less distinct proximally (Plate 57, No. 269; Plate 60, No. 280). The five distal rows are composed of three teeth each, but the proximal two are fused into roughened bars. There are also some very short sensory setae interspersed through the toothed area. The basal podomere has only one large seta, about 35μ long, attached to the anterior edge in the distal portion (Fig. 11).

The dorsal apex is joined to two chitin rods which are operated by muscles extending to the side of the shell, just anterior to the closing muscles (Fig. 7). These muscles do not penetrate the body wall, but extend through soft tissues (Plate 15, Nos. 88, 89; Plate 35, Nos. 210, 211). They apparently adjust the angle of the basal podomere of the mandible. Scars of these muscles are often misinterpreted as those of additional closing muscles.

The second podomere of the protopodite is attached at the side of the

basal podomere and about 200μ from the dorsal tip (Fig. 12). It projects anteriorly, and forms the basal unit of the palp. It is 65μ long and subelliptical in cross-section; the height tapers from 60 to 30μ, and the width from 30 to 25μ. There is a shallow cup on the outer dorsal side into which the base of the exopodite plate is set (Fig. 12). Near the distal end of the podomere are two ventral, strong-toothed setae 90μ long. It is not known what special use is made of these unusually well-developed setae.

The exopodite plate is a very delicate structure, and can only be seen clearly in a stained specimen. It is about 50μ long and bears seven setae. These setae are shrunken to small diameter in a diaphane-mounted dissection (Plate 58, No. 271), but in a freshly dissected animal, they are seen to have expanded bulbous bases and "feathered" edges. The six terminal setae are 100μ long, but the one attached at the mid-point of the anterior edge is only about one-half that length (Plate 56, No. 264).

The first podomere of the endopodite is only 20μ long and 30μ in diameter. Distally it has two dorsal and four ventral setae. The dorsal setae are of unequal length, the longer measuring 130μ and the shorter only 60. The ventral four setae, varying from 50 to 70μ in length, are attached to a scale to form a comb-like structure, very similar to that of the natatory setae on the antenna.

The second podomere of the endopodite is 45μ long and 25μ in diameter. All of the setae are on the distal portion. On the inner face there are two comb-like structures, the dorsal one having three setae 60μ long and the ventral one having four setae 100μ long. These latter extend beyond the terminal claws. In addition, there are three isolated setae: one at the dorsal apex 50μ long, a second on the inner face about 30μ long, and a third on the ventral border only 20μ long.

The third podomere of the endopodite terminates the palp. It is only 15μ long and 15μ in diameter. At the distal end it bears three claws, all equally developed and about 60μ in length. These claws are almost constantly in use to pass food backward to the mouth.

The basal podomere is connected by muscles both to the dorsal part of the shell (Plate 31, Nos. 192, 193) and to the endoskeleton (Plate 5, Nos. 17, 18). Two small muscles extend dorsally from each mandible, and four large and at least three small muscles connect it to the endoskeleton. These latter are arranged in a complicated pattern, making it difficult to discern the exact number, even in 10μ sections. They cross one another (Plate 5, No. 19), permitting the adjustment of the mandible to many positions. Their primary purpose is to pull the teeth together in the atrium in the chewing process, and they may all be called adductors until their individual functions are understood in greater detail. The two muscles to the dorsal part of the shell act as retractors, and also perhaps as diduc-

tors. The muscles from the center of the shell valve to the chitin processes attached to the dorsal tip of the mandible (Fig. 7) serve as diductors and adjustors.

The second podomere of the protopodite does not appear to have muscles for independent movement.

The first podomere of the endopodite has one extensor and three flexors connecting its proximal rim to the posterior rim of the basal podomere (Fig. 11).

There is apparently only one other muscle in the palp. This is a flexor extending from the base of the terminal podomere back to the dorsal proximal edge of the first podomere of the endopodite. Extension of the podomeres of the endopodite must be accomplished by elasticity of the joints, returning the podomeres to a fixed position when the flexor muscle relaxes.

The nerves of the mandible are connected to the ventral chain of ganglia. The sensory nerve cord connects to a small ganglion in the basal podomere (Plate 31, No. 195). From this ganglion one branch extends down into the distal end to the teeth and the accompanying small sensory setae, and a second branch goes into the second podomere to a second small ganglion. From this ganglion in the base of the palp, a small nerve bundle extends to the end of the palp (Fig. 6).

The "mandible gland," which lies in the distal portion of the basal podomere, is discussed under "Gland M."

Forehead and Upper Lip

The whole front of the body of the ostracod is bounded by a blunt, reinforced chitin case constituting the forehead and upper lip. These two divisions are not separated, but are fused together into one unit (Fig. 13). This unit, like other sections of the body wall, is made up of two distinct types of chitin. There is a distinct framework of strong chitin rods. The spaces bounded by this rigid framework are filled by thin flexible chitin which is fused to it — like the glass panes in a leaded window. The whole encases the soft tissues within.

Each side of the forehead has a strong chitin process on the surface which terminates anteriorly in a curved fork (Fig. 13, delta). These fit against the outer rims of the antennules, as has been described. There are also two chitin rods on each side which do not lie on the surface (Fig. 13, alpha and beta). These rods are connected posteriorly. The anterior end of the dorsal rod is set against the triangular inset in the base of the antennule, and the anterior end of the ventral rod is set into a small socket in the outer rim of the base of the antenna (Fig. 14). The boundary of the forehead and upper lip is marked by a horizontal U-shaped chitin rod around the anterior end of the body (Fig. 13, gamma).

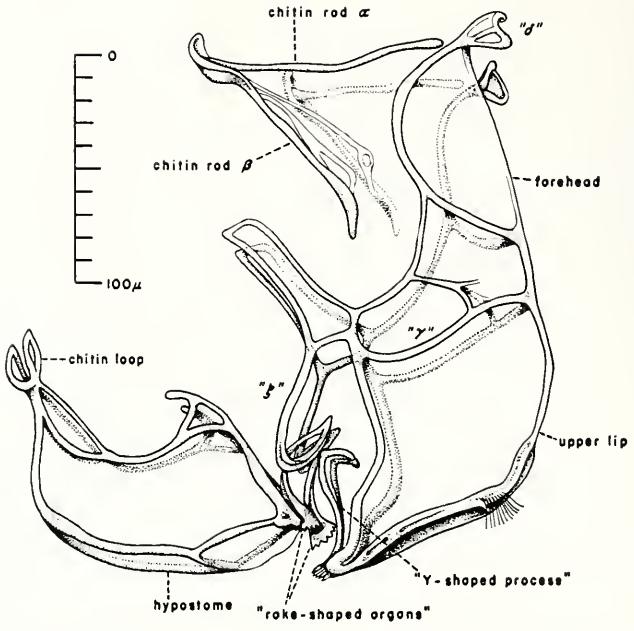


FIG. 13. Chitin framework of the forehead, upper lip, and hypostome as seen from the right side.

The upper lip has been appropriately described by Claus (1893, p. 28) as a *helmförmiger Aufsatz* (helmet-shaped structure). The anterior end is bluntly rounded (Fig. 15), and the sides are subparallel. The ventral surface is further reinforced by a number of elliptical chitin rods, which are concentric anteriorly and converge posteriorly.

The posterior part of the upper lip forms the forward boundary of the atrium, or mouth opening. This portion of the mouth has a chitin lining equipped with numerous hairs directed inwardly and dorsally. The lining has a slight groove along the median plane, and is strengthened by a vertical chitin process (Fig. 16). This structure was referred to by Claus (1893, p. 30) as *Epipharyngealleisten* (epipharyngeal rods). The writer feels that this designation is misleading, and proposes the descriptive term "Y-shaped process" in its place. The narrow spoon-like base of the "Y" is ventral, and attached to the chitin lining; the arms of the structure are directed dorsally and anteriorly (Fig. 15). The tips of the arms have short hook-like projections pointing anteriorly, lying along the sides of the esophagus (Fig. 13). The Y-shaped process is operated by a group of muscles connecting it to the anterior portion of the upper lip (Fig. 4).

The posterior ventral rim of the upper lip has a notched border (Fig. 13). The roughened rim is not regularly notched, so that it cannot be

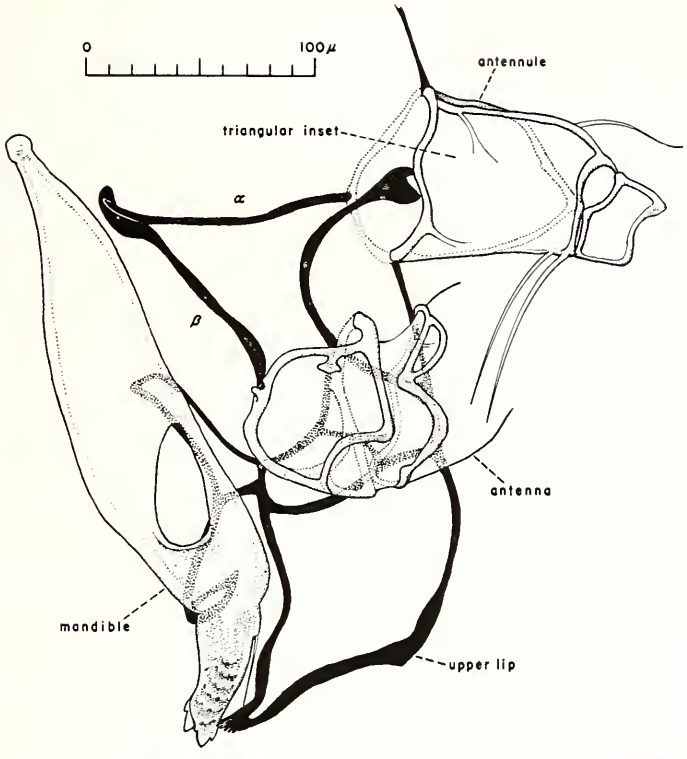


FIG. 14. Chitin framework of the forehead and upper lip are shown in solid black. The bases of the antennule, antenna, and mandible are shown in their respective positions.

said to be toothed. The upper lip has very little independent motion, and the rasping is done primarily by the mandibles, abetted by the rake-shaped organs.

The horizontal U-shaped chitin rod marking the boundary of forehead and upper lip is joined on its posterior ends by vertical chitin rods (Fig. 13, zeta). These lie along the sides of the esophagus. At the ventral end, these rods terminate in narrow triangular chitin processes pointing inward at the back of the mouth but failing to meet in the median plane.

Posteriorly the upper lip is slightly indented at the sides to accommodate the large basal podomeres of the mandibles, which bear the true masticatory teeth on their ends (Fig. 14). The indentation allows the teeth to meet in the center of the atrium.

HYPOSTOME

The hypostome or lower lip is located posterior to the atrium. It forms a median sternum-like structure on the ventral side of the body.

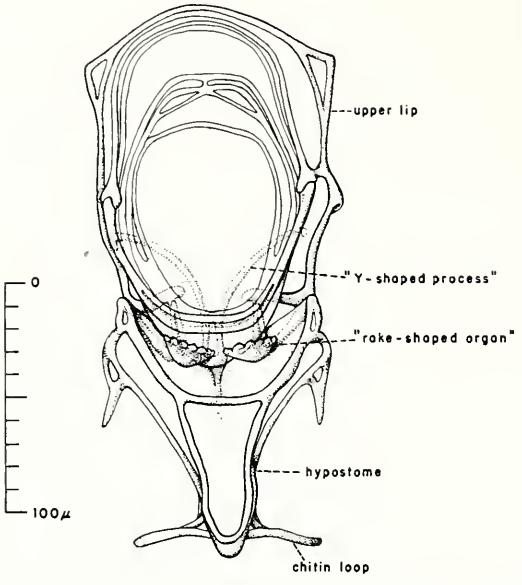
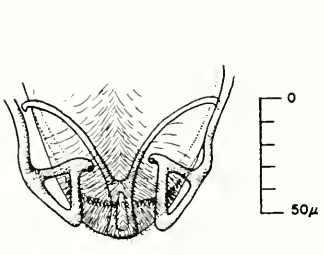


Fig. 15. Hypostome and upper lip as seen from below and slightly to the front.



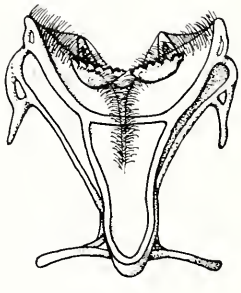


Fig. 16 Fig. 17

Fig. 16. Front part of the mouth as seen from above and to the rear. Fig. 17. Hypostome as seen from below. The rake-shaped organs are shown in place.

It is about 110μ long and 100μ wide at the front. The maxillae lie along the sides, and the first thoracic legs are attached to the posterior tips.

The hypostome is shaped like the breast of a bird, with the posterior-anterior positions reversed. It may also be described as similar to the rear one-half of a fishing dory. The flattened bottom of this structure has an A-shaped chitin framework, with the apex posterior (Fig. 17). The dorsal framework is V-shaped. Dorsal and ventral portions are joined together anteriorly by two slanting chitin rods (Fig. 13), and

posteriorly by two vertical rods set very close together and converging toward the posterior point of the base.

The posterior stem is somewhat upturned, and at its dorsal termination is joined by a chitin girdle-shaped structure with elongate loops extending laterally. These loops are each 40μ long (Fig. 15). The first thoracic legs are suspended from the outer tips of these loops (Fig. 20).

The broad anterior of the hypostome is the rear lining of the atrium. There are two soft lobes at each side called the paragnaths (Fig. 3). These are covered with hairs which are directed toward the well-defined median groove (Fig. 17).

Two small masticatory appendages are embedded in the tissue of the hypostome at the rear of the atrium. Each of these rake-shaped organs has a vertical shaft 20μ long, joined ventrally to the center of a horizontal bar of equal length bearing nine teeth. The three teeth nearest the median plane are somewhat fused at their bases. Long, inwardly directed hairs line the outer edges of the shafts of these embedded rake-shaped organs (Plate 85, No. 372). These hairs form a curtain across the back of the atrium, and they may be used in straining certain food particles, although this has not been established.

At the atrium, the ventral part of the hypostome is narrower than the dorsal. This ventral indentation matches that of the upper lip, and together they form wide lateral V-shaped notches. In these notches the mandibles fit closely when they are chewing. The sides of the hypostome are also incurved somewhat to accommodate the maxillae.

The chitin of the body wall above the hypostome is flexible, permitting movement of the hypostome by the muscles which connect it to the endoskeleton. There are three pairs of these muscles (Fig. 4). The first is attached where the rake-shaped organs are imbedded; the second at the dorsal anterior part, and the third pair near the center of the dorsal chitin rods. The movement of the hypostome and the attached rake-shaped organs is forward and back. Resemblance of this action to that of a mammalian lower jaw is marred only by the horizontal (rather than vertical) orientation.

Both sensory and motor nerves of the hypostome are connected to the ventral chain of ganglia (Fig. 6).

Maxillae

The maxillae are greatly modified appendages. The basal podomeres partially surround the middle portion of the hypostome, and point forward toward the atrium (Plate 57, No. 270). The terminal "masticatory" processes are aligned laterally (Fig. 19), and serve only to pass food particles toward the mouth. The maxillae serve a second function, that of respiration. The large branchial plate is in constant motion, stirring the

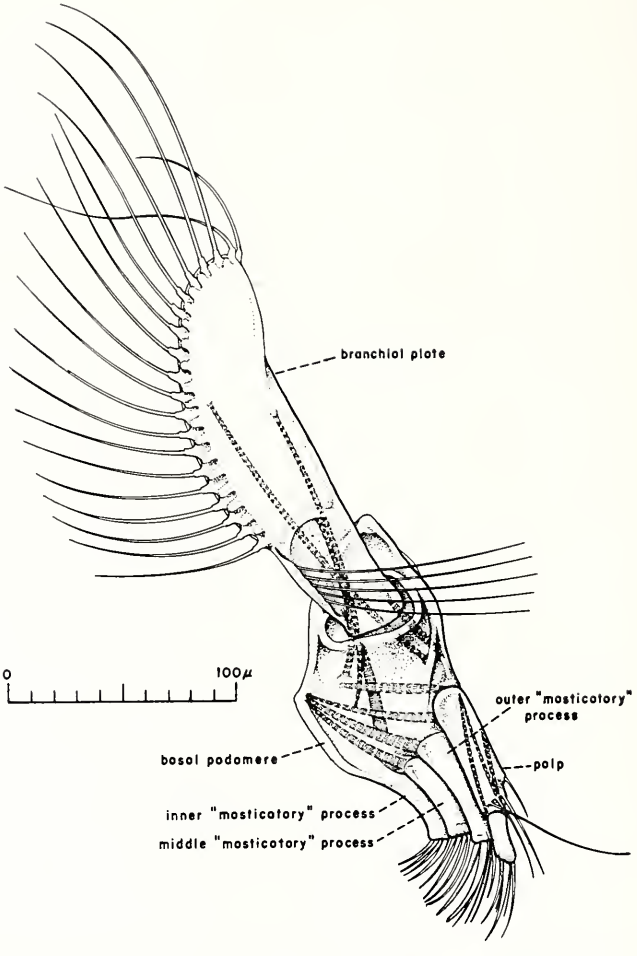


Fig. 18. Right maxilla as seen from the outer side and slightly to the rear.

water inside the shell to speed up the absorption of oxygen by the body wall.

The basal podomere curves inward at the top and terminates in a forked process which Claus (1893, p. 37) termed the *Endbügel* (Fig. 19). The motion of the whole maxilla is controlled by this dorsal process, which acts as a fulcral point. There is no correct description of the arrangement of this fulcrum in literature. First, it must be pointed out that above the hinge point of the first thoracic leg and the chitin loop of the hypostome, there is a long chitin structure (Fig. 20). This structure has two median flanges which diverge toward the anterior end to form a groove. The dorsal chitin process of the maxilla narrows to a

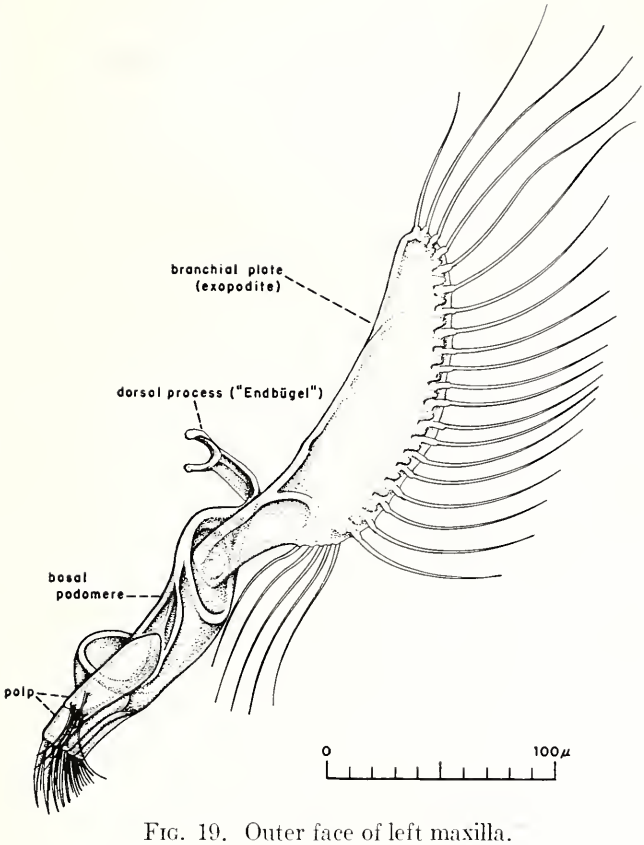


FIG. 19. Outer face of left maxilla.

curved rod immediately below the terminal fork. This curved portion fits into the groove of the chitin structure over the first thoracic leg (Fig. 2; Plate 59, No. 274; Plate 60, No. 276). The terminal fork, which is directed forward, prevents the maxilla from slipping downward through the groove.

The curved basal podomere is about 180μ long (Plate 57, No. 268), although when seen from the side it usually appears shorter. The dorsal part has already been described above. The ventral part has an inside cup fitting close against the side of the hypostome. From this cup the three "masticatory" processes and the palp project downward.

The problem of what portion of this appendage represents the endopodite is not simple. The middle and outer "masticatory" processes and the palp are set off from the basal portion by definite sutures (Fig. 18). This observation was also made by Claus (1893, p. 36), who concluded that the middle process was the first podomere of the endopodite, the outer process was the second, and the palp represented the third and

fourth podomeres of this highly modified endopodite. This is a logical analysis, for these members are definitely set off from the basal podomere.

This leaves the inner "masticatory" process as the only one of the basal podomere. This process is 40μ long and about 15μ in diameter. The distal end is blunt and bears seventeen setae. Only seven of these are well developed, about 20μ long; some are very insignificant and can only be seen from below, since otherwise they are hidden by the larger setae.

The outer side of the basal podomere has a chitin-rimmed socket to which the large branchial plate is attached. This plate is modified exopodite. The plate itself is 180μ long and 50μ wide near the middle. It lies nearly horizontal. The ventral rim is fringed with twenty-five well-developed setae. These vary from 70 to 120μ in length. The proximal five setae point down; the others are directed posteriorly, and between their bases are reinforced by short chitin elements (Plate 56, No. 266). The setae are feathered by very delicate secondary seta, which become invisible in balsam or diaphane mounts.

The orientation of the entire maxilla is frequently misunderstood, and it has been illustrated in many incorrect ways. The dorsal process of the maxilla must lie above the first thoracic leg, as described above. From this point of the maxilla curves outward and forward to the socket where the branchial plate is attached. Then the maxilla continues forward and down and flares inward to form the inner cup, to which the "masticatory" processes and the palp are attached. The inner process is a direct continuation of the basal podomere. The processes and the palp are normally arranged in an almost horizontal plane, with the setae pointing forward. The inner processes of the left and right maxillae lie adjacent near the median plane (Plate 74, No. 324).

The position of the branchial plate must be studied in its relation to the rest of the body of the ostracod. We must note that the closing muscles of the shell extend all the way through the soft inner body tissues, and do not penetrate through the body wall or the chitin lining of the hypodermis of the shell. Therefore, the body wall joins the chitin lining of the hypodermis *below* the closing muscles. (Plates 3 and 4). This forms the dorsal boundary of the open space inside the shell, to which the free-moving branchial plate is limited by necessity. It is obviously impossible for the branchial plate to occupy a vertical position, for then it would be cutting through the closing muscles themselves. Whenever the branchial plate is shown out of its normal position so that other structures can be shown, this should be explained in the text. Normally the branchial plate lies almost horizontal, along the side of the shell (Plate 35, No. 210), and covers the third thoracic leg (Plate 24, Nos. 152-154).

The middle "masticatory" process, the first podomere of the endopodite, is 40μ long and about 15μ in diameter. It is blunt at the distal end,

and has nine setae, only six of which reach significant length. The longest is nearly 40μ long.

The outer "masticatory" process is nearly 50μ long and slightly less than 20μ in diameter. Because of the variety of claws and setae attached to it, this podomere has been termed *the* masticatory process, and is said to be of taxonomic significance. One strong seta 25μ long is attached on the outer border, a few microns from the end. This is followed in order by two long narrow setae, two claws, and one tapering seta, all of them terminal. The claws of this podomere are significant in the separation of many of the Cypridae. They are relatively simple in the case of *Cypridopsis vidua*. They are about 40μ long, tapering, and with a long groove along the inner face. The sides of the claws flare slightly near the middle and again near the end, but they are not notched, as are many others of the Cypridae.

The palp contains two podomeres, representing the third and fourth podomeres of the endopodite. It lies outside the "masticatory" processes. The proximal podomere of the palp is slightly over 50μ long and 20μ in diameter. One seta 40μ long is attached on the outer edge of this podomere 10μ from the distal end. Nearer the end is a comb-like structure with four setae 40μ long. These are evidently sensory. The distal podomere of the palp is quite small, less than 25μ long and only 10μ in diameter. It is armed with terminal setae and claws. There are two strong outer claws and one inner claw 30μ long, and three small setae set in the center.

The musculature of the maxilla is complex. Most of the action used to pass food toward the mouth is imparted to the entire appendage by muscles from the endoskeleton. These muscles are attached to the anterior and posterior edges of the cup-shaped opening (Fig. 5). It must be remembered that the maxilla swings from the dorsal process, which acts as a fulcral point. Therefore, the terms "flexor" and "extensor" are not applicable to these muscles from the endoskeleton.

The palp is operated by one flexor and one extensor muscle attached to the inside of the basal podomere. In addition, the second podomere of the palp also has independent action; it has one flexor and two extensor muscles. The flexor muscle extends back to the outer proximal edge of the first podomere. The two extensors also connect to the outer edge of the first podomere, one to the middle and one to the proximal tip.

The middle and outer "masticatory" processes have muscles connecting them to the basal podomere, but their independent movement is very limited. The inner "masticatory" process, a part of the basal podomere, has no muscles at all.

The large branchial plate is operated by four muscles, so arranged that the plate can be waved from side to side, raised and lowered, and

even turned on its long axis. Two of these muscles are attached at the base of the plate, one at the front and one at the rear. The other two extend into the plate for over half its length, and impart the rotational motion. One muscle extends from the ventral margin of the plate to the forward part of the basal podomere. The second muscle goes from the dorsal margin of the plate, passes inside the first muscle, and is attached to the rear part of the base (Fig. 18). The attachment of the branchial plate to the socket in the basal podomere is made by very elastic chitin, and the plate itself is flexible. The rhythmic beating of the branchial setae can be seen through the shell of the living ostracod, although individual setae cannot be distinguished.

The nervous system of the maxilla branches from the ventral chain of ganglia. There is a large ganglion in the cup of the basal podomere, with branches into the branchial plate, the palp, and each of the "masticatory" processes. The ganglion is laterally compressed, but measures about 30μ wide and 50μ long.

First Thoracic Legs

The first pair of thoracic legs in ostracods of the family Cypridae are adapted for feeding, and do not resemble the other thoracic legs. Early workers on the ostracods, noting the resemblance of these first thoracic legs to the maxillae in form and function, designated them as the "second maxillae."

In the family Cytheridae there are three pairs of thoracic legs, all similar and adapted for crawling. Each of these legs is uniramous, and they appear to be identical.

It is certainly logical, therefore, to assume that the ostracods of other families also have one pair of maxillae and three pairs of thoracic legs, rather than two pairs of maxillae and only two pairs of legs. This is now the accepted interpretation of these appendages.

In the Cypridae the first leg retains the biramous character of the typical crustacean appendage. Therefore, the divergence of the Cypridae and the Cytheridae probably occurred very early in the history of the ostracods. In the former the first leg retains its biramous character but has been modified in function; whereas, in the latter it has lost the exopodite but still serves as a walking appendage.

Cypridopsis vidua has an L-shaped protopodite, with the two original podomeres completely fused and the boundary no longer marked. The vertical stem is articulated with the rear portion of the hypostome. The dorsal portion of the protopodite is almost completely rimmed with a collar of chitin rods. One of these rods on the inner face is modified as a hook which fits over the tip of one of the loops of the girdle-shaped process of the hypostome (Figs. 20, 21). This apparently acts as a fulcrum to

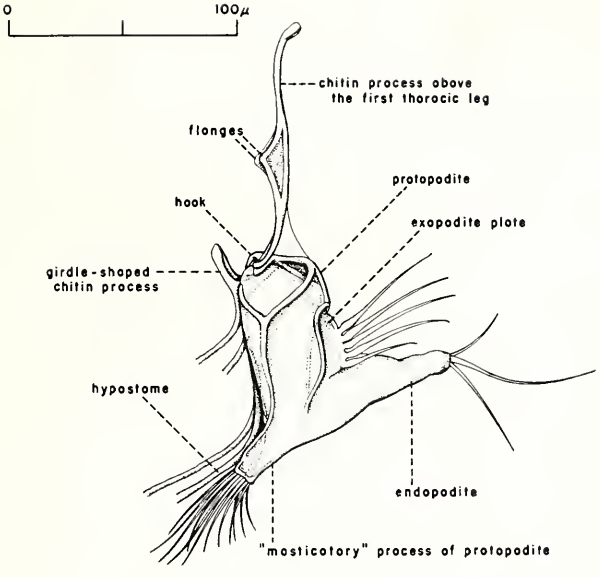


FIG. 20. Outer face of left first thoracic leg. The attached chitin process and the posterior part of the hypostome are also shown.

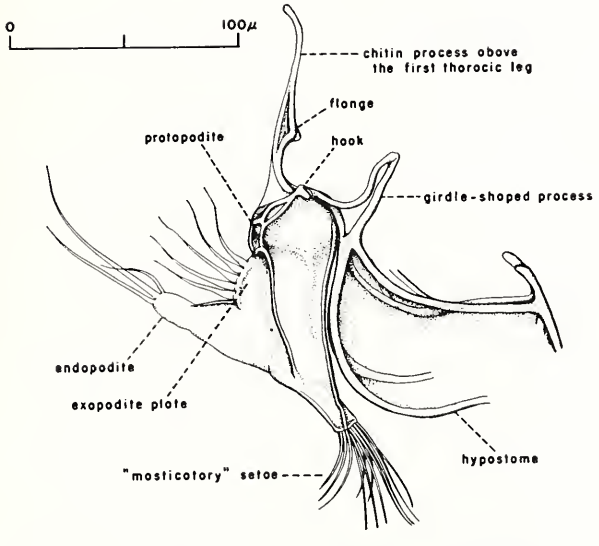


FIG. 21. Inner face of left first thoracic leg, showing the method of attachment to the hypostome.

control movement of the leg. This distal end of the protopodite lies more nearly horizontal and serves as an accessory "masticatory" process. It is equipped with twelve setae for passing food forward to the mouth. These setae are spread in a nearly horizontal plane, the longest about 50μ long. When the leg is directed forward, these setae reach to the atrium.

The endopodite is represented by a posterior continuation of the L-shaped protopodite, giving the whole leg the general form of an inverted T. This rear endopodite palp is not sharply set off from the protopodite. It is composed of a single elongate podomere (Plate 71, No. 310). There are three terminal setae. In syngamic species of the Cypridae, the endopodite of the male is composed of two podomeres forming a weak chela used for holding the female during copulation. There is a slight constriction of the endopodite palp of *Cypridopsis vidua* about 20μ from the distal end, which may represent the setting off of a second podomere; however, there is no chitin rim to mark the junction, and the writer prefers to regard the palp as made up of a single podomere.

The exopodite is a plate bearing setae. It is set on to the protopodite immediately dorsal to the endopodite palp. The five setae have enlarged bases, and are all about 50μ long. They are extremely difficult to see except in heavily stained sections (Plate 71, Nos. 310-311). A large, lobed gland, called "gland N" in this paper, empties through a duct, which passes through the dorsal part of the protopodite of this leg and opens at the base of the exopodite plate (Fig. 3).

The musculature of the first thoracic leg is very simple. The endopodite palp and the exopodite plate do not appear to have independent movement. The only muscles apparent in *Cypridopsis vidua* are attached to the proximal rim of the leg and connect it to the endoskeleton (Fig. 5). One is fastened to the posterior part of the rim, and the other to the anterior part. Rome (1945, p. 114) describes additional muscles in the first thoracic leg of *Herpetocypris reptans*, some of which are attached to the dorsal region of the shell. These muscles are either absent or so inconspicuous in *Cypridopsis vidua* that they are not discernible in 10μ sections.

The sensory nerves of this leg connect to the ventral chain of ganglia. There is a broad ganglion in the protopodite, with a branch into the base of the endopodite palp. This ganglion is very thin, despite its large area when seen from the side. Nerves from the distal end connect to the "masticatory" setae.

There is a strong chitin structure dorsal to the first thoracic leg which is not a part of the leg, but acts as a reinforcing connection from the first leg to the maxilla. This structure is over 100μ long, and is formed of a long chitin rod shaped like an integral sign, with two median flanges extending anteriorly (Fig. 20). This chitin process has its base at the

point where the hook of the leg fits onto the loop of the hypsostome. Normally it lies almost vertical. The two triangular flanges form a notch into which the dorsal process of the maxilla fits. This arrangement is described in the discussion of the maxilla.

The first thoracic legs have the protopodite stems parallel, and nearly vertical. The "masticatory" processes at the ends are pointed inward, and lie ventral to and somewhat inside the processes of the maxilla (Plate 57, No. 270). The endopodite palps are directed outward, and lie outside the bases of the second thoracic legs. A complete needle dissection is necessary to uncover the details of the chitin rim around the upper part of the first leg, since it is concealed by the branchial plate of the maxilla (Fig. 2).

Second Thoracic Legs

The second pair of thoracic legs are very conspicuous appendages, being projected out as soon as the shell is opened. They are used in walking and clinging to inclined surfaces. The powerful end claw can be strongly flexed, so that the dorsal surface is used to support the rear part of the body in walking (Fig. 34).

The second thoracic legs were referred to by earlier writers as the first thoracic legs, since the true first legs of the Cypridae were thought to be second maxillae.

Each of these second thoracic legs is uniramous. It is composed of six podomeres, two of the protopodite and four of the endopodite. The protopodite is set nearly vertical in the middle of the ventral half of the body, close to the median plane. The endopodite extends horizontally toward the posterior end. The terminal claw is curved downward (Fig. 2).

The two podomeres of the protopodite are unique, and partially fused together. The first has an intricate network of strong chitin rods (Fig. 22). It bulges outward in the middle and enlarges distally to form a chitin collar which fits around the second podomere (Fig. 23). The entire protopodite is firmly attached to the body, and has very limited movement.

The second podomere of the protopodite is hemispherical and fits into the chitin collar on the distal end of the basal podomere (Fig. 22). It does not have independent movement, being more or less fused to the basal podomere, but serves as an area for attachment of many of the muscles operating the endopodite. There is a small seta on the anterior surface.

The first podomere of the endopodite is strongly constructed and distinct. It is 60μ long and about 45μ wide. The proximal rim fits against a fulcral point on the basal podomere of the protopodite. The ventral margin bears a fringe of very minute setae, and the distal end has a strong seta over 50μ long.

The second and third podomeres of the endopodite are distinct but

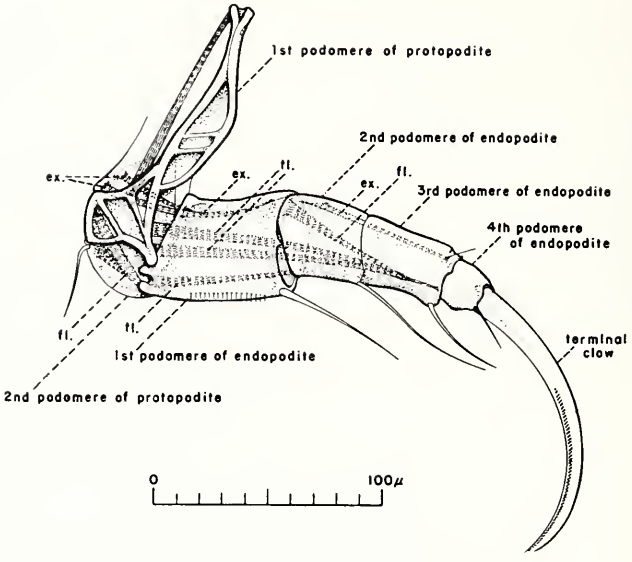


FIG. 22. Outer face of left second thoracic leg.

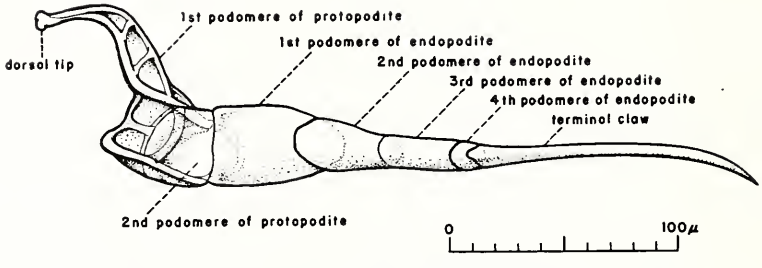


FIG. 23. Right second thoracic leg as seen from above.

fused together, and act as a single unit. Each has a strong ventral seta at its distal end. The third also has a small dorsal seta. These podomeres are laterally compressed to about 15μ thickness.

The terminal podomere of this leg is small. Distally it has a large claw over 100μ long and a delicate seta only 30μ long. The curved claw serves as a foot in walking (Fig. 33). It has numerous small teeth along the ventral margin. The podomere has a ventral chitin projection extending back inside the third podomere of the endopodite; the flexor muscles are attached at the end of this projection.

There are two muscles from the protopodite to the endoskeleton (Fig. 5). One is attached to the dorsal tip of the basal podomere, and the other to the ventral part. Muscles have not been found leading to the dorsal region of the shell, although such muscles are present for the antennule,

antenna, and mandible. There is also a muscle from the dorsal tip of the first to the second podomere of the protopodite (Fig. 22). The presence of this muscle suggest that the fusion of the two is not complete, and that there is some little movement possible.

The first podomere of the endopodite is lowered by a broad band of flexor muscles extending to the anterior area of the second podomere of the protopodite (Fig. 22; Plate 11, Nos. 53, 56). There is no corresponding extensor muscle, and the first podomere apparently cannot be raised without moving the second and third podomeres also.

The second and third podomeres of the endopodite are fused together and act as a single unit. Ventrally they are operated by a flexor muscle extending to the proximal rim of the first podomere of the endopodite (Fig. 22). Dorsally they are controlled by extensor muscles connected to the anterior area of the second podomere of the protopodite.

The terminal podomere and its large claw have great amplitude of movement. Extended, the podomere lies horizontal with the tip of the claw pointing downward (Plate 59, No. 272). Flexed, it lies vertical with the tip of the claw pointing forward (Plate 59, No. 273). When the whole leg is flexed, the dorsal edge of the claw is turned into a ventral position (Fig. 33). The terminal podomere is operated dorsally by an extensor muscle attached to the proximal area of the second podomere of the endopodite. The ventral margin of the terminal podomere has a chitin prolongation inside the penultimate podomere. Three strong flexor muscles are attached to this process. The first of these is fastened to the *dorsal* part of the proximal rim of the second podomere of the endopodite (Plate 11, No. 55). The other two muscles extend all the way forward into the second podomere of the protopodite (Plate 34, No. 206).

The sensory nerves of the second leg connect to the ventral chain of ganglia without an enlargement to form a separate ganglion, such as is present in the antennule, antenna, mandible, maxilla, and first thoracic leg.

Third Thoracic Legs

The third thoracic legs are the most flexible of all the appendages, and are used to keep the body and the inside of the shell free of foreign materials. They are attached to the body immediately behind the dorsal tips of the second thoracic legs.

Each of these legs is uniramous, and normally lies close to the body in the form of a modified "U." The protopodite is directed downward, the antepenultimate podomere backward, and the penultimate podomere upward. However, the unusual protopodite cannot only be moved forward, backward, outward, and inward, but can be enrolled on itself a full 180° to bring the distal end of the leg into the anterior region of the

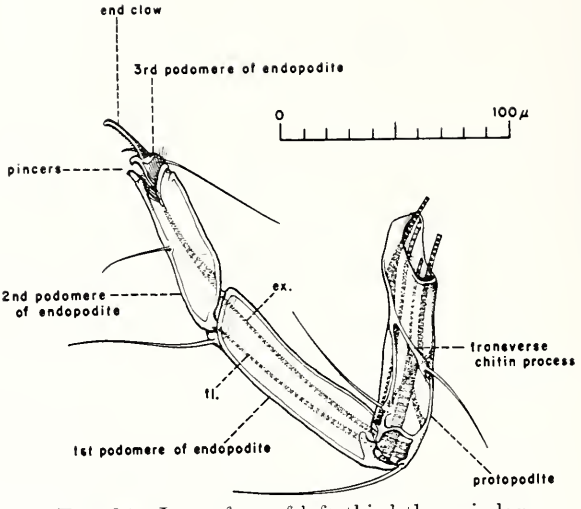


FIG. 24. Inner face of left third thoracic leg.

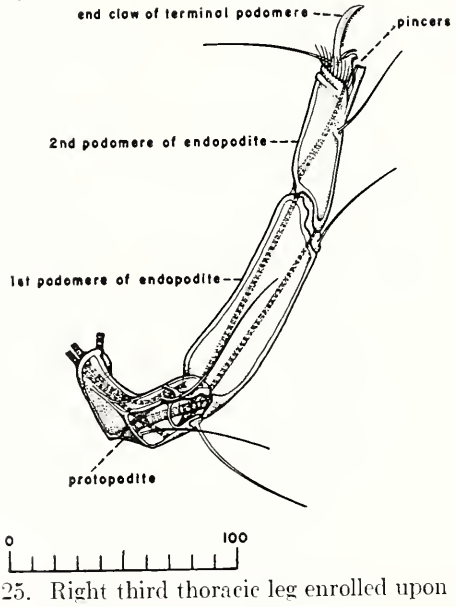


FIG. 25. Right third thoracic leg enrolled upon itself.

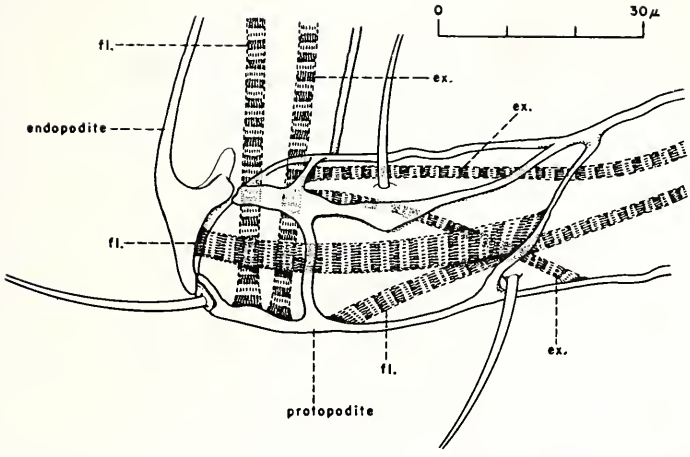


FIG. 26. Inner face of left third thoracic leg showing details of musculature of the protopodite and the proximal part of the endopodite.

shell (Fig. 25). The terminal podomere and the distal tip of the penultimate podomere act as the two jaws of a pincers, seize small particles of irritating material, and eject them from the shell. This unique structure shows the degree of specialization of the ostracod appendages.

The protopodite is difficult to see in the living ostracod, even in species having transparent shells. It lies under the branchial plate. There are two podomeres of the protopodite, but they are in an advanced state of fusion. The line of separation of the two podomeres is marked by the arrangement of the muscles and by a transverse chitin process on the inner face, but on the outer face there is no mark of separation at all. The protopodite acts as a very supple, flexible unit. It is over 100μ long. As stated above, it is able to turn upon itself a full 180° to direct the leg forward. The inside face of this portion of the leg is characterized by an intricate frame of chitin rods which control the enrolling motion and provide a fulcrum on which the endopodite pivots. This face bears three setae: one at the ventral end of the first podomere, one in the middle of the dorsal area of the second podomere, and the third at the ventral tip of the second podomere. This last seta may represent the reduction of the exopodite, but this is a matter of conjecture. The outer face of the protopodite is made of very thin chitin, with no strengthening structures.

The first podomere of the endopodite is about 100μ long and 20μ wide. It bears one well-developed seta at its ventral tip (Fig. 24).

The second podomere of the endopodite is shorter, and bears one long seta on the middle of its ventral margin. Distally the ventral border is extended in a tooth-like structure (Plate 60, No. 277). This forms the lower jaw of the pincers structure. On the dorsal side, the semicircular

chitin rim is fringed with numerous short, sensory hair-like setae. These evidently aid in locating foreign materials.

The distal podomere is very short, but quite essential to the functioning of the leg. It is joined to the preceding podomere on the dorsal side by an elastic ligament. The ventral margin forms a chitin hook, which serves as the dorsal jaw of the pincers. Distally this podomere has a toothed claw about 25μ long. This appears to be used as a kicking structure to dislodge particles which cannot be easily removed by the pincers. There is also a short seta attached near the base of this claw. On the dorsal side of the podomere is a long, backward-directed seta (Plate 60, No. 277).

The musculature of the protopodite is highly complex. The muscles in the case of *Cypridopsis vidua* are quite small in most cases, and cannot be entirely worked out. Rome (1947, p. 122) has described three groups of muscles for *Herpetocypris reptans* which could not be recognized for this species: first, muscles from the left leg joined to those of the right on a little chitinous device in the middle of the body; second, muscles extending to the endoskeleton; and third, muscles extending to the dorsal region of the valve. There are two muscles of the protopodite which pass into the body (Fig. 24). These are attached to the distal part of the first podomere. Two other muscles extend from the proximal rim of the protopodite to the distal part of the second podomere, where they are attached to the chitin framework. They are used in the enrolling process (Fig. 25). The muscles attached to the dorsal margin may logically be called extensors, and those attached to the ventral margin may be called flexors. There is also an extensor muscle from the ventral margin of the first podomere to the dorsal part of the chitin framework of the second podomere (Fig. 26). This muscle also assists in the enrolling process, and is here classified as an extensor because its contraction provides tension on the dorsal part of the second podomere.

The first podomere of the endopodite has a chitin projection near its proximal end, which fits against a similar projection at the distal end of the protopodite (Fig. 26). These form a fulcrum to control movement of the endopodite. A strong muscle is attached to the endopodite proximal to the fulcrum, and extends to the transverse chitin process separating the two podomeres of the protopodite (Fig. 24). Contraction of this muscle moves the endopodite downward, and it is here called a flexor (Fig. 26). Rome (1947, p. 123) designates the corresponding muscle in *Herpetocypris reptans* as extensor, apparently because it brings the endopodite into a straight line with the protopodite, and thus "extends" it. The writer believes it is much simpler to label all muscles which move podomeres ventrally as flexors, regardless of the particular angle which the podomere makes with the preceding one. Similarly, all muscles moving podo-

meres dorsally would be extensors. This plan assumes that the evolution of a podomere changes the angle it makes with the preceding podomere, rather than reversing its dorsal and ventral positions. The first podomere of the endopodite has no extensor muscle, but depends upon the combined action of the flexor and extensor muscles for the second podomere (Fig. 26; Plate 27, No. 177).

The second podomere of the endopodite is operated by one flexor and one extensor muscle, both attached to the ventral border of the protopodite near its distal end (Fig. 24).

The terminal podomere is operated by a single muscle, which acts as an adductor to close the pincers.

The sensory nerves from the third leg are attached to the ventral chain of ganglia, and do not have a separate ganglion. Separate nerves from the upper and lower jaws of the pincers unite in the protopodite (Fig. 6).

Genital Lobes

The external chitinous parts of the genital system are generally imperfectly understood. The lobes themselves are half ellipsoids set side by side near the median plane. They lie behind the thoracic legs and in front of the furcae.

The key to the arrangement of the whole genital system is the fact that there are two pairs of genital openings. The two vaginal openings lie near the center of the lobes, on the inner faces, and are rimmed with heavy chitin frames. In syngamic species they are used in copulation, and lead to the seminal receptacles. There are separate distinct uterine openings, through which the eggs are discharged. They are normally very long horizontal slits along the inner edges of the genital lobes, extending behind the vaginal openings (Fig. 27). In the process of egg laying, the genital lobe is forced outward to provide a sufficiently large opening.

The vaginal opening has a rather complex chitin structure. The opening itself is directed toward the posterior end of the animal. It has an elliptical frame (Fig. 28, alpha and beta), which is joined at its dorsal and ventral tips by a semicircular rod of chitin which arches toward the anterior end (Fig. 28, gamma). This strengthening rod lies along the inner face of the genital lobe, and near its ventral juncture with the frame of the opening it is divided to form a hole (Fig. 29). A separate chitin structure extends through this hole, curved like a buckle. Bergold (1910, p. 28) described this as a chitin "stick," and that designation is used here. The outer edges of this chitin "stick" are marked by small pustules, to which muscles are attached to operate the vaginal openings. The muscles connect to the outer ventral wall of the genital lobe. Their contraction pulls the chitin "stick," which then turns the framework of the opening. In a syngamic species, this would make it more accessible for the male in

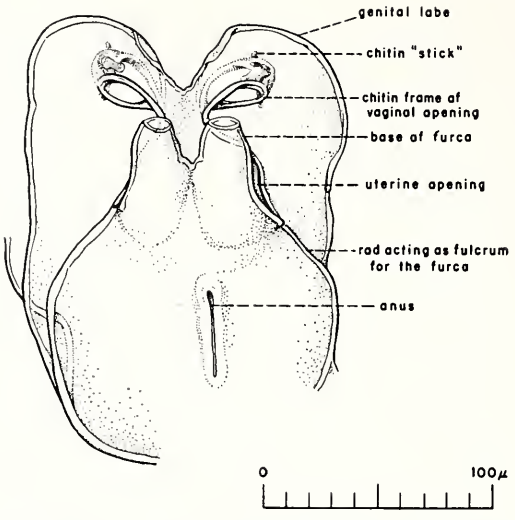


Fig. 27. Genital lobes and posterior portion of the body as seen from below and to the rear. Distal portions of the furcae are removed to show the vaginal openings.

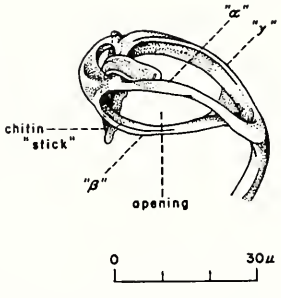


Fig. 28. Chitin framework of the right vaginal opening as seen from below.

copulation. The "stick" is enclosed by the genital lobe (Figs. 3, 4; Plate 49, No. 241; Plate 59, No. 272).

The pair of uterine openings are not nearly as conspicuous as the vaginal openings. They are elongate in the long direction of the animal, and lie immediately anterior to the furcae (Figs. 3, 4). The actual opening is difficult to find in microtome sections, being closed except during the period of egg laying. In those specimens having eggs in the end sections of the uterus, the opening is distended and can be located accurately (Plate 39, No. 221; Plate 40, No. 222; Plate 50, No. 243). The uterine openings are operated by numerous muscles attached to the periphery, and connected to the genital lobe and to the posterior body wall (Fig. 4).

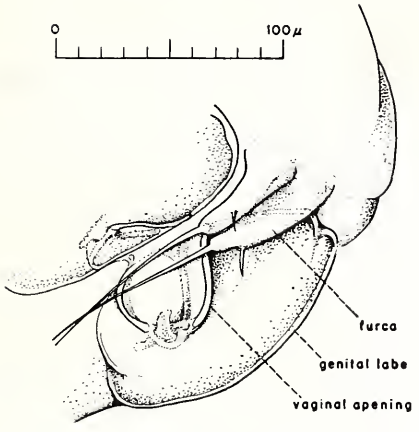


FIG. 29. Posterior portion of the body as seen from the left side and below.

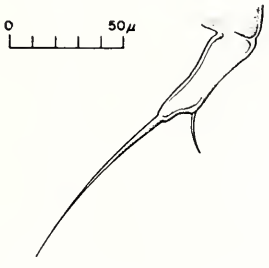


FIG. 30. Inner face of right furca.

The sensory and motor nerves are connected to the posterior part of the ventral chain of ganglia (Fig. 6).

FURCAE

The pair of furcae are attached to the posteroventral part of the body, immediately behind the genital lobes. Many of the fresh water ostracods possess furcae which are very strong and each is equipped with robust claws. However, the subfamily Cypridopsinae, to which *Cypridopsis vidua* belongs, is characterized by reduced furcae, each of which terminates in a long seta or "flagellum."

The furca apparently serves only a sensory function in *Cypridopsis vidua*. The base is about 50μ long, and tapers gradually for about three-fourths of its length, then more sharply until it is only a few microns at the point where it joins the terminal seta. This long seta is about 80μ long, and tapers throughout its length to a very delicate tip (Fig. 30; Plate 50, Nos. 242, 243). There is a second small seta 20μ long on the

dorsal edge of the base, attached at the point where the tapering of the base changes abruptly.

There is a vertical chitin rod fitted against the mid-point of the base of the furca, which acts as a fulcrum. This rod is curved around the posterior part of the body, embedded in the body wall. Dorsally the rod splits into two branches. The posterior branch is a place of attachment for muscles operating the furca (Fig. 5).

Nerves of the furca are connected to the posterior end of the ventral chain of ganglia.

The Eye

The "single" eye of the ostracod is not a simple organ. It is made up of two lateral elements and one median. It lies in the most anterior-part of the body a little below the dorsal rim of the shell. When the shell is gaped open, the eye can see through the space between the valves, with only the body wall of the forehead to interfere with the vision. When the shell is closed, however, direct vision is sacrificed for protection. Even under such adverse circumstances, the animal is able to distinguish light from shadow.

The framework of the entire eye structure is black and opaque. This pigment forms a backdrop for the three parts of the eye, so that the sensitive cells in each can receive light only from a given direction. Three optic cups are set into deep depressions in the pigment, one on each side, and a third slightly below and at the front. Each of these optic cups has a tapetum and is equipped with sensitive nerve cells. In each lateral cup the tapetum forms two basins to accommodate the twin lenses. The number of sensitive cells can be determined, provided the specimen is prepared carefully, oriented precisely, and cut in very thin sections. The writer did not attempt the exacting procedure. Novikoff (1908, p. 85) reported ten to fifteen cells in each of the lateral cups and seven to eight in the frontal cup. Rome (1947, p. 79) counted the sensitive cells in the eye of *Herpetocypris reptans* as follows: the frontal cup = 8, upper part of posterior basin of each lateral cup = 6, lower part of the posterior basin of each lateral cup = 4, and anterior basin of each lateral cup = 3.

The crystalline lenses of the eye serve to concentrate the light onto the sensitive cells, and also to anchor the eye in place. The frontal cup has a single large lens, which in *Cypridopsis vidua* is heart-shaped, with two dorsal lobes (Plate 61, No. 282). Each lateral optic cup contains two lenses. These are rounded, except for the flat surfaces where the two are in contact, and for the elongate projections which hold the eye in place. There are four projections, one on each of the lateral lenses. The two anterior projections diverge and end at the forehead, near the inside

boundaries of the antennules (Plate 61, No. 281). They are attached, and it is possible that the eye can be moved slightly by the movement of the antennules. The two posterior projections diverge toward the rear, and are embedded in the connective tissues of the head (Plate 20, No. 134).

There are three optic nerves connecting the nerve cells of the eye with the protocerebrum. There is one from the frontal median element (Plate 15, No. 85; Plate 42, No. 226), and one from each of the two lateral elements (Plate 15, Nos. 86, 88; Plate 42, No. 227). These nerve cords are very smooth and cylindrical.

Endoskeleton

The endoskeleton is completely encased within the body, and therefore can be studied only by sections. Although the endoskeleton was properly described by Claus (1893, p. 57) and by Vávra (1891, p. 11), its nature was misunderstood by Klie (1926, p. 10) who confused it with the framework of the body.

The muscle arrangement in the ostracod differs from that in the higher crustaceans. In the lobster, for example, the appendages of each segment are operated by muscles attached to the surrounding section of hardened carapace. In the ostracod, however, the hardened armor is in the form of the two valves of the shell; and the wall of the pouch-like body hanging inside the shell is, for the most part, very delicate and supple and structurally unsatisfactory for muscle attachment. These factors critically limit the pattern of muscle arrangement. Many muscles from the appendages are attached to the dorsal region of the shell; some of the muscles from the alimentary tract are attached to a framework of chitin rods embedded in the body wall; and other muscles from the appendages, alimentary tract, and excretory glands are fastened to the endoskeleton in the middle of the body.

The endoskeleton is composed of chitin. It lies behind the esophagus, above the ventral chain of ganglia, and between the mandibles. There are projections from the plate-like center of the endoskeleton pointing toward the various appendages. Muscles are attached at the ends of these projections. The projections toward the antennules and antennae are fused into wing-like processes extending outward and upward (Plate 64, No. 288; Plate 69, No. 303). There is also a posterior ventral extension to which the muscles of the maxilla and the first thoracic leg are attached (Plate 70, No. 306).

The endoskeleton itself is suspended by a pair of muscles from the dorsal region of the shell (Plate 11, No. 54). The contraction of these muscles compensates the forces exerted on the endoskeleton by the other muscles (to appendages, hypostome, etc.).

There are muscles from the endoskeleton to the antennules, the antennae, the mandibles, the esophagus, the hypostome, the maxillae, the first thoracic legs, the second thoracic legs, excretory gland A's, excretory gland C's, and the closing muscles. This last muscle, connecting the endoskeleton with the closing muscles of the shell, is a subject of controversy. Rome (1947, p. 83) denied its existence. There are muscles from the endoskeleton which appear to terminate at the junction of the closing muscles with the chitin process which joins closing muscles of the opposite sides (Plate 63, No. 286; Plate 23, No. 147). These muscles lie above those going to the maxillae, and are definitely attached to the endoskeleton. The writer is of the opinion that they are also attached to the chitin process joining the closing muscles of right and left sides, as Vávra (1891, p. 11) and others believed.

The writer has also examined sections of *Candona crogmaniana* Turner, which has a markedly different endoskeleton. In this case it has a complex net of delicate chitin rods, with no such large masses of chitin as are present in *Cypridopsis vidua*. The endoskeleton probably differs with each species.

Excretory Gland A — The Gland of the Antennule

The excretory glands lying on the sides of the esophagus and in front of the ducts from the liver to the stomach are conspicuous structures in frontal sections, but they were not described until 1910, when Bergold (1910, p. 12) gave a very good account of them. They lie within the limits of the body, and empty out immediately below the antennules through a duct. Since Bergold referred to the antennules as the "first antennae," he called these the "glands of the first antennae."

The glands are not located in the antennules ("first antennae"), and there is no evidence that their functioning benefits these appendages any more than any other part of the body. Each of them is here called simply an "excretory gland A," to distinguish it from other excretory glands.

Each gland is roughly triangular in shape and spread out horizontally. It is about 30μ in its longest direction, and has a duct 20μ long (Plate 3, Nos. 10-12; Plate 22, No. 144; Plate 65, No. 290). It contains four or five large cells, each containing several small nuclei. No fluid has been observed in the cavity.

A large muscle is attached to the posterior point of the gland, leading back to the endoskeleton (Fig. 4; Plate 3, Fig. 11; Plate 15, Fig. 89). Contraction of the muscle stretches the gland, narrows its diameter, and forces out any secretion it may contain.

Excretory Gland B — The "Shell Gland"

This pair of glands is very complex, and may actually represent the combination of two pairs of glands. They are located in the epidermis of

the shell, and in many species can be seen through the shell. They are seen with difficulty in living *Cypridopsis vidua* because of the color pattern on the shell.

These glands were first recognized by Zenker (1854, p. 38), who referred to them as *Milz* (spleen). His description was incomplete. Claus (1895, p. 13) gave complete details of the gland, and compared the structure in various Cypridae. Additional contributions were made by Bergold (1910, p. 13).

The "shell glands" of the ostracod appear to be homologous to the green glands of the higher crustacea and to the shell glands of the Cladocera.

Each gland is composed of three parts: a glandular duct with several lateral diverticula; a rear sac which empties into the inside (at the junction of the base of the antenna with the hypodermis of the shell) through a short duct; and an end sac of secreting cells, connecting to the rear sac through a narrow duct (Fig. 31).

The glandular duct is the largest of the three parts (Fig. 1). It lies entirely within the hypodermis, anterior to the body (Plate 3, Nos. 10-12; Plate 8, No. 39; Plate 14, Nos. 81-83; Plate 42, No. 227). It has eight to ten short diverticula which increase the volume of the lumen. The cells surrounding the duct have large oval nuclei (Plate 32, Nos. 197, 198), and number about eight in *Cypridopsis vidua*. They seem to bear no particular arrangement with respect to the diverticula, sometimes being located at the ends, and at other times lying between adjacent diverticula. The cells around the glandular duct are set off from the epidermal cells and are connected to the walls of the epidermis by trabecular processes. Claus (1895, p. 14) referred to the spaces in the hypodermis as blood lacunae. No fluid has been seen in the glandular duct of *Cypridopsis vidua,* but the writer also examined sections of *Candona crogmaniana* Turner, in which the diverticula are found to be partially filled with a clear substance which stains an orange color with Ehrlich's haematoxylin and eosin.

The rear sac of the gland is an ellipsoidal cavity about 40μ in diameter. The glandular duct empties into it with no apparent change in diameter. The rear sac lies posterior to the junction of the hypodermis lining with the body wall, with about half its volume extending into the region of the body (Plate 1, Nos. 3, 4; Plate 15, No. 87; Plate 20, No. 135). The four or five cells forming the rear sac are large and each contains several nucleoli. The sac also has an enveloping meshwork of fibrous processes. The end sac also empties into this rear sac through a narrow canal (Fig. 1). The rear sac discharges the products it receives from the glandular duct and the end sac through a short tapering duct which opens between the antenna and the lining of the shell. This duct is difficult to find except in transverse sections (Plate 15, No. 85). The emptying of

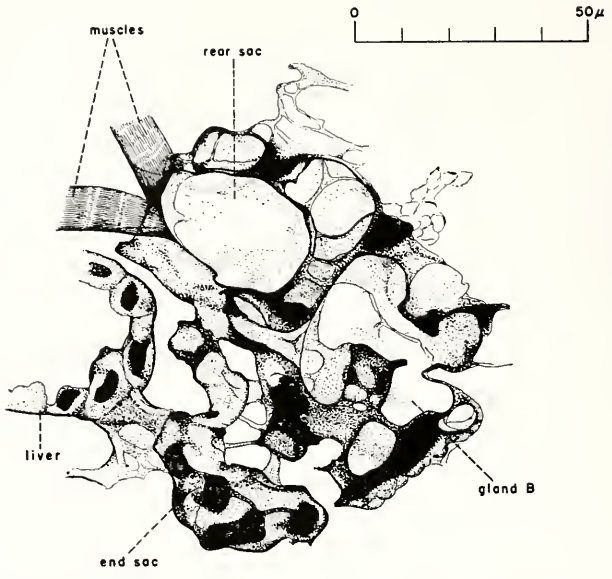


Fig. 31. Ten-micron longitudinal section through excretory gland B. The right side of the drawing is anterior.

the rear sac is accomplished by two small muscles attached to the posterodorsal part connecting it to the wall of the hypodermis (Figs. 1, 31).

The end sac is located immediately anterior to the liver, to which it is connected by tissue (Plate 2, No. 7; Plate 32, No. 196). It is composed of about six large cells with circular nuclei, which stain the same color as the cells of the liver. The lumen is very narrow. It connects to the rear sac by a narrow canal about 30μ long (Fig. 31).

It is impossible at this time to tell what the evolutionary history of excretory gland B has been. It apparently corresponds to an original segmental nephridium. The end sac seems to be an added feature. The boundaries of the ancestral segments have disappeared in the ostracod, and the development of the shell has influenced the arrangement of the body elements. Only three of the numerous nephridia in the ancestor have survived. One of these, the one under discussion in this section, is located almost entirely in the hypodermis of the shell. Certainly this gland deserves additional study, for it quite possibly holds the key to the history of the ostracod shell.

Excretory Gland C — The Maxillary Gland

This gland was first described by Bergold (1910, p. 18). The sole reason for calling it a "maxillary gland" is that the orifice is located immediately behind the maxilla. The ostracod has no segmental boundaries

and the number of appendages are reduced from that of other crustacea, so there is no assurance that this nephridial structure is actually part of the maxillary segment. It is here called excretory gland C.

There is a point of confusion which should be clarified for other workers in ostracod morphology, in case it has not already been discovered by them. The term "maxillary gland" has been used for two entirely different structures. The term is referred to in this paper as it was originally applied by Bergold. However, Yatsu (1917, pp. 435-39) Okada (1926, p. 478), and possibly others have used the term "maxillary glands" for some elongate glands in the upper lip of certain marine ostracods. These glands are the source of the bioluminescence which characterizes these species. The glands were first discovered by Müller (1890, p. 243-49), who described them only as glands in the upper lip. His description and illustrations depict them as large, elongate glands filling most of the upper lip. They empty individually through pores in the outside ventral wall of the upper lip. Some of these pores are located on odd cone-like projections. The illustrations of both Yatsu and Okada leave no doubt that they were describing these glands. It is unfortunate that they selected "maxillary glands," a term already in use and also very inappropriate as applied to glands which produce luminescent substances. No homologous glands have ever been found in fresh-water ostracods.

The pair of these glands is found near the center of the body behind the closing muscles. Each gland lies immediately to the outside of the corresponding gland N (Plate 63, Nos. 285, 286; Plate 64, Nos. 287, 288). The gland is foursided in frontal section (Plate 64, No. 287), roughly circular in sagittal section (Plate 10, No. 47; Plate 27; No. 178), and triangular in transverse section (Plate 17, No. 98). From these sections we can construct the general form as that of a truncated pyramid which is almost completely inverted. The two outside corners of the gland are affixed to the body wall, and the posterior inside corner is anchored by branching tissues which penetrate into the interior of the body (Plate 64, No. 287). The fourth corner, the inside anterior, is attached to muscles leading to the nearby endoskeleton. The anterior portion of the gland narrows downward into a tiny duct, which is contorted in a flattened S-shape (Fig. 3; Plate 64, Nos. 287, 288; Plate 65, No. 289). The orifice of this duct is in a slight indentation of the body wall immediately behind the maxilla. The contraction of the muscle to the endoskeleton narrows the lumen of the gland and forces the contents out through the ventral duct.

The cells of this gland are the same type as those composing excretory gland A and the rear sac of excretory gland B. The several nucleoli of each cell are small and inconspicuous. No substance has been observed in the lumen of the gland.

The Liver or Hepatopancreas

The livers or hepatopancreases are paired glands lying in the hypodermis layers of the valves and emptying their solution into the stomach through ducts. They secrete a large portion, if not all, of the digestive juices.

Each of these large glands is nearly 200μ long and 40μ in diameter in the posterior half (Plate 8, Nos. 35-37). The anterior half extends horizontally to a width of over 60μ (Plate 1, No. 4). The posterior end is in the posteroventral quadrant of the hypodermis, from which point the liver curves upward and forward until the anterior end is at the side of the stomach (Fig. 1). There is a large lumen which is always partially or wholly filled with fluid. The short, horizontal duct from the lumen tapers to a small orifice in the front part of the stomach (Plate 2, No. 6).

The food ball in the stomach is surrounded by a substance which shows the same properties as that in the livers, and there is no reason to doubt that they are the same. The large blocky cells of the liver have large nuclei, and differ from the narrower elongate cells of the stomach wall. This strongly suggests that the liver produces all of the digestive fluids, while the stomach absorbs the nourishment of the food.

Gland L — Gland of the Upper Lip

This pair of glands was first described by Claus (1895, p. 12). They are located in the upper lip and open to the rear in the mouth, near the place where the atrium narrows into the esophagus (Plate 6, Nos. 21, 22; Plate 14, Nos. 78, 79; Plate 24, No. 150; Plate 30, No. 188; Plate 34, No. 206).

Each gland is about 30μ in diameter, roughly spherical in shape, and set in the center of its half of the upper lip. There is no large lumen, and the duct leading to the mouth is small and made of thin tissue. The gland is held in place by this duct and by a thin connective tissue extending to the anterior wall of the upper lip. The wall of the gland is very definite in cross-sections, but in the whole animal it is sometimes obscured by subdermal cells which have the same appearance as the cells of the gland. The cells of the gland can be seen more easily in a needle dissection of the whole animal than in any of the sections, due to the strong absorption of stain in the outer parts of the gland. In a needle dissection the cells' borders can be seen, showing about eight cells. Each cell has several small nucleoli.

Gland L is one of the few glands of the ostracod which suggests a specific function by its location. Whatever solution is produced, it is emptied into the mouth. The gland might be called the salivary gland without gross error of judgment. The food upon reaching the stomach is immediately embodied in a smooth, ellipsoidal mass, the food ball (Plates 1, 2).

What role the fluid secreted by gland L plays in preparing the particles for incorporation in the mass already in the stomach is only a matter of conjecture, at present.

"Gland M" — The Gland (?) of the Mandible

Schreiber (1922, pp. 530-31) described an unusual gland which had not been previously recognized, located in the distal portion of the basal podomere of the mandible. This multiple gland, according to the description, is composed of about thirty small glands, each consisting of a single cell, all enclosed by a loose membrane. Most of the cells lie clustered in the dorsal part of the glandular structure, but several are isolated in the ventral part. Each cell has a tiny duct leading down from it. Three or four of these ducts open above the constricted part of the toothed area, but the majority of them converge into ducts opening to the outside through circular openings in the teeth (according to Schreiber).

Schreiber's original description of these cells compares them with those of *Dytiscus marginalis*, as described by Casper (1913, p. 443). These cells form a mandibular gland. *Dytiscus* is a predaceous diving beetle. Now, although the ostracod and the diving beetle belong to the same phylum, and both are freshwater forms, we should use extreme caution in stating that structures are homologous. Indeed, the ostracod is such a modified little animal that it is difficult to make certain direct comparisons with the higher crustaceans (Malacostraca), to which it is more closely related.

The arrangement described by Schreiber is present in *Cypridopsis vidua* (Plate 6, No. 24; Plate 35, No. 209; Plate 43, No. 229). There are small elongate cells about 1½ to 2μ in diameter located dorsal to the mandibular teeth, with little cord-like connectives less than ½μ in diameter converging and extending into the teeth. However, the writer has seen no openings for these small connectives; and whether the connectives are nerve fibers (as they appear to the writer) or are tubular ducts (as Schreiber believed) is not critically defined in 10μ sections with a magnification of 850 diameters. The "gland" cells stain the same color as the nerve cells with Ehrlich's haematoxylin and eosin. Cells of gland N and gland O show much darker borders and more granular protoplasm with the same treatment. So the cells in question appear to be sensory nerve cells, with nerves extending into the teeth.

Rome (1947, p. 105) studied the cells in the mandible of *Herpetocypris reptans* and concluded that the structures were scolopoïdes, with the terminal filaments ending in the teeth and setae at the distal end of the basal podomere.

The writer uses the term "gland M" in this paper. He does not believe Schreiber's theory, and he agrees with Rome in that the cells are nerve

cells. Detailed work is needed to determine the nature of the distal ends of the nerve fibers, and whether there are any openings in the teeth. Thinner sections and higher magnifications with the electron microscope may bring additional evidence as to what particular sense is registered by this group of cells.

Gland N — The Gland of the First Thoracic Leg

Each of this pair of glands lies in the middle of the body behind the closing muscles and the endoskeleton, on the inner side of the corresponding excretory gland C. The two N glands lie side by side next to the median plane (Plate 63, No. 286). Claus (1895, p. 18) gave the first account of this gland in 1895, calling it the *Kieferdrüse* (gland of the jaw) to correspond to his term for the first thoracic leg, *Kieferfuss* (jaw-foot).

Each gland is reniform, slightly lobed, with distinct borders. It is about 30μ in diameter. The two inner lobes extend above the ventral chain of ganglia (Plate 10, No. 52; Plate 24, Nos. 150, 151). There is a distinct duct in the center of the gland (Plate 64, No. 288), which extends beyond the glandular section into the shaft of the first thoracic leg (Plate 5, No. 19) and opens at the base of the exopodite plate of that appendage (Fig. 3).

There are apparently no muscles attached to this gland, so that it is not comparable with the nephridial structure of the excretory glands. The internal structure in the case of *Cypridopsis vidua* differs from that of other Cypridae. The cell boundaries are not distinct, the glandular portion appears granular, and the nuclei are obscured by the very dark outer area, which becomes opaque with absorbed stain (Plates 63, 64). The writer has examined sections of *Candona crogmaniana* Turner for comparison, and found that the gland in that species has very obvious cell boundaries and large nuclei set toward the outer wall away from the duct.

The nature of the secretion and its utilization are unknown. The development of this gland varies in individuals. Further investigations could be made by isolating individuals of the eighth instar into differing environments where factors of pH of the water, temperature, types of food available, light, etc., are controlled. As soon as the animals had molted into the adult stage, and survived for a given period, they could all be killed and sectioned, and the glands examined. In that way, perhaps, the function of this and other glands could be determined, or at least logically conjectured.

Gland O — The Copulation Gland

This gland was described first by Bergold (1910, p. 28), and later by Fassbinder (1912). The two accounts do not agree in all details.

The gland is very well developed in *Cypridopsis vidua,* even though it is a parthenogenetic species (Plate 4, No. 13). It is elongate, about 30μ in diameter and 50μ long (Plate 48, Nos. 238, 239; Plate 49, No. 240). It lies above and outside the vaginal opening to which it is connected by a duct. The writer has a section where an egg is in the lower part of the uterus, adjacent to the gland (Plate 51, No. 245; Plate 52, No. 246). There does not appear to be any duct connecting the uterus with the gland, as was described by Fassbinder (1912, p. 567: ". . . geht der Eileiter aus einem sehr engen Abschnitt in einem viel umfangreicheren drüsigen Teil über, welcher der von Bergold beschreiben Copulationsdrüse entspricht.") In frontal section this gland is seen to have a distinct lumen (Plate 40, No. 222). The boundaries of each cell are somewhat irregularly disposed. The protoplasm is granular in appearance, and the nucleus contains several nucleoli.

The use of gland O is not known. Its secretion may be of some value in copulation, as Bergold suggested. Although it appears well developed in a parthenogenetic species, such as *Cypridopsis vidua,* we cannot say that it is not copulatory in function, for we know that disuse is not necessarily accompanied by the reduction and disappearance of an organ. The writer has not seen any duct connecting gland O to the uterus, so Fassbinder's suggestion that the gland secretes the shell of the egg seems highly improbable. For the secretion to reach the uterus, it would have to pass successively through the duct of gland O, the "copulation bladder," out through the vaginal opening, and into the uterine opening. Additional research is needed, particularly with the larger Cypridae, to establish the finer details of this gland.

The Digestive System

The ostracod has a complete system of digestive organs from the mouth to the anus. This includes the atrium (mouth), esophagus, stomach, intestine, rear gut, and anus.

The atrium is bounded on the two sides by the toothed ends of the mandibles, on the front by the upper lip, and on the rear by the hypostome. The mandibles have a masticatory and rasping action in preparation of food particles, and can actually "bite off" pieces of solid material. Most of the food, however, consists of numerous fine particles of algae passed into the mouth by the mandibular palps, the maxillae, and the first thoracic legs. Some accessory chewing action is accomplished by the rake-shaped organs embedded in the front of the hypostome. Very small particles are probably obtained by straining through the curtain of long hairs which reaches to the median plane from the front edges of the hypostome. It is quite possible that the animal can selectively route the food either to go through or to by-pass this strainer. The hypostome can

move forward and back; and although the upper lip is rigidly attached to the head, the Y-shaped chitin process at the front of the atrium can also move forward and back (Fig. 4). Gland L, probably a salivary gland, empties into the upper part of the mouth (Fig. 3).

The esophagus is a very muscular portion of the tract. Muscles completely encircle the opening (Plate 5, No. 19). There are also muscles to the forehead, upper lip, and endoskeleton, which by their contraction can distend the opening (Fig. 4; Plate 10, No. 52; Plate 11, No. 53).

The esophagus opens into the stomach. At the place of entrance there are two structures which serve to move the food quickly into the stomach. The first is a powerful tongue-shaped organ which Claus (1895, p. 5) described as a *Wulst* (swollen hump), and Bergold (1910, p. 5) referred to it as a *dorsaler Wulst*. The writer has retained this very appropriate term for this structure. The dorsal wulst projects to the rear, and fits closely against a corresponding structure called the "ventral wall of the front stomach" or the "ventral duplicature." This feature has a concave front surface, however. A cross-section of the passageway between them is crescentshaped, with the horns of the crescent pointed forward (Plate 3, No. 12).

The dorsal wulst is surrounded by a hard cuticle bearing rows of small hairs. These hairs (miniature setae) are directed upward, and push the food particles into the stomach. There is a median groove in the free upper end of the dorsal wulst (Plate 3, No. 9). The dorsal wulst is operated by powerful muscles extending to the front wall of the upper lip (Plate 10, No. 52); these muscles have been referred to in the literature as "pharynx muscles." Other muscles extend across the base of the structure (Fig. 4). In immature individuals or in adults which have recently molted, the bobbing motion of the dorsal wulst can be seen through the shell.

The ventral duplicature is much smaller than the dorsal wulst, but is similarly armed with a hard cuticle bearing setae. It is attached at its front end, with the rest of the structure hanging free (Plate 10, No. 51; Plate 34, No. 205). Two sets of small muscles cross the basal part (Fig. 4), one from the esophagus to the rear wall of the structure, and the other from the stomach wall to the front part of the structure.

The stomach is a large organ in which most (if not all) of the digestion takes place. It is suspended from the dorsal part of the shell by a bundle of tissues (Plate 10, No. 49; Plate 29, No. 184). Ducts from the two livers enter the front part of the stomach from opposite sides (Plate 2, No. 6). The walls of the stomach are made of three layers. The outermost is a thin layer of longitudinal muscles; the middle is a thin layer of circular muscles; and the innermost is a thick layer of epithelial cells. This lining is the true digestive layer, and is made up of cylindrical to

prismatic cells filled with very finely granular protoplasm. The cell walls are distinct, and the nucleus lies in the outer half of each cell. These cells are altered considerably by prolonged dessication in alcohol, and the best sections are those most quickly prepared. Although the liver secretes most of the enzymes used for digestion, the epithelial lining of the stomach may also contribute substances to act on the food. A food ball in the stomach is always surrounded by digestive fluid, but in the rear gut there is seldom a vestige of such fluid. It is possible, however, that some resorption of nourishment continues in the rear gut portion of the alimentary tract.

There is a short section where the tract is constricted and surrounded by heavy muscles, which is here called the intestine. Here the longitudinal and circular muscles are to be seen in their fullest development (Plate 1, Nos. 2-4). The movement of the food ball from the stomach to the rear gut is quite as involved a procedure as the final voiding through the anus. Different specimens have shown the following three conditions: (1) food ball in the stomach only (rare); (2) food balls in both the stomach and rear gut (usual case) (Plate 2, No. 6; Plate 10, No. 48); and (3) food ball in the rear gut only (Plate 33, No. 203). This suggests that the feeding and digestive processes are not continuous, but periodic, although the animal appears to spend most of its time grazing on algal growths.

The rear gut is a cavity lined with the same kind of epithelial cells as the stomach, though not so well developed. Some resorption of nutrition may take place here, but the food balls (changing to fecal pellets) are noticeably smaller than those in the stomach.

The anal opening is an elongate slit made of soft thin chitin (Plate 38, No. 219). It is not muscled at the termination, and the muscles acting as a sphincter lie at the end of the rear gut (Plate 10, No. 49).

The Nervous System

The main features of the nervous system are quite obvious in all stained sections. The central portion consists of the well-developed cerebrum, a circumesophageal ganglion, and a ventral chain of fused ganglia. There are also small ganglia in the antennules, antennae, mandibles, maxillae, and first thoracic legs which are connected to the central portion of the system. There is also a network of small motor nerves from the central portion connected to the various muscles.

The cerebrum has been studied in detail by Turner (1896, pp. 20-44) and later by Hanström (1924, pp. 31-38). It is divided into three portions which can be discerned only by a study of the nerves, for they are not marked off by any constrictions. These three portions are the protocerebrum, the deutocerebrum, and the tritocerebrum.

The protocerebrum is located in the forehead above its junction with the upper lip. It is gently rounded at the top and enlarges downward to the deutocerebrum. The sensory nerves leading into the protocerebrum are the three optic nerves, one from the frontal optic cup and one to each of the two lateral optic cups (Plate 14, Nos. 83, 84; Plate 42, Nos. 226, 227).

The deutocerebrum lies below the protocerebrum. The front is blunt and two wings extend outward toward the rear (Plate 68, Nos. 299, 300). There are two pairs of sensory nerves leading into this portion of the cerebrum. The first pair comes from the antennules (Plate 10, No. 52; Plate 42, No. 227), and the second pair comes from a network of sensory nerves in the anterior part of the shell. The latter pair is difficult to follow in sections, but apparently enters into the epidermis of the valves in front of the ducts which connect the livers and the stomach. There are also motor nerves leading out from the deutocerebrum to the antennules and the dorsal region of the body.

The tritocerebrum has a flattened front with two small forward-projecting ridges at the sides and large extensions outward toward the rear (Plate 68, No. 301; Plate 69, No. 302). Sensory nerves from the antennae lead into the tritocerebrum (Plate 69, No. 303).

The circumesophageal ganglion is composed of two connectives between the cerebrum and the ventral chain of ganglia, one on either side of the esophagus (Plate 23, No. 147; Plate 29, No. 185; Plate 43, No. 229; Plate 69, Nos. 303, 304). Motor nerves extend upward to the antennae and frontal region and downward to the upper lip (Fig. 6).

The sensory nerves of the upper lip are joined to a second ring of nerve tissue around the esophagus, the peribuccal ring (Fig. 6). This ring is attached to the central nervous system at the junction of the circumesophageal ganglion and the ventral chain of ganglia.

The ventral chain of ganglia begins anteriorly with a subesophageal enlargement and tapers posteriorly to the furcae, with local enlargements between each pair of postoral appendages (Plate 11, No. 53; Plate 15, No. 86; Plate 34, No. 206). The anterior end of the ventral chain lies below the endoskeleton, and has a hole in the middle to accommodate the muscles from the endoskeleton to the hypostome (Plate 70, Nos. 306, 307). Sensory nerves join the ventral chain from the mandibles, the maxillae, the thoracic legs, the posterior portion of the valves, the genital region, and the furcae. There are also motor nerves extending out to the muscles of the oral and postoral regions of the body (Fig. 6).

The Valves

The body of *Cypridopsis* is enclosed by two valves which are hinged together along the middle one-third of the dorsal margin. These two

valves are very nearly alike, but are not exact mirror images of each other. There are small differences to be seen on close inspection, as will be described later.

The two valves are closed by muscles through the center of the body. When these muscles relax, the elastic ligament on the dorsal margin has the tension released upon it and contracts, pulling the valves open. When the valves are thus gaped open, the appendages can be thrust out of the boundaries of the shell for locomotion, feeding, and other life processes.

Each valve is composed of two major divisions: (1) a layer of soft sensitive tissues called the *epidermis* or *hypodermis,* enclosed by chitin, and (2) a layer of hard calcium carbonate coated with chitin. This latter layer forms the so-called *outer lamella,* bounding the epidermis on the outside, and the adjoining *duplicature,* rimming the inside edge of the epidermis (Fig. 32).

Many writers have methodically described the hard parts of the valves first. Perhaps this approach has been induced by two facts: (1) the hard parts of the shell are taxonomically the most important parts of the animal, and (2) they are the parts preserved as fossil. In their enthusiasm over the hard parts, some writers have even chosen to regard the epidermis as an incidental layer of tissue filling the space between the hard parts on the outside and a lamella of chitin on the inside. This is faulty analysis. It has led to unfortunate choices in terminology which make it difficult to understand the true nature of the valves.

A more logical order of discussion is called for. It must be borne in mind that each time the animal molts, the calcareous and chitinous parts of the valves are shed, and only the soft epidermis remains with the animal as a basic and necessary part of its anatomy. The epidermis is the *stable* part of the shell in the ostracod's ontogeny. It determines the form of each new set of hard parts which it secretes. Therefore, the study of the shell should begin with the epidermis, and the calcareous and chitinous layers should be described in their relation to it.

The Epidermis or Hypodermis

Claus (1893, p. 17) described the soft tissues in each valve as a hypodermis composed of two layers, an outer and an inner. Fassbinder (1912, pp. 566-67) referred to the same tissues as an outer hypodermis and an inner hypodermis. Rome (1947, p. 68) calls them an epidermis with two layers of epithelial cells. Although the terminology is varied, most writers agree on the actual anatomical details. The soft, skinlike portion of each valve has an outer and an inner layer of cells which apparently secrete the hard parts. The distribution of these cells is disturbed only by excretory gland B, the liver, and the ovary which all lie within this epidermis.

The cells which form the two layers in the epidermis may be referred

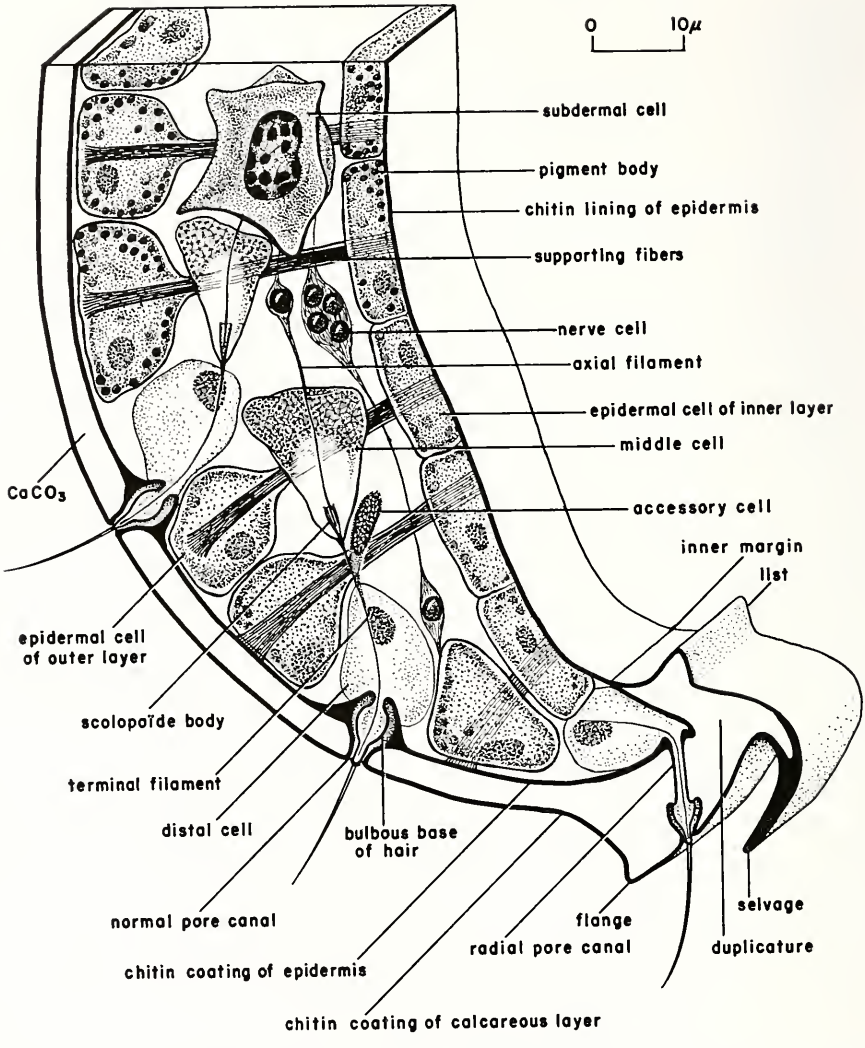


FIG. 32. Diagrammatic section through the anterior ventral part of the right valve as seen from the front.

to as *epidermal cells.* These are the *Hypodermiszellen* of Claus (1893, pp. 19-20). By function they are the epithelial type of cells, as Rome stated. The two layers are not similar in the case of *Cypridopsis vidua.* The outer layer is composed of subangular cells approximately 10μ in diameter. Each cell is distinct (Plate 1, No. 4; Plate 2, No. 7). The cells of the inner layer, on the other hand, are flat and form a more regular continuous layer. They are closely joined to the chitin lining of the epidermis (Fig. 32).

The two layers of epidermal cells are not in contact, but have a space between them. This space is transversed by numerous *supporting fibers,* which act as reinforcing girders from the chitin lining to the chitin coating of the epidermis (Plate 2, Nos. 5-8). These supporting fibers divide the space between the layers of epidermal cells into *lacunae.*

Lying free in the lacunae are large angular *subdermal cells,* which are also found in the hypostome and the upper lip. There are very few of these cells in the epidermis of *Cypridopsis vidua.* The subdermal cells are not attached at any point of their boundaries (Plate 2, No. 6). Various earlier descriptions of the subdermal cells were made, but Claus (1893, pp. 19-20) was the first to give an accurate account which left no confusion between the subdermal and the epidermal cells. Rome (1947, p. 68) claimed to have observed movement of the subdermal cells in the epidermis.

The epidermal and subdermal cells can be distinguished from each other by several characteristics. The subdermal cells lie free in all cases; but the epidermal cells are fixed in place, normally by transverse supporting fibers passing through the middle part of the cell, and in the region of the ovary, liver, and excretory gland B by trabecular fibers parallel to the surface of the epidermis. The epidermal cells in the "striped" areas of the shell have numerous small black bodies of pigment enclosed in their protoplasm, giving the dark color; there are no pigment bodies in the subdermal cells. The epidermal cells also have smaller nuclei than the subdermal cells (Fig. 32).

The function of the subdermal cells has never been established definitely. Claus (1893, p. 20) made the logical suggestion that they serve the function of blood cells. Yet no explanation of their circulation has been offered; and the means by which they could eliminate waste products and carry oxygen to the tissues poses an even greater problem.

In addition to its function of secreting the hard parts of the valve, the epidermis is equipped with many "hairs" (actually little setae), sensitive to touch, which project through pores in the hard parts and serve to warn the animal when the shell nears contact with outside objects. Each hair is actually a projection of the chitin coating of the epidermis. The hair has a bulbous base, and the perforation through the calcareous and chitinous layers forms a spherical cavity, concentric to the base of the hair. In many cases the chitin coating of the epidermis is indented before turning outward to form the base of the hair. In extreme cases the depth of this invagination reaches 8μ (Plate 52, No. 247; Plate 53, No. 248). The sensitivity of the hair is due to a complex arrangement called a *scolopoïde* by Rome (1947, p. 72), similar to that found in insects. Scolopoïdes are found also in connection with the setae of the various appendages. Each of these innervating processes extends from the base

of the hair (or seta) to a basal nerve cell, and consists of: a distal cell, terminal filament, accessory cell, scolopoïde body, middle cell, and axial filament. The terminal filament has its distal end lying free in the base of the hair and its proximal end attached to a scolopoïde body in the distal end of the middle cell. The scolopoïde body is a narrow cone of sensitive fibers, with its apex directed outward and joined to the terminal filament. The axial filament extends from the nerve cell into the middle cell, where its distal end lies free within the cone-shaped scolopoïde body. Any displacement of the hair brings its base in contact with the terminal filament, which then moves the scolopoïde body on its other end; this brings the sensory filaments in the cone of the scolopoïde body in contact with the axial filament which carries the impulse to the nerve cell. The distal cell is attached to the base of the hair and to the terminal filament; it is a specialized epidermal cell and lies in the outer layer of epidermal cells. The distal cell is large, like the other epidermal cells. The accessory cell is small, and is attached to the proximal half of the terminal filament by a cycoplasmic extension. It does not appear to have any direct control in the functioning of the scolopoïde. The middle cell has a distinct cell wall, and has a large vacuole in the distal end where the scolopoïde body is located. It is pear-shaped, with the protoplasm more or less restricted to the rounded proximal end.

Most of the hairs extend through *normal pore canals,* but there are some which are found along the junction of the outer lamella and the duplicature, reaching through *radial pore canals.* The radial pore canals are quite narrow except for a conical enlargement near the end (Fig. 32). The conical base of the hair fits into this enlargement, and does not extend the full length of the pore as in the normal pore canal.

Hard Parts of the Valves

The epidermis is in contact with a chitin covering over most of its surface; in the central dorsal area it opens on the inside to the body itself. The covering on the inside wall may be designated as a *chitin lining of the epidermis* and on the outside wall as a *chitin coating of the epidermis* (Fig. 32). The chitin lining of the epidermis (together with the duplicature) has been referred to as the inner lamella of the shell (Claus 1893, p. 6; Bradley 1941, p. 8). When used for ostracods, "inner lamella" has an entirely different meaning from that which it has when used for pelecypods. Confusion has resulted, and there is little to recommend the further use of the term.

The chitin lining of the epidermis folds back upon itself near the center of the valve, and is then known as the *body wall.* There is no change in composition and no structure to mark the division between the two. It may be said that the soft tissues of the body are held up in a chitin pouch,

which is a continuation of the chitin linings of the two surrounding valves.

The calcareous parts of the shell, as stated above, are the outer lamella and the duplicature. The term "outer lamella" has been used by Bradley (1941, p. 8) to include the calcareous part, the chitin coating of the epidermis, and the chitin coating of the calcareous layer. Again, this is a question of terminology. In this paper, "outer lamella" and "duplicature" are used in reference to calcareous parts only.

The outer lamella and the duplicature are "welded" together at the anterior, ventral, and posterior borders of the shell by a chitin layer. This chitin layer joins onto the junction of the chitin lining and the chitin coating of the epidermis, and is tranversed by the radial pore canals (Fig. 32). The line along which these three chitin layers come together is called the *line of concrescence* by Bradley (1941, p. 9) and *Verwachsungslinie* by Müller (1898, p. 258).

Both the outer lamella and the duplicature have a waxy chitin covering. The line of contact of the chitin lining of the epidermis and the chitin coating of the duplicature is the inner margin. It marks the proximal limit of the duplicature.

The character of the border of the outer lamella, the duplicature, and their chitin coatings is of specific value in ostracod taxonomy. In *Cypridopsis vidua* the left valve overlaps the right valve throughout the perimeter. However, the valves are nearly the same size, and the overlap is made by thin projections around the border.

The structures of the border areas are quite complex. Not only do the structures of one valve differ from those directly opposite in the other valve, but structures change radically from one point to another around the perimeter of each valve. The closure is accomplished in the simplest instances by razor-like projecting ridges of the duplicatures, called the *selvages* by Bradley (1941, p. 10), which overlap and produce a seal along their contact areas. The selvage is the *Saum* of Müller (1898, p. 258) and later German workers. The selvage varies from a low, blunt ridge to an elongate delicate structure, and in some cases is curved outward (Fig. 32). In some sections the selvage is paralleled by an outer ridge, the *flange*, and/or an inner ridge, the *list* (*Leiste* of Müller). The flange may be developed at the welded area as a structure shared by the outer lamella and the duplicature, or it may be confined to the outer lamella alone. The flange does not always form the outer margin of the shell, and sometimes occurs as a small ridge on the outside of the shell when the selvage is unusually well developed and forms the outer margin. The flange is separated from the selvage by a portion of the shell called the *flange strip*. This may form a groove, which is known as the *flange groove*. The list is usually not as well developed as the selvage. The part of the duplicature lying between the selvage and the list is the *selvage*

strip, and when this forms a groove, that is called the *selvage groove*. The part of the duplicature between the list and the inner margin is the *list strip*.

The space enclosed between the outer lamella and the duplicature is termed the *vestibule* by Bradley (1941, p. 8). In living specimens, this space is occupied by the distal portion of the epidermis. In fossil species having only the calcareous parts of the shell preserved, the term "vestibule" has more significance.

Although the Cypridae are said to have no teeth, there are in *Cypridopsis vidua* along the median dorsal border several interlocking small corrugations which serve the function and have the form of "microteeth." In the right valve these are found on a flat vertical surface outside the selvage (Fig. 7; Plate 66, No. 291). The corresponding "microteeth" in the left valve are on the thickened edge of the selvage.

Immediately posterior to this toothed area the selvage of the left valve occurs in the middle of the marginal face and turns up sharply. It fits very intimately into a deep incurved flange groove of the right valve (Fig. 7; cf. Gauthier 1939, Fig. 6D). This evidently functions much the same as the pseudocardinal tooth arrangement in schizodont pelecypods.

The posterior region has an unusually well developed duplicature which extends beyond the line of concrescence to form a large vestibule space. The right valve has a flange, selvage, and a small rounded ridge corresponding to the list. The list lies next to the inner margin. The left has a selvage extending outside the flange of the right valve, a wide selvage strip, and a weakly developed list next to the inner margin. Thus, in this region the selvages of the two valves lie widely separated.

In the center of the ventral border, both valves have only thin, very wide selvages, which lie almost horizontal. The lip-like selvage of the left valve completely overlaps that of the right when the shell is closed. Tips of both selvages are turned outward.

In the anteroventral region the selvage of the right valve is turned strongly outward (downward) and there is development of the flange and the list (Fig. 32). In the left valve the selvage projects forward at an angle to fit against the flange of the right valve. There is a slight development of a flange in the left valve, but it has no connection with the closure. As seen from the side, the line of concrescence in the right valve lies between the flange and the selvage, while in the left valve it lies to the inside of the selvage.

In the anterior end there is some question as to the limits of the inner margin. By definition, the inner margin marks the proximal extent of the duplicature. When a valve of *Cypridopsis vidua* is broken and the anterior end is tilted under double polarized light, the calcareous portion

of the duplicature appears to be limited to about 40μ in width. There is a pattern of interlacing grooves on the thickened chitin in the anterior region. This grooved area is sharply set off proximally by a curved line (Fig. 7). It seems that the chitin lining of the epidermis and the chitin covering of the duplicature continue in contact with each other beyond the inner limit of the calcareous duplicature to form the grooved area. The grooves do not show any significant structure, and they seem to be functionless. The right valve has a selvage turned strongly outward and a small marginal flange. In addition, the right valve also has a row of about fifteen tubercles on the outer lamella near the margin. These vary both in size and in number in individuals of the same clone. The left valve has no tubercles, and the selvage embraces the flange of the right valve in a well-developed overlap. The flange of the left valve is a low, rounded rim which does not enter into the closure.

Very little has been written about the structure of the calcium carbonate in the shell. Dudich (1929, p. 257) set up a classification of the crustacean shell as follows:

I. Achalicodermal: lacking a calcareous layer.
II. Chalicodermal: calcareous layer present.
  1. Amorphochalicose: calcareous material amorphous.
  2. Morphochalicose or crystallichalicose: calcareous material crystalline.

According to this classification, the ostracod shell is chalicodermal, since it contains calcium carbonate. It is further morphochalicose, because the calcium carbonate is crystalline. Under double polarized light, the ostracod shell shows extinction parallel to the orientation of the nicols, with illumination of the rest of the shell (Plate 67, Nos. 293-296). This shows the mineral of the shell to be anisotropic. The same results are obtained when the shell is tilted and when it is viewed from the dorsal edge. Therefore, the mineral is cryptocrystalline, with some (if not all) of the crystals at right angles to the surface of the shell.

X-ray Diffraction Study of the Ostracod

An X-ray powder pattern was made to determine the nature of the shell material. *Cypridopsis vidua* specimens were removed from the aquarium by means of a pipette to avoid contamination with bottom sediments. The ostracods were filtered from the sample and allowed to dry for twelve hours. Several hundred specimens were then packed into an acetate tube about 1 mm. in diameter. The X-ray machine was the copper-target type, and was used with a nickel filter. The tube containing the ostracods was mounted in a collet in the center of a circular metal camera 14 cm. in diameter, and rotated throughout the exposure by a small motor. An exposure of one hour forty-five minutes was found to give good results.

D Measurements from an X-ray Powder Pattern Photograph of Ostracods, Compared with the D Measurements of Calcite and Quartz.

Ostracods		Calcite[1]		Calcite[2]		alpha-Quartz	
Angstrom units	Intensity	Angstrom units	Intensity	Angstrom units	Intensity	Angstrom units	Intensity
4.495	vf	...	...	...	...	...	...
4.25	f	...	...	...	...	4.25	0.25
3.867	f	...	...	3.877	m	...	...
...	...	...	...	3.36	m	...	...
3.340	st	...	...	...	...	3.35	1.00
3.205	vf	...	...	...	...	...	...
3.020	vst	3.04	1.00	3.03	vst	...	...
2.851	vf	...	...	...	...	...	...
...	...	...	...	2.80	f	...	...
2.700	vf	...	...	...	...	...	...
2.576	vf	...	...	...	...	...	...
2.478	m	2.49	0.20	2.495	m	...	...
...	...	...	...	...	...	2.45	0.15
2.276	m	2.28	0.24	2.308	m	2.29	0.10
...	...	...	...	...	...	2.23	0.06
...	...	...	...	...	...	2.12	0.09
2.084	m	2.09	0.20	2.102	m	...	...
1.987	vf	...	...	1.997	vf	...	...
...	...	...	...	...	...	1.97	0.08
1.928- 1.921	m	1.92	0.32	1.912	st	...	...
1.905	m	...	...	...	...	...	...
1.88	m	1.87	0.24	...	...	...	...
1.826	f	...	...	...	...	1.82	0.25
...	...	...	...	...	...	1.82	0.25
...	...	...	...	1.79	vf	...	...
...	...	...	...	1.689	vf	...	...
1.671	vf	...	...	...	...	1.66	0.08
1.602	m	1.60	0.16	1.615	m	...	...
...	...	...	...	...	...	1.54	0.20
1.524	m	1.51	0.12	1.524	m	...	...
1.48	vf	1.475	0.05	1.479	vf	...	...
...	...	...	...	...	...	1.450	0.02
1.438	f	1.439	0.08	1.435	m	...	...
1.417	f	1.425	0.05	...	...	...	...
1.378	vf	...	...	...	...	1.375	0.25
1.360	vf	1.35	0.03	1.36	vf	...	...
1.339	vf	...	...	...	...	...	...
1.295	vf	1.295	0.05	1.296	f	1.299	0.04
...	...	...	...	...	...	1.256	0.03
1.250	vf	1.243	0.03	1.241	f	...	...
1.233	vf	...	...	...	...	...	...
...	...	...	...	...	...	1.228	0.03
1.201	vf	...	...	...	...	1.200	0.06
1.181	f	1.179	0.03	1.185	m	1.180	0.08
1.155	m	1.15	0.05	1.156	m	1.155	0.01
1.145	vf	...	...	...	...	...	...
...	...	...	...	1.124	vf	...	...
...	...	...	...	...	...	1.080	0.04
1.064	vf	...	...	1.063	vf	...	...
1.047	m	1.045	0.06	1.047	m	1.048	0.02
1.038	f	...	...	1.040?	vf	...	...
...	...	...	...	...	...	1.035	0.01
1.011	f	1.014	...	1.014	vf	1.015	0.01
0.990	vf	...	...	0.987	f	...	...
0.978	vf	...	...	...	...	...	...
0.964	f	...	...	0.967	f	...	...

D Measurements from an X-ray Powder Pattern Photograph of Ostracods, Compared with the D Measurements of Calcite and Quartz.

Ostracods		Calcite[1]		Calcite[2]		alpha-Quartz	
Angstrom units	Intensity	Angstrom units	Intensity	Angstrom units	Intensity	Angstrom units	Intensity
0.944	f	...	...	0.944	m	...	...
...	...	...	...	0.925	vf	...	...
...	...	...	...	0.902	m	...	...
...	...	...	...	0.891	m	...	...
...	...	...	...	0.875	f	...	...
...	...	...	...	0.863	m	...	...
...	...	...	...	0.854	f	...	...
...	...	...	...	0.843	m	...	...

Key: vst — very strong; st — strong; m — medium; f — faint; vf — very faint.

[1] The figures in the first column for calcite and for alpha-quartz were taken from the file cards in the chemistry department, University of Illinois.

[2] The d measurements for calcite listed in the second column were computed from the s distances given by Heide (1924), according to the formula

$$A = \frac{7.68}{\sin (0.714\, s)}.$$

This formula is based on the average conversion factors required to derive the strong intensity lines of calcite, aragonite, and mu-$CaCO_3$ as given by Heide.

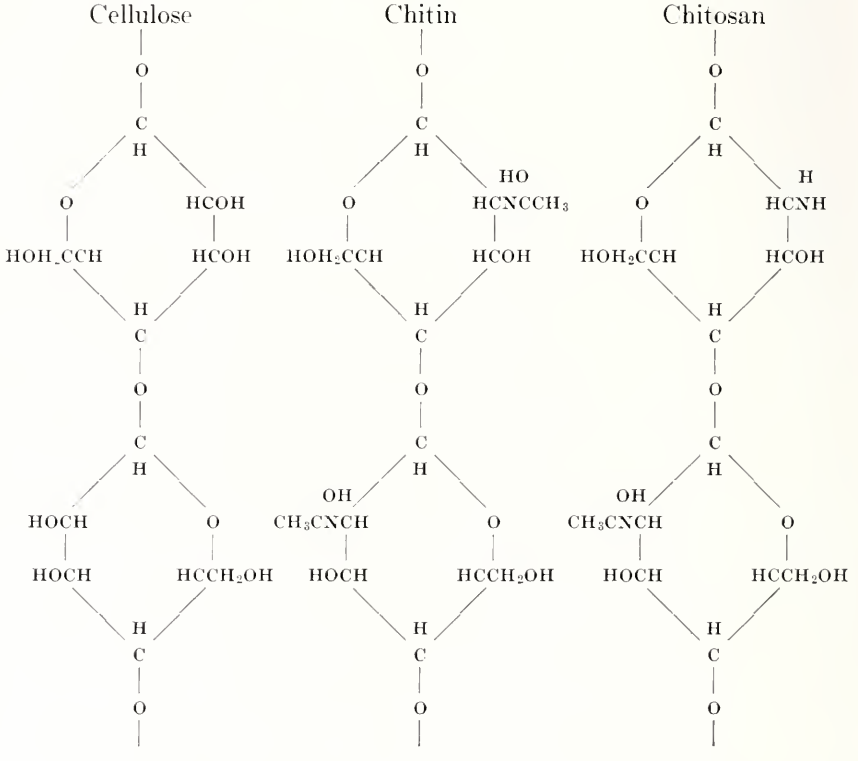
The computed d distances are given in Angstrom units.

The X-ray analysis shows calcite and alpha-quartz present. There is no indication of either aragonite or mu-$CaCO_3$ (vaterite B of Gibson, Wyckoff, and Merwin, 1925, p. 331). The intensity of the lines corresponding to calcite on the film indicates that there was a considerable quantity present in the ostracod sample. The alpha-quartz may all be attributed to the siliceous skeletons of diatoms present in the stomachs of the ostracods.

It will be noted that there are some additional lines which do not correspond to either calcite or quartz. These may possibly be lines from organic remains of the ostracod, from the chitin, or from some mineralogic contamination. The preparation of the original sample excluded any appreciable quantity of impurities, and it is not known whether or not the ostracod eats quantities of clay and other minerals with its food.

The lines with the greatest d values may be indications of organic remains of some type. The clarity of the lines indicates the crystalline nature of the material. The lines do not appear to come from chitin. Clark and Smith (1936, p. 875) show powder patterns of chitin from the lobster *Homarus americanus* to be very diffused, indicating an almost amorphous structure. Chemically, chitin is identical with cellulose except that the secondary hydroxyl on the alpha carbon atom of the latter is substituted by an acetamide group. Chitosan is closely related to chitin. The formulas given here are those given by Clark and Smith (1936, p. 864). There is no evidence at the present time that the substances of crustacean shells called chitin by the zoologists are identical with the

prepared substances called chitin by the chemists. Clark and Smith (1936, p. 864) found that lobster shell material treated with dilute nitric acid, heated for four hours with 20 per cent NaOH, bleached with permanganate and bisulphite, and finally dehydrated with alcohol and ether, produced a chitin nitrate, which was crystalline, probably orthor-



hombic. Chitosan was also prepared from lobster chitin by the action of fused KOH at 180° C., and was found to produce orthorhombic crystals. Meyer and Pankow (1935, p. 590) prepared chitin from the tendons of *Palinurus vulgaris* by treating it with caustic soda, hydrochloric acid, and finally extraction by alcohol. They were then able to obtain definite lines on an X-ray powder pattern of the substance. Again, the crystalline substance from which the powder pattern was made was not in its natural biological occurrence.

The writer made an X-ray powder pattern of dried *Daphnia longispina*, since these cladocerans do not have any calcium carbonate in their shells, which are said to be made entirely of chitin. The film showed only very diffuse halos of high d values (approximate values of 4.5 and 11.7 at the center of the diffuse bands). These match diffuse halos on the

powder photograph of the ostracods, but the lack of definition excludes the conclusion that they are both caused by chitin.

Secretion of the Shell

There do not appear to be any special cells which secrete the shell material. It seems to be formed by all of the epidermal cells. Furthermore, there is no apparent difference between those epidermal cells of the inner layer which secrete only chitin and those which secrete the duplicature. The whole process of shell secretion in the ostracod is entirely different from that in the pelecypod. The pelecypod adds material continuously as the mantle grows; and although the growth is rapid during the summer and inhibited during the winter months, it cannot be said to be discontinuous. The ostracod, by contrast, sheds the entire shell with each molting and secretes a new one, of different size and shape. The actual process of shell formation may show rhythmic activity, as Zschorn (1937, pp. 323-48) found to be the case for other arthropods.

No one has investigated the biochemical conditions which initiate the molting process and those which stimulate the sudden precipitation of chitin and calcium carbonate for the new shell. Fassbinder (1912, pp. 556-57) established that the immediate source of the calcium carbonate was from the body of the ostracod and not from the water. On April 26 he isolated seven instars, including those of *Cypris pubera, Cypris virens,* and *Cypris fuscata.* All were placed in calcium-free water and fed on sphagnum moss, which is acid and noncalcareous. The old shells were removed after each animal molted to insure that there was no outside source of calcium carbonate. The first animal molted on April 27 and the sixth on the morning of May 2; the seventh animal did not molt. On the evening of May 2 all the specimens were killed, and were found to have hard shells. The calcium carbonate for the shell material must have been stored up by the sixth animal at least five days previous to the molting.

How the calcium carbonate is obtained and stored up by the animal has been studied very little for the ostracod. However, the important work of Mann and Pieplow (1938, pp. 1-17) on the calcium carbonate changes in the crayfish during molting may have some bearing on the problem of the ostracod. They found that prior to the molting, the total weight of the crayfish shell is reduced to only one-fourth its normal value, with a proportionate decrease in its calcium content. The progressive decrease in the weight of the shell is accompanied by the appearance and growth of gastroliths in the stomach of the crayfish. These gastroliths contain calcium, but not in sufficient quantities to make up for all of the decrease in the shell. They then analyzed the calcium content of the blood during the molting process and found it to be 150 per cent of its

normal value. After the molting process the gastroliths decrease and disappear as the shell increases in weight and proportionate calcium content. However, the gastroliths are evidently not a source of the calcium for the new shell, since (1) the calcium content of the shell after the gastroliths are lost is approximately three times the calcium content of the original gastroliths, and (2) the rate of calcium increase in the new shell is the same before the disappearance of the gastroliths as it is after. If the gastroliths contributed to the shell, there should be a rapid rate of addition *pari passu* with the diminution of the stones. The mechanical abrasion of grinding in the stomach is cited as an explanation of the depletion and disappearance of the gastroliths. Mann and Pieplow then conducted feeding experiments on newly molted crayfish to determine the source of the calcium. One group was placed in normal tap water and left without food for twenty-one days. The shell was paper-like and elastic. The animals were then fed on Chara, rich in calcium, for an additional twenty-six days. The shells were unchanged. A second group of crayfish was placed in soft water and fed on Chara; at the end of thirty-two days the shells were little hardened and still elastic. The third group were placed in flowing hard water without food; at the end of thirty-two days the shells were completely hardened. The crayfish, Mann and Pieplow concluded, derive the calcium for the new shell from external sources and specifically from a large quantity of hard water. It was also found that feeding with the flesh of other crayfish, rich in calcium, failed to produce calcium increase in molted animals. These investigations show an entirely different situation in the case of the crayfish from that reported for the ostracod. Fassbinder's experiment, showing that the ostracod can store calcium for the shell before the molting takes place, has already been discussed. It is possible that the phylogenies of the crayfish and the ostracod have produced not only morphological differences, but also differences in their biochemical processes.

There is apparently another difference between the crayfish and the ostracod in regard to calcium assimilation. Experiments have shown that the diet affects the weight and shape of the ostracod shell. Fassbinder (1912, p. 563) set up two cultures of *Cypris pubera* O. F. Müller, a normally smooth shelled form. One culture was fed on a diet of crushed snails, rich in calcium. Animals in this culture developed a secondary thickening of the shells, marked by conspicuous anterior and posterior protuberances. Animals in the second culture were fed on a plant diet and maintained the typical smooth form. Unless the history of the individuals had been known, most certainly those on the calcium-rich diet would have been classified as a distinct species.

Wohlgemuth (1914, p. 21) conducted a converse experiment with *Cyprinotus incongruens* Ramdohr. Animals were fed on a near-starvation

diet, and developed saddle-shaped indentations in the posterior dorsal border. Others in a control culture were of the normal shape.

Any ecological study of ostracods should include the food supply as a possible cause of exotic shell shapes occurring within a given species.

The Closing Muscles

The muscles which serve to close the two valves have been referred to as the closing muscles (*Schliessmuskeln*, Vávra 1891, p. 11; Claus 1893, p. 14), adductors (Sharpe 1918, p. 790; Hoff 1942, p. 42), and occlusor muscles (G. H. Fowler 1909, p. 221). Muscles from the two valves are joined in the center of the body to a short, chitinous rod. The distal ends of the muscles are attached to the chitin coating of the epidermis, which is in turn fastened to the calcareous layer. There is no evidence that the muscle fibers penetrate into the calcareous layer.

The muscle fibers, which are striated, change their character as they enter the epidermis layer. The fibers diverge to cover a larger area, and are no longer striated. The distal tips of the individual fibers appear to be enlarged where they join onto the chitin layer. Where the closing muscles penetrate through it, the epidermis lies in contact with the chitin layer (Plate 3, No. 9; Plate 22, No. 145; Plate 23, No. 146). The epidermis in these areas is composed of very finely granular protoplasm, and has no epidermal cell nuclei. The chitin in contact with the ends of the fibers from each muscle appears to differ from that in the remainder of the valve; in *Cypridopsis vidua* there is a secondary deposit of chitin in the form of a low flat boss, to which the fibers are attached. There is one boss for each muscle. These bosses are clearly set off from the rest of the chitin layer by distinct lines of demarcation.

It is very difficult in the whole valve to tell whether the bosses are present or not, for they have very little relief, and are apparently composed of the same material as the rest of the chitin. It is the writer's opinion that the bosses are so firmly welded to the chitin coating of the epidermis that they are molted with the other hard parts of the valves. This means that these areas are of special significance in the formation of the new shell. The chitin coating of the epidermis is apparently secreted after the calcareous layer, since it separates the $CaCO_3$ deposits from the epidermis which must have secreted them. Then the epidermis at the ends of the muscle fibers must have a supplementary secretion of chitin to fasten the muscles to the hard parts of the shell.

The muscle scars found on fossil ostracods are of different types as well as designs. As seen from the inside surface of the valve, some are raised areas, some are depressions, and some have many small pits. A complete study of all living species might throw some light on the original differences in muscle attachment. However, it should also be considered

that the differences may arise in part from selective replacement in the fossil forms. If the thin boss and a part of the epidermis attached to it were preserved, then the fossil form would have a strongly raised process marking the former position of the muscle; but if the rest of the epidermis were replaced and the portion with the muscle fibers were lost (by decay), then the fossil would have only depressions as muscle scars. If the muscle fibers penetrated through the epidermis in large bundles, then the muscle scar could bear many pits. Since muscle scars are used in the taxonomy of fossil forms, they deserve special study. Actually, very little is known about them at the present time.

Respiration

The ostracod has no special structure for obtaining oxygen from the water in which it lives. Many writers have suggested that respiration is carried on by absorption through the epithelium, which includes the body wall and the lining of the epidermis of the shell (Edwards 1857, p. 118; Claus 1895, p. 28; Bernecker 1909, pp. 583-630; Blochmann 1915, p. 391; and others).

Even preliminary observations of ostracods show that they require oxygen for life. They do not occur in waters which are oxygen-deficient.

At the present time morphological studies have neither confirmed the respiratory role of the epithelium nor cast any doubt upon it. The exopodite plates of the maxillae are sometimes referred to as the respiratory plates because they serve to circulate a fresh supply of water in the space within the shell. They are in constant motion. There are no special respiratory structures in the plates themselves.

Reproductive System

Cypridopsis vidua is a parthenogenetic species, apparently at all times, despite the statement by Weismann (1880, p. 83) that this species is only temporarily parthenogenetic, and the report of a male by Spandl (1925, p. 118). The latter is seriously questioned by Klie (1938a, p. 132). The writer has maintained a culture through a period of two years, has examined adult individuals at intervals throughout that period, and has never seen a male.

The reproductive system of *C. vidua* contains the same parts as that found in syngamic species, with no reductions whatsoever.

It must be made clear at the beginning that there are two distinct portions of the system: the first is the circuit followed by the egg, and includes the ovaries and uteri; the second part is normally used in the reception and storage of sperm, and includes the vaginas, the "copulation bladders," the spiral canals, and seminal receptacles. The left half of the system is a mirror image of the right half, but the two are not connected in any portion.

The ovaries originate in the hypodermis layer of the valves in the posterior part of the animal. Each curves backward and downward, forming approximately two-thirds of a circle, then extends forward and upward parallel to the liver (Fig. 1). It then passes into the body, where it is known as the uterus or egg tube.

The ovary of the ostracod offers an unusual opportunity for the study of oögenesis, for the time of development of an egg cell can be estimated from its position in the ovary. The first few microns of the ovary forms a syncytium where the eggs originate. The various stages in parthenogenetic development of ostracod eggs was first adequately described by Woltereck (1898, pp. 602-8), who worked with *Herpetocypris reptans* Baird and *Cyprinotus incongruens* Ramdohr. He distinguished two major zones of development: the *germinal zone,* where the eggs originate, and the *growth zone,* where the many changes in the eggs occur. The growth zone is divided into three parts: (1) the synapsis zone, in which the chromosomes are isolated at one side of the cell, (2) a "differentiation" zone, in which the egg cells become distinguishable from the nurse cells, and (3) the growth zone (restricted sense), in which the yolk is added to the egg and further developmental changes take place in the egg and nurse cells. The oöcytes produced in the germinal zone pass through a stage of synizesis (called simply "synapsis" by Woltereck) exactly the same as that in the sexual egg (Wilson 1925, p. 793). Weismann and Iskikawa (1888, p. 21) state that the parthenogenetic development is diploid, and only one polocyte is present. It is typical of the whole animal kingdom that female-producing eggs always develop with the diploid number of chromosomes. The developing egg increases its yolk content from two sources: the first is from the yolk nuclei or vitelline bodies within the cell; and the second is from separate nurse cells, whose nutritive substances are sacrified to the egg. These nurse cells develop with the same synizesis as the true egg cells; indeed, Claus (1893, p. 21) believed them to be abortive eggs, whose destiny it was to supply vitelline content to the functional egg cells which had followed the same path with more success. The nurse cells are exhausted in their progress through the ovary, and they do not appear in the uterus.

The ovary turns into the body and becomes the uterus without conspicuous change. The actual opening or passageway from one to the other lies posterior to the duct from the liver to the stomach (Plate 36, No. 215). The uterus has a normal diameter of about 30μ, but can be distended to 100μ to pass the eggs. The outside wall of the uterus has a well-defined boundary; the inner wall (bounding the lumen) is irregular (Plate 37, No. 216). There are two sections of the uterus, not sharply separated, based on the wall structure. The initial part is made up of large cells with very finely granular protoplasm and some trabecular tissue, giving it a spongy appearance (Plate 36, No. 214). In contrast,

the remainder of the duct contains large glandular cells (Plate 36, No. 215). The use of these cells is still only conjectured. The most logical use of the cells in the posterior part of the uterus is to secrete the double-walled shell of the egg (Müller 1894, p. 150: "Der scharf abgesetzte glockenförmige Endabaschnitt ist von einem hohen Cylinderepithel ausgekleidet. Er dürfte sowohl als Befruchtungsraum dienen als auch eine Eihülle liefern."). The egg shell is complete upon leaving the animal. Another suggested use of the cells is to furnish a secretion for formation of the threads used to anchor the eggs (Woltereck 1898, p. 601: "Die Fäden und ihre ursprüngliche Dehnbarkeit beobachtet man unter dem Mikroskop. — Das Spinnsekret wird, nach einer schriftlichen Mittheilung, die ich der Güte des Herrn Hofrath Claus verdanke, wahrscheinlich von einer Drüse am Ausgang des Oviducts geliefert."). It seems quite possible that both of these functions may be performed by the glandular section. The opening of the uterus is on the inner face of the genital lobe (Plate 40, No. 222). It is narrow and much elongated, difficult to see unless it is distended by an egg in the end portion of the tube.

The rigid framework of the vagina has been discussed with the genital lobe. It leads to the spiral canal, which terminates in the seminal receptacle. There is some disagreement as to the nature of the connection of the vaginal opening and the spiral canal. Bergold (1910, p. 28) reported that the vaginal opening led to a large copulation bladder, situated above the chitin framework, which tapered at the anterior end into the spiral canal. Fassbinder (1912, p. 567) did not believe in this arrangement, and described the connection as simply horn-shaped, with the smaller end connected to the spiral canal. The writer has found an intermediate condition in *Cypridopsis vidua*, where there is an enlarged tubular section curving forward and upward to the more rigid spiral canal (Plate 39, No. 221; Plate 49, No. 240). This tubular section is lined with glandular-type cells, and lies to the inside of gland O, which it resembles very much. It is here called "copulation bladder," to correspond to Bergold's designation. The "copulation bladder" does not seem to be appropriately named: apparently it does not function as a collecting place, or *bladder,* but is actually the *vagina*. Unfortunately, this latter term has been applied to the chitin framework of the opening.

Gland O, the "copulation gland" of Bergold (1910, p. 28), has already been described. It empties near the opening by a narrow duct.

The spiral canal is unusually well developed, even though the species is parthenogenetic. From its junction with the "copulation bladder" it passes to the outside of the genital region and forms a tightly wound ball before ending at the posterior end of the seminal receptacle (Plate 53, No. 248). The canal is remarkably uniform throughout its length, about 6μ outside diameter and 4μ inside diameter (Plate 40, No. 222).

The total length is over 850μ, but it is wound into a mass only 60μ in diameter.

The seminal receptacle, which in this species never contains any sperms, is an elongate tube lying horizontal in the posterior part of the animal (Plate 38, No. 219). It is connected with the spiral canal at the rear. It is filled with a clear fluid substance, which might (in syngamic species) serve as nourishment for the sperms until they are used. The anterior blind end of the receptacle terminates in an unturned nipple-shaped structure (Plate 48, No. 238). This structure may be the *Pol* which was described by Zenker (1854, p. 43) as being opposite the entrance opening, and which Bergold (1910, p. 34) was unable to find.

There is another phase of the female genital system which is a subject of disagreement, and which applies to the syngamic species directly. A great deal has been written about how the sperm get into the seminal receptacle, but very little about how they get from the receptacle to the uterus, where the eggs are fertilized. Only one opening of the receptacle has been found, and that opens into the spiral canal; thus the entrance is also the exit for the sperms. Klie (1926, p. 37) and others have stated that the spiral canal leads into the end section of the uterus, apparently believing that the vaginal and the uterine openings are one and the same. The writer has seen no internal connection between the vagina and the uterus. Bergold (1910, p. 35) offered a logical solution to the problem, suggesting that the sperm travel out of the vaginal opening and into the uterine opening when the two are in contact. The muscles attached to the chitin "stick" pull the upper part of the vaginal framework downward, turning the structure so that the opening faces directly to the rear. This action brings the vaginal opening closer to the uterine opening, and additional contraction of the muscles may bring the two in contact. There is also a broad band of muscles connecting the anterior and posterior ends of the genital lobe, which by contraction would move the two openings closer together (Plate 49, No. 241). This explanation of how the sperm travel from the storage space (seminal receptacle) to the fertilization room (rear section of the uterus) fits the observed morphological facts very well.

It has been definitely established that one species *Cyprinotus incongruens* Ramdohr, may reproduce either by parthenogenesis or by syngamy. Reports of this species in nature shows that males and females have been found in central Germany, Hungary, and North Africa, but only females are reported in western and northern Europe and central United States. This geographic distribution of parthenogenetic and syngamic races of the species cannot be explained on the basis of climate, food supply, or size of the bodies of water. There is no morphologic difference between the two reproductive types.

Experiments carried out by Wohlgemuth (1914, pp. 57-63) show that the parthogenetic condition may be induced in cultures. With all males removed, the females reproduced parthenogenetically. All of the young were females, and neither males nor spermatozoa were found on examination of the animals. Parthenogenesis was not a result of the isolation of a syngamically produced female, for the cultures continued to reproduce with no males. The ostracods from which the cultures were started continued to be syngamic.

Wohlgemuth (1914, pp. 62-63) was able to reverse the experiment, producing a syngamic form from a parthenogenetic, in only one case. An originally syngamic form of *Cyprinotus incongruens* was changed to the parthenogenetic form by isolation of the females as above. Then females from this race were fed on excrement and brown algal residue and returned to the syngamic condition. These cultures were maintained on a minimal diet of potato peelings and continued to reproduce male and female offspring by syngamy. Four separate cases of changes from parthenogenetic to syngamic races in nature have been observed by Wohlgemuth (1914, p. 65) with no seasonal return to parthenogenesis.

The exact role of the sperm in syngamic reproduction of ostracods is at present only conjecture. After a study of the structure and motility of ostracod sperm, Lowndes (1935, pp. 35-48) concluded that the sperms were nonfunctional, and that copulation has continued in the ostracods after its fertilizing function was lost. If copulation is an instinctive vestigial habit without reproductive significance, there still remains the problem of why impregnated females produce young of both sexes, while those which remain virgin produce only female young.

IV. Biology

The descriptions of life processes in this section are based primarily on observations of *Cypridopsis vidua*. There are some important ecological relationships which are not represented in the life history of this species, and these are also included in this paper and credited to the proper species. This is done to give a full picture of ostracod biology and relationships.

The Egg and Embryonic Development

The eggs of *Cypridopsis vidua* are green in color. Each egg is nearly spherical in shape, approximately 105μ in diameter. It has a double-walled cover of chitin impregnated with calcium carbonate. The inner wall is concentric to the outer, separated from it about 5μ all around. The inner wall is held in place by numerous small chitin processes connecting to the outer wall.

The embryonic development of the egg has been studied for *Herpetocypris reptans* Baird and *Cyprinotus incongruens* Ramdohr by Woltereck (1898, pp. 609-23), for *Cypris ovum* Jurine (= *Cyclocypris laevis* O. F. Müller) and *Notodromas monacha* (O. F. Müller) by Schliep (1909, pp. 390-431), and for *Cyprinotus incongruens* Ramdohr by Müller-Calé (1913, pp. 113-70). The results of their investigations show that the cleavage is total and equal. The first two divisions are meridional, and the next five are alternately latitudinal and meridional, resulting in a 128-celled blastosphere. Differentiation of the cells into entoderm and ectoderm begins after the eighth division. The writer has not sectioned any eggs of *Cypridopsis vidua*, and the very minute pits on the surface of the egg shell make observation of the contents impossible.

The rate of development of ostracod eggs has a phenomenal range, depending primarily upon the desiccation to which the eggs are subjected. Sharpe (1917, p. 797) tells of an instance of samples of dried mud being sent to England from Jerusalem and *Cypris* being raised therefrom after a lapse of from twenty-four to thirty years. Sars frequently described faunas which were raised by him in Norway from dried mud samples shipped from distant lands, including South Africa (1895, pp. 1-56), Australia (1889, 1896), and South America (1901).

This ability to withstand desiccation is attributed by Wohlgemuth (1914, p. 37) to the presence of a watery fluid between the two walls of the cover. Woltereck (1898) observed that the two walls of the egg lie

in close contact while the egg is in the uterus, and do not separate until the egg is expelled. The space between the walls then fills with "water," but whether this comes from an external or an internal source is not clear. The egg also contains a very large amount of yolk material, which according to Klie (1926, p. 30) may be a factor in sustaining life in the egg over such unusually long periods.

Wohlgemuth (1914, p. 37) found that eggs of *Herpetocypris reptans* would withstand drying of over a year, although this species did not occur in his collections from ponds which annually dried up. There is only one type of egg for ostracods, and winter eggs, such as the cladocera produce under unfavorable conditions, are never found. It seems likely that the eggs of all ostracod species are able to survive at least short periods of drying out.

Ostracod eggs also have a great tolerance of cold, and temperature has an important effect on the rate of development. It has been found by Wohlgemuth (1914, p. 42) that eggs of *Cyprinotus incongruens* kept at a temperature equivalent to that of their natural environment (9-11° C.) required fifteen days from the time they were laid until they hatched; other eggs placed at the same time in water kept at room temperature (17-19° C.) needed only seven days to hatch; and a third group of eggs placed in an artificially warmed aquarium (28-30° C.) hatched in only three days.

When the egg hatches, it splits in a smooth plane into two equal halves. Usually the two hemispheres remain attached together by a small bit of unbroken chitin of the outer wall, but this is a very delicate connection and is broken with the slightest disturbance. No studies have been made to determine whether the position of the break in the egg shell bears any relation to the orientation of the nauplius inside.

The Process of Egg Laying

The eggs of *Cypridopsis vidua* are laid in the algae lining the bottom of the aquarium. It would be a very difficult operation indeed to observe the process in nature, and it can only be assumed that the animal would choose a similar site in her natural environment.

The operation of the actual laying of the egg is difficult to observe because of the opacity of the shell. The mother animal stands motionless in the algae with the valves partially opened at the beginning of the process. When attempts were made to orient the shell on its back, so that the procedure could be seen to better advantage, the disturbed female partially closed the valves and apparently ceased egg laying operations. It may be that the second and third thoracic legs assist in the removal of the egg and pass it forward before the ejection from the shell, for when the egg emerges from between the valves, it comes from the middle

of the ventral border. This agrees with the observation of Klie (1926, p. 39) who suggested that the secretion of the gland of the first thoracic leg (gland N) may play an important role in the egg laying process.

The eggs are laid singly, and not in clusters. *Cypridopsis vidua* does not have an enlargement of the uterus to serve as a storage chamber for the eggs, as does *Candona*. Of the many females of *C. vidua* examined in this study, both by microtome and by needle dissections, the maximum number of eggs found at any one time in both of the paired uteri was three. Wohlgemuth (1914, p. 38) reports as many as eight eggs laid by *C. vidua* at one time. There are many periods of egg laying, so that the progeny of any one female are spaced over a long period of time. This is discussed more fully in a following section on the rate of reproduction.

The place where the female chooses to lay the eggs appears to bear a relationship to the oxygen content of the water. Wohlgemuth (1914, p. 41) conducted an experiment with three cultures of *Cyprinotus incongruens* to determine the effects of environment on the site of deposition of the eggs. He found that in the culture with abundant algae and a sandy bottom, the eggs were laid on the bottom; in the culture with a few plants and a sandy bottom, the eggs were deposited under water half way up the side of the aquarium; but in a culture without plants and a mud bottom, the eggs were laid *above* the surface of the water.

It is not possibile to say whether this seeking of an oxygen-rich environment is caused by the extraordinary respiration requirements of the female during the egg laying process, or by an instinct which nature uses to insure a favorable environment for the eggs themselves.

The Process of Molting

The growth of the arthropods is characteristically discontinuous. Unlike the pelecypod or the gastropod, which have their soft parts exposed along one side and can increase their armor by small increments to keep pace with their body growth, the arthropod is completely encased by a hard covering which must be broken open and shed each time the animal adds to its body size. The ostracod is a typical arthropod. Each molting of the shell introduces an animal differing from that of the previous stage, not only in size but also in form. The old appendages may change their form and function, and entire new appendages are added quickly before the new armor is secreted. Each molting is a very crucial short interval in the life history of the ostracod.

Relatively nothing is known about the biology of the molting process. In other words, no one knows what internal reconstructions or what organic phenomena presage the act of molting; and observers cannot agree even on how the animal escapes from his chitinized confines when they

become insufficient for his needs. Wohlgemuth (1914, p. 43) from his observations on *Cyprinotus incongruens,* believed that the animal shed the antennules first, then the other appendages in order toward the rear. Schreiber (1922, p. 491) observed the molting of *Eucypris virens* and concluded that the rear appendages were the first to be freed from the old skeleton and the antennules were last. It is possible that the process varies with different species.

The writer has observed one animal complete the molting, and has killed three others in various stages of the process. The molting takes at least two hours. It is accomplished by barely perceptible movements with prolonged intervals in which the animal is apparently motionless. A peculiarity that conspicuously marks the complicated procedure is that the old shell, the old body wall, and the old covering of the appendages, all are left lying approximately in their original attitude. It requires close inspection indeed to determine how the animal, now crawling away and secreting a new covering, could have escaped at all!

The ostracod which completed the molting was first observed lying on its side at the bottom of a culture dish. The branchial plates were in normal rapid motion, but the animal did not attempt to right itself with the antennae. The valves were slowly spread abnormally wide, so that the animal came to rest on its back with the appendages upward. The first break of the covering occurred when the chitin lining of the left valve suddenly burst and the new shell thrust forward about 10 μ, as though propelled by a spring. This was followed by a rippling motion in the right valve, and a short time later the new valve emerged on that side. Thirty minutes had elapsed since the observation began. The edges of the new valves were remarkably smooth, not crumpled at all. Slowly the rift in the chitin lining spread toward the rear, following the inner margin of the ventral edges, and allowing more of the new valves to spring out. The outward movement of the new valves seemed to create a tension on the body wall in the region of the head. The body wall separated from the lining of the valves in the dorsal part of the head region. The antennules were then withdrawn meticulously and ever so slowly from their enclosing sheath, like fingers from a glove. The antennae followed, and then the other appendages. The shell in the posterior region was freed from the old chitin lining. This lining then acted as a spring, permitting the old body wall and appendage coverings to be pushed upward, away from the body. Using the antennae, the animal rather freely clambered out through the front of the old skeleton. As soon as the animal was free, the elastic lining of the old valves sprung back into place, partially concealing the splits which served as an exit. Even a coating of the ligament was shed, so that the valves remained united. The animal lay motionless for some time, then gingerly brought itself upright with the aid

of the antennae and began feeding. It had successfully passed from the eighth to the ninth instar stage. The animal was eating two hours and fifteen minutes after it was first observed, but the writer does not know how long it had been in the original position on its side.

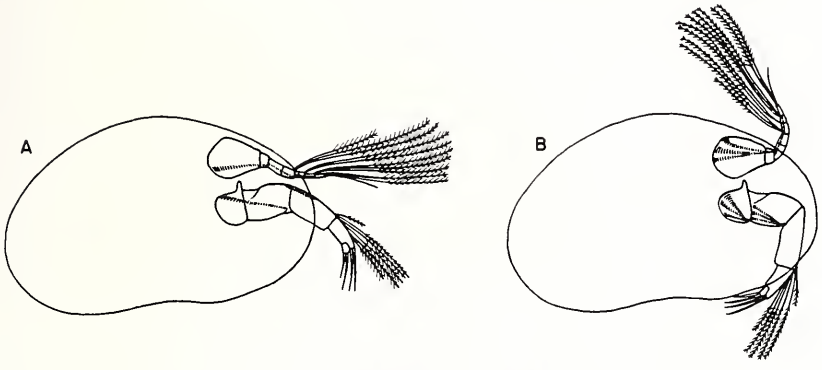


FIG. 33. Swimming movements of *Cypridopsis vidua*. A. The forward extension of the natatory setae. B. The backward thrust of the antennules and antennae.

A second specimen was killed for study in the first stages of the seventh molting. The new valves had not yet broken through, but were seen to be buckled under the old valves in three broad warps. The old valves were not extended as far as were those of the first case.

The third specimen was killed when the two valves had begun separation from the old ones. It was the eighth molting. The left valve was completely free, while the right had only broken through at the anterior edge. This unsymmetrical progression made the animal appear to have three valves, one right and two left.

The fourth specimen was also in the eighth molting. The two new valves were still imprisoned in the posterior region, but the antennules were completely withdrawn, and were found to be complete, even to the natatory setae.

It would appear from these observations that the process of molting is somewhat irregular, depending upon where the chitin happens to split.

By the time the new shell emerges from the cast-off skeleton, it is rigid; however, no study was made of the rate of addition of calcium carbonate. This could be done by using doubly polarized light, and noting the appearance and spread of the lighted areas. Fassbinder (1912, p. 555) stated that the precipitation began in the anterior end of the shell.

SWIMMING

The ostracod propels itself forward in swimming by swift, powerful strokes of the antennules and antennae. The very long setae of the antennules are thrust quickly upward and back, and in unison the setae of

the antennae are thrust downward and back (Fig. 33). This four-oared motion of the two antennules and two antennae permits the animal to swim freely at an observed speed of 10 mm./sec. when alarmed, despite the heavy burden of the shell.

The nauplius or first instar spends most of its time swimming, and is seldom observed on the bottom of the aquarium. The adult usually swims short distances, stopping for longer periods of time to feed on the bottom. However, when the water close to the bottom becomes foul and low in oxygen, the adults also spend much of their time swimming near the top, and feed on the algae on the sides of the aquarium.

Walking

The second thoracic leg seems to be essential to the walking gait of the adult ostracod. The younger instars, in which the second leg has not developed, spend little time on the bottom. Their locomotion on the floor of the aquarium appears limited to clambering with the two antennae. The amount of time the animal spends in walking increases with each instar, and many adults do no swimming for long periods of time, but walk over the surface of the algae and even burrow into it.

The motion of the ostracod in walking is rather smooth, despite the fact that it "hops" rather than "ambles." The legs move in unison rather than alternately. To understand the motion, let us follow through a complete cycle. The claws of the antennae support the weight of the anterior part of the ostracod, while the claws of the second thoracic legs similarly support the posterior part. The complete cycle of the motion involves six phases, as follows: (1) the body is horizontal, the second legs are so strongly flexed that the weight rests on the convex *dorsal* edge of the claws, and the antennae are partially flexed; (2) the antennae are straightened, elevating the front part of the shell; (3) the extensor muscles of the second legs contract, rocking the end claws forward on the convex surface, and pushing the body forward; (4) the end claws of the antennae are shifted forward to a new position; (5) the flexor muscles of the antennae contract, pulling the shell forward; (6) the second leg is flexed and shifted forward, bringing the animal to the first position again (Fig. 34).

pH Tolerance

The pH value was determined for the water in an aquarium where the *Cypridopsis vidua* fauna was increasing rapidly, and was found to be 7.8. The pH value of water from Crystal Lake, Urbana, Illinois, where *Cypridopsis* is abundant, was found to be approximately 7 in the summer.

Reed and Klugh (1924, p. 274) conducted faunal surveys of two pools in close proximity, one in limestone and one in granite. *Cypridopsis vidua*

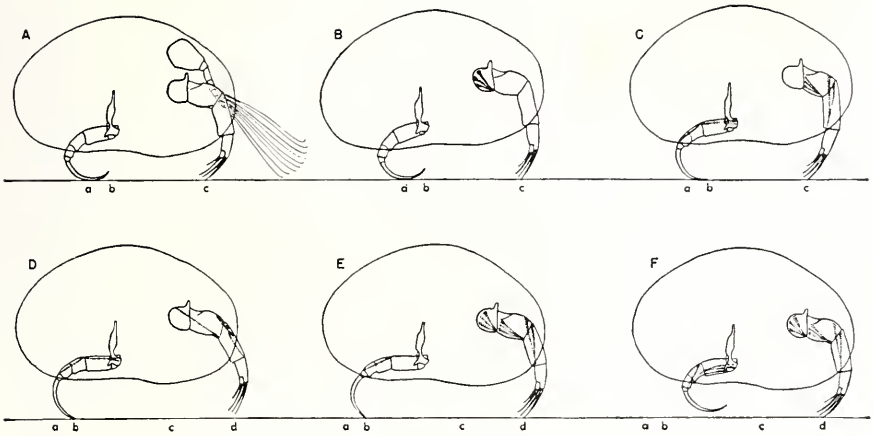


Fig. 34. Walking movements of *Cypridopsis vidua*. A. At rest. B. Antennae extended to lift the anterior end of the body. C. Antennae thrust backward and the body rocked forward on the end claws of the second thoracic legs. D. Antennae lifted free and extended to new positions (from c to d). E. Flexing of the antennae and the farthest extension of the second legs. F. Second thoracic legs lifted free and brought forward to new positions. The cycle then repeats from B. Fig. A. shows the antennules in position to "explore" the area immediately in front of of the ostracod. The muscles shown are those used in each phase of the movement.

was reported in the granite pool where the pH was 6.2 to 6.8, but was absent from the limestone pool.

Klugh (1927, pp. 42-43) used HCl and NaOH to control the pH in a set of experiments to determine the pH range of freshwater ostracods. He found that *Cyprinotus incongruens* could survive two days in pH = 4, one day in pH = 10, and none were killed in pH =7 and pH= 8. *Cypria exsculpta* could survive one day in pH = 4, seven days in pH = 10, and none were killed in pH = 6 and pH = 7. His specimens were from pools having pH less than 7.2.

No experiments or collections have ever been made to determine if a species can become adapted to pH values outside its experimental range. This would be especially valuable in the interpretation of the environments of fossil species.

Heat and Cold Tolerance

The tolerance of heat and cold differs for species reproducing in the early spring and those reproducing in summer. The forms which reproduce in the cold temperatures of early spring can withstand being frozen fast in the ice, but expire at warm temperatures. On the other hand, the species which typically reproduce during the hot summer months die in

very cold water, but maintain normal living processes at very warm temperatures.

Cypris ornata O. F. Müller and *Cypris virens* Jurine could only be sustained at a temperature of 16-18° C. for a maximum of three days, according to Schreiber (1922, pp. 497-98). *Cypridopsis vidua* and *Cyprinotus incongruens* Ramdohr, "summer" forms, were placed in the sun in July where the mid-day temperature was 34° C. and continued swimming about freely; under the same conditions *Cypris ornata* and *C. virens,* "early spring" forms, ceased all swimming activity and crept about on the floor of the container.

The tolerance of cold is phenomenal for certain species. Korschelt (1914, pp. 106-20) conducted a series of experiments with *Cypris virens* Jurine and *Cyclocypris laevis* O. F. Müller. At 7 P.M. on January 23 ostracods were placed in water with a temperature of 4° C. and the water was then frozen; on January 25 the ice was melted and one *Cypris* and one *Cyclocypris* were still living; observations were continued until February 24, a which time both animals were still strong. In a second experiment, ostracods were placed at 7 A.M. on January 24 in water at a temperature of 4° C., the water was frozen, and the ice was broken into pieces so that no trace of water could remain; on January 26, one *Cyclocypris* was still living and appeared completely fresh; it was still living on February 24 when observations were discontinued. In a third experiment, at 9:30 P.M. on February 5 ostracods were placed in a small quantity of water at 4° C., which was then frozen into a piece of ice the size of a walnut; on February 6 four *Cyclocypris* and two *Cypris* were still alive, and were still living on February 26. Schreiber (1922, p. 498) found that *Cypris ophthalmica* Jurine could also be frozen fast in ice without apparent ill effects, but that individuals of *Cyprinotus incongruens,* a "summer" form, showed marked effects when brought to a temperature of 2° C. They sank to the bottom and their color faded to the yellowish tint typical of dead individuals of the species; they crept slowly about the bottom with their shells half-open. They could not withstand the temperature of 2° C. for longer than twenty-four hours. Other *Cyprinotus incongruens* were placed in a container which was slowly cooled to 2° C. during a six-hour period; the temperature was maintained at that level for two to three hours, then gradually warmed to 11° C. The animals died after two to three days.

No experiments have been made with *Cypridopsis vidua* to determine its cold temperature tolerance. The writer has taken samples from Crystal Lake, Urbana, Illinois, in early December when the temperature of the air was between 5 and 10° C. The *Cypridopsis vidua* in the samples were very few, about half adults and half intermediate instars. All of

them were very sluggish when first examined, but upon warming to room temperature they became quite active.

Relation of Heat and Growth

The writer found that in laboratory cultures kept at room temperatures *Cypridopsis vidua* developed from the egg to sexual maturity in approximately one month. Ferguson's (1944, p. 719) records of field collections indicate that the species in nature requires over two months for full development. There is no information on the quantity or quality of food supply available for the ostracods in Ferguson's data, so that food cannot be ruled out as a contributing factor to the slower growth rate. However, the writer believes that the temperature effects were chief factors causing the difference in rate.

Klugh (1927, p. 46) has done the only quantitative work on the relation of heat to the rate of growth in ostracods. He kept twenty immature instars of *Cyprinotus incongruens* Ramdohr at a temperature of 12 to 13° C. for one week, and twenty other instars of the species at a temperature of 17 to 31° C. during the days and 7 to 12° C. during the nights. The ostracods at he lower temperature showed an average increase of 204μ for the week, while those at the higher daytime temperature increased an average of 553μ during the same period. Food and light were the same for the two cultures.

It is apparent that the relation of heat to the ostracod in nature is a complex ecological problem. If we consider the ostracod as a faunal constituent, then the amount of heat supplied to its environment will affect the amount and type of its food supply, the thermal gradient of the water, the nature of the bottom sediments, the activity and food requirements of its natural enemies, the number of generations in a given time, the amount and type of protective screening vegetation, the hydrogen ion concentration of the water, and possibly other factors. The increase of the species is thus much more complicated than the growth of the individual in its relation to heat. Field records indicate that each species reaches its greatest abundance when the temperature of the water is most favorable for its reproduction and growth, but specific data are insufficient to substantiate this conclusion as true without exception. All available information on habitat and biotic relationships should be considered in the study of this problem.

Phototaxis

Cypridopsis vidua individuals can be segregated in a culture dish by exposing a large area of the dish to a very strong light for a few minutes. The animals will all be found in the unlighted area, away from

the source of light. If half of the area under a flat-bottomed dish is made white and the other half black, and the whole is exposed to strong overhead light, more animals will be found over the black nonreflecting surface after a few minutes. This has proved to be an efficient means of isolating ostracods in a culture, so that individuals can be obtained for study. Yet if placed in darkness for an hour, most individuals will immediately head toward light of any intensity.

Towle's (1900, pp. 345-65) experiments with this species also showed that the positive response is temporary (longer in duration when the animal has not previously been exposed to light), while the negative one persists as long as the animal is in motion. The animal's direction is reversed when the animal is mechanically stimulated. Towle concluded that mechanical stimulation is responsible for reversal of heliotropic reaction, but the writer has observed that reversal of direction will result with mechanical stimulation with even illumination, so that light cannot be credited as a factor.

Yerkes (1900, p. 412) found that *Cypris virens* swam the second half of the distance toward the light source more rapidly than the first half, and that it swam quicker in strong than in weak light. Thus the intensity of the light is proportional to the intensity of the stimulation effect it produces on the ostracod.

The chemical condition of the water also appears to be a very decisive factor in phototaxis. Ostwald (1907, pp. 384-408) found that with other Entomostraca, the addition of macerated quince to the water changed a strongly positive heliotropic reaction to a strongly negative one, and vice versa, with the temperature maintained the same. He also found that temperature increase can change a positive to a negative reaction, and vice versa. These results emphasize that one series of observations is entirely inadequate to describe the phototactic reactions of a species.

The strength of the initial heliotropic response is phenomenal. Yerkes (1900, p. 419) found that when an acid barrier is placed in their path, the directive influence of light is sufficient to lead ostracods (*Cypris virens*) to their destruction. Franz (1910, p. 331) also found that the phototaxis of lower animals is abnormally strong, stronger than the drive of hunger or sex. It should be borne in mind in any ecological study, therefore, that the directive power of the light may bring ostracods into harmful environments which they would otherwise avoid.

Relation of Light and Growth

Cultures of *Cypridopsis vidua* placed in full sunlight during the day did not increase in numbers, and some of them died after several weeks. The aquaria placed in the sunlight was not provided with any large types of vegetation or artificial shading. Cultures placed in strong indirect sun-

light survived for two years. These results cannot be attributed wholly to the effect of light, for no means were used to control the temperature of the aquaria placed in the sun, and undoubtedly the water temperatures became unfavorable during the middle of the day. The experiment shows that ostracod cultures can survive for as long as two years without direct sunlight.

These results of the ultimate increase of cultures is at variance with the results obtained by Klugh (1927, pp. 45-47) on the individual growth rate of *Cyprinotus incongruens* Ramdohr as affected by light. His elaborate experiments were so designed that temperature and food supply was constant for all cultures. One typical experiment showed that instars in full light grew an average of 189μ per week; those in 50 per cent grew 155μ per week; those in 20 per cent light grew 92μ per week; and those in total darkness only 57μ per week. Klugh also found that the instars were affected by the color of the light. Filters of approximately equal light transmission were used, and the ostracods subjected to red light increased an average of 83.4μ per week, to green light an average of 180.7 microns, and blue light an average of 205.9 microns.

The light requirements vary for the species. Some species of freshwater ostracods have even been described by Klie (1931, pp. 161-68; 1934, pp. 193-99; 1936, pp. 1-13) from caves and other underground waters of Europe. No experiments have ever been conducted to determine the effects of light on the growth rate for these species which are adapted to total darkness.

Rate of Reproduction and Life Span

On December 2, 1947, the writer isolated ten adults of *Cypridopsis vidua* into separate small vials. Since this species is parthenogenetic, all the young produced in each vial would represent a clone. Each individual was supplied at the beginning with a culture of algae for food. Distilled water was added from time to time to make up for losses by evaporation. The conditions of light, temperature, and aeration were maintained the same for all ten ostracods during the course of the experiment.

At the end of the thirty-four days, an examination of the contents of each vial was begun. All of the living ostracods were removed and measured, to determine what stages they had reached. Although the females were in uniform environments, there were great variations in the number of young produced. This may be attributed, in part at least, to differences in their ages, for the adults were originally selected at random. The results of the final counts are shown in Table 1. Three of the females died without leaving any progeny, while one produced fifty-three young. The clone in vial B contained offspring in eight different stages; and although three of the young had already reached maturity, it seems highly unlikely

TABLE 1

Vial	Instar 1	2	3	4	5	6	7	8	Adults	Total Young	Days	Remarks
A	..	..	7	16	2	2	1	..	1	28	34	
B	..	6	5	6	10	7	13	3	4	53	35	
C	1	4	1	2	..	1	1	..	1	10	35	2 fertile eggs
D	..	..	1	3	..	5	..	1	1	10	35	3 fertile eggs
E	..	5	..	..	2	..	..	1	1	8	36	
F	..	..	..	..	..	..	..	2	1	2	36	
G	..	..	..	..	2	1	4	..	..	7	36	Female died
Total young	1	15	14	27	16	16	19	7	3	118		

that any of the younger instars were granddaughters of the original ostracod. The clone in vial C ranged from fertile eggs to a seventh instar. The spacing of the young in vial E indicates that the eggs were not laid continuously, but in groups at intervals. It seems highly probable that the females in vials F and G were older, for they ceased egg production shortly after their isolation.

The results of the experiment indicate that: (1) the female lays eggs at intervals, and not all at one time; (2) the complete cycle of growth can be completed in thirty-five days; (3) a female may survive beyond her capacity to lay eggs; and (4) under favorable laboratory conditions, ostracods will reproduce during the winter, although in nature they do not normally produce young during that season.

There are very few studies of the occurrence in nature of *Cypridopsis vidua*. Wohlgemuth (1914, p. 55) maintained the species in a culture throughout the year, but only found it in nature during the months of May, June, July, and August. Müller (1900) also reported it in September. Ferguson (1944, p. 719) found adults in nature from February through December, late instars in April, May, and June and in August, September, and October, and young instars in April and August. He believed from his investigations that there are two broods per year for the species.

The longest life span recorded for *Cypridopsis vidua* is 134 days reported by Korschelt (1920, p. 73). Schreiber (1922, p. 504) found that the animals lived as adults 113, 53, 47, 40 and a fewer number of days.

We see, therefore, that there must either be more than two broods per year to maintain the species, or the development of the eggs must be

greatly retarded in cold water during the winter. Ferguson's observations of young instars in April probably corresponds to the general burst of life in fresh water in the spring. The warming of the upper layers and the sudden appearance of additional food must have affected even the small pond which Ferguson used for his study. The writer obtained plankton samples from Crystal Lake, Urbana, Illinois, a small body of water without active flow. Samples were taken at intervals from April through October, 1947, and from March through early December, 1948. Both young instars and adults of *Cypridopsis vidua* were present in all collections, although the numbers present in the spring and summer months were about ten times those in December.

It would seem that reproduction takes place the year around in nature, but the survival rate is much greater during the favorable spring and summer months than during the rigorous late fall and winter months.

Food

The food supplied to cultures of *Cypridopsis vidua* consisted of the small spherical algae which Klugh (1927, p. 77) included under the term "palmella forms." No attempt was made to follow these algae through their reproductive cycle to determine their generic status, but it is assumed that they are included in Klugh's listing of palmella forms: *Palmella, Chlorella, Gloeocystis, Chlorobotrys, Botrydiopsis, Chlorosphaera, Palmellococcus, Pleurococcus, Schizochlamys, Sphaerocystis, Tetraspora, Chlorococcum, Planktosphaeria, Protococcus,* and *Heterococcus.*

It was found advantageous to raise cultures of the algae. The algae were collected from the same habitat as the ostracods, and small amounts were added to the aquaria. At the same time were added small quantities of detritus derived from boiled egg yolk which had been grated into water, decomposed bacterially for a month at warm temperature, and strained through a 100-mesh screen. It was found that this material gave greater growth of algae than similar additions of humus or of macerated leaves. It was also found that the growth was slightly greater in pond water than in distilled water. No experiments were made with prepared chemical solutions, such as Molisch Solution. The algae increased in sufficient quantity so that amounts could be withdrawn for stocking other aquaria before adding the ostracods. In some cases the algal increase in the water was sufficient to offset depletion by the ostracods, but frequently secondary additions from the stock of algae were found to be necessary.

An examination of the stomach contents in needle dissections of animals collected at Crystal Lake, Urbana, Illinois, showed that the diet of *Cypridopsis vidua* also includes the following: diatoms of the family Naviculaceae, including the genera *Pinnularia, Brebissonia,* and *Am-*

phora; Chlorophyaceae of the family Desmidiaceae, tentatively identified as *Tetmemorus* and *Gymnozyga;* and one flagellate, probably *Trachelomonas.*

Klugh (1927, p. 54) listed palmella forms, *Chaetophora elegans,* and *Conferva bombycina tenuis* from his examination of *Cypridopsis vidua* stomachs. Sharpe (1918, p. 798) reports that the species has been observed making skeleton leaves.

The food of fresh-water ostracods in general was investigated by Wohlgemuth (1914, p. 20). He stated that of twenty-one species he was able to raise in cultures, only *Notodromas monacha* (O. F. Müller) could not be raised on an altered diet. He found that the other species could also be brought to a diet of potato, crushed snails, or horse flesh. This is not in accord with the writer's experience with *Cypridopsis vidua.* All cultures died out when supplied with meat, both cooked and raw, and in varying quantities.

Commensalism in Ostracods

There are no biocoenotic relationships or associations known for *Cypridopsis vidua.*

No ostracods are known to have adopted a parasitic habit, although Marshall (1903, pp. 117-44) first described *Entocythere* as a parasite of the crayfish *Cambarus.* This relationship was later shown by Hoff (1942b, pp. 63-73) to be only commensal.

There are only two commensal genera of fresh-water forms reported. One of these, *Sphaeromicola,* is limited to Europe, and the other, *Entocythere,* has only been found in the United States and Mexico. All the relationships have been with other crustaceans, with the ostracod clinging to appendages of its larger relative to take advantage of the currents of water with incoming food. *Sphaeromicola topsenti* Paris lives on the isopods *Caecosphaeroma burgundum* Dollfuss and *C. virei* Dollfuss (Klie 1926, p. 54). *Sphaeromicola dudichi* Klie clings to the burrowing amphipod *Chelura terebrans* (Klie, 1938b, pp. 317-22). The species of *Entocythere* are commensal on the crayfish *Cambarus* (Hoff 1942b, pp. 63-73; Roija 1942, pp. 201-4).

Taxonomic work on the American ostracods has been limited, and other instances of commensalism, and possibly parasitism, may be discovered.

Parasites of Ostracods

Although no parasites were found in the writer's collections of *Cypridopsis vidua,* internal parasites have been reported by Hoff (1942a, p. 10) in fresh-water forms from Illinois.

Larval stages of cestodes and acanthocephalans have been found parasitizing fresh-water ostracods. The cestodes were species which as adults

parasitize aquatic birds. Mràzek (1890, pp. 226-48) found cercocysts of *Taenia coronula* Dujardin in the ostracod *Cyclocypris ovum* Jurine. Lindner also found larvae of *Drepanidotaenia gracilis* Keal in *Candona, Dolerocypris,* and *Cypria* (Klie 1926, p. 53).

The ostracod *Cypria globula* has been found by Ward (1940, pp. 327-47) to be the first intermediate host of *Neoechinorhynchus cylindratus* (Van Cleave), the adult of which parasitizes the largemouthed black bass. Hoff (1942a, p. 10) also found acanthocephalan larvae in several species of ostracods.

There are also ectoparasites found on fresh-water ostracods which may not be very damaging to their hosts. The ciliate protozoans *Rhabdostyla ovum* Kent and *Opercularia lichtensteini* Stein have been found on Cypridae (Klie 1926, p. 53).

Marine ostracods are beset with additional types of parasites. G. W. Müller, found *Cythereis* badly damaged by undetermined nematodes (Klie 1926, p. 53). Monod (1932, pp. 1-8) discovered that *Cypridina* serves as host for two different parasites, a copepod larva of the family Choniostomatidae and an isopod *(Cyproniscus)* of the family Cryptoniscidae.

V. Immature Stages

The growth of an ostracod becomes apparent only at intervals when the animal sheds the old carapace and secretes a new one. Each instar, or molt stage, must be regarded as a completely integrated living unit, performing locomotion, feeding, respiration, and the other life processes. Each molting of the ostracod introduces an animal differing from that of the previous stage. The molting is quickly followed by a revision of the tissues, before the new covering of chitin is secreted. Entire new appendages and organs are added, and the structure of previous appendages is drastically changed. A most remarkable feature of this discontinuous growth system is the change in function of an appendage, which may be used as a walking leg in one instar and as an accessory feeding mechanism in the next.

The morphology of the various instars has been described by Claus, G. W. Müller, Schreiber, and Scheerer-Ostermeyer. At first, a comparison of their reports seems to show great variance. However, a detailed comparison of their descriptions reveals that the differences arise not from the observation of what is present in any one instar, but from the *interpretation* of the appendages in immature individuals. The same appendage which Claus describes as an incipient second leg is referred to by Müller as an incipient furca. Thus the order of appearance of the various appendages differs considerably according to different authors, although their observations are in agreement.

Claus (1868, pp. 151-66) made the first extensive study of early instars. He gave the following order of appearance of the appendages and sex organs, based on *Cypris ovum* and *C. fasciata:*

Instar	Appendages —									
1	Al	An	Md							
2	Al	An	Md	(Mx)	....	(L2)				
3	Al	An	Md	Mx	....	(L2)				
4	Al	An	Md	Mx	(L1)	(L2)				
5	Al	An	Md	Mx	L1	(L2)	. . . . .			(Fc)
6	Al	An	Md	Mx	L1	L2	(L3)	. . . . .		Fc
7	Al	An	Md	Mx	L1	L2	L3	(Ov)	. . . . .	Fc
8	Al	An	Md	Mx	L1	L2	L3	Ov	(Gn)	Fc
9	Al	An	Md	Mx	L1	L2	L3	Ov	Gn	Fc

Al = antennule
An = antenna
Md = mandible
( ) = *anlagen,* incomplete
Mx = maxilla
L1 = first thoracic leg
L2 = second thoracic leg
L3 = third thoracic leg
Ov = ovary
Gn = genitalia
Fc = furca

The next contribution was that of G. W. Müller (1894, p. 182), who gave the following sequence for the Cypridae:

Instar	Appendages —									
1	Al	An	Md							
2	Al	An	Md	(Mx)	. . . . .					(Fc)
3	Al	An	Md	Mx	. . . . .					(Fc)
4	Al	An	Md	Mx	(L1)	. . . . .				(Fc)
5	Al	An	Md	Mx	L1	(L2)	. . . . .			Fc
6	Al	An	Md	Mx	L1	L2	(L3)	. . . . .		Fc
7	Al	An	Md	Mx	L1	L2	L3	(Ov)	. . . . .	Fc
8	Al	An	Md	Mx	L1	L2	L3	Ov	(Gn)	Fc
9	Al	An	Md	Mx	L1	L2	L3	Ov	Gn	Fc

This system was followed in general by Schreiber and Scheerer-Ostermeyer later, and it agrees with the observed facts for *Cypridopsis vidua*. It will be seen that the number of appendages for each stage in the two analyses is the same. In Müller's system the furca appears early and the body appendages are added in orderly sequence from the anterior to the posterior, which agrees with the pattern observed for other crustaceans.

The orderly appearance of new appendages led Müller to propose a theory that would account for the rate at which they appear. One new appendage is added at each molt stage except the third. Müller (1894, p. 179) postulated that the second maxilla was lost late in the history of the ostracod, and that the original ostracod added one appendage at each instar. With this second maxilla (which does not develop in the present ostracod) represented by a dash, the sequence in the ostracodal ontogeny assumes the orderly arrangement:

Instar	Appendages and Organs —									
1	Al	An	Md							
2	Al	An	Md	(Mx)	. . . . .					(Fc)
3	Al	An	Md	Mx	(—)	. . . . .				(Fc)
4	Al	An	Md	Mx	—	(L1)	. . . . .			(Fc)
5	Al	An	Md	Mx	—	L1	(L2)	. . . . .		Fc
6	Al	An	Md	Mx	—	L1	L2	(L3)	. . . . .	Fc
7	Al	An	Md	Mx	—	L1	L2	L3	(Ov)	Fc
8	Al	An	Md	Mx	—	L1	L2	L3	Ov (Gn) . . .	Fc
9	Al	An	Md	Mx	—	L1	L2	L3	Ov Gn . . .	Fc

Whether Müller's postulate is justified or not, it offers an explanation of the appendage sequence.

First Instar

The shell of the first instar, or nauplius, is wellrounded, reflecting the elliptical shape of the egg shell from which it hatches. The shell is very

weakly calcified. The eye is large in relation to the size of the shell. The three pairs of appendages are antennules, antennae, and mandibles. Each antennule consists of four podomeres set upon a stump or projection of the body, so that it functions as five podomeres. There are only five setae, three of which are terminal (Chart 4). The antenna has two podomeres set on a long projection from the body. The terminal podomere has a constriction one-third of the length from the end, but does not appear to be completely divided. It is of note that the penultimate podomere bears a short cylindrical seta on its ventral border, which later develops into the "sense club." The mandible is pediform, composed of two short podomeres set on an elongate extension of the body. There is a strong seta at the end of this backwardly directed appendage. The base of the mandible has an anterior lobe which lies at the side of the mouth.

The mouth itself is set far back on the body, in the posterior half of the shell. An enlargement of the alimentary tract can be seen through the transparent shell, with only a slight medium constriction to set it off into a stomach proper and a rear gut. There are two lateral livers opening into the stomach, but they do not reach to the epidermis of the valves. Schreiber (1922, p. 511) isolated first instars of *Cyprinotus incongruens* without food, and found that they molted at the same time as those with adequate food supply. It is entirely possible that the ostracod passes through the first instar stage utilizing remnants of the yolk as nourishment.

Excretory gland B has been described for *Cyprinotus incongruens* in the first instar (Schreiber 1922, p. 509), but it could not be discerned in stained total mounts of *Cypridopsis vidua*.

Second Instar

The first molting of the valves initiates the second instar. The shell is larger and slightly thicker. The rim of the shell is still very simple. The eye is approximately the same size as in the first instar, and is still located near the middle of the shell. The antennule is still composed of four distinct podomeres and a basal projection of the body. The antenna is now made of three distinct podomeres set on a long projection from the body. The "sense club" is now on the antepenultimate podomere, so the division of the terminal podomere resulted in the increased number in this instar. The terminal claws of the terminal and penultimate podomeres are only weakly developed as setae. The mandible is greatly altered from its pediform structure of the first instar. The basal podomere is completely set off and equipped with incipient teeth at its distal end. The leg-like development which was directed posteriorly in the previous stage is turned 180° about the base, and now becomes modified as the

palp. This palp, composed of three distinct podomeres, is set onto a projection of the basal protopodite, and represents the endopodite. There are also the beginnings of the mandibular exopodite plate.

The *anlagen* of two new appendages are interpreted as the maxilla and the furca. The maxilla is a swollen section of the body with a nipple-shaped pointed projection at the anterior ventral corner. There is also a slight lobing of the body in the dorsal posterior area, which may be interpreted as the *anlagen* of the exopodite plate. The furca is represented by a strong stump-like projection of the body with a long terminal seta extension (Chart 4).

The mouth has shifted to the middle of the body. The digestive system more closely resembles the final arrangement. The livers are still simple lobes and do not reach the epidermis of the valves.

Third Instar

The third instar is marked by the further development of the appendages already present, and no new *anlagen* appear. The antennules consist of the same number of podomeres, and the main change is the increased length of the natatory setae. The antenna has the same form, but the natatory setae appear in abbreviated length. The mandible is also essentially unchanged. The basal podomere is stronger and more elongate, of approximately the definitive form. The end of the maxilla is divided into "masticatory" processes but without a palp. The exopodite plate bears six setae. The furca is of the same form as in the second instar, a stump of the body with a long, strong seta, and still has not assumed its definitive form.

There is a pair of knob-like body extensions between the maxillae and the furcae which Claus (1868, p. 155) interpreted as the beginnings of the first thoracic legs. These lobes are not sufficiently developed to be regarded definitely as the *anlagen* of the first legs.

The mouth is still in a median position.

Fourth Instar

The outline of the shell of the fourth instar (Chart 4), like those of the other instars, was drawn from all measurements of all specimens plotted in Chart 1. This composite outline does not show any inbuckling of the ventral border as was described by Claus (1868, p. 156) and by Schreiber (1922, p. 519).

The antennule has five podomeres. The antenna has the same approximate form as before, but with stronger end claws and three natatory setae. The second podomere of the protopodite of the mandible is now separated from the basal podomere, but the general form remains the

same. The maxilla approaches the definitive form with the addition of an unmembered palp, and the increase in the number of setae on the respiratory plate.

There is a definite *anlage* of the first thoracic leg, a roughly triangular plate with the forward corner attached to the body, the ventral lobed corner hanging free, and the rear corner equipped with a short curved claw. The ventral part is the incipient "masticatory" process of the protopodite, and the rear part is the endopodite.

The furca is strongly developed, proportionately larger than the final form.

The mouth is shifted slightly forward. The livers still do not reach into the valves. The cerebrum can be discerned in this stage.

Fifth Instar

The shell of the fifth instar has a more complex rim and a thicker structure. There is also a better-defined color pattern, very similar to that of the adult.

The antennule is composed of the same five podomeres with an increase in the length of the natatory setae. The antenna is also changed very little, with the three natatory setae reaching to the mid-point of the end claws. The mandible is increased only in size. The palp of the maxilla is now divided into two podomeres, and the respiratory plate is larger and equipped with approximately ten setae. The first thoracic leg is further developed. The "masticatory" process bears three short setae at its distal end. The endopodite has two distinct podomeres set onto a projection of the protopodite, and bearing a strong curved claw at the end. This backwardly directed pediform process appears to perform the functions which are later taken over by the second thoracic leg.

There is an *anlage* of the second thoracic leg. This is an elongate, backwardly directed process of the body, terminating in a very blunt claw-like process. It is attached above and immediately behind the first thoracic leg.

The furca approaches the definitive form, with the terminal seta reduced to the "flagellum" typical of the Cypridopsinae.

The liver extends laterally into the epidermis of the valve, but is not recurved toward the ventral posterior end.

Sixth Instar

In the sixth instar for the first time the ostracod has all of the appendages present. The remaining ontogenetic stages show further development of the appendages and the *anlagen* and completion of the sex organs.

The antennule has six podomeres with well-developed natatory setae. The antenna has the same number of podomeres, and the natatory setae reach to the end of the terminal claws. The mandible, which already

reached its definitive form, is slightly larger. The maxilla also has reached its definitive form in the previous instar, except for the number of setae, which are increased in this instar. The first thoracic leg has a "masticatory" process with a few setae, a three-membered endopodite with three terminal setae, and the *anlage* of the exopodite plate. The second thoracic leg has three podomeres set one to a projection of the body, and a well-developed, slightly curved terminal claw. There are also two short setae on the ends of the ventral borders of the penultimate and antepenultimate podomeres.

The *anlage* of the third thoracic leg is an elongate, backwardly directed process of the body with a stubby chitin claw at the end. It resembles the *anlage* of the second thoracic leg in the fifth instar.

The furca has the definitive form, including the small seta on the dorsal edge.

One of the most remarkable features of microtome sections of these immature instars is the lack of well-defined boundaries for the internal organs. Differentiation of the cells continues to the adult stage, and the early *anlagen* of some organs are difficult to distinguish from the connective tissue in which they are embedded. The ventral chain of ganglia is proportionately much larger than in the adult stage. L glands are present in the large upper lip, but they are not set off sharply from the surrounding tissues. The dorsal wulst is very well developed by this instar. The livers are distinct, and recurve posteriorly a short distance in the epidermis of the valves. The muscles connecting the mandibles to the endoskeleton are very large and well-defined. The eye differs from that of the adult only in the lesser amount of pigment. The rake-shaped organs are already well advanced, and possess eight teeth each. The contents of the stomachs show that the diet is approximately the same as that of the adult, composed largely of small spherical algae.

Seventh Instar

The seventh instar has all of the appendages well defined, and the *anlagen* of the sex organs. The internal structures become more distinct, but do not approach the final form.

The antennule is composed of six podomeres set onto a basal projection of the body. The natatory setae are better developed than in any previous instar. The antenna approached the definitive form, except for the protopodite, which is not divided into separate podomeres but remains as an elongate lobe of the body. The mandible is only increased in size. The maxilla shows greatest change in the exopodite plate, which is much larger and equipped with the definitive number of setae. The first thoracic leg is considerably altered; the endopodite palp is no longer separated into podomeres, and the exopodite plate is much larger. The

second thoracic leg has the definitive number of podomeres, but the end claw is proportionately smaller than that of the adult. The third thoracic leg is small but otherwise complete.

With an acid fuchsin stain the ovaries can be seen in the epidermis layers of the valves. There is no development of the genital lobes and the external genitalia.

The upper lip is still much larger than in the final form (Plate 91, Nos. 390-93). Gland L is present, but lacks the smooth outline which characterizes it in the adult (Plate 91, No. 390). The dorsal wulst is very large (Plate 91, No. 392). The excretory glands A (Plate 91, No. 391) and B (Plate 91, No. 390) can be located, but have irregular outlines. The *anlagen* of the spiral canals do not show any passageways through them (Plate 93, No. 401).

The chitinous rake-shaped organs are well developed and have eight teeth each (Plate 92, No. 397). The endoskeleton is large and distinct (Plate 92, No. 395). The teeth of the mandible are arranged in seven rows (Plate 96, No. 416).

The muscles of the appendages appear to agree with those of the adult, as seen in the microtome sections (Plates 89-96). The mandibular and the closing muscles are large and well developed.

The nervous system has all the elements present, but the cerebrum is in proportion smaller (Plate 90, No. 389) and the ventral chain of ganglia larger (Plate 92, No. 395) than in the adult.

Eighth Instar

The eighth instar resembles the adult very closely except for size. The appendages are all in the definitive form. The greatest change from the previous instar is the shifting of the mouth forward and the development of the genital lobe. Excretory gland C and gland O have not appeared in definite form.

The spiral canals and the other genital organs in the genital lobe are still only *anlagen* (Plate 81, Nos. 360, 361). Gland N is also incompletely developed (Plate 88, No. 380).

The cerebrum is much larger than in the seventh instar (Plate 85, No. 372) and the ganglia of the various appendages are more distinct.

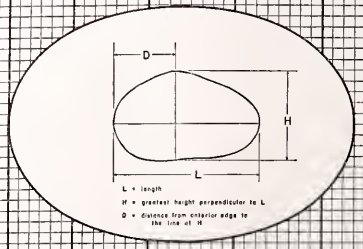
The Adult

The adult differs from the eighth instar in (1) stronger chitinous development of the appendages; (2) completion of the internal glands; (3) addition of the external chitinous genital structures and the completion of the sex organs; (4) enlargement of the dorsal posterior portion of the valves, greater thickness, and more complex rim structures; and (5) the shifting of the mouth forward with corresponding changes in the shape of the upper lip.

Chart 1

CHART I

SIZE DISTRIBUTION OF 500 SPECIMENS



DISTANCE ⟶ HEIGHT ⟶

INSTAR I INSTAR II INSTAR III INSTAR IV INSTAR V INSTAR VI INSTAR VII INSTAR VIII ADULT

LENGTH ⟶

AVERAGES OF STAGES			
	L	H	D
I	132.2	92.0	56.4
II	155.5	108.0	64.6
III	188.2	123.8	75.4
IV	226.6	145.6	91.9
V	269.8	169.7	109.7
VI	333.4	203.8	139.4
VII	416.0	250.5	174.2
VIII	528.0	316.2	225.9
IX	617.0	372.6	281.5

VI. Variations in Size of Instars

After a culture of *Cypridopsis vidua* had been maintained for several months, the residue in the bottom of the aquarium was removed for examination. Five hundred valves were selected at random, and outline drawings were carefully made with the use of the camera lucida. These drawings were then measured for length, height, and distance from the anterior edge to the line of greatest height (see Chart 1), using the proper scale to the nearest 5μ interval. Then the area of each drawing was measured with a polar planimeter, and the readings converted to square microns.

An effort was made to orient the shells at right angles to the line of sight when the drawings were made, but some distortion could not be avoided. The length was measured as the greatest length of the outline drawing, without reference to the position of the hinge or any other structure. The height was then measured as the greatest height at right angle to the length. The lines of length and height were marked on each drawing, and the distance from the anterior edge of the shell to the line of greatest height was measured along the line of the length.

A plot of the length vs. height and of the length vs. distance from the anterior edge to the line of greatest height is shown in Chart 1. It can be seen that the measurements fall into nine groups, one for each growth stage or instar. However, there are overlaps in the measurements of heights for adjacent instars; we can state with assurance that height alone is not a certain criterion for determining to what instar a given shell belongs.

There is no direct linear relationship of the length vs. height as shown in Chart 1. Therefore, the ratio of the height/length is not a constant for a species, but varies within an instar and also from one instar to another.

Brooks' Law

Fowler (1909, p. 224) proposed a formula for the growth of ostracods which he termed Brooks' Law. He believed that during growth, each stage increases at each molt by a fixed percentage of its length, which is approximately constant for the species and sex. This may be expressed as a formula:

$$L_{(n+1)} = L_n(k+1),$$

where k is the constant percentage for the species and sex and L_n repre-

sents the length of any molt stage. Skogsberg (1920, p. 132) applied this formula to several species of marine ostracods, and the large variations between computed and observed lengths led him to state that Brooks' Law should be applied with extreme caution. Table 2 shows the observed and computed lengths of instars for *Cypridopsis vidua*. The variations in the last three stages are too great for the formula to be of value in this species.

TABLE 2

Comparison of Actual Length with Length Computed by Brooks' Law.

Instar	Observed Length	Computed Length [a]
1	132.2	132.2
2	155.5	158.6
3	188.2	190.3
4	226.8	228.4
5	269.8	274.1
6	333.4	328.9
7	418.0	394.7
8	528.0	473.2
9	617.0	567.8

[a] Computed from $L_{(n+1)} = L\ (0.20 + 1)$

VII. Variations in Shape of Instars

A comparison of shape of two valves is not a simple matter of choosing descriptive terms. There are no large structures on the surface of *Cypridopsis vidua,* and this lack of ornamentation compels us to seek criteria in the general outline of the valves. A complete study should include the thickness, as well as the length and height, but the writer found it very difficult to obtain an accurate reading for this factor. With the very small instars a slight change in the angle at which the valve is viewed will cause considerable variation in the readings. The thickness in fossil specimens is found to be deformed more than any other diameter through the shell, and many species are rarely found without crushed sides. Since thickness is difficult to measure accurately in modern specimens and has only limited application to fossil specimens, it was not included in this study.

"Elongation"

A simple height/length ratio for each instar will give a comparison of the "elongation" of the shell. Table 3 shows this ratio is largest for the first instar and lowest for the seventh and eighth instars. The first instar has the most shortened outline, therefore, and the seventh and eighth instars have the most elongated outlines. If we start with the egg, which has a ratio of 90 to 100 per cent (spherical), we find a general elongation

Table 3

Instar	Average Height *microns*	Average Length *microns*	Height/Length *per cent*
1	92.0	132.2	69.6
2	106.0	155.5	68.2
3	123.8	188.2	65.8
4	145.6	226.8	64.2
5	169.7	269.8	62.9
6	203.8	333.4	61.2
7	250.5	418.0	60.0
8	316.2	528.0	60.0
9	373.0	617.0	60.4

of the outline of the shell through the eighth instar. The adult shell (ninth instar) is found to have a slightly greater increase in height than in length from the previous instar.

"Bluntness"

The distance from the anterior edge to the line of greatest height is an indication of the "bluntness" of the front of the shell. The shell with the greatest degree of bluntness would have the greatest height at the anterior end, and one with a low degree would have the greatest height in the middle. The "bluntness" factor, it will be noted, can only be applied to those ostracods with a convex hinge line.

Charts 3 and 4 show the relationship of three factors: length, height, and distance from the anterior edge to the line of greatest height. These were plotted on a percentage basis so that direct comparisons could be made between instars. Chart 2 has smooth curves of height vs. length and of distance from the anterior edge to the line of greatest height vs. length, based on the information shown on Chart 1. Chart 3 shows the percentage relations of the three factors mentioned above, taken at 5-μ intervals from Chart 2. Chart 4 gives percentage relations of the three factors based on the average figures for each instar.

Table 4 gives the ratios of distance from the anterior edge to the line of greatest height/length for each instar. This shows the greatest degree of bluntness to be in the third instar, and the least degree to be in the adult (ninth instar).

These observations hold for the single species under observation and, whereas other ostracods may show similar progressive shifts in bluntness, each should be investigated independently before valid generalizations can be made.

Table 4

Ratios of Difference from the Anterior Edge to the Line of Greatest Height/Length.

Instar	Average Distance[a] *microns*	Average Length *microns*	Distance/Length *per cent*
1	56.4	132.2	42.7
2	64.6	155.5	41.5
3	75.4	188.2	40.1
4	91.9	226.8	40.5
5	109.7	269.8	40.7
6	139.4	333.4	41.8
7	174.2	418.0	41.8
8	225.9	528.0	42.8
9	282.0	617.0	45.6

[a] Distance from the anterior edge to the line of greatest height.

"Roundness"

In addition to these measurements of "elongation" and "bluntness," the valves can also be compared for "roundness" from the ratio of the area of the outline figure to the area of a circumscribed circle. The ratio

Chart 2

CHART 2

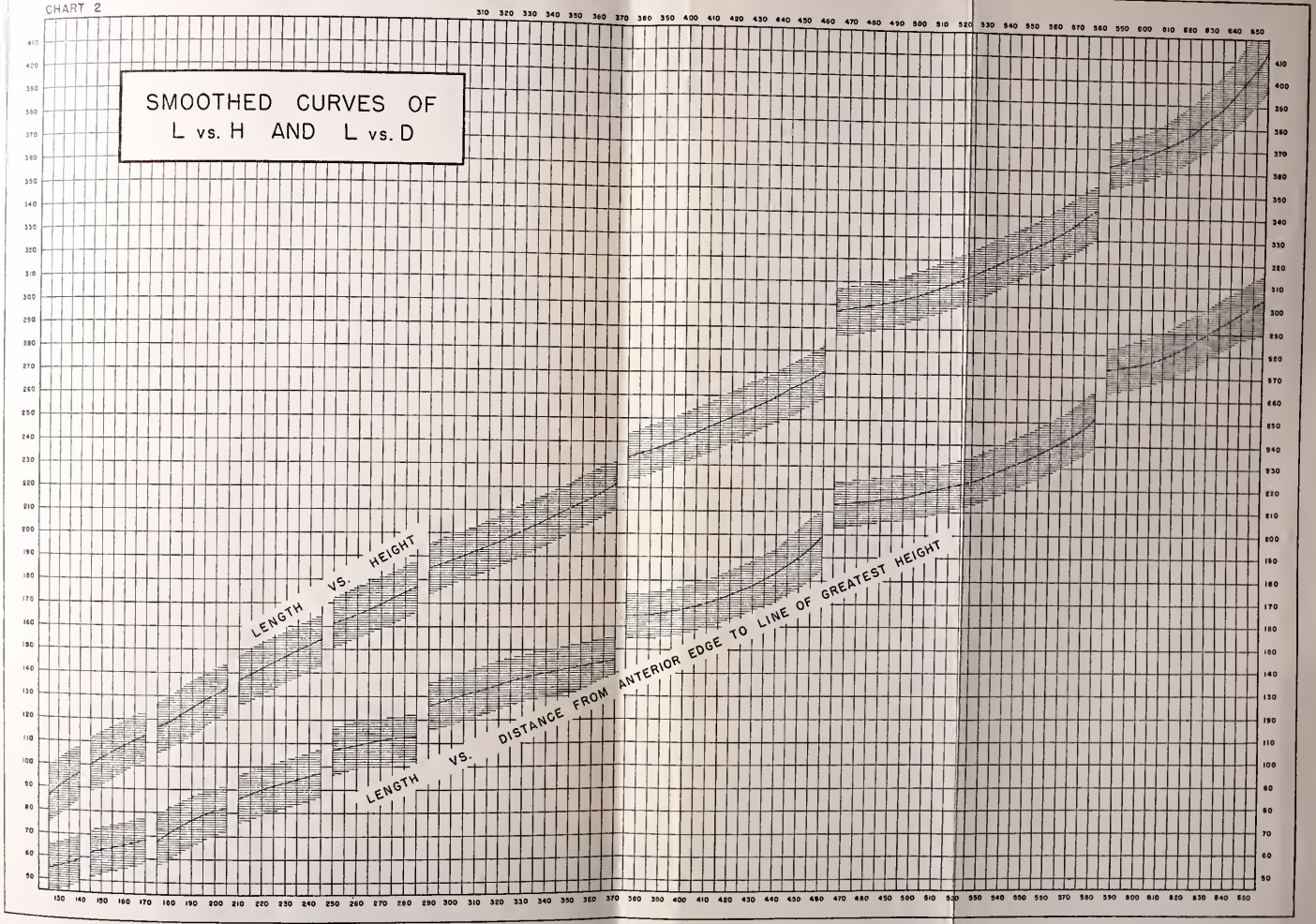

SMOOTHED CURVES OF
L vs. H AND L vs. D
LENGTH VS. HEIGHT
LENGTH VS. DISTANCE FROM ANTERIOR EDGE TO LINE OF GREATEST HEIGHT

TABLE 5

Comparison of Roundness of the Valves.

Instar	Average Area of the Valve	Area of Circumscribed Circle	Area of Valve / Area of Circle
	sq. μ	*sq. μ*	*per cent*
1	10,059	13,726	73.3
2	13,227	18,991	69.7
3	18,426	27,818	66.2
4	26,485	40,399	65.6
5	36,479	57,171	63.8
6	54,345	87,301	62.3
7	83,198	137,228	60.6
8	131,963	218,957	60.3
9	180,847	298,993	60.5

for each instar is shown in Table 5. The greatest degree of roundness is found in the first instar, and the least degree is found in the eighth instar. The adult has a more rounded outline than the eighth instar, and the additional space inside is utilized by the sex organs which reach their full development only in the final stage.

APPLICATIONS OF HUXLEY'S CONSTANT DIFFERENTIAL GROWTH-RATIO FORMULA

J. S. Huxley (1924, p. 895; 1932, pp. 6-8) first proposed a formula for comparison of relative growth rates which has been used in many statistical studies in embryology and growth. His formula is based on the assumption that the ratio of the relative growth-rate of an organ (or a particular dimension) to the relative growth-rate of the body remains constant for a given species and sex. If y is the size of an organ, and x is the size of the rest of the body, then

$$\frac{dx}{dt} = axG \text{ and } \frac{dy}{dt} = byG,$$

where a is the specific constant of the body, b is the specific constant of the organ, G is derived from conditions of growth, and dt is a time interval. Since the organ and the rest of the body are growing under the same environmental conditions, the value of G is the same in both equations, and therefore

$$\frac{dy}{dx} = \frac{by}{ax}.$$

Integration reduces this equation to

$$y = Cx^{b/a}$$

which can also be expressed as

$$y = Cx^{k}$$

where k is the constant differential growth-ratio, by definition the same as b/a, the ratio of the relative growth-rate of the organ to the relative growth-rate of the body. C is a constant arising from the integration.

The general application of this formula has been to specific organs as compared to the rest of the body, but it is equally applicable to other dimensions as compared to the total length.

It is not to be supposed that the value of k will not vary throughout the life of any organism, but it is of importance because it gives a quantitative evaluation of growth in any given growth cycle.

The equation $y = Cx^k$ can also be written as

$$\log y = k \log x + \log C.$$

This form is easier to use in the determination of the values of k and C over a range of measurements.

It is obvious from Tables 2 and 3 that the height and the distance from the anterior edge to the line of greatest height do not have constant ratios with the length throughout the ostracod's ontogeny. Huxley's formula can be applied to determine if the *rate* of their growth has a constant ratio to the relative growth-rate of the length. The computed values for height agree remarkably well with the actual measurements in all of the immature instars.

TABLE 6

Instar	Measured length	Measured height	Computed height [a]	Measured distance	Computed distance [b]
1	132.2	92.0	90.3	56.4	56.2
2	155.5	106.0	104.5	64.6	66.0
3	188.2	123.8	124.2	75.4	79.8
4	226.8	145.6	146.9	91.9	96.0
5	269.8	169.7	171.9	109.7	114.0
6	333.4	203.8	208.1	139.4	140.5
7	418.0	250.5	255.2	174.2	175.8
8	528.0	316.2	315.2	225.9	221.5
9	617.0	373.0	362.8	282.0	258.5

[a] $h = Cl^K$, where $C = 1.0965$, $k = 0.903$.

[b] $d = Cl^K$, where $C = 0.4467$, $k = 0.99$. Distance refers to the distance from the anterior edge to the line of greatest height.

The computed values for the distance from the anterior or edge to the line of greatest height do not vary greatly from the actual measurements, except in the adult. The values of C and k in each case are median values obtained from computations for each instar stage.

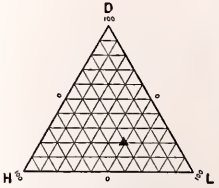
We see from this statistical study that the proportions of the ostracod shell have a nearly constant differential growth ratio in all of the immature instars, but change in the adult.

Chart 3

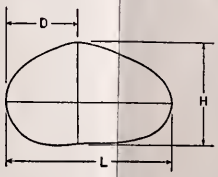
CHART 3

100 PER CENT 3-FACTOR DIAGRAM

SHOWING THE PERCENTAGES OF LENGTH, HEIGHT, AND DISTANCE FROM ANTERIOR EDGE TO LINE OF GREATEST HEIGHT FOR EACH 5-MICRON DIVISION OF LENGTH IN INSTAR STAGES OF *CYPRIDOPSIS VIDUA*



COMPLETE DIAGRAM TO SHOW POSITION OF THE ENLARGED SECTION



DISTANCE

FROM ANTERIOR EDGE TO LINE OF GREATEST HEIGHT

HEIGHT

LENGTH

SMALL FIGURES ARE LENGTHS OF SPECIMENS (FROM SMOOTH CURVES)

D'Arcy Thompson's Graphic Expression of Growth-Gradients Applied to Valves of Instars

D'Arcy Thompson (1917, Chapter 17) devised an application of the principle of Cartesian co-ordinates to the problem of animal form. A rectangular grid of co-ordinates laid over the figure of an original form can be enlarged and deformed to bear the same relationship to the figure of the form in an advanced stage. The size and amount of this deformation in any part of the grid is an index to the relative amount of growth.

Although the results may give a clear presentation of the growth-gradients acting to change the shape of an organ or a species, they are only qualitative. In a smooth outline, such as that of many ostracods, there are no "guide points" to be followed through the various instars, and this method of comparison offers a general pattern of the changes which occur.

Figure 35 shows outlines of the instars centered on the lines of greatest height and greatest length. Each of the outlines is based on average measurements from all the specimens used in this study. Figure 36 shows the graphic analysis of the growth pattern prepared according to the system of D'Arcy Thompson. It can be seen that the dorsal anterior quadrant has not grown as fast as the rest of the shell. We may say that its heterogony (relative rate of growth as compared to the growth of the entire shell) is negative, and that the value of the k in Huxley's formula is less than 1.0 for this quadrant is positive throughout the development. The dorsal posterior quadrant appears to be heterogonically negative through the eighth instar, and changes abruptly in the final instar. It would also appear that the heterogony of the ventral posterior quadrant is negative through the fifth instar, but becomes positive in the later instars. As we see in the following section, quantitative work on the same outline drawings (Fig. 35) reveals that the graphic method gives false results in some instances. Considerable caution is required in the evaluation of D'Arcy Thompson's method, for it does not tell with certainty whether the growth of any part is heterogonically positive (greater than the rest of the body), isogonic (the same as the rest of the body), or heterogonically negative (slower than the rest of the body).

Schmalhausen's Formula Applied to Valves of Instars

Schmalhausen (1927, p. 48; 1930, p. 294) has developed a formula for the true growth-rate (G_y) of an organ for a period of time from t to t_1 during which time the size of the organ increases from y *to* y_1:

$$G_y = \frac{\log y_1 - \log y}{0.4343\ (t_1 - t)}\ .$$

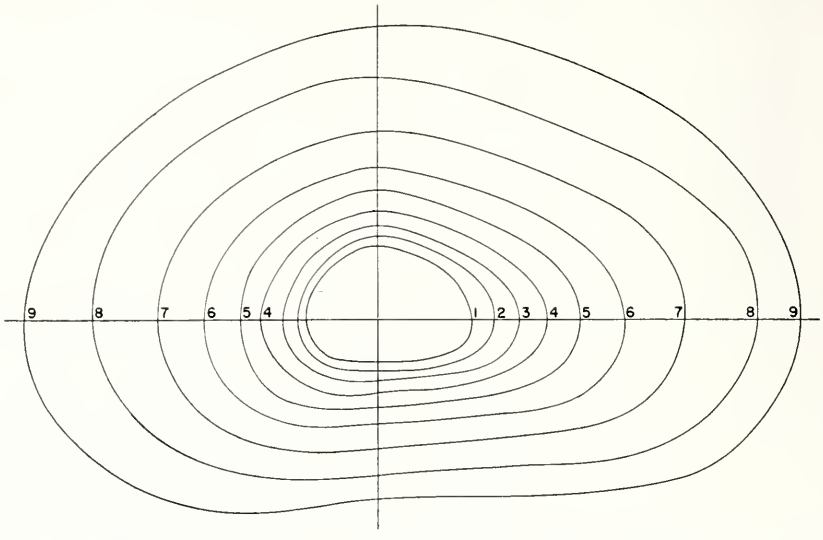


Fig. 35. Average outlines of the various instars in lateral view, based on camera lucida drawings of all specimens listed in Chart 1.

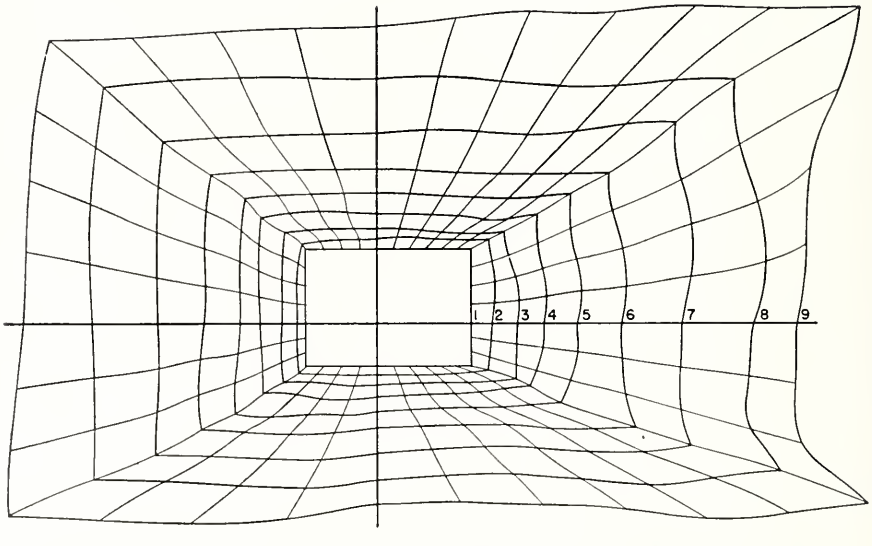


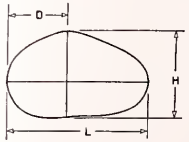
Fig. 36. D'Arcy Thompson's system of Cartesian co-ordinates applied to the average outlines of instars shown in Fig. 35.

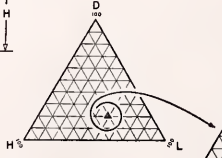
Chart 4

CHART 4

100 PER CENT 3-FACTOR DIAGRAM

SHOWING THE PERCENTAGES OF AVERAGE LENGTH, HEIGHT, AND DISTANCE FROM ANTERIOR EDGE TO MAXIMUM HEIGHT FOR EACH INSTAR STAGE.





KEY

A1 = ANTENNULE
A2 = ANTENNA
Md = MANDIBLE
M1 = MAXILLA
L1 = FIRST THORACIC LEG
L2 = SECOND THORACIC LEG
L3 = THIRD THORACIC LEG
G = GENITAL LOBE
F = FURCA
( ) = ANLAGEN

The true growth-rate of the body during the same period of time can be similarly expressed:

$$G_x = \frac{\log x_1 - \log x}{0.4343\ (t_1 - t)}.$$

The constant differential growth-ratio (k) is the ratio of these two formulas:

$$k = \frac{G_y}{G_x} = \frac{\log y_1 - \log y}{\log x_1 - \log x}.$$

This k is the same as the k in Huxley's formula.[1] This formula is based on the total volume or weight, but it can also be applied to areas, since the factor $\frac{2}{3}$ in both numerator and denominator will cancel.

The area (in lateral view) of quadrants can therefore be compared quantitatively with the area of the entire valve. Table 7 gives the values of k for the quadrants of the ostracod valves, covering the growth in-

TABLE 7

Constant Differential Growth-Ratios by Quadrants.

Quadrant	Instar interval 1-2	1-3	1-4	1-5	1-6	1-7	1-8	1-9
Dorsal anterior	0.66	0.87	0.89	0.90	0.93	0.87	0.84	0.95
Ventral anterior	0.99	1.07	1.08	1.07	1.06	1.05	1.31	1.25
Ventral posterior	1.22	1.17	1.10	1.08	1.07	1.04	1.16	0.96
Dorsal posterior	1.11	0.99	0.95	0.98	0.97	0.99	0.85	0.93

tervals from the first instar to the other instars in sequence. This statistical treatment shows clearly that growth in any given instar is not constant throughout the development, and that during any one interval the growth varies from one quadrant to another. When we compare these results with Thompson's system of Cartesian co-ordinates, we see immediately that the numerical analysis has greater validity than the graphic in evaluating growth.

[1] The transformation:

$$\log y_1 = k \log x_1 + (\log y_0 - k \log x_0),$$

where y_0 is the size of the organ at its first appearance, and x_0 the corresponding size of the rest of the body. Since $(\log y_0 - k \log x_0)$ will be a constant,

$$\log y_1 = k \log x_1 + \log C$$
$$y_1 = C x_1^k.$$

VIII. Relation of Appendages and Internal Organs to the Shape of the Valves in Instars

Each instar bears a definite relation to the preceding and the following instars, since they are all only stages of the same animal. The continuity of substance is accompanied by *progressive* changes of form. Each part of an animal bears a definite relation to the other parts, and the summation of these parts (the total animal) functions to carry on those processes necessary for its survival in its environment — for if the animal does not function successfully then the species cannot survive.

Since the carapace is the most important taxonomic structure of the ostracod, we are interested in any valid correlations between the shape of the valves in the instars and the appendages and internal organs. A mathematical comparison of the appendages and organs to the shell can give a quantitative evaluation of the rates of growth which cannot be attained by mere observation. However, any formula must be applied with discretion.

Schmalhausen's formula may be stated

$$k = \frac{\log y_{(n+1)} - \log y_n}{\log x_{(n+1)} - \log x_n},$$

where n and $n + 1$ are successive instars, and k is the constant differential growth-ratio for the interval between them. As we have seen, this formula can be applied to areas as well as volumes. It would be a difficult task, subject to numerous errors, to determine the volume or weight of an appendage in an ostracod. However, we can use a planimeter to determine the areas of appendages and valves seen in lateral view, provided all drawings are made to scale and each drawing is based on a number of individuals to give average values. The errors of this method are not sufficient to destroy its quantitative value.

Table 8 lists the computed values of the constant differential growth-ratios of the appendages and portions of the valves. A complete analysis of ostracod structure should also include the digestive system, the nervous system, the glands, and connective tissues, but these were not measured in sufficient cases to warrant their inclusion.

Study of the data in Table 8 has led the writer to believe that the growth of individual appendages is relevant to the growth of the enclosing portion of the valves. In general, the growth profile of the ap-

pendages and the rest of the body is directly reflected in the growth profile of the valves. There is agreement of growth-ratios of appendages and sections of the valves in individual instars, and there appears to be concomitant variation of these two factors through the complete growth cycle. Inasmuch as the ostracod apparently derives no external functional advantage from the changes in shell shape, it may be assumed that such changes bear some degree of relevance to internal structures. If this is true, then our logic in seeking relationships between appendages and valves is valid, and we have not committed a fallacy of *cum hoc ergo propter hoc.*

First to Second Instar

During this interval the greatest growth of an appendage occurs in the mandible, which has changed from its pediform structure in the first instar to its typical form. In the process of reorganization, the mandible has moved from the middle of the posterior half of the valve toward the anterior end; the ⅝-¾ increment of the valve (from which the mandible moved) has a growth-ratio of 0.89, while the ½-⅝ increment (to which the mandible shifted) has a growth-ratio of 1.10. The influence of the mandible on the valve is also seen in the large growth-ratio of the posteroventral quadrant. The maxilla appears as a small *anlage* in the second instar; the value of k would therefore be infinity for this interval, but such an interpretation is meaningless.

Second to Third Instar

The antenna and the mandible show the greatest growth of the appendages. Both are shifted forward from their previous positions. This agrees with the high ratios in the anterior half of the valve. The maxilla and the small furca have low growth-ratios, and there is a corresponding trend in the posterior half of the valve.

Third to Fourth Instar

The distribution of appendages in the fourth instar is somewhat different from that of the third. The position of the mouth has been shifted forward so that the mandibular palp, the antenna, and the antennule are now closer to the anterior end. The anterior one-fourth of the valve has a low growth-rate, just as do the antennule and the antenna. The large ratio in the ¼-⅜ interval of the length corresponds to the forward shift of the large mandibular palp and the base of the antenna. The maxilla and the adjacent mid-sections of the valve have large growth-ratios.

It may be noted here that the growth-ratios for the increments intercepted by intervals of the length do not always agree with the growth-ratios of the quadrants of the valve. Chart 4 shows that the distance

TABLE 8

Constant Differential Growth-Ratios of Appendages and Portions of the Valves of Instars.

Organ	Instar interval 1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
Antennule	1.05	0.52	0.16	0.98	0.68	1.05	0.70	2.33
Antenna	0.00	1.05	0.74	1.27	0.10	1.78	1.08	1.83
Mandible	2.07	1.52	0.26	1.66	0.17	1.17	1.13	2.18
Maxilla	...	0.48	1.25	1.15	0.65	1.40	1.35	1.90
1st leg	...	...	...	3.81	0.00	0.89	0.84	1.92
2nd leg	...	...	...	...	3.61	0.56	1.89	2.23
3rd leg	...	...	...	...	...	2.77	1.02	2.52
Furca	...	0.23	1.08	—0.90	0.39	0.00	1.85	1.26
Increments of the Valve Intercepted by Intervals of the Length								
Anterior								
0-1/8	0.76	1.08	0.91	1.43	0.91	0.92	0.98	0.81
1/8-1/4	1.20	1.09	0.96	1.00	1.00	0.95	0.97	0.91
1/4-3/8	1.28	1.02	1.09	0.91	0.94	1.01	1.02	0.90
3/8-1/2	1.02	1.04	1.02	0.91	0.99	0.99	1.01	0.93
1/2-5/8	1.10	0.93	1.05	0.93	1.01	1.04	0.99	1.04
5/8-3/4	0.89	1.05	0.96	0.93	1.05	1.00	1.00	1.14
3/4-7/8	1.01	0.91	1.02	1.00	1.06	1.04	1.02	1.18
7/8-1	1.17	0.80	0.89	1.21	1.06	1.05	1.00	1.15
Posterior								
Quadrant								
Anterodorsal	0.66	0.93	1.01	0.96	1.01	1.03	1.14	1.05
Anteroventral	0.99	1.13	1.09	1.06	1.03	0.98	0.97	1.20
Posteroventral	1.22	1.13	0.98	1.02	1.04	0.93	0.91	0.79
Posterodorsal	1.11	0.89	0.89	1.05	0.94	1.05	0.98	1.00

from the anterior edge to the line of greatest height reaches its minimal value in the third instar, and increases in all subsequent instars. This means that a different proportion of the length is included in the anterior quadrants in each instar. Slight differences in the growth gradient along the mid-dorsal edge can shift the apex of the valve forward or back, and thereby influence the position of the dividing line between the two anterior and the two posterior quadrants. Thus the increments of the valve intercepted by intervals of the length offers a clearer picture of growth changes in the valves than that offered by the quadrants.

FOURTH TO FIFTH INSTAR

The first leg has an unusually high growth-ratio, and has assumed a pediform structure in its endopodite in the fifth instar. On the other hand, the furca actually decreases in size; this is the only negative growth-ratio encountered in the ostracod. The whole form of the furca is changed, and the robust pediform structure of the fourth instar is re-

placed with the delicate degenerate caudal appendage typical of the Cypridopsinae. It seems to be more than coincidence that when the pediform structure of the thoracic region is taken from one appendage (the furca in this case) and transferred to another (the first leg), the former has a low or even negative growth-ratio while its successor has a *strong counterbalancing growth-ratio.* The same situation occurs in the following growth interval where the second thoracic leg develops a pediform structure at the expense of the first leg. This indicates that a pediform structure is necessary for the thoracic region, and that the ostracod will develop it at the expense of other appendages.

In this interval the strong growth of the antenna is reflected in the large growth-ratio of the anterior portion of the valve.

The development of the first leg and the *anlage* of the second leg extends the length of the body toward the posterior end of the valve (see Chart 4), where the growth-ratio is relatively large.

Fifth to Sixth Instar

In this growth interval the second thoracic leg develops into a pediform structure, while the palp of the first leg begins to lose its pediform aspect. The increase of the thoracic pediform appendage again holds true; the second thoracic leg has a large growth-ratio, while its predecessor (the first leg) shows no growth during this interval.

The antennule, antenna, mandible, and maxilla are all located in the anterior half of the valve. These appendages have low ratios, and so does the anterior half of the valve.

The second thoracic leg is a large appendage and its large ratio is reflected in the ratios of the posterior half of the valve. The ratios of the quadrants show also that the growth of the valve is centered in the posteroventral region.

Sixth to Seventh Instar

In this interval all appendages are present. The third thoracic leg, present as an *anlage* in the sixth instar, has a large growth-ratio.

The large ratios of the antenna and mandible have a corresponding large ratio only in the ¼-⅜ increment of the valve. The posterior half of the valve has larger growth-ratios than the anterior half, probably caused by the *anlage* of the ovary, which overshadows the growth profile of the appendages.

Seventh to Eighth Instar

The antenna, mandible, and maxilla show strong growth, as does the ¼-⅜ and ⅜-½ increments of the valve.

The large ratios of the posterior half of the valve are probably related jointly to the large increase of the large second thoracic leg and to the *anlage* of the genital system.

Eighth to Ninth Instar

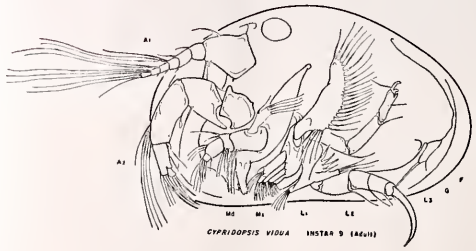
All of the appendages show large growth-ratios as they assume the robust character of the adult. The large growth of the posterior half of the valve is related directly to the full development of the genital lobe.

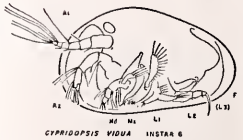
Chart 5

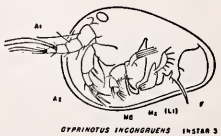
CHART 5

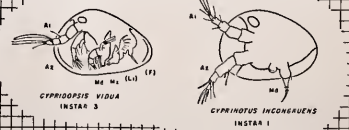
AVERAGE SIZES OF INSTAR STAGES OF FOUR SPECIES

SHOWING THE OVERLAPPING OF LENGTHS AND HEIGHTS









CYPRIS OVUM

CYPRIDOPSIS VIDUA

CYPRIS FASCIATA

CYPRINOTUS INCONGRUENS

HEIGHT ⟶

LENGTH ⟶

IX. Height-Length Ratio as a Valid Character for Determination of Species

Height-length ratio has been used by various taxonomists as specific character. They have supposed that a given height-length ratio is associated with all instar stages of a species and they have assigned many of the small ostracod valves of Paleozoic age to a particular species on the basis of their having the proper height-length ratio.

It is a difficult process to draw all the boundaries of a living ostracod species, where the appendages, the soft inner parts, and the fine details of the shell are all present for examination. It seems unjustified to base a classification on the ratio of two measurements in fossil forms, where the appendages are absent and the shape of the valves is often distorted in the process of burial and fossilization.

To test the dictum that the height-length ratio has specific significance, the writer has compared the valves of living ostracods in which the species are known to be definite by laboratory cultures. In a comparison of species of *Cypridae,* the writer has found the ratio theory to be fallacious in limitation of species. Chart 5 is based on the averages of the instars of *Cypris fasciata* Müller (averages from Claus 1868, p. 164; figure constructed from description and figures of other instars of this species), *Cypris ovum* Jurine (averages from Claus 1868, p. 164), and *Cyprinotus incongruens* Ramdohr (averages and figures from Schreiber 1922) plotted on the same chart of height vs. length as *Cypridopsis vidua* O. F. Müller. The dotted areas show the ranges of instars of *C. vidua.* When the *average* heights and lengths of some instars of the other species fall within the range of *C. vidua,* it is plausible that many of the individual specimens of the different species have the same precise height and length, and therefore, the same ratio. Even if two species did not have the *same* height and length, the *ratio* of height to length could be the same for individuals of both species.

An inspection of the figures shown in Chart 5 for comparison suggests that an evaluation of factors other than height and length, such as the distance from the anterior edge to the line of greatest height, would serve to separate many of the individuals with duplicated height-length ratios into their proper species.

However, it seems likely that if all possible diameters are compared for specimens, some species will be found to have overlaps with others.

Using current techniques and measurements, it is probable that some of the fossil smooth Cypridae are divided into "form species," which contain more than one actual species.

Ostracods can increase in importance as geologic indices only when new criteria are found to improve the taxonomic classification. Since the valves are the only parts preserved, except in rare instances, they should be studied in greater detail in both living and fossil forms. The patterns of muscle scars, particularly those in the dorsal area, may give additional information. Such patterns are difficult to work out in living species, but the value of the information promises to outweigh the time and effort necessary for its achievement.

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Plates

Plate 1

Nos. 1-4. Adult *Cypridopsis vidua* O. F. Müller, 10μ frontal sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from the dorsal area to the ventral.

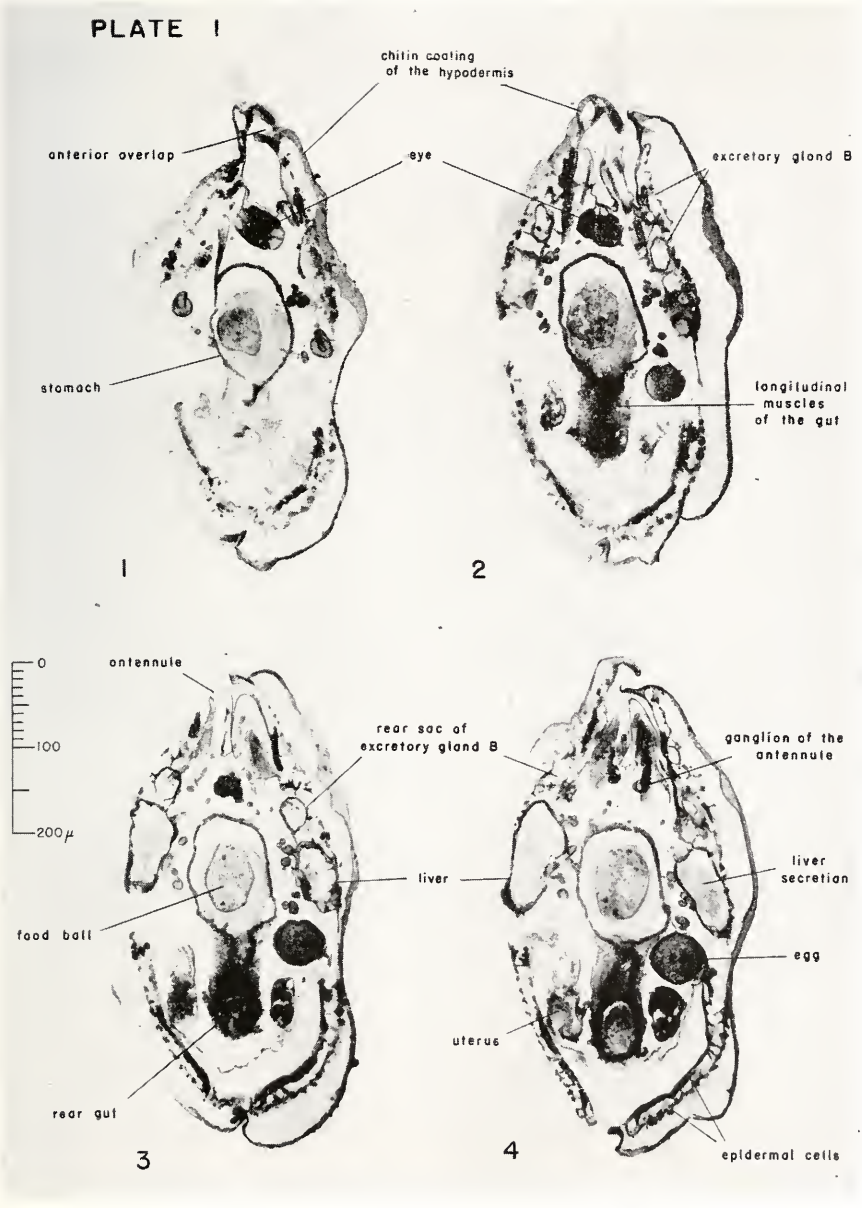


PLATE I
chitin coating
of the hypodermis
anterior overlap
eye
excretory gland B
stomach
longitudinal
muscles
of the gut
1
2
0
100
200μ
antennule
rear sac of
excretory gland B
ganglion of the
antennule
liver
liver
secretion
food ball
egg
uterus
rear gut
epidermal cells
3
4

Plate 2

Nos. 5-8. Adult, 10μ frontal sections. These sections follow those shown in Plate 1.

PLATE 2

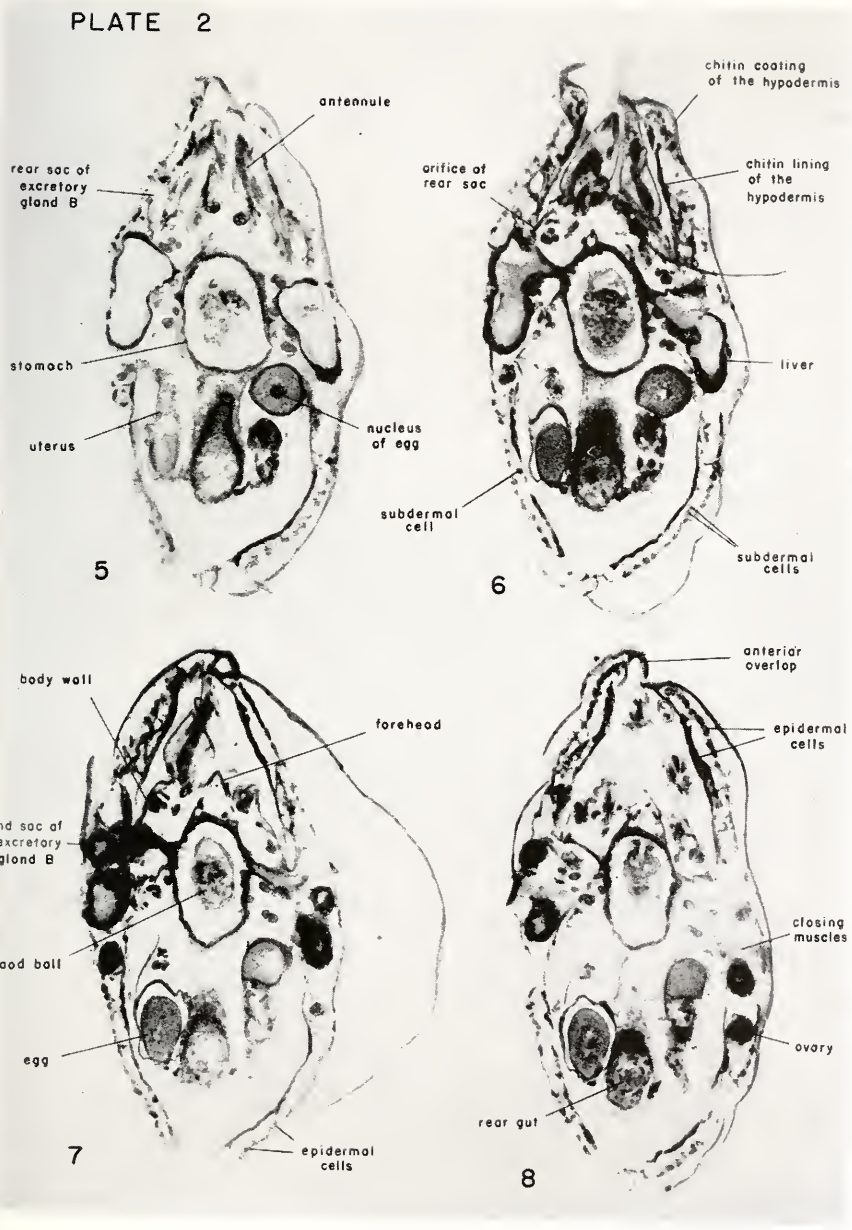

antennule
rear sac of excretory gland B
stomach
uterus
nucleus of egg
5
chitin coating of the hypodermis
orifice of rear sac
chitin lining of the hypodermis
liver
subdermal cell
subdermal cells
6
body wall
forehead
end sac of excretory gland B
food ball
egg
epidermal cells
7
anterior overlap
epidermal cells
closing muscles
ovary
rear gut
8

Plate 3

Nos. 9-12. Adult, 10μ frontal sections. These sections follow those shown in Plate 2.

PLATE 3

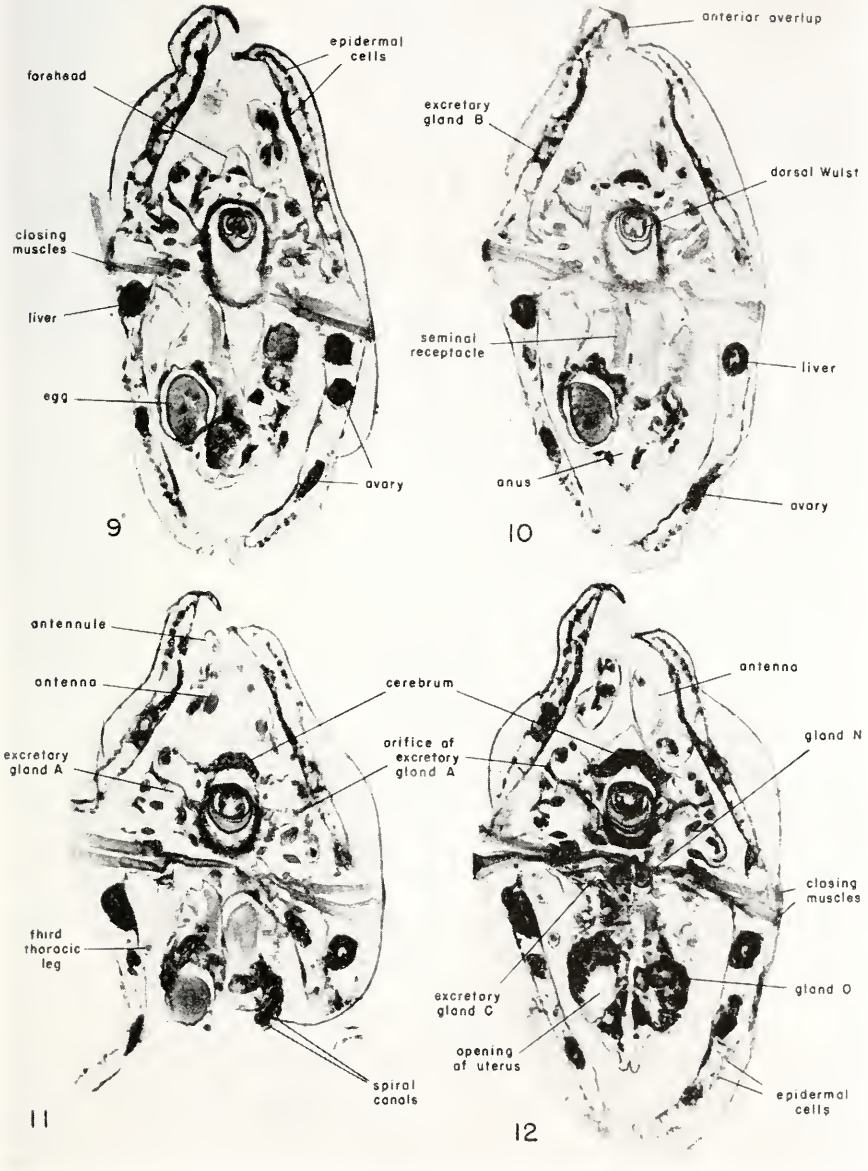

epidermal cells
forehead
closing muscles
liver
egg
ovary
9
anterior overlap
excretory gland B
dorsal Wulst
seminal receptacle
liver
anus
ovary
10
antennule
antenna
excretory gland A
cerebrum
third thoracic leg
spiral canals
11
antenna
orifice of excretory gland A
gland N
closing muscles
gland O
excretory gland C
opening of uterus
epidermal cells
12

Plate 4

Nos. 13-16. Adult, 10μ frontal sections. These sections follow those shown in Plate 3.

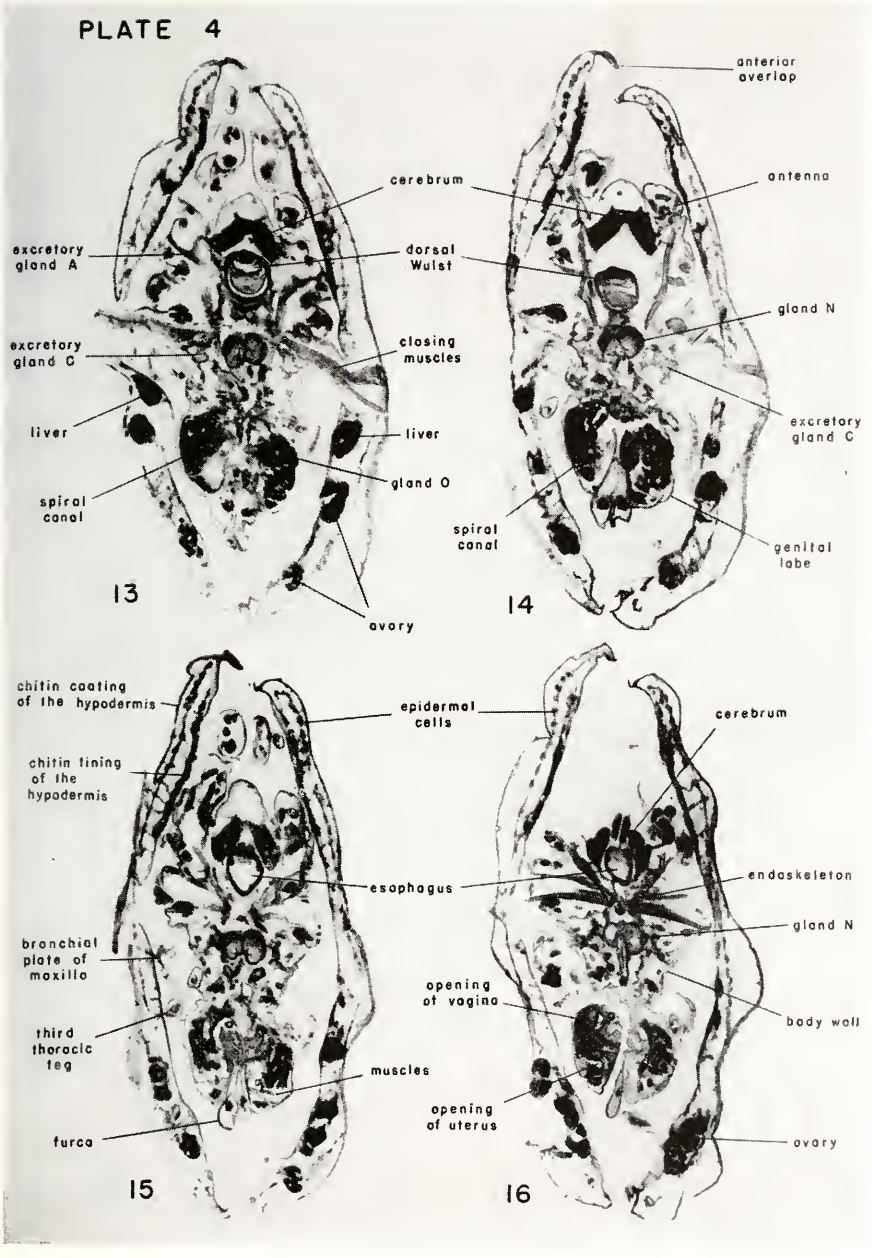


PLATE 4
cerebrum
excretory gland A
dorsal Wulst
excretory gland C
closing muscles
liver
liver
gland O
spiral canal
ovary
13
anterior overlap
antenna
gland N
excretory gland C
spiral canal
genital lobe
14
chitin coating of the hypodermis
epidermal cells
chitin lining of the hypodermis
esophagus
branchial plate of maxilla
third thoracic leg
muscles
furca
15
cerebrum
endoskeleton
gland N
opening of vagina
body wall
opening of uterus
ovary
16

Plate 5

Nos. 17-20. Adult, 10μ frontal sections. These sections follow those shown in Plate 4.

PLATE 5

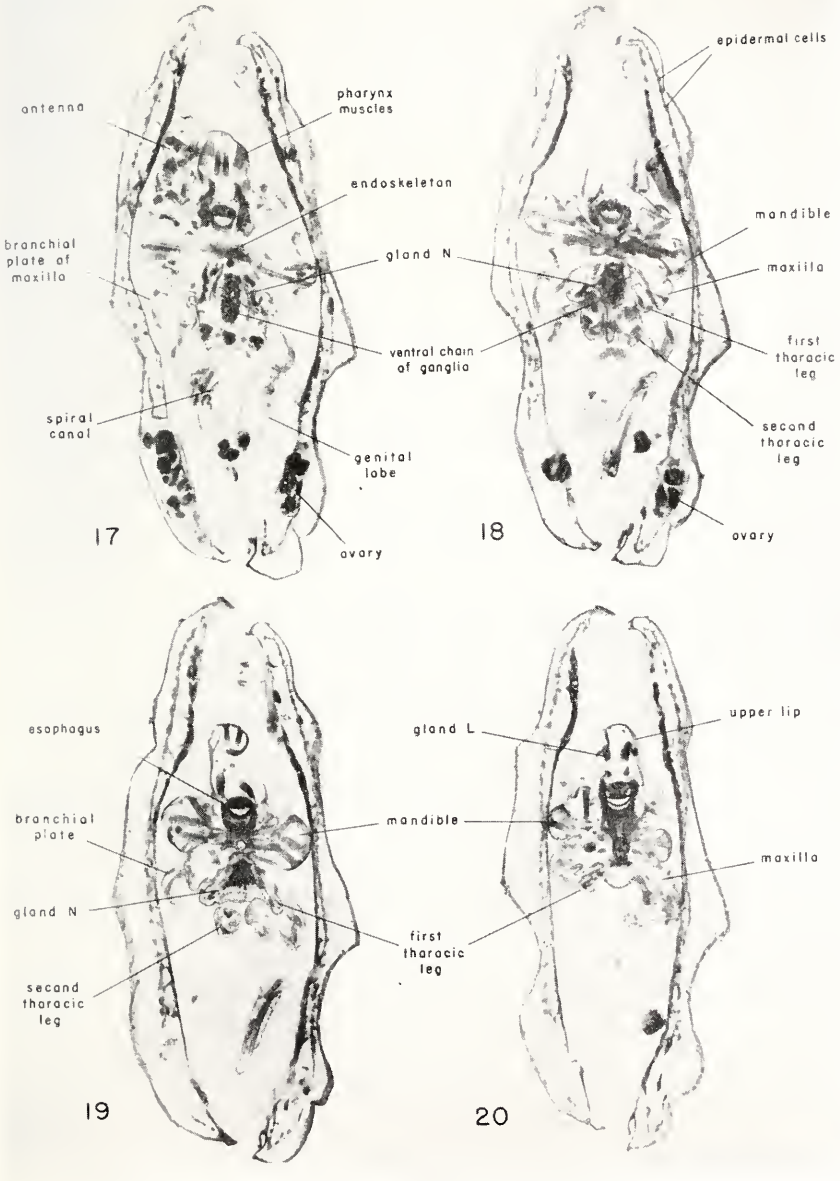

antenna
pharynx muscles
endoskeletan
branchial plate of maxilla
gland N
ventral chain of ganglia
spiral canal
genital lobe
ovary
17
epidermal cells
mandible
maxilla
first thoracic leg
second thoracic leg
ovary
18
esophagus
branchial plate
gland N
second thoracic leg
mandible
first thoracic leg
19
gland L
upper lip
maxilla
20

Plate 6

Nos. 21-24. Adult, 10μ frontal sections. These sections follow those shown in Plate 5.

PLATE 6

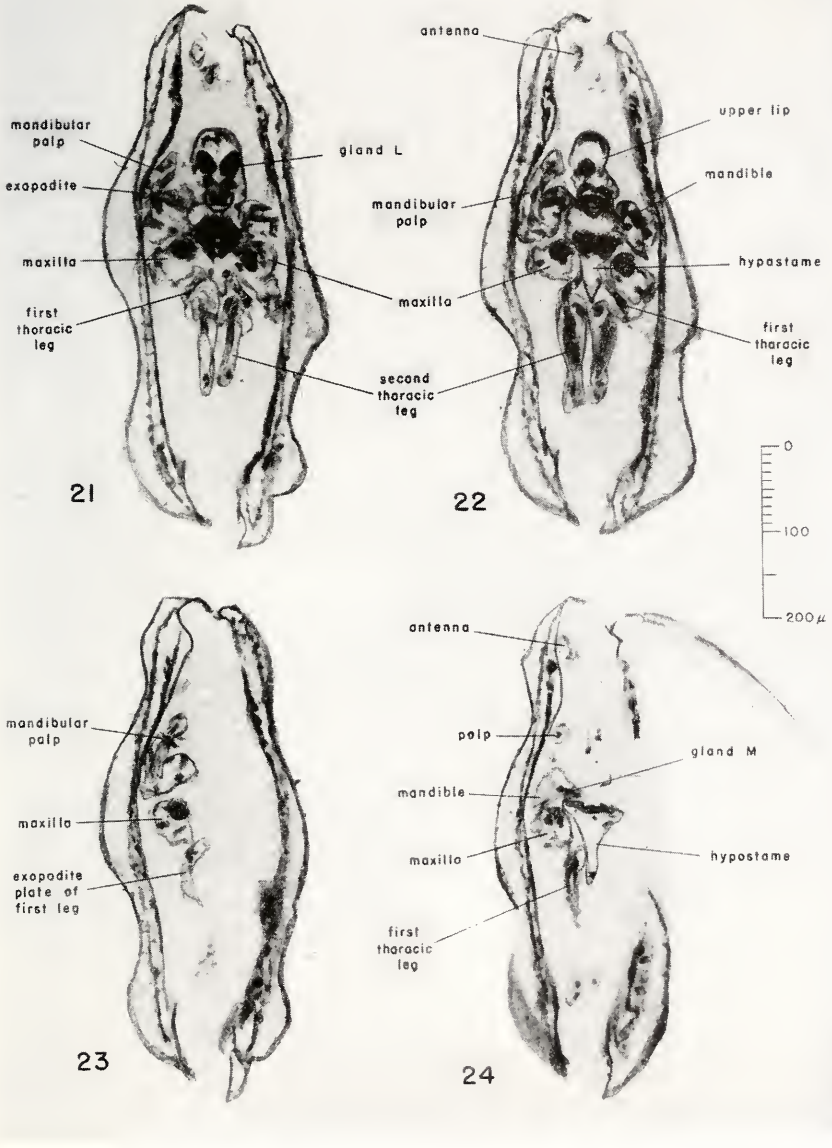

mandibular palp
exopodite
maxilla
first thoracic leg
gland L
maxilla
second thoracic leg
21
antenna
upper lip
mandible
mandibular palp
hypostame
maxilla
first thoracic leg
22
0
100
200 μ
mandibular palp
maxilla
exopodite plate of first leg
23
antenna
palp
gland M
mandible
maxilla
hypostame
first thoracic leg
24

Plate 7

Nos. 25-28. Adult, 10μ frontal sections. These sections follow those shown in Plate 6, and reach to the ventral border of the shell.

Nos. 29-34. Adult, 10μ sagittal sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from the left to the right side.

PLATE 7

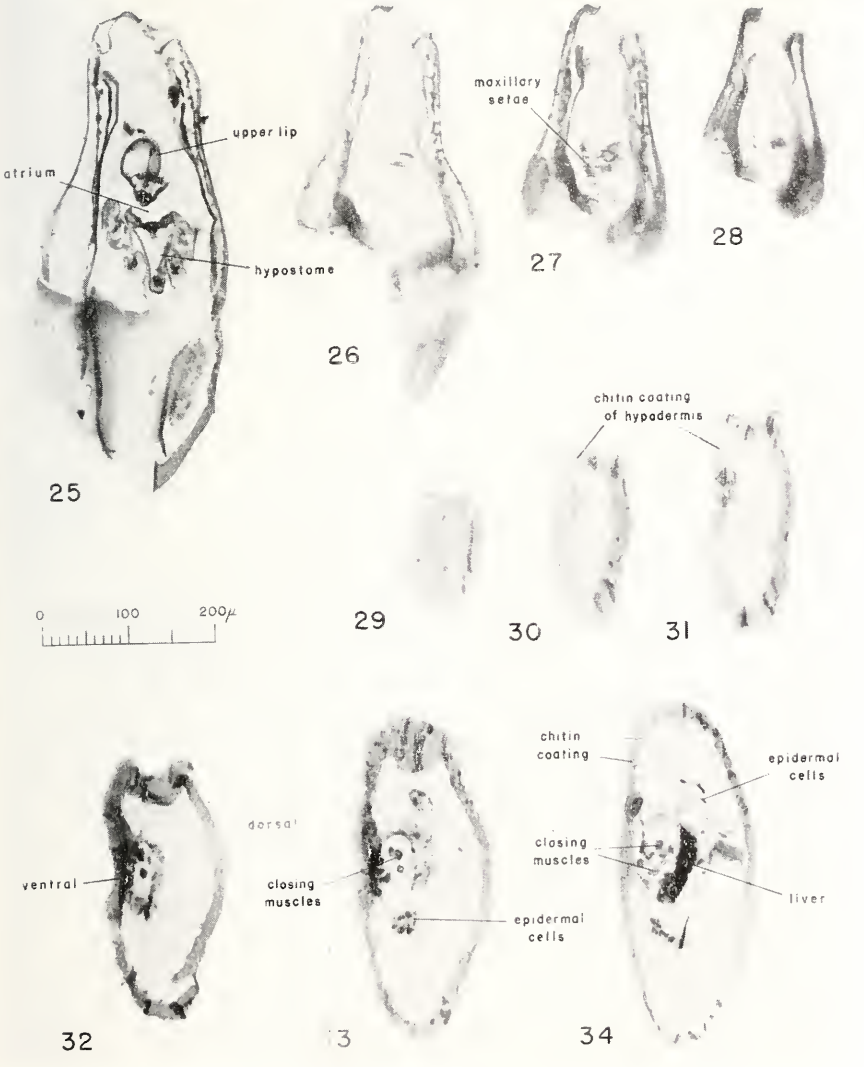

upper lip
atrium
hypostome
25
26
maxillary setae
27
28
chitin coating of hypodermis
29
30
31
0
100
200μ
ventral
dorsal
closing muscles
32
3
chitin coating
epidermal cells
closing muscles
liver
epidermal cells
34

Plate 8

Nos. 35-40. Adult, 10μ sagittal sections. These sections follow those shown in Plate 7.

PLATE 8

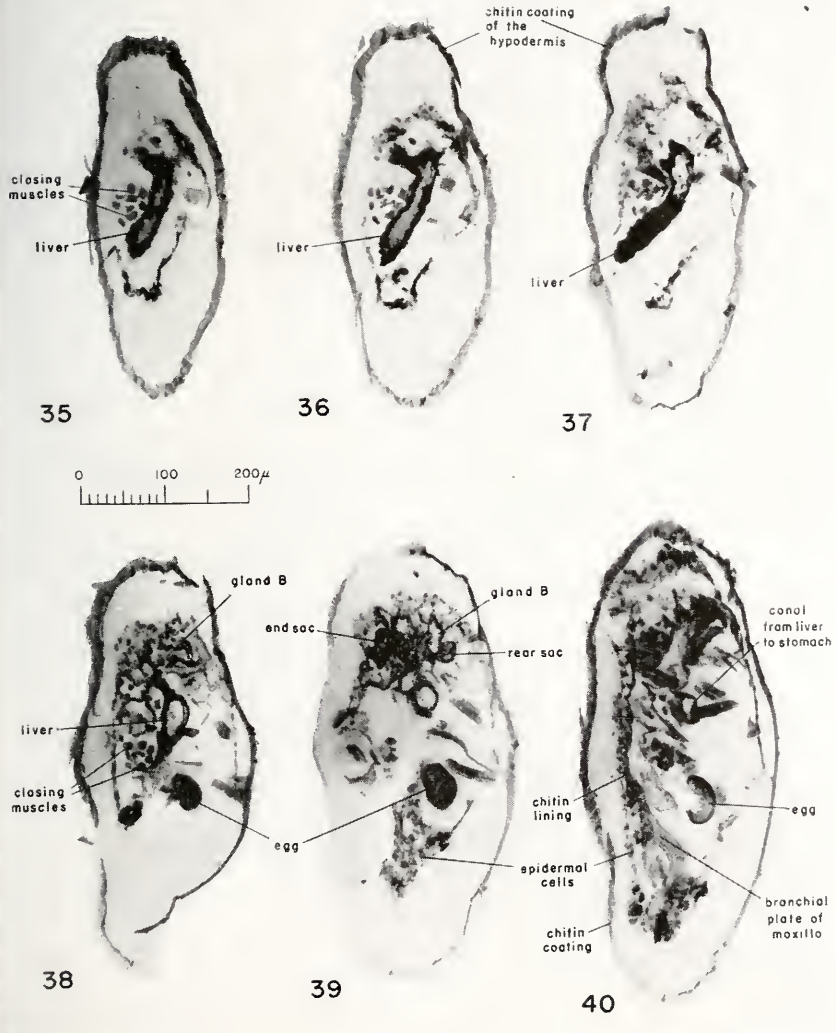

chitin coating of the hypodermis
closing muscles
liver
liver
liver
35
36
37
0
100
200μ
gland B
end sac
gland B
rear sac
conal from liver to stomach
liver
closing muscles
egg
chitin lining
egg
spidermal cells
branchial plate of maxilla
chitin coating
38
39
40

Plate 9

Nos. 41-46. Adult, 10μ sagittal sections. These sections follow those shown in Plate 8.

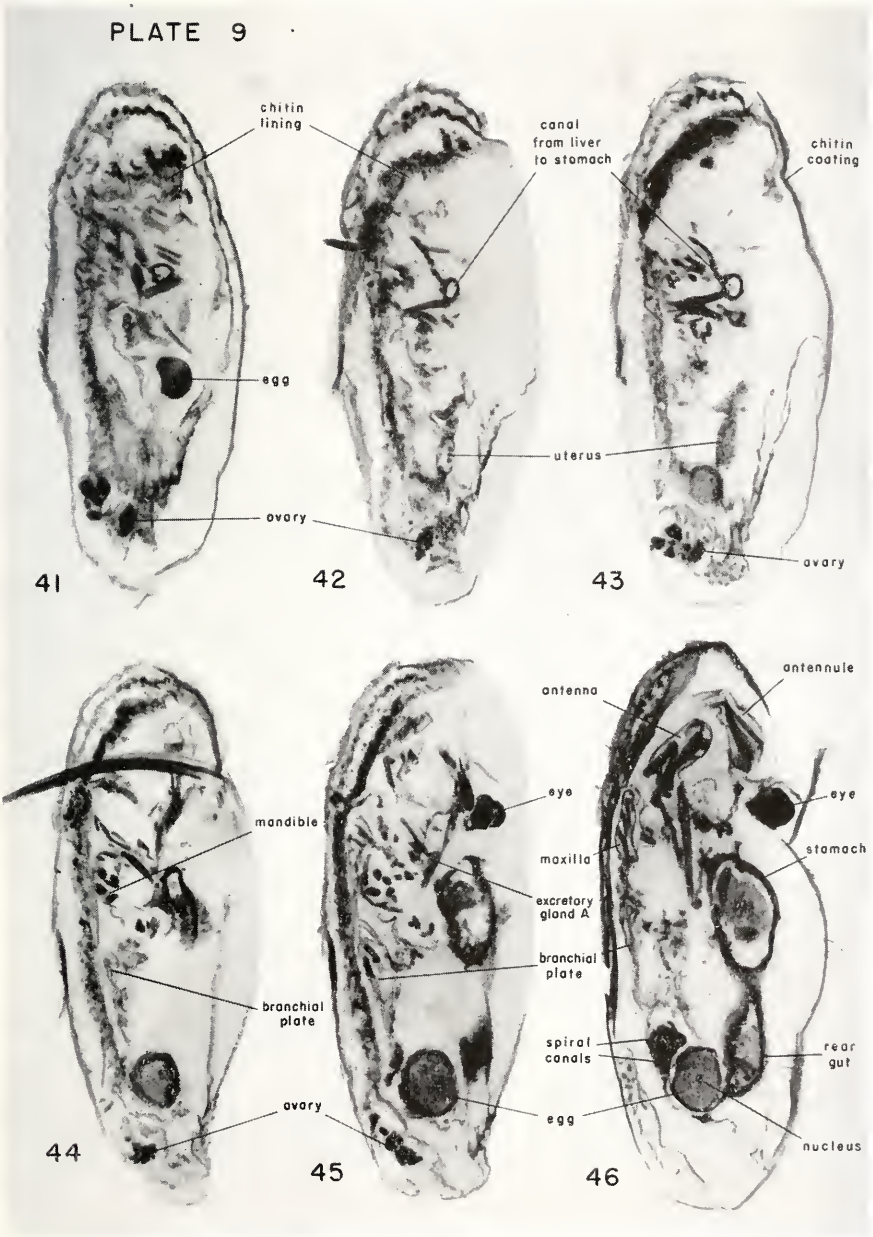


PLATE 9
chitin lining
egg
ovary
41
canal from liver to stomach
uterus
42
chitin coating
ovary
43
mandible
branchial plate
ovary
44
eye
excretory gland A
egg
45
antennule
antenna
eye
stomach
maxilla
branchial plate
spiral canals
rear gut
nucleus
46

Plate 10

Nos. 47-52. Adult, 10μ sagittal sections. These sections follow those shown in Plate 9.

PLATE 10

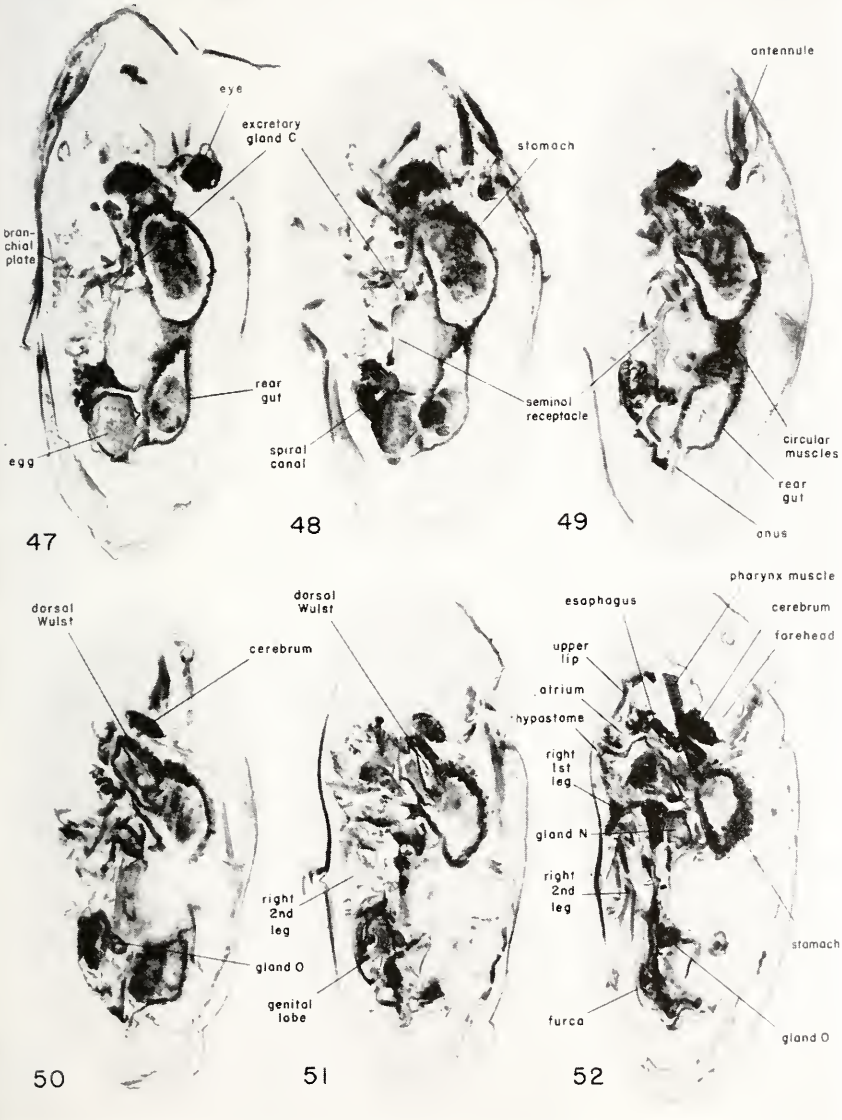

eye
excretory gland C
branchial plate
rear gut
egg
spiral canal
stomach
seminal receptacle
antennule
circular muscles
rear gut
anus
47
48
49
dorsal Wulst
cerebrum
right 2nd leg
gland O
dorsal Wulst
genital lobe
pharynx muscle
esophagus
cerebrum
forehead
upper lip
atrium
hypostome
right 1st leg
gland N
right 2nd leg
stomach
furca
gland O
50
51
52

Plate 11

Nos. 53-58. Adult, 10μ sagittal sections. These sections follow those shown in Plate 10.

PLATE II

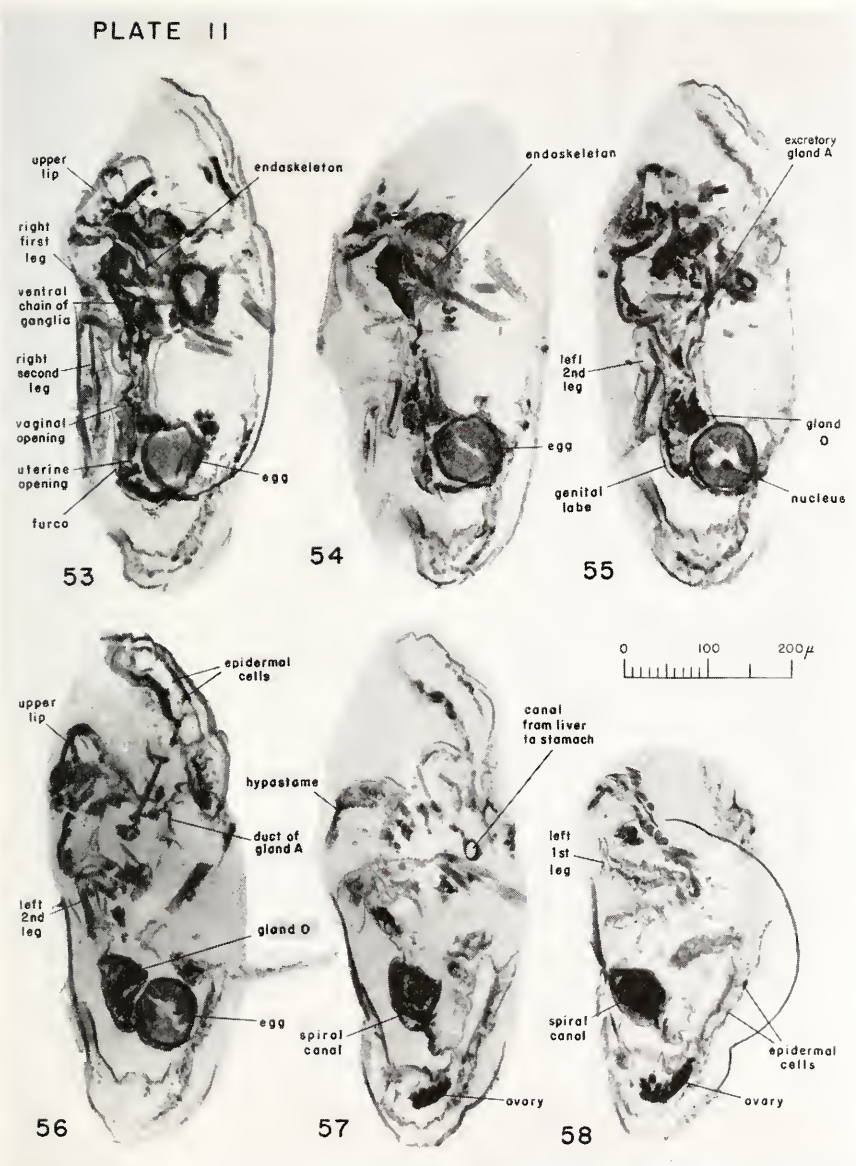

upper lip
endaskeleton
right first leg
ventral chain of ganglia
right second leg
vaginal opening
uterine opening
egg
furca
53
endaskeleton
egg
54
excretory gland A
left 2nd leg
gland O
genital labe
nucleus
55
epidermal cells
upper lip
hypostome
duct of gland A
left 2nd leg
gland O
egg
56
canal from liver to stomach
spiral canal
ovary
57
0
100
200μ
left 1st leg
spiral canal
epidermal cells
ovary
58

Plate 12

Nos. 59-64. Adult, 10μ sagittal sections. These sections follow those shown in Plate 11, and conclude the sequence which began on Plate 7, No. 29.

PLATE 12

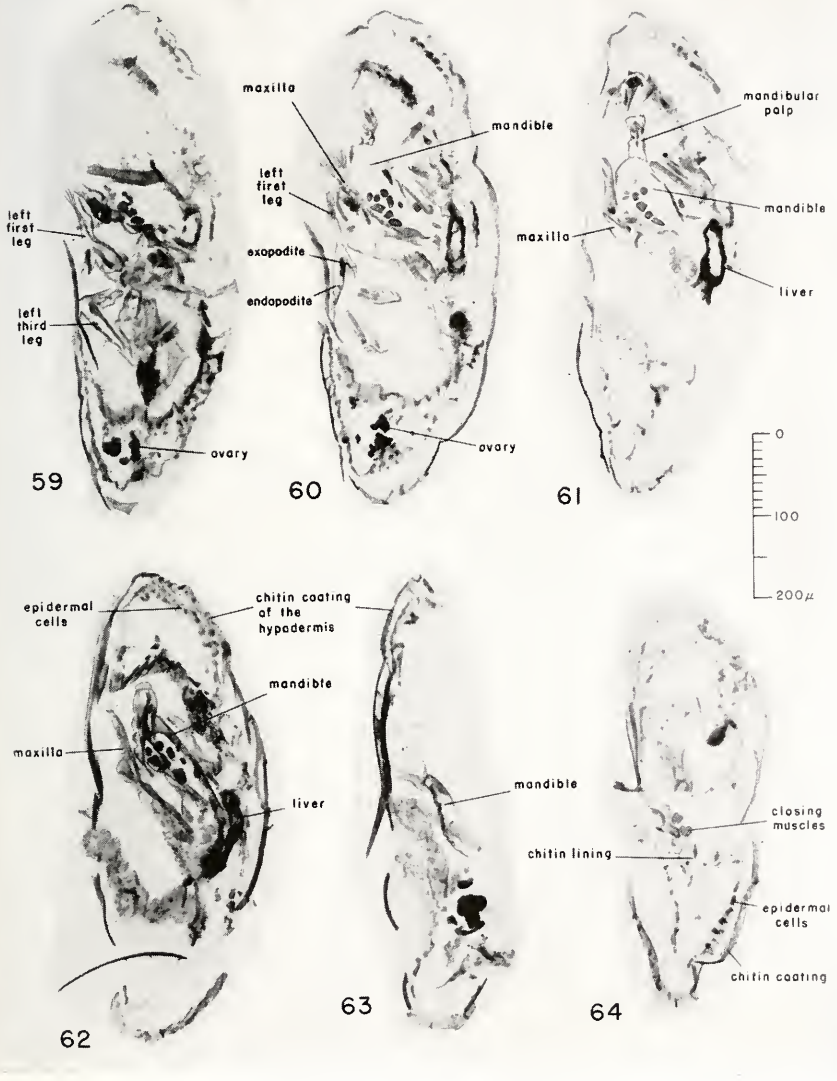

left first leg
left third leg
ovary
59
maxilla
mandible
left first leg
exopodite
endopodite
ovary
60
mandibular palp
mandible
maxilla
liver
61
0
100
200μ
epidermal cells
chitin coating of the hypodermis
mandible
maxilla
liver
62
mandible
63
closing muscles
chitin lining
epidermal cells
chitin coating
64

Plate 13

Nos. 65-75. Adult, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from the anterior to the posterior end.

PLATE 13

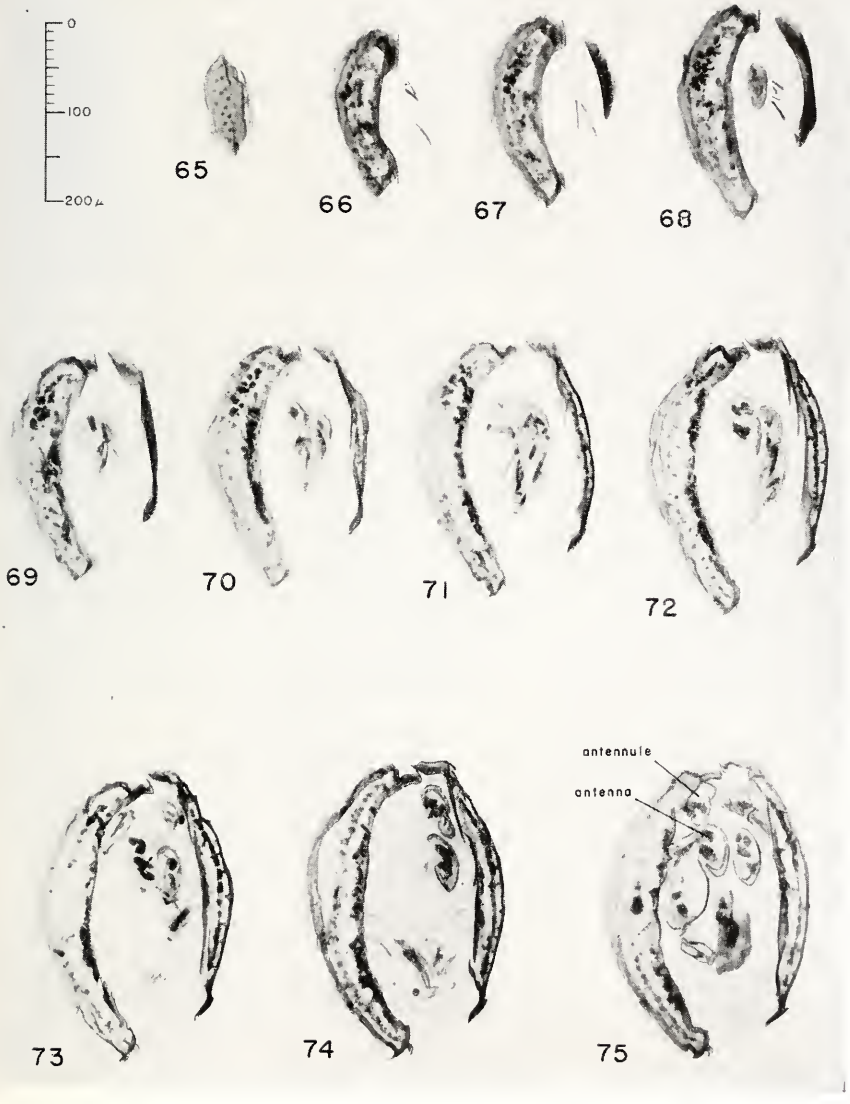


Plate 14

Nos. 76-84. Adult, 10μ transverse sections. These sections follow those shown in Plate 13.

PLATE 14

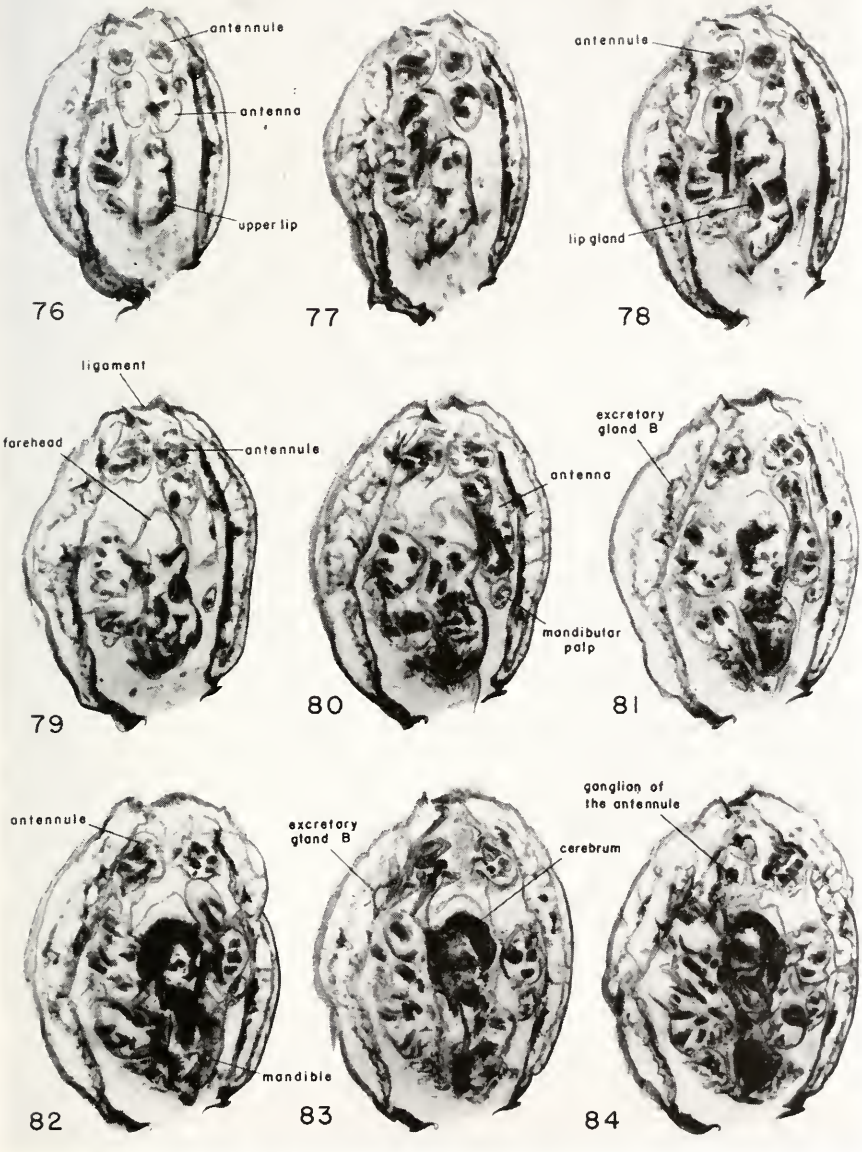

antennule
antenna
upper lip
76
77
antennule
lip gland
78
ligament
forehead
antennule
79
antenna
mandibular palp
80
excretory gland B
81
antennule
mandible
82
excretory gland B
cerebrum
83
ganglion of the antennule
84

Plate 15

Nos. 85-90. Adult, 10μ transverse sections. These sections follow those shown in Plate 14.

PLATE 15

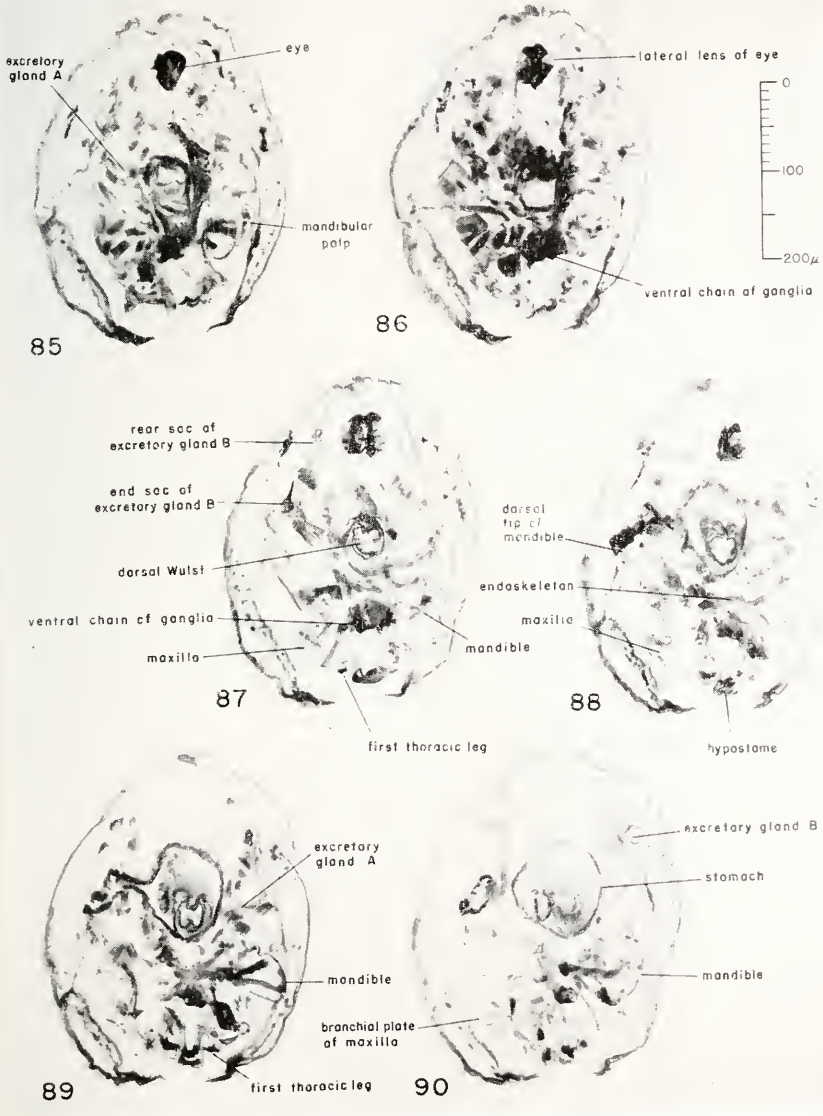

excretory gland A
eye
mandibular palp
85
lateral lens of eye
0
100
200μ
ventral chain of ganglia
86
rear sac of excretory gland B
end sac of excretory gland B
dorsal Wulst
ventral chain of ganglia
maxilla
mandible
first thoracic leg
87
dorsal tip of mandible
endoskeleton
maxilla
hypostome
88
excretory gland A
mandible
branchial plate of maxilla
first thoracic leg
89
excretory gland B
stomach
mandible
90

Plate 16

Nos. 91-96. Adult, 10μ transverse sections. These sections follow those shown in Plate 15.

PLATE 16

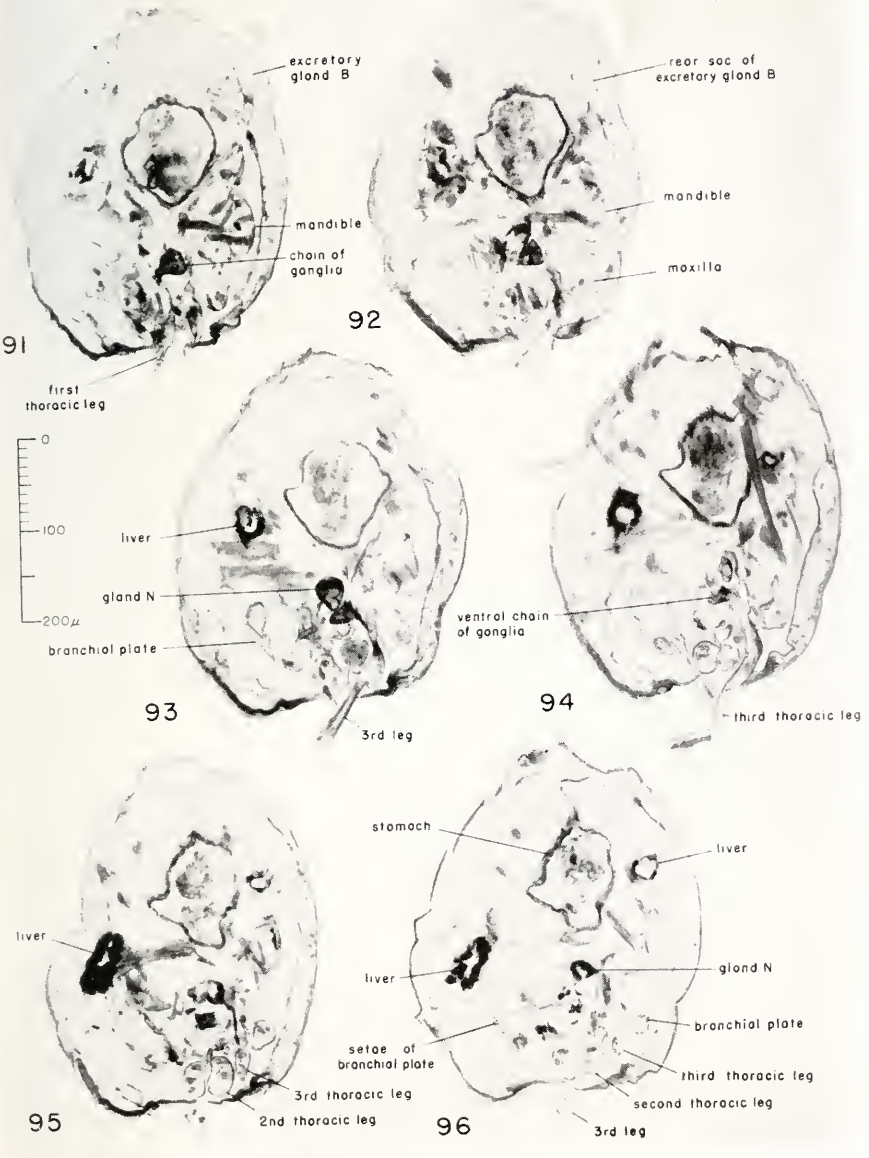

excretory gland B
mandible
chain of ganglia
91
first thoracic leg
reor soc of excretory gland B
mandible
maxilla
92
0
100
200μ
liver
gland N
branchial plate
93
3rd leg
ventral chain of ganglia
94
third thoracic leg
liver
95
3rd thoracic leg
2nd thoracic leg
stomach
liver
liver
gland N
branchial plate
setae of branchial plate
third thoracic leg
second thoracic leg
96
3rd leg

Plate 17

Nos. 97-102. Adult, 10μ transverse sections. These sections follow those shown in Plate 16.

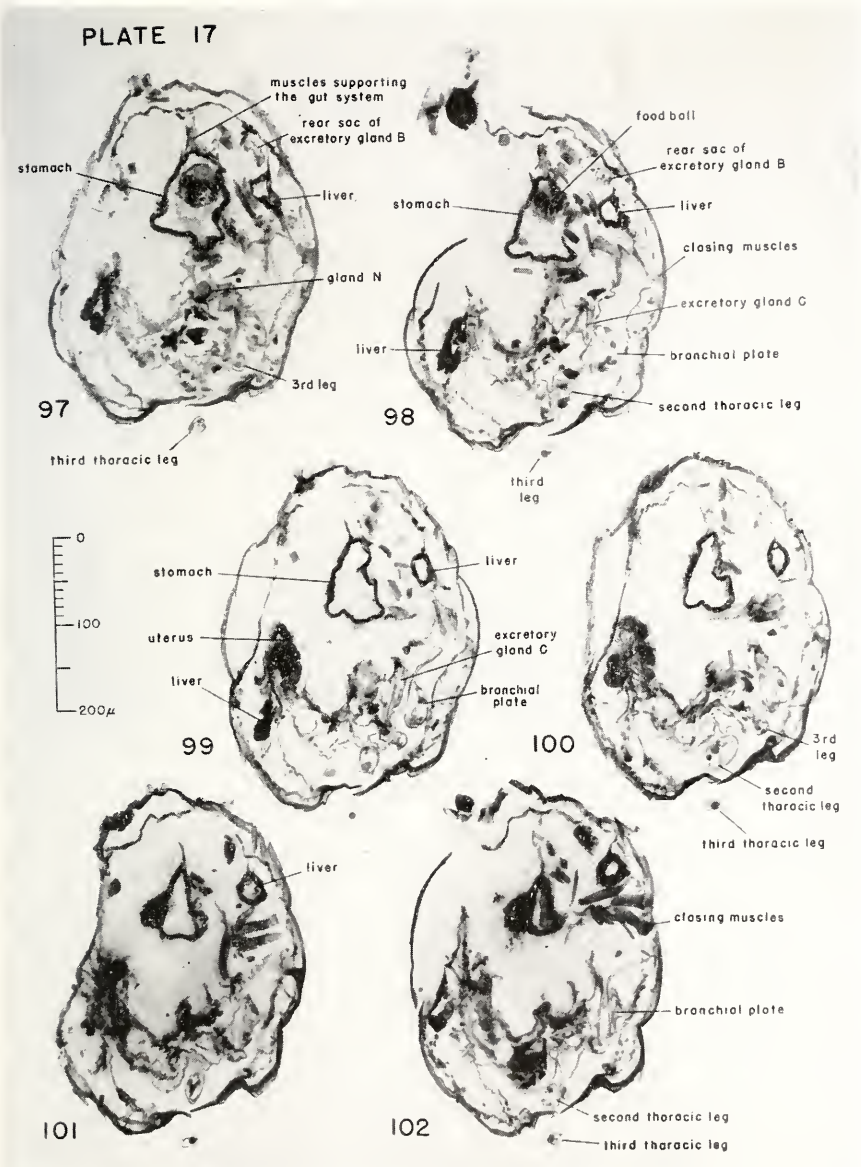


PLATE 17
muscles supporting the gut system
rear sac of excretory gland B
stomach
liver
gland N
3rd leg
97
third thoracic leg
food ball
rear sac of excretory gland B
stomach
liver
closing muscles
excretory gland C
liver
branchial plate
second thoracic leg
98
third leg
0
100
200μ
stomach
liver
uterus
excretory gland C
liver
branchial plate
99
100
3rd leg
second thoracic leg
third thoracic leg
liver
101
closing muscles
branchial plate
second thoracic leg
third thoracic leg
102

Plate 18

Nos. 103-111. Adult, 10μ transverse sections. These sections follow those shown in Plate 17.

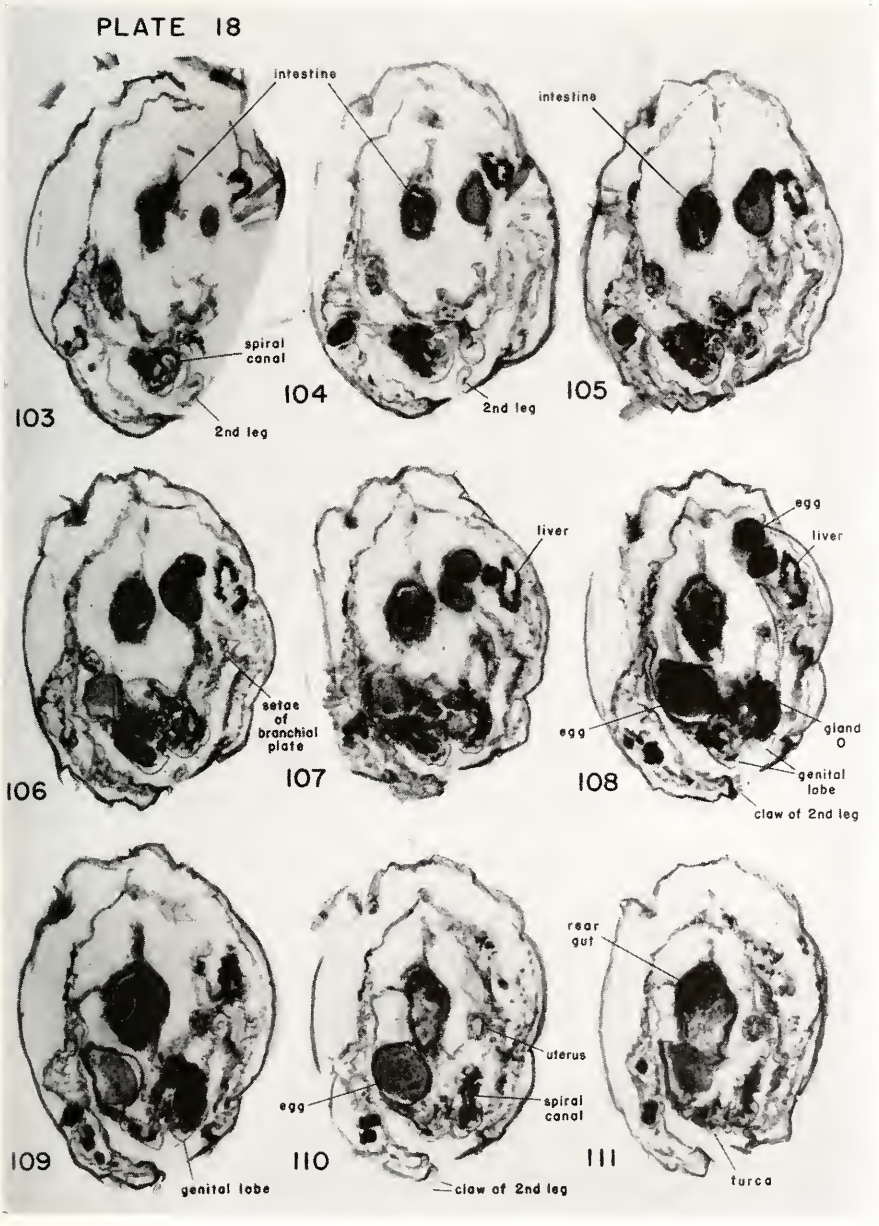


PLATE 18
intestine
spiral canal
2nd leg
103
intestine
2nd leg
104
intestine
105
setae of branchial plate
106
liver
107
egg
liver
egg
gland O
genital lobe
claw of 2nd leg
108
109
genital lobe
egg
uterus
spiral canal
claw of 2nd leg
110
rear gut
furca
111

Plate 19

Nos. 112-120. Adult, 10μ transverse sections. These sections follow those in Plate 18.

PLATE 19

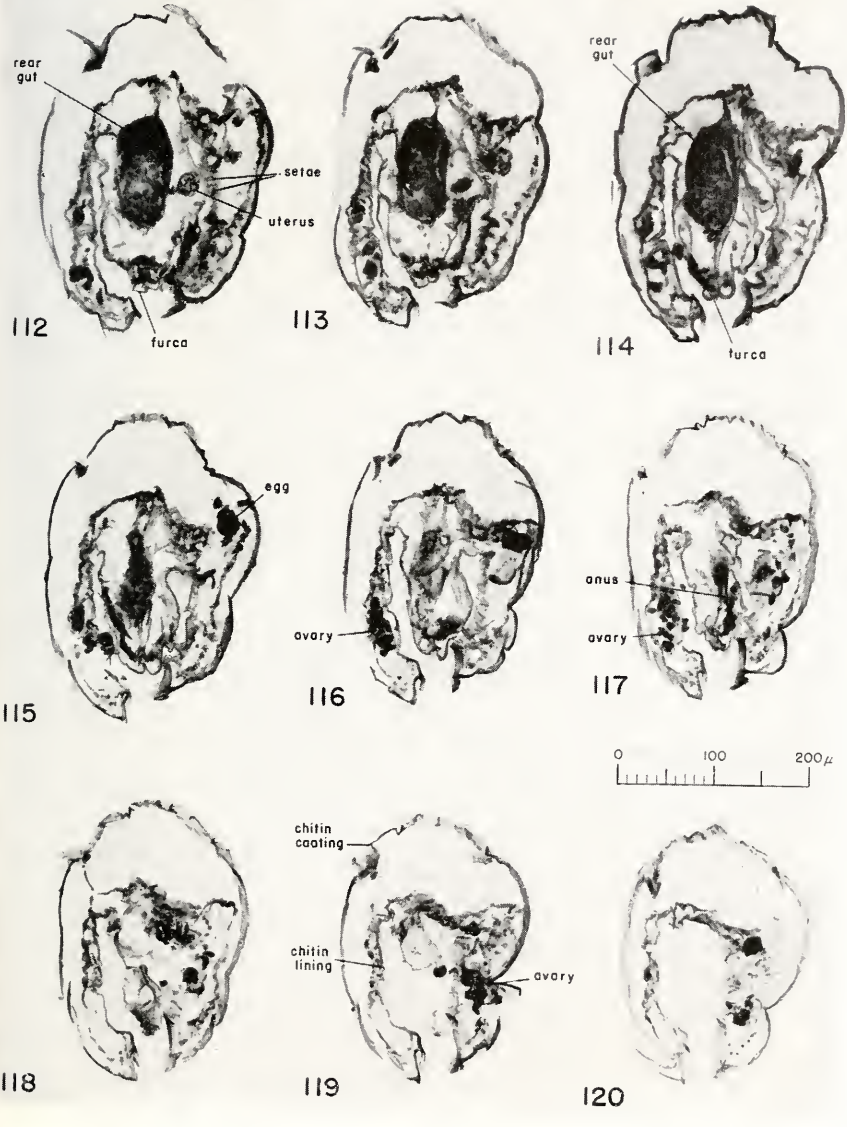

rear gut
setae
uterus
furca
112
113
rear gut
furca
114
egg
115
ovary
116
anus
ovary
117
0
100
200μ
chitin coating
chitin lining
ovary
118
119
120

Plate 20

Nos. 121-127. Adult, 10μ transverse sections. These sections follow those shown in Plate 19, and conclude the sequence of transverse sections which began in Plate 13.

Nos. 128-135. Adult, 10μ frontal sections, stained with Ehrlich's haematoxylin and eosin. These sections progress from the dorsal to the ventral edge.

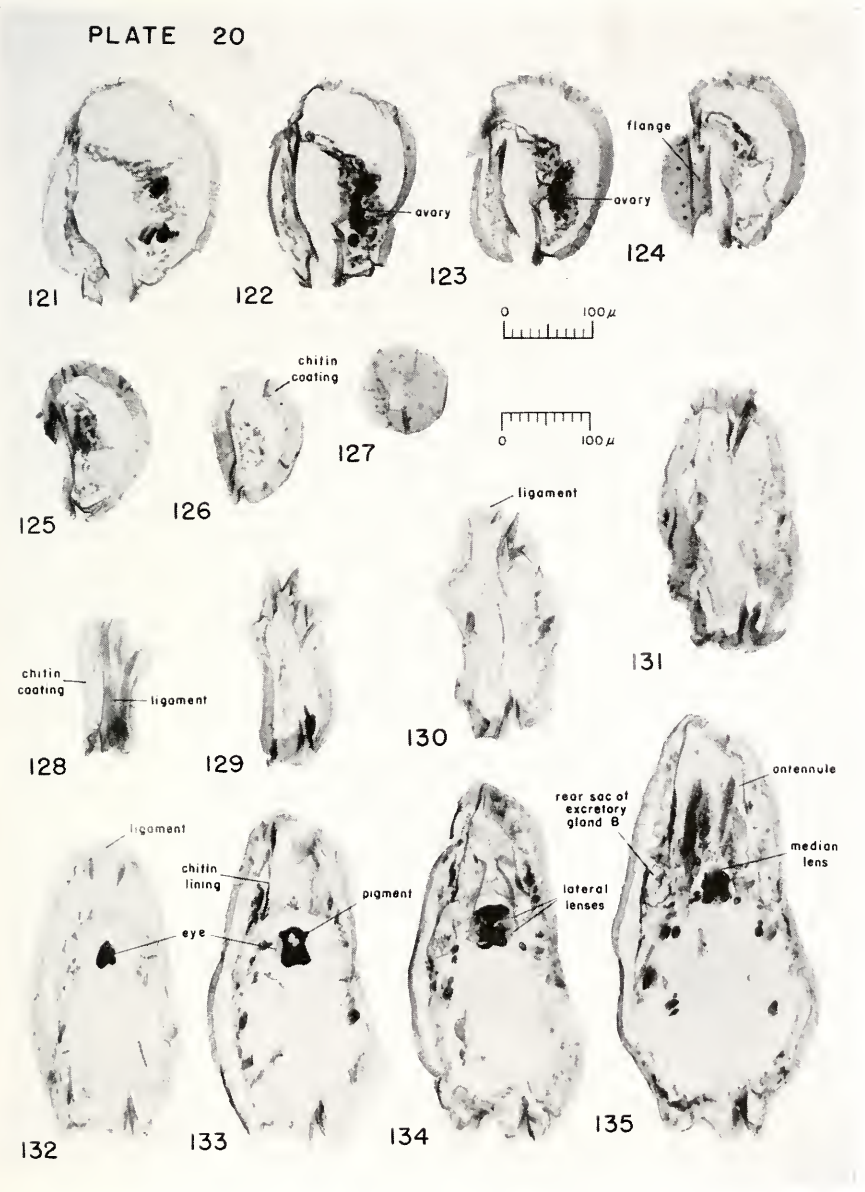


PLATE 20
121
122
ovary
123
ovary
flange
124
0
100μ
125
chitin coating
126
127
0
100μ
ligament
131
chitin coating
ligament
128
129
130
ligament
chitin lining
pigment
eye
132
133
134
rear sac of excretory gland B
antennule
median lens
lateral lenses
135

Plate 21

Nos. 136-161. Adult, 10μ frontal sections. These sections follow those shown in Plate 20 beginning with No. 128.

PLATE 21

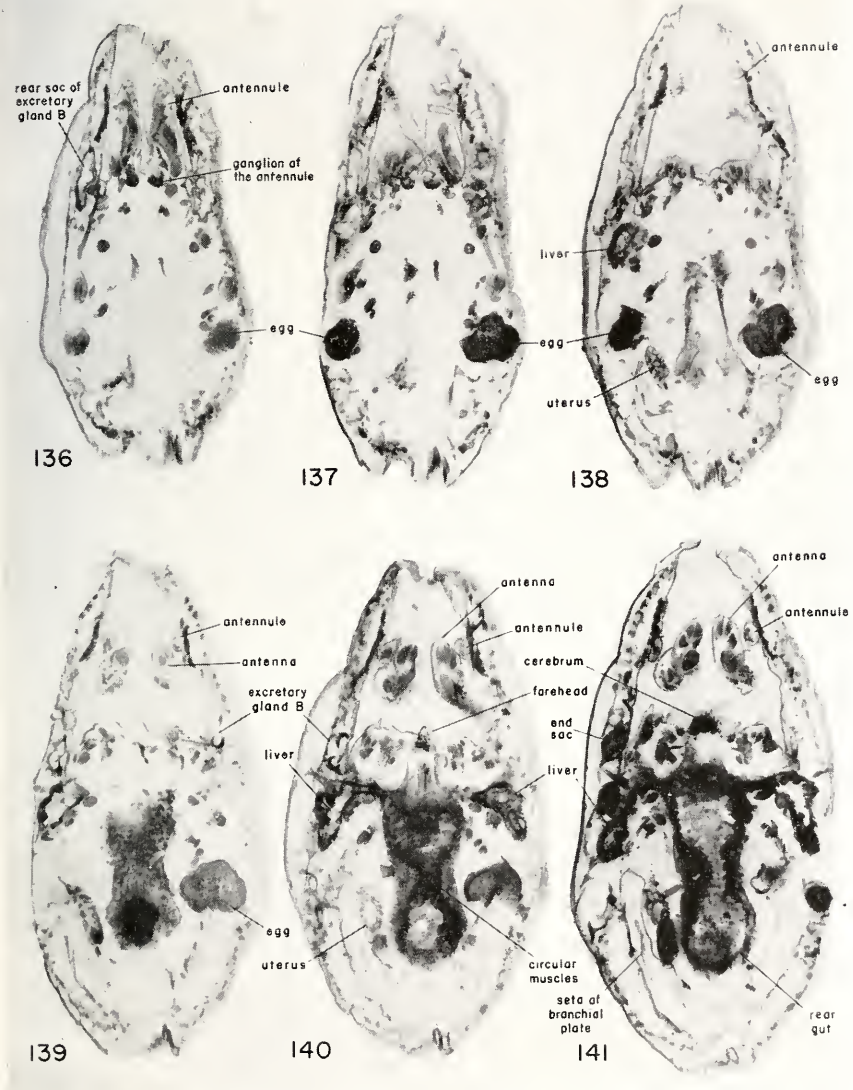
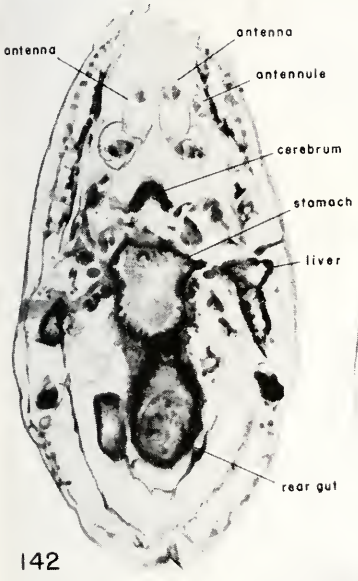

rear sac of excretory gland B
antennule
ganglion of the antennule
egg
136
137
antennule
liver
egg
uterus
egg
138
antennule
antenna
excretory gland B
liver
egg
uterus
139
antenna
antennule
cerebrum
forehead
end sac
liver
circular muscles
seta of branchial plate
140
antenna
antennule
rear gut
141

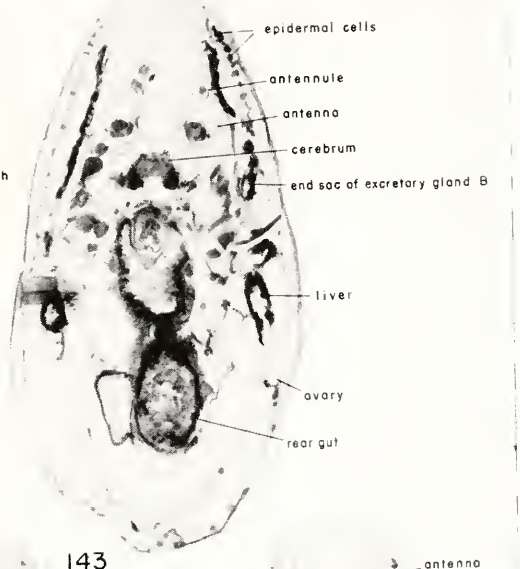
Plate 22

Nos. 142-145. Adult, 10μ frontal sections. These sections follow those shown in Plate 21.

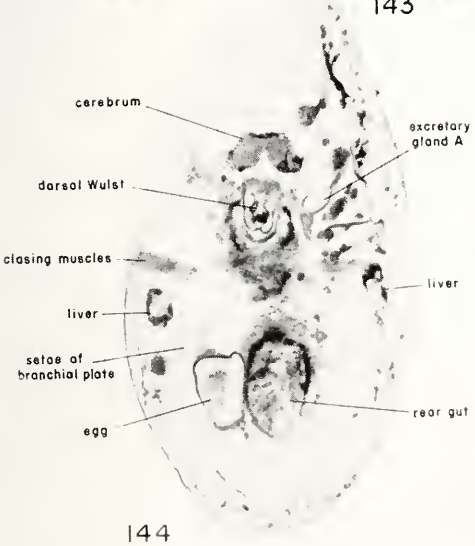
PLATE 22



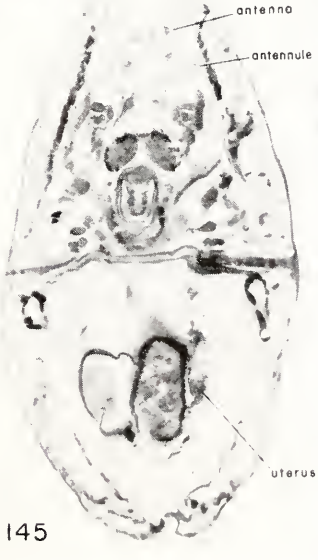
142



143



144



145

Plate 23

Nos. 146-169. Adult, 10μ frontal sections. These sections follow those shown in Plate 22.

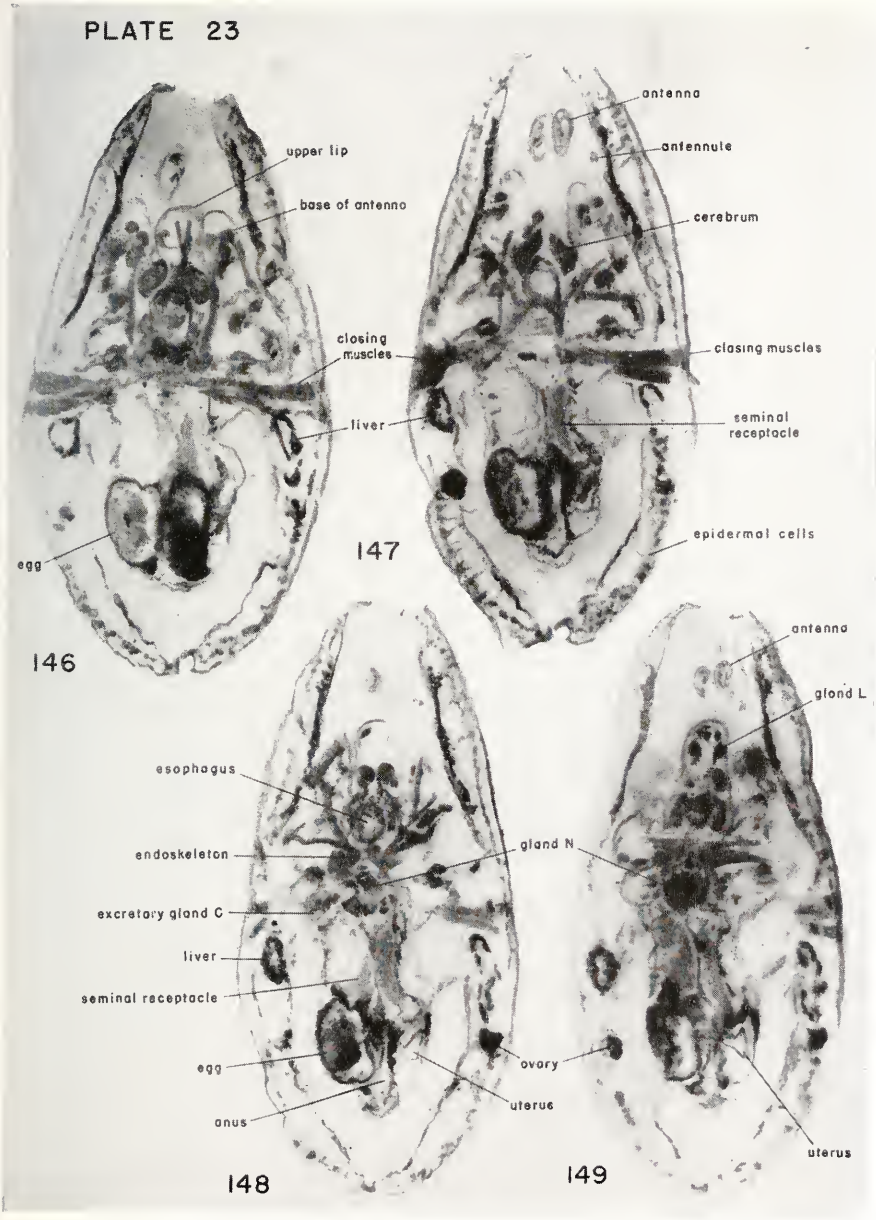


PLATE 23
upper lip
base of antenna
closing muscles
liver
egg
146
antenna
antennule
cerebrum
closing muscles
seminal receptacle
epidermal cells
147
esophagus
endoskeleton
excretory gland C
liver
seminal receptacle
egg
anus
gland N
ovary
uterus
148
antenna
gland L
uterus
149

Plate 24

Nos. 150-154. Adult, 10μ frontal sections. These sections follow those shown in Plate 23.

PLATE 24

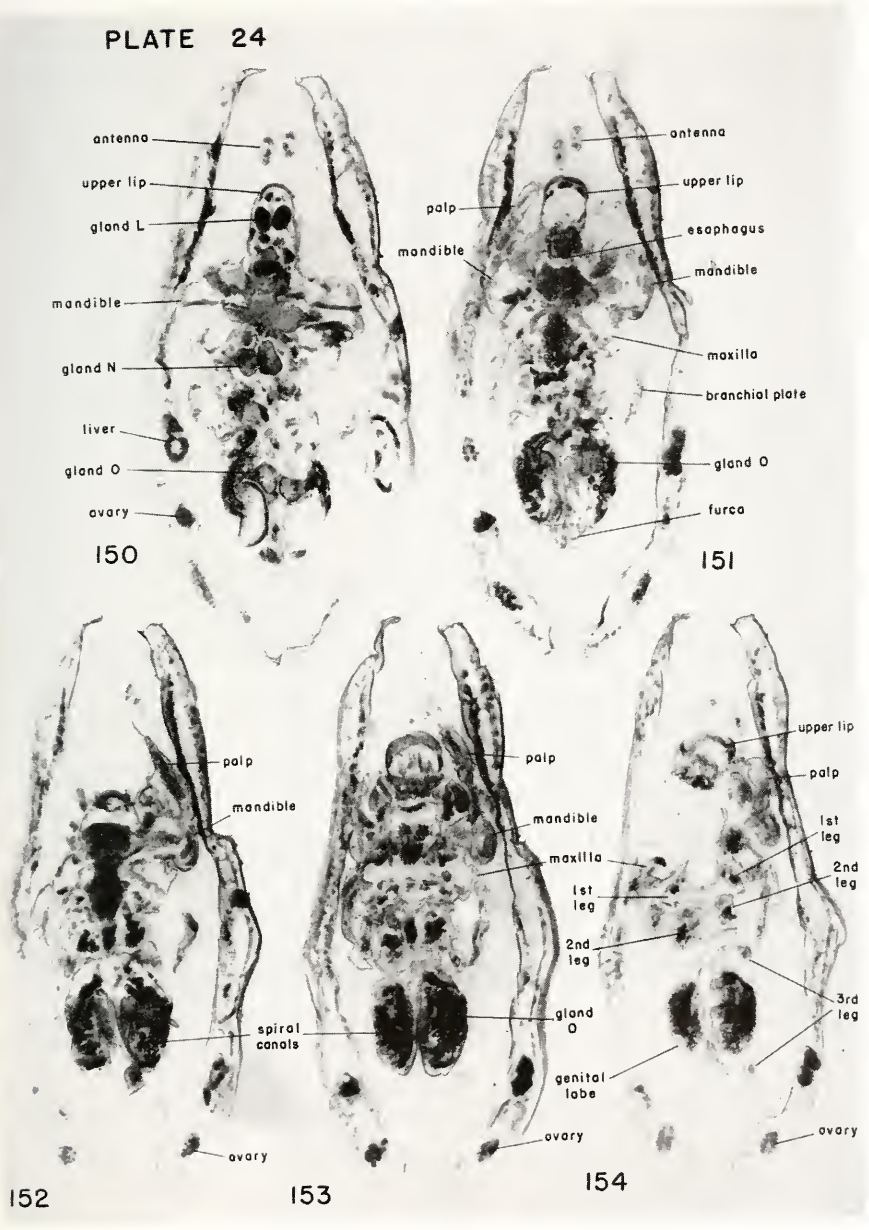

antenna
upper lip
gland L
mandible
gland N
liver
gland O
ovary
150
antenna
upper lip
palp
esophagus
mandible
mandible
maxilla
branchial plate
gland O
furca
151
palp
mandible
spiral canals
ovary
152
palp
mandible
maxilla
1st leg
2nd leg
gland O
ovary
153
upper lip
palp
1st leg
2nd leg
3rd leg
genital lobe
ovary
154

Plate 25

Nos. 155-161. Adult, 10μ frontal sections. These sections follow those shown in Plate 24, and conclude the sequence of frontal sections which began in Plate 20, No. 128.

PLATE 25

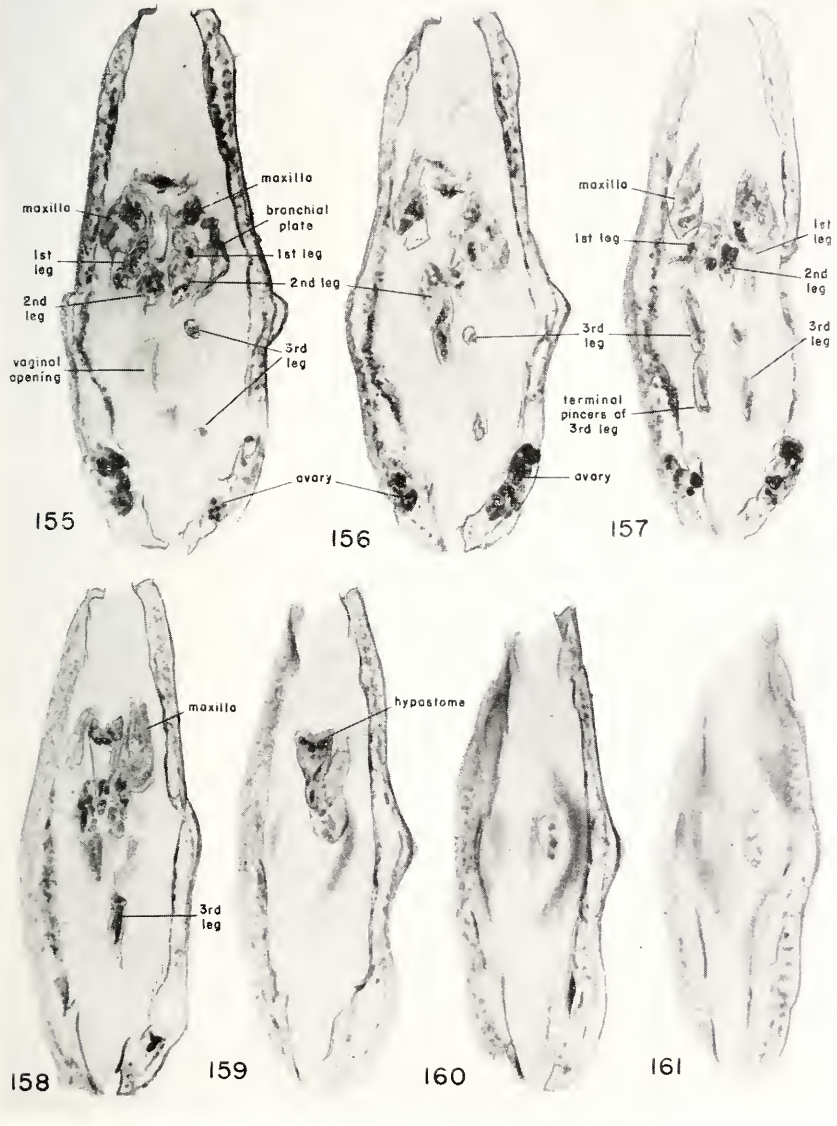

maxilla
maxilla
branchial plate
1st leg
1st leg
2nd leg
2nd leg
2nd leg
3rd leg
vaginal opening
ovary
155
maxilla
1st leg
1st leg
2nd leg
3rd leg
3rd leg
terminal pincers of 3rd leg
ovary
156
maxilla
1st leg
1st leg
2nd leg
3rd leg
3rd leg
157
maxilla
3rd leg
158
hypostome
159
160
161

Plate 26

Nos. 162-173. Adult, 10μ sagittal sections, stained with Ehrlich's haematoxylin and eosin. These sections progress from left to right.

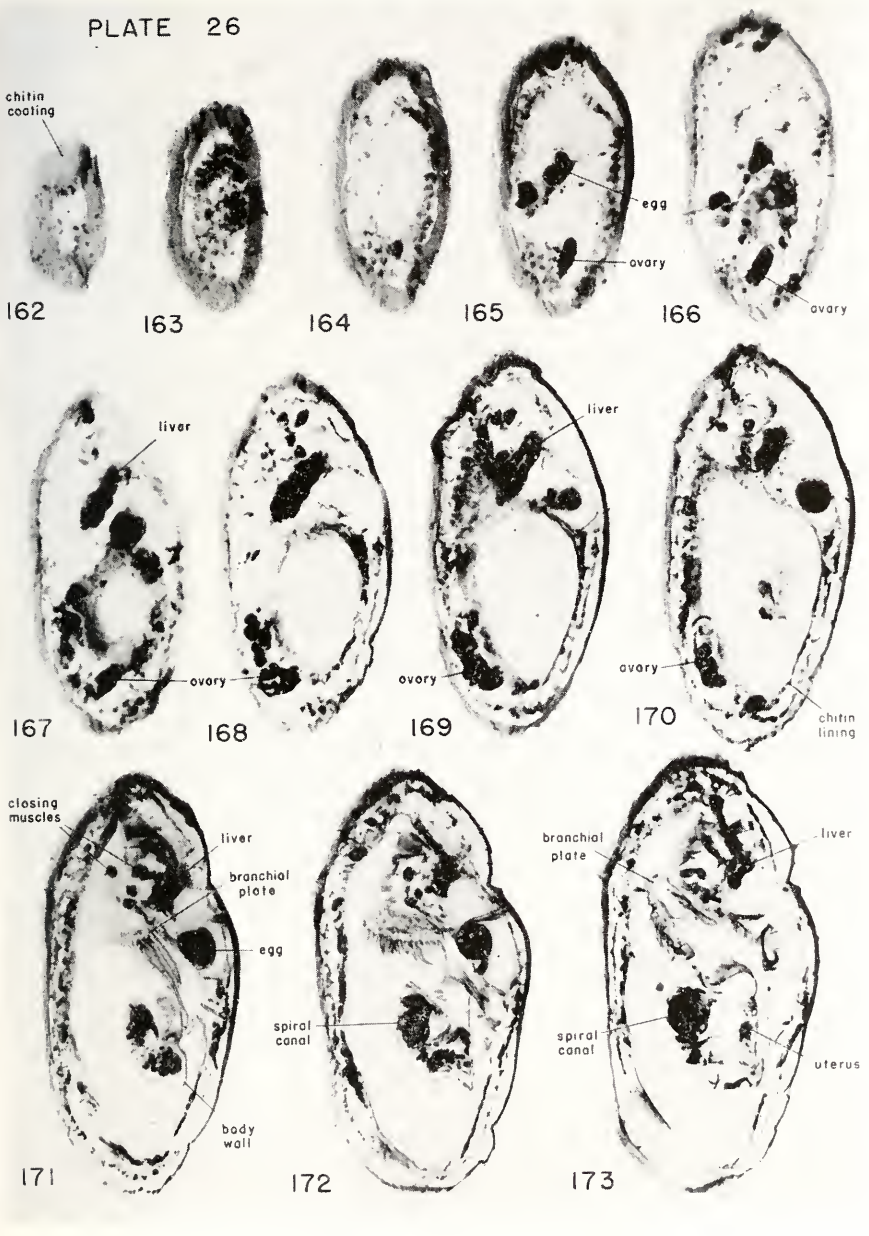
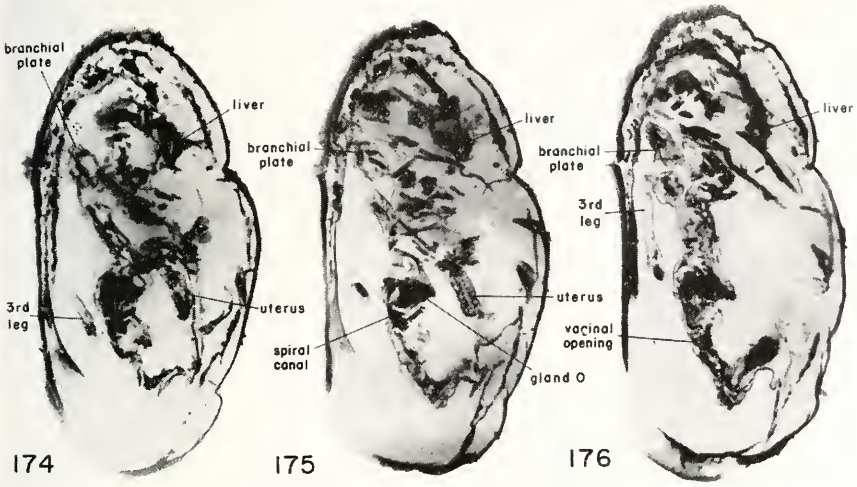


PLATE 26
chitin coating
egg
ovary
ovary
162
163
164
165
166
liver
ovary
liver
ovary
ovary
chitin lining
167
168
169
170
closing muscles
liver
branchial plate
egg
body wall
spiral canal
branchial plate
liver
spiral canal
uterus
171
172
173

Plate 27

Nos. 174-178. Adult, 10μ sagittal sections. These sections follow those shown in Plate 26.

PLATE 27


branchial plate
liver
3rd leg
uterus
174
liver
branchial plate
uterus
spiral canal
gland O
175
liver
branchial plate
3rd leg
vaginal opening
176

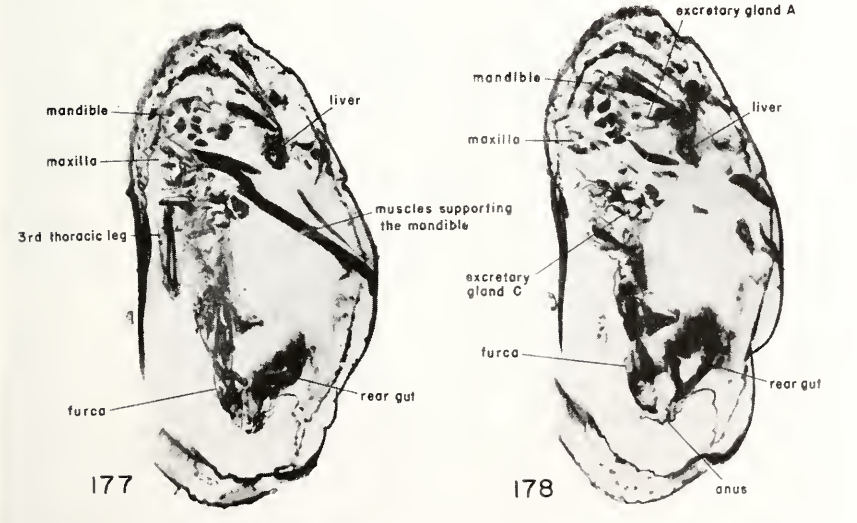

mandible
liver
maxilla
muscles supporting the mandible
3rd thoracic leg
furca
rear gut
177
excretory gland A
mandible
liver
maxilla
excretory gland C
furca
rear gut
anus
178

Plate 28

Nos. 179-182. Adult, 10μ sagittal sections. These sections follow those shown in Plate 27.

PLATE 28

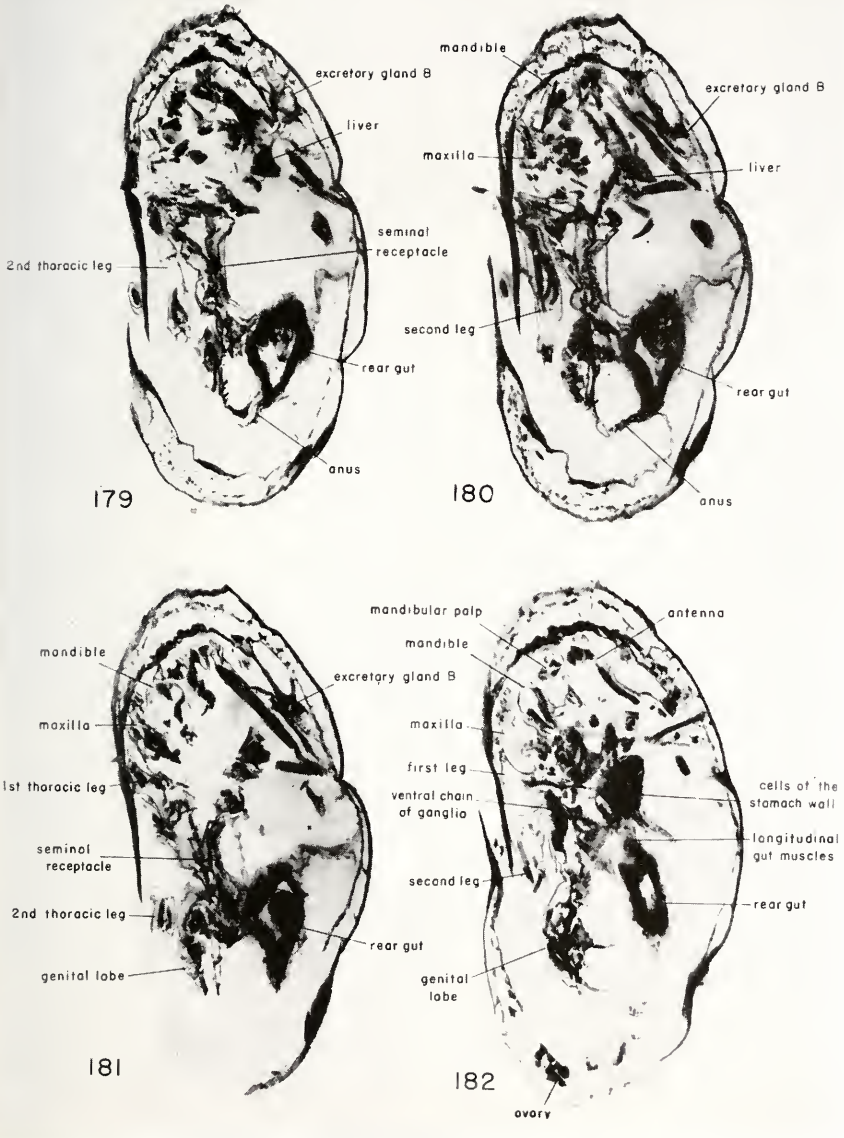

excretory gland B
liver
seminal receptacle
2nd thoracic leg
rear gut
anus
179
mandible
excretory gland B
maxilla
liver
second leg
rear gut
anus
180
mandible
maxilla
1st thoracic leg
seminal receptacle
2nd thoracic leg
genital lobe
excretory gland B
rear gut
181
mandibular palp
antenna
mandible
maxilla
first leg
ventral chain of ganglia
second leg
genital lobe
ovary
cells of the stomach wall
longitudinal gut muscles
rear gut
182

Plate 29

Nos. 183-186. Adult, 10μ sagittal sections. These sections follow those shown in Plate 28.

PLATE 29

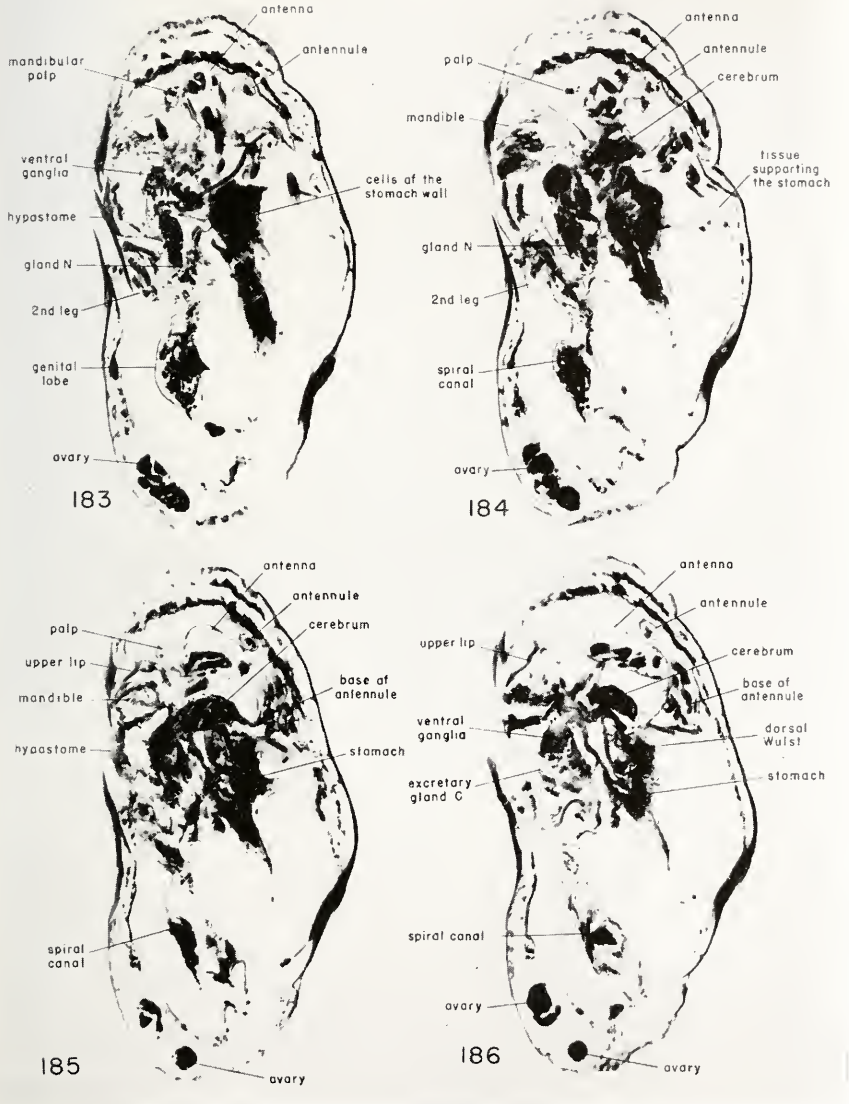

antenna
antennule
mandibular palp
ventral ganglia
cells of the stomach wall
hypostome
gland N
2nd leg
genital lobe
ovary
183
antenna
antennule
palp
cerebrum
mandible
tissue supporting the stomach
gland N
2nd leg
spiral canal
ovary
184
antenna
antennule
palp
cerebrum
upper lip
base of antennule
mandible
hypostome
stomach
spiral canal
ovary
185
antenna
antennule
upper lip
cerebrum
base of antennule
ventral ganglia
dorsal Wulst
excretary gland C
stomach
spiral canal
ovary
186
ovary

Plate 30

Nos. 187-191. Adult, 10μ sagittal sections. These sections follow those shown in Plate 29.

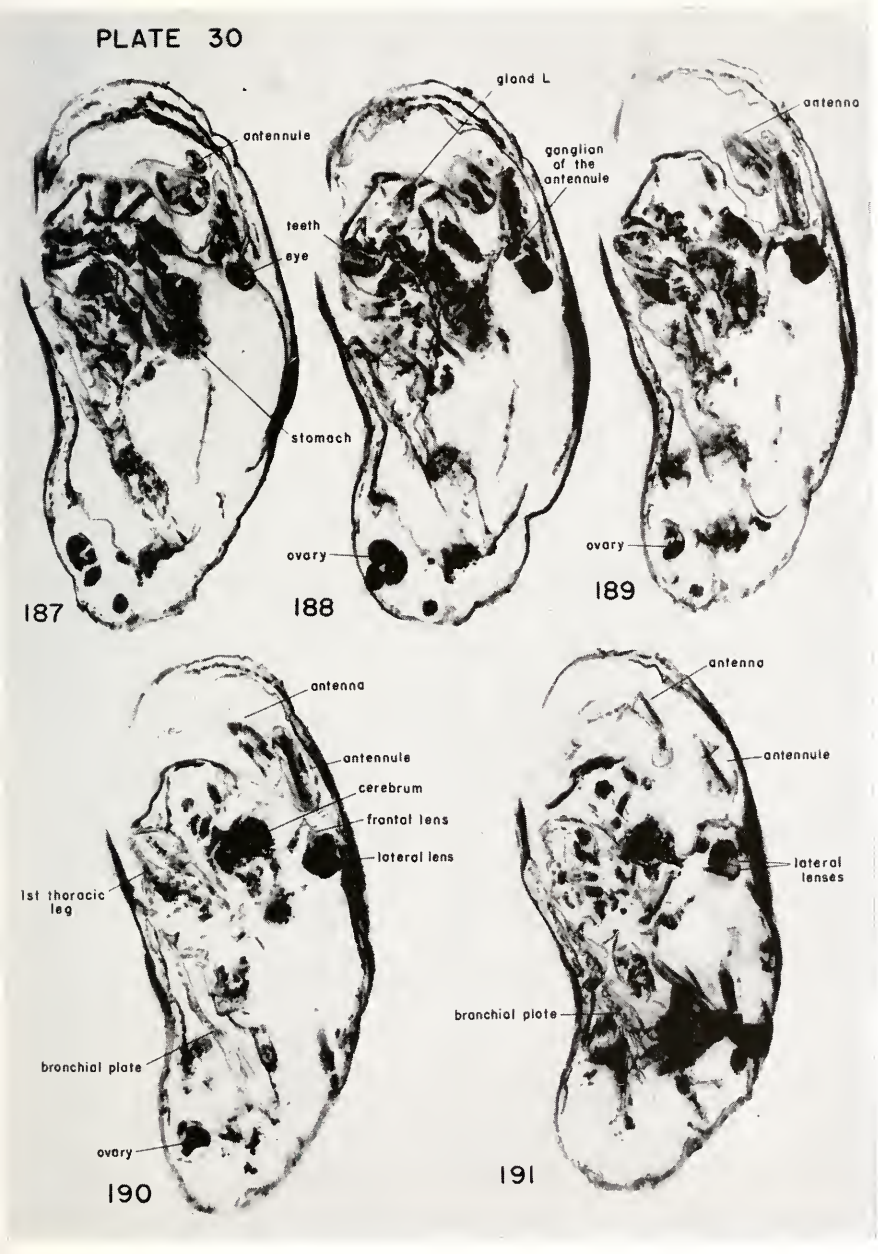


PLATE 30
antennule
teeth
eye
stomach
187
gland L
ganglion of the antennule
ovary
188
antenna
ovary
189
antenna
antennule
cerebrum
frontal lens
lateral lens
1st thoracic leg
bronchial plate
ovary
190
antenna
antennule
lateral lenses
bronchial plate
191

Plate 31

Nos. 192-195. Adult, 10μ sagittal sections. These sections follow those shown in Plate 30, and conclude the sequence of sagittal sections which began in Plate 25.

PLATE 31

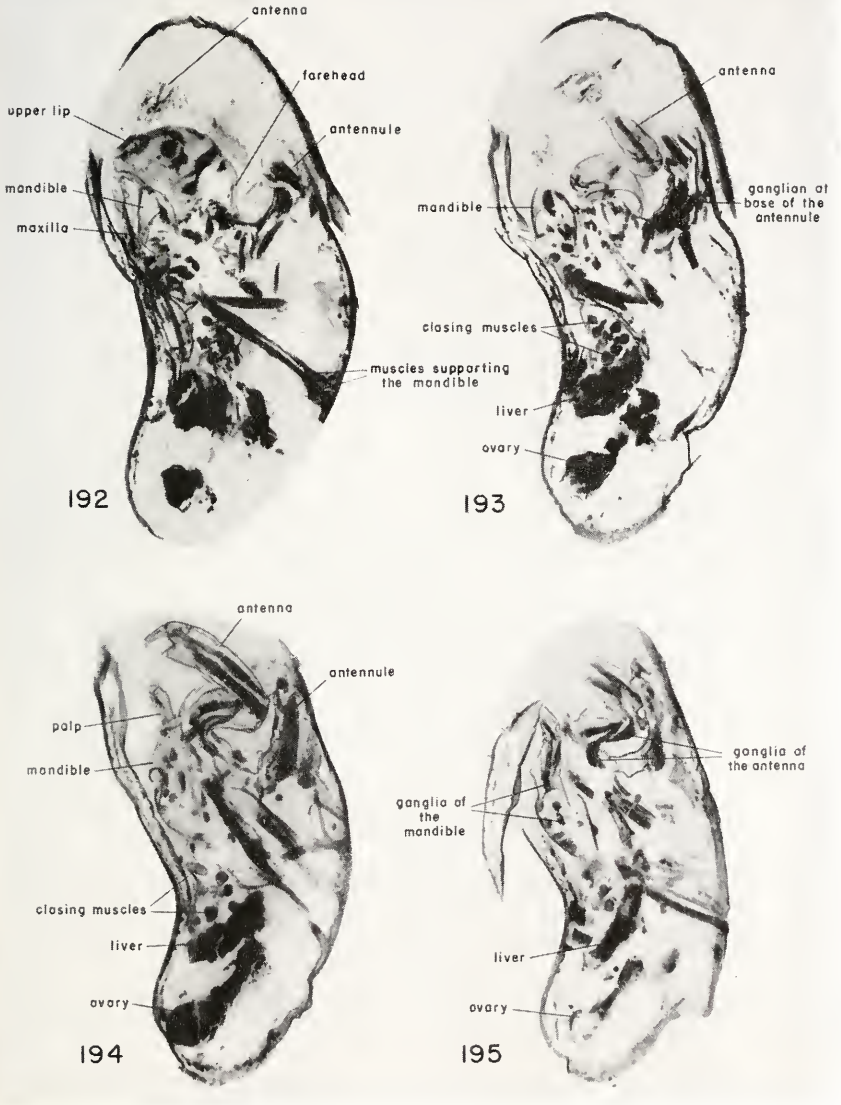

antenna
forehead
upper lip
antennule
mandible
maxilla
muscles supporting the mandible
192
antenna
ganglion at base of the antennule
mandible
closing muscles
liver
ovary
193
antenna
antennule
palp
mandible
closing muscles
liver
ovary
194
ganglia of the antenna
ganglia of the mandible
liver
ovary
195

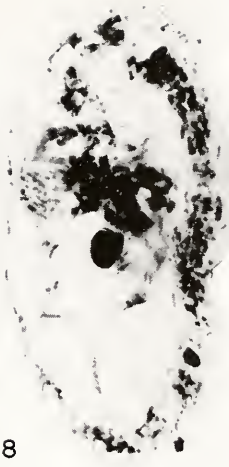
Plate 32

Nos. 196-200. Adult, 20μ sagittal sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from the right side to the left.

PLATE 32

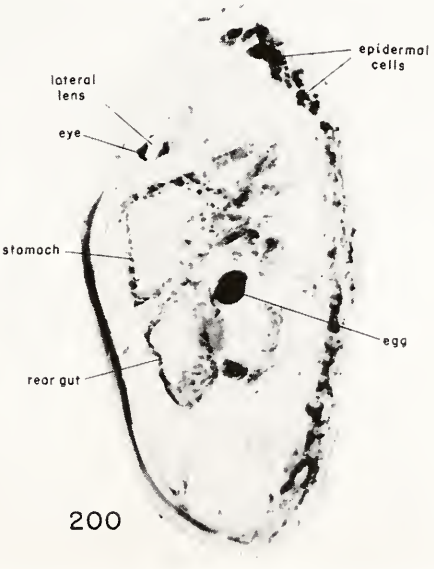
196

197



198

199



200

Plate 33

Nos. 201-204. Adult, 20μ sagittal sections. These sections follow those shown in Plate 32.

PLATE 33

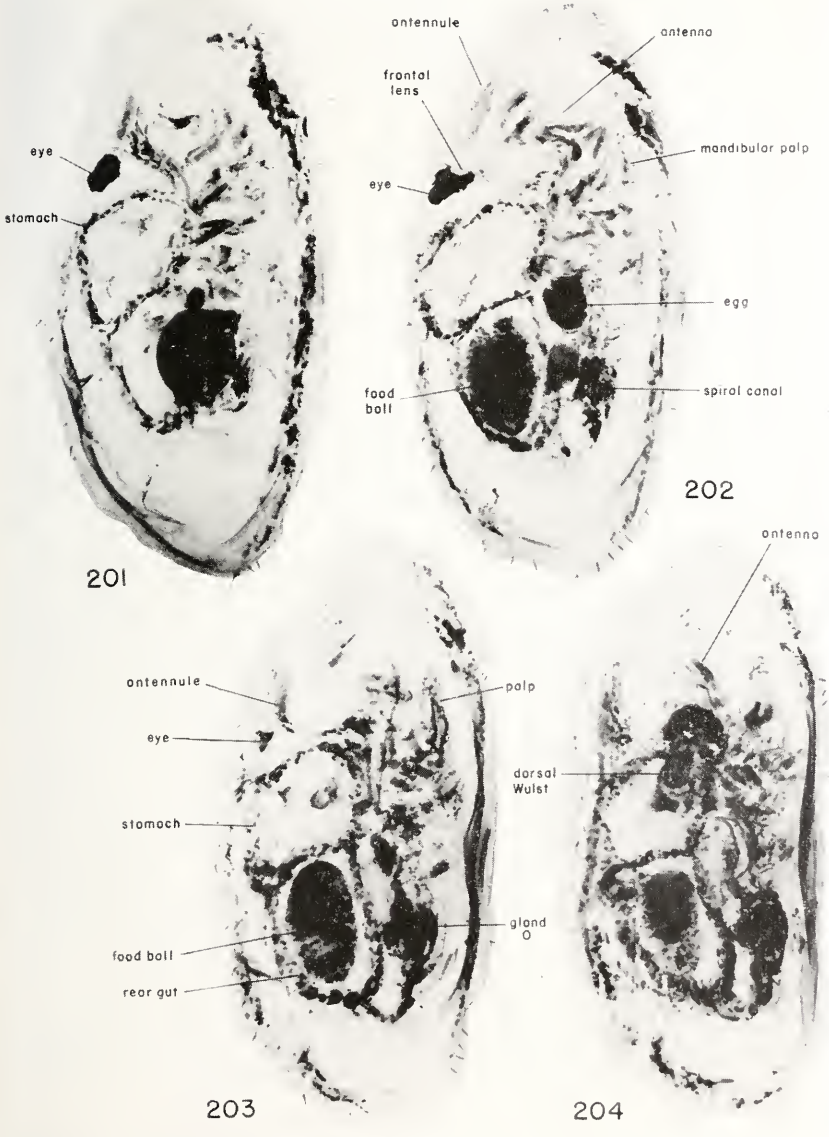

eye
stomach
201
ontennule
frontal lens
eye
antenna
mandibular palp
egg
food ball
spiral canal
202
ontennule
eye
stomach
food ball
reor gut
palp
gland O
203
ontenna
dorsal Wulst
204

Plate 34

Nos. 205-208. Adult, 20μ sagittal sections. These sections follow those shown in Plate 33.

PLATE 34

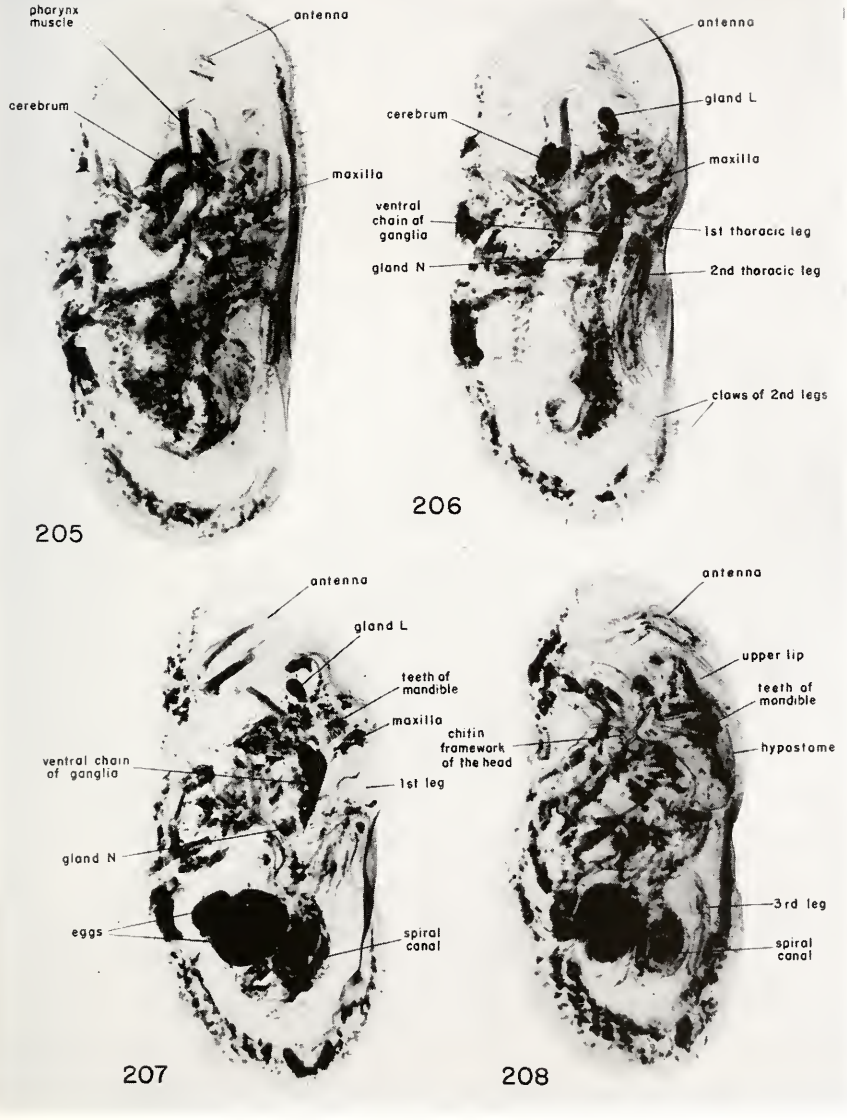
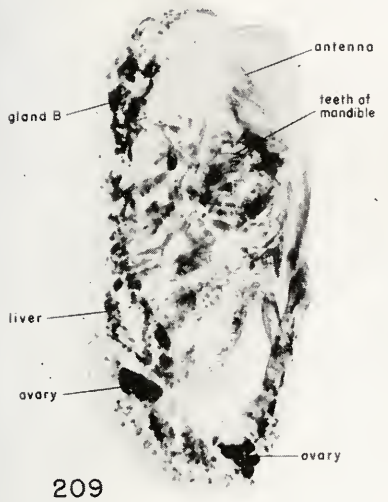

pharynx muscle
antenna
cerebrum
maxilla
205
antenna
gland L
cerebrum
maxilla
ventral chain of ganglia
1st thoracic leg
gland N
2nd thoracic leg
claws of 2nd legs
206
antenna
gland L
teeth of mandible
maxilla
ventral chain of ganglia
1st leg
gland N
eggs
spiral canal
207
antenna
upper lip
teeth of mandible
chitin framework of the head
hypostome
3rd leg
spiral canal
208

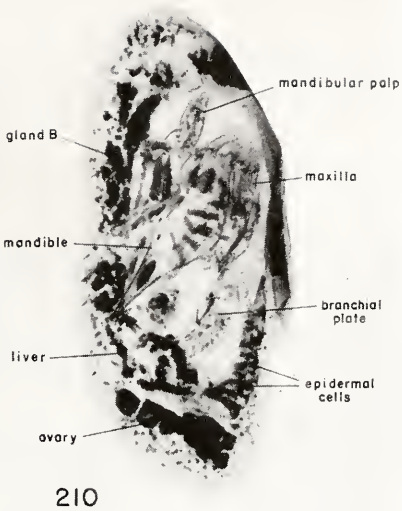
Plate 35

Nos. 209-213. Adult, 20μ sagittal sections. These sections follow those shown in Plate 34, and conclude the sequence of sagittal sections which began in Plate 32.

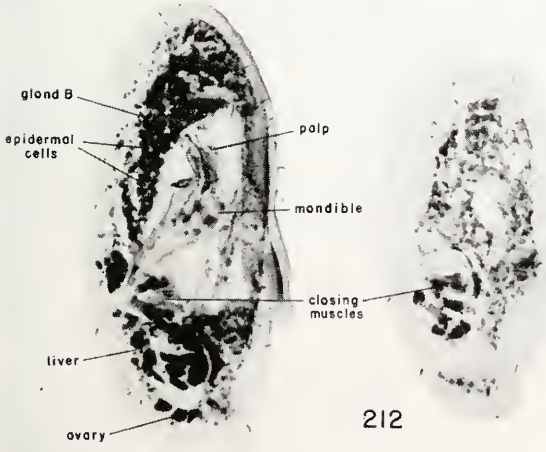
PLATE 35



209



210



211

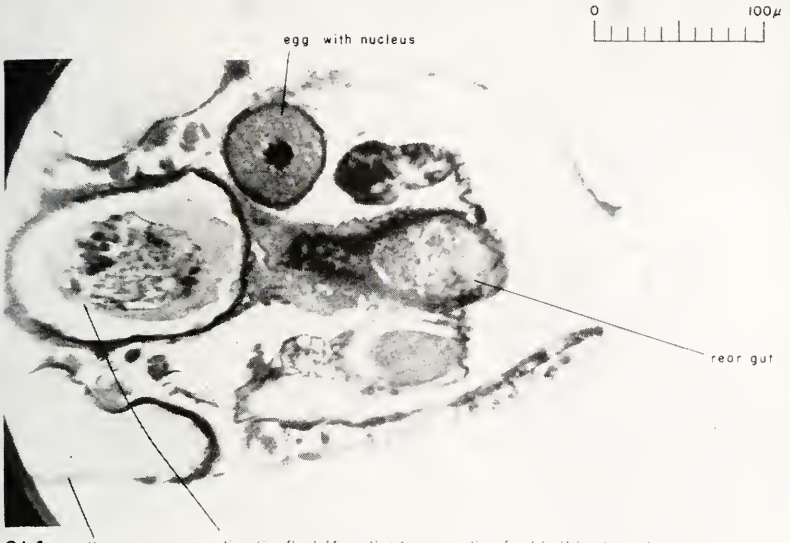
212

213

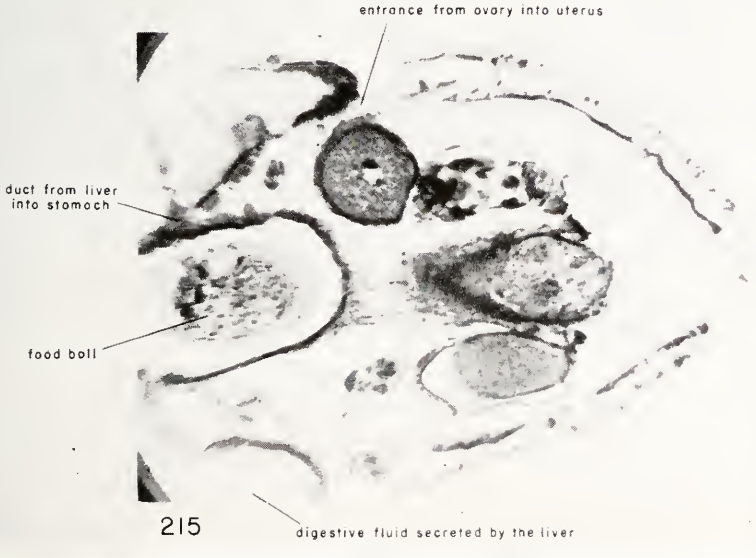
Plate 36

Nos. 214-215. Adult, 10μ frontal sections, stained with Ehrlich's haematoxylin and eosin. These sections progress from dorsal to ventral.

PLATE 36



214

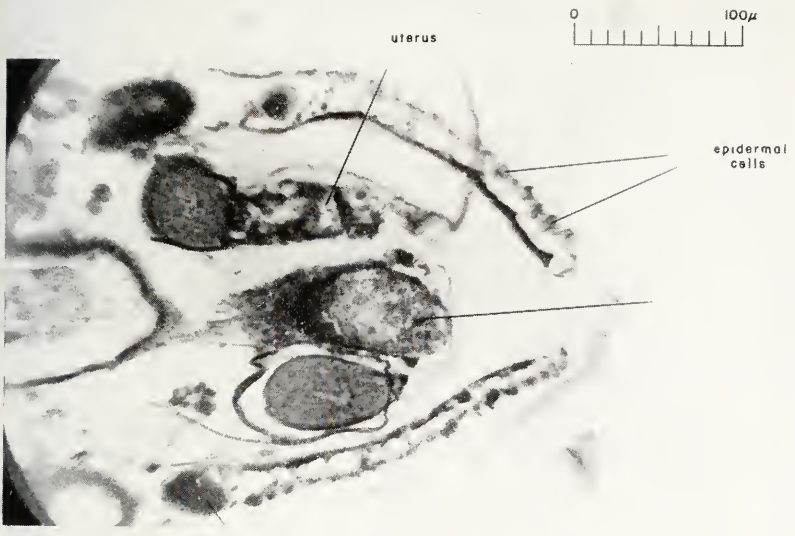


215

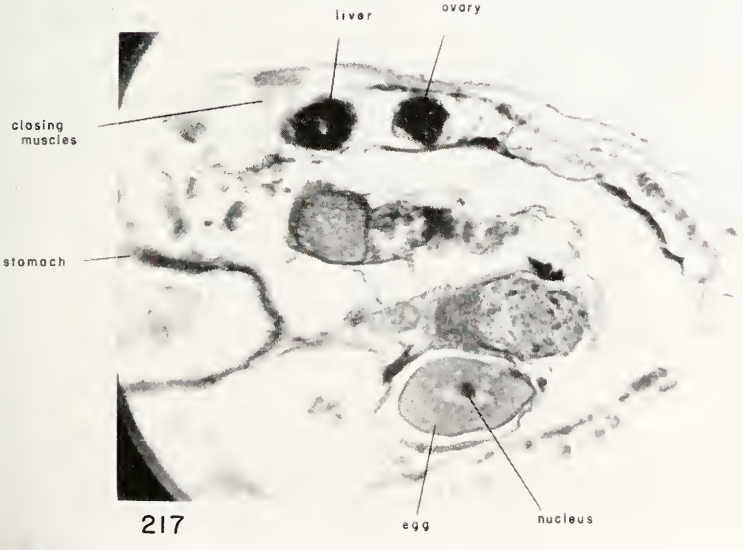
Plate 37

Nos. 216-217. Adult, 10μ frontal sections. These sections follow those shown in Plate 36.

PLATE 37



216

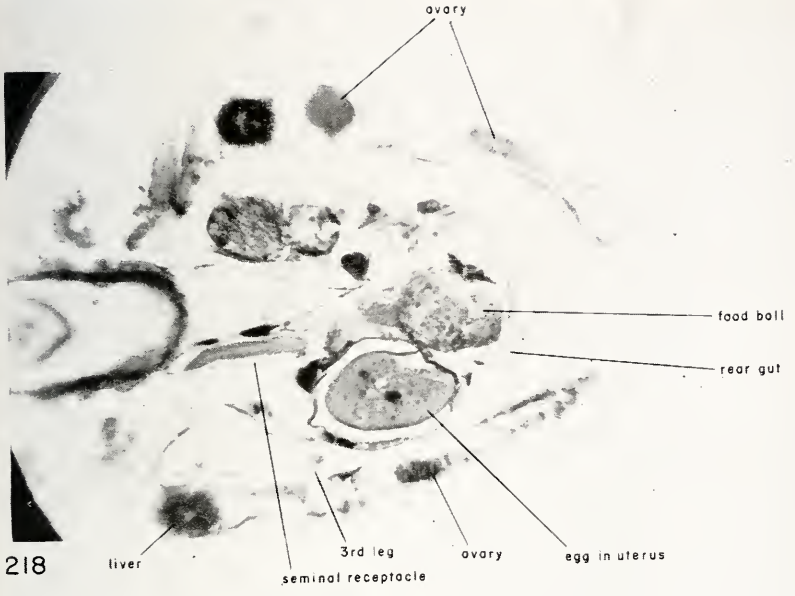


217

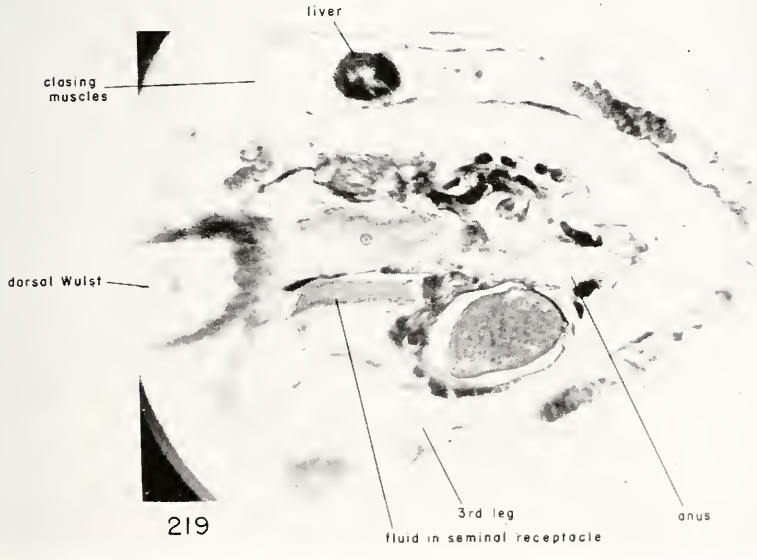
Plate 38

Nos. 218-219. Adult, 10μ frontal sections. These sections follow those shown in Plate 37.

PLATE 38



218

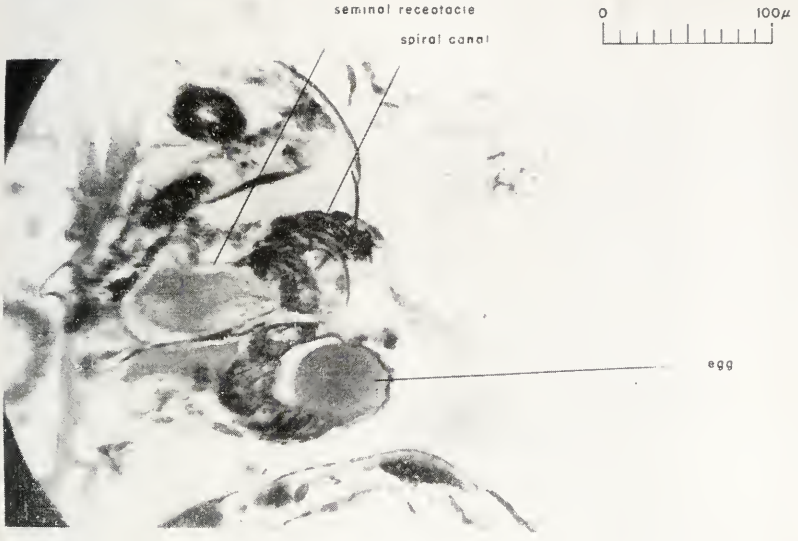


219

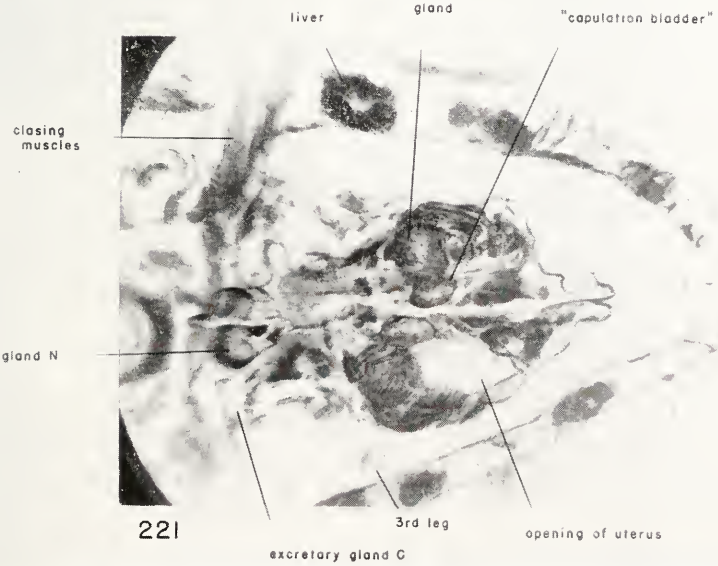
Plate 39

Nos. 220-221. Adult, 10μ frontal sections. These sections follow those shown in Plate 38.

PLATE 39



220



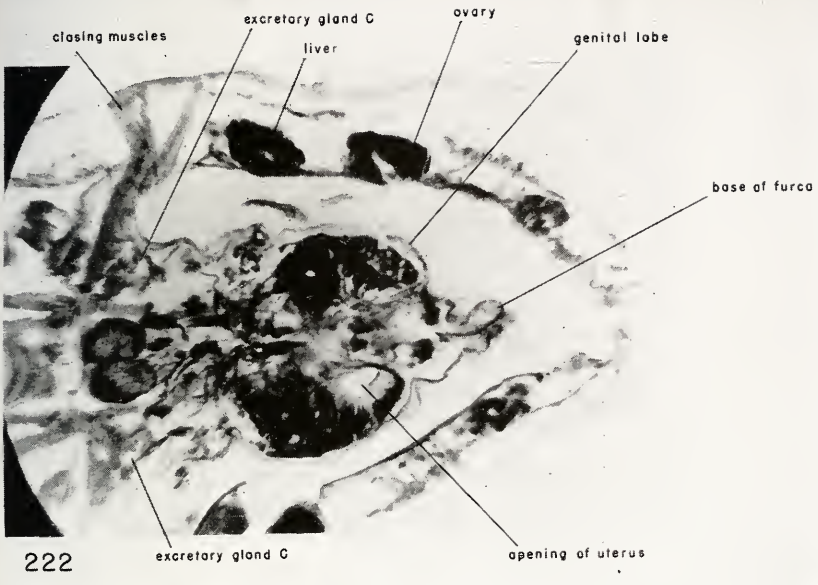
221

Plate 40

No. 222. Adult, 10μ frontal section. This concludes the sequence of frontal sections which began in Plate 36.

No. 223. Adult, 10μ transverse sections. The dorsal end of the section is at left. The following sections progress from anterior to posterior.

PLATE 40


closing muscles
excretory gland C
liver
ovary
genital lobe
base of furca
222
excretory gland C
opening of uterus

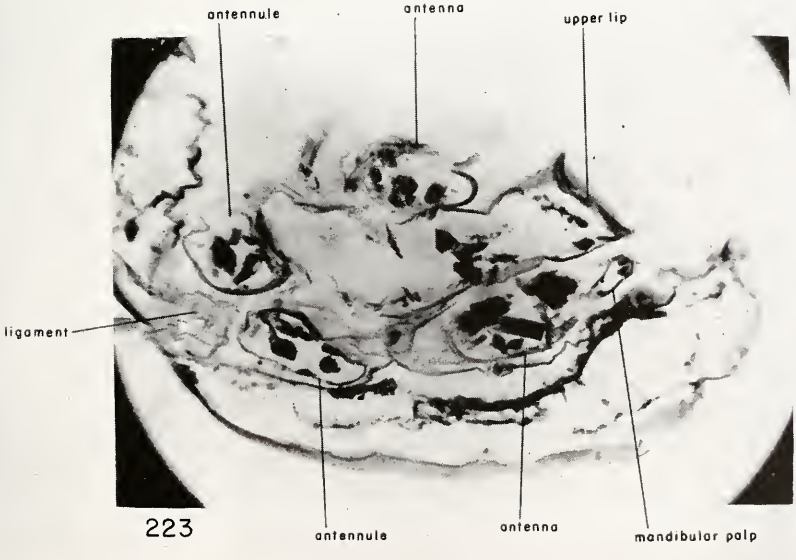
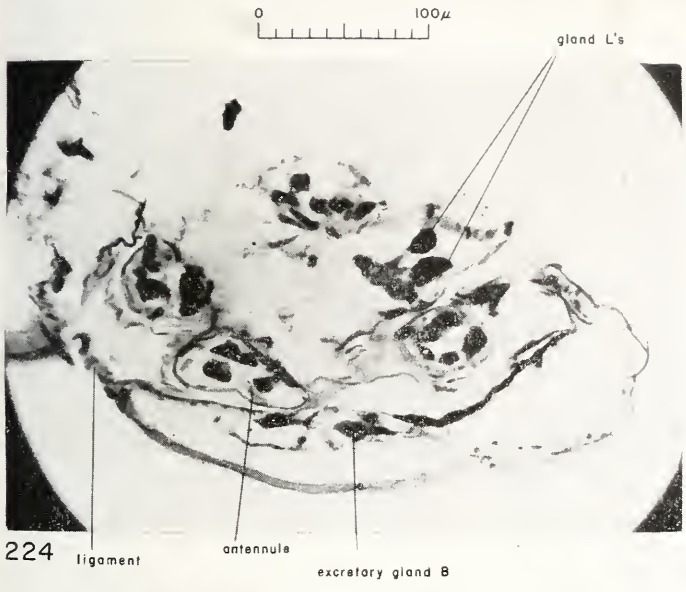

antennule
antenna
upper lip
ligament
223
antennule
antenna
mandibular palp

Plate 41

Nos. 224-225. Adult, 10μ transverse sections. These sections follow that shown in No. 223.

PLATE 41


0
100μ
gland L's
224
ligament
antennule
excretory gland B

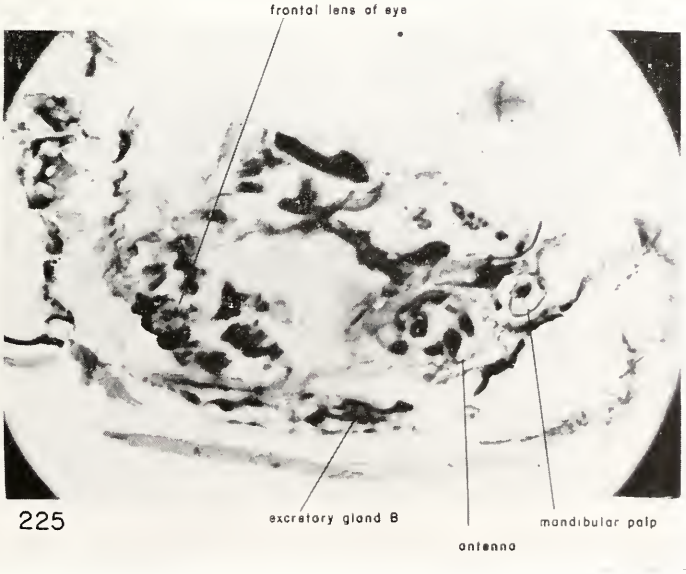
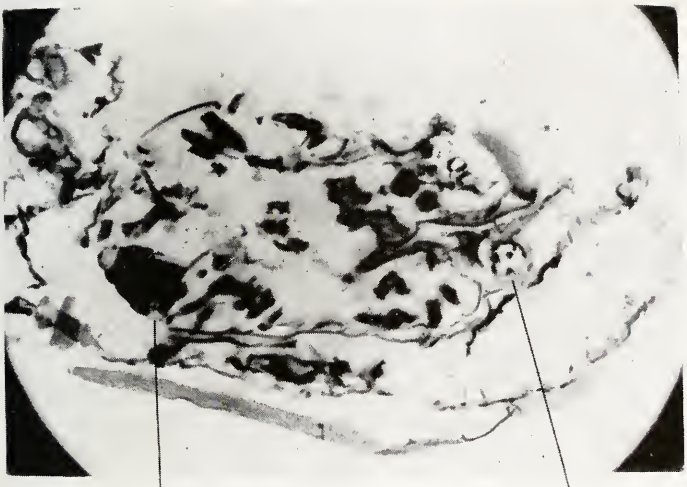

frontal lens of eye
225
excretory gland B
antenna
mandibular palp

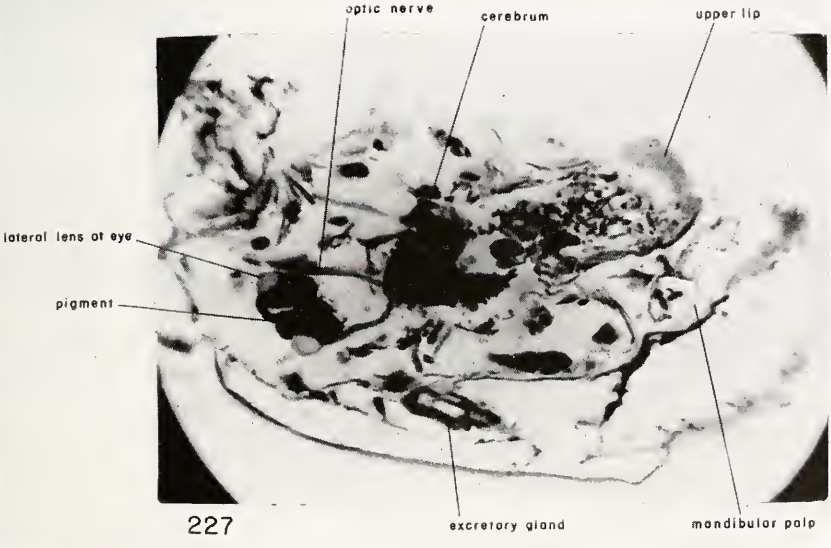
Plate 42

Nos. 226-227. Adult, 10μ transverse sections. These sections follow those shown in Plate 41.

PLATE 42



226

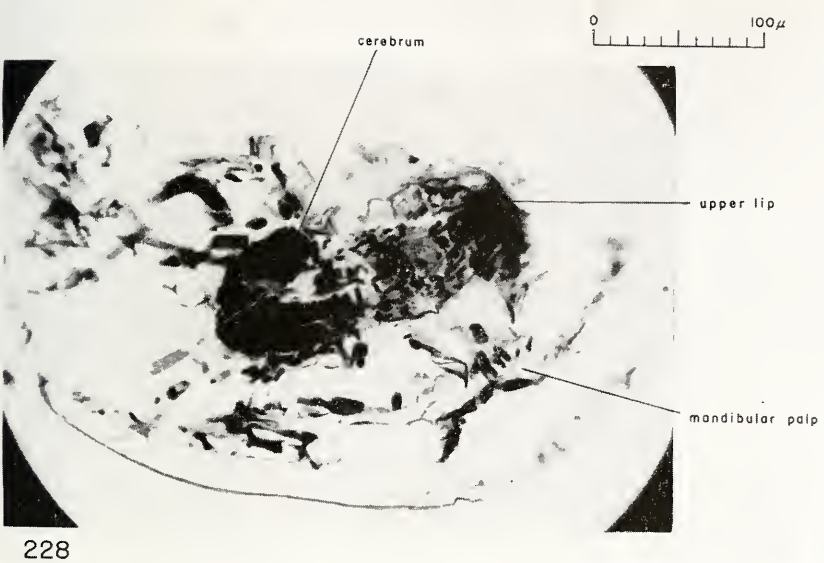


227

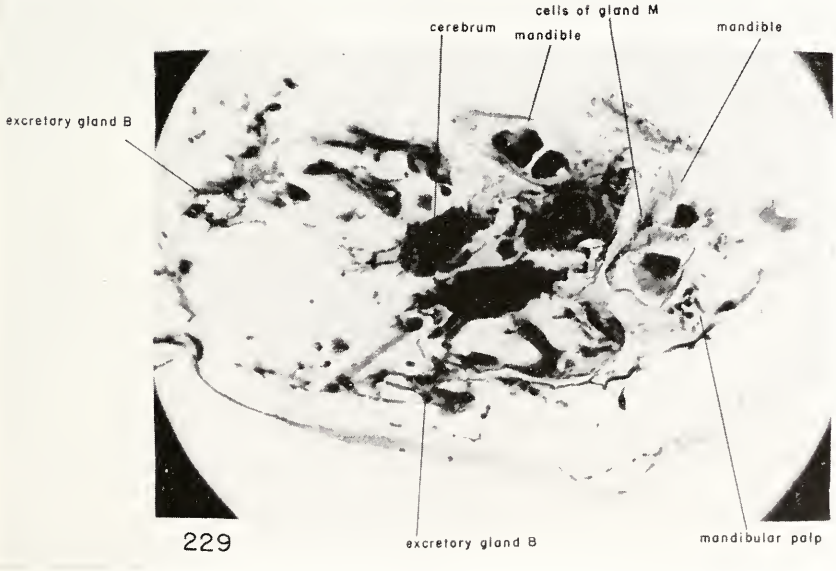
Plate 43

Nos. 228-229. Adult, 10μ transverse sections. These sections follow those shown in Plate 42.

PLATE 43



228

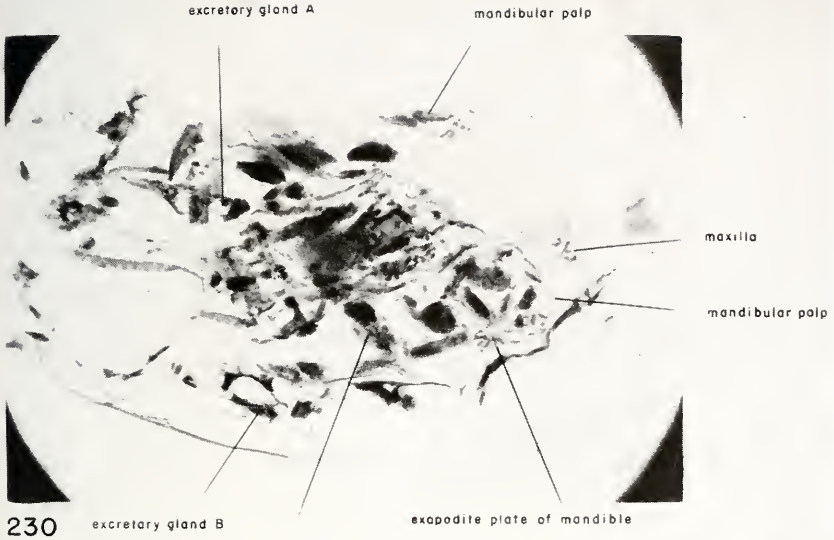


229

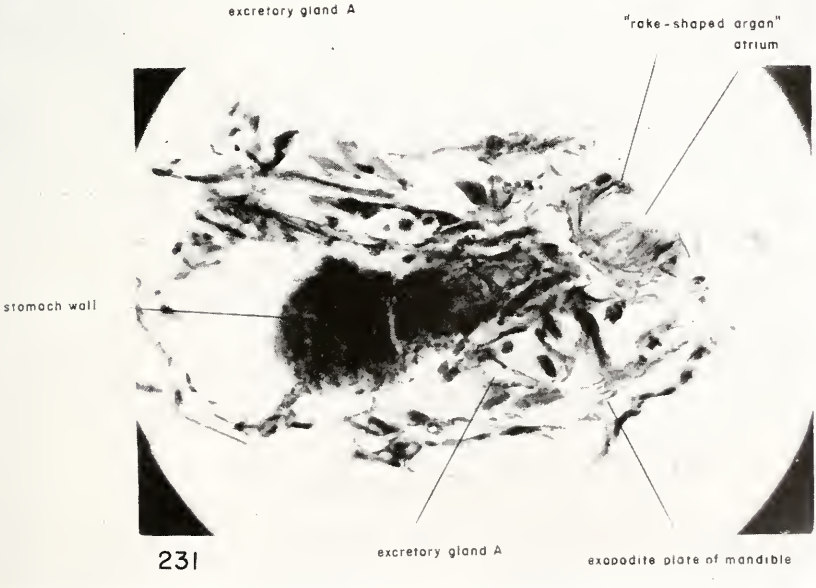
Plate 44

Nos. 230-231. Adult, 10μ transverse sections. These sections follow those shown in Plate 43.

PLATE 44



230

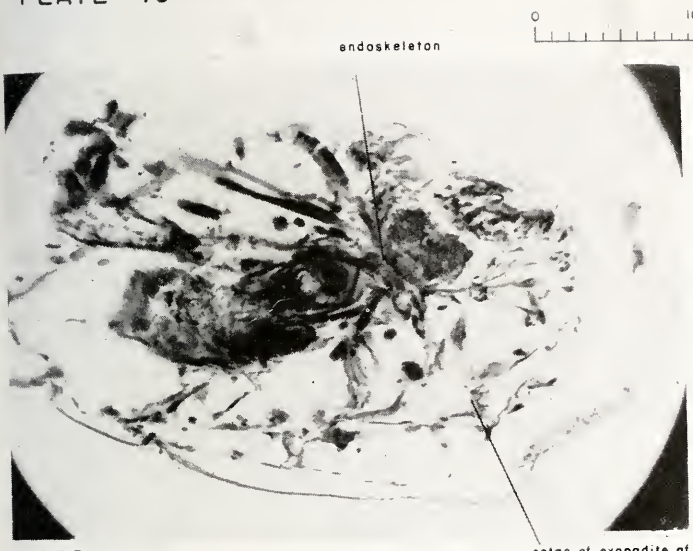


231

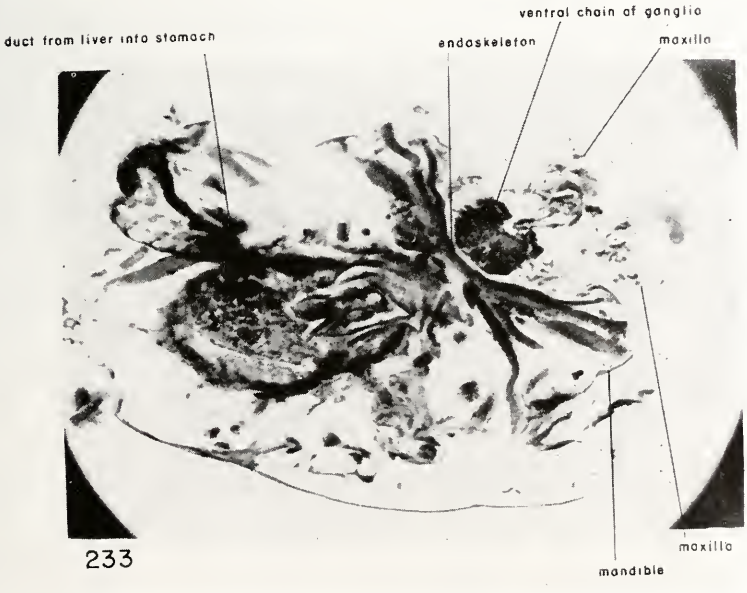
Plate 45

Nos. 232-233. Adult, 10μ transverse sections. These sections follow those shown in Plate 44.

PLATE 45



232

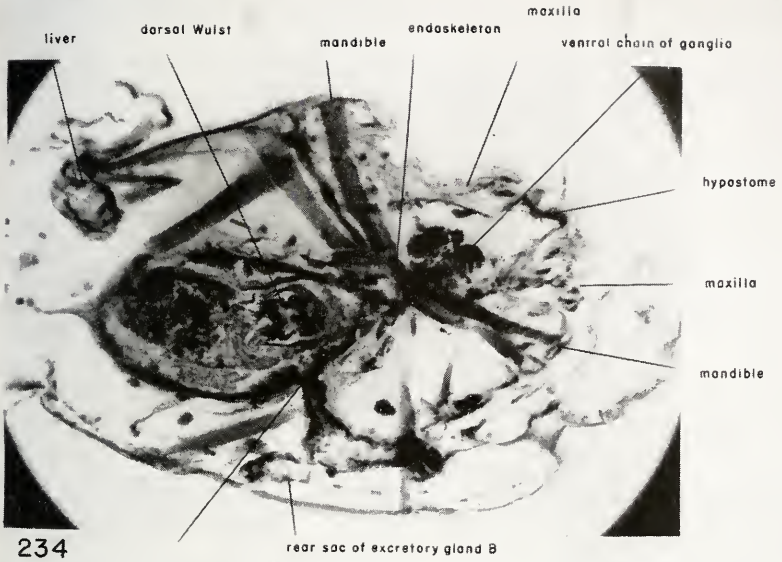


233

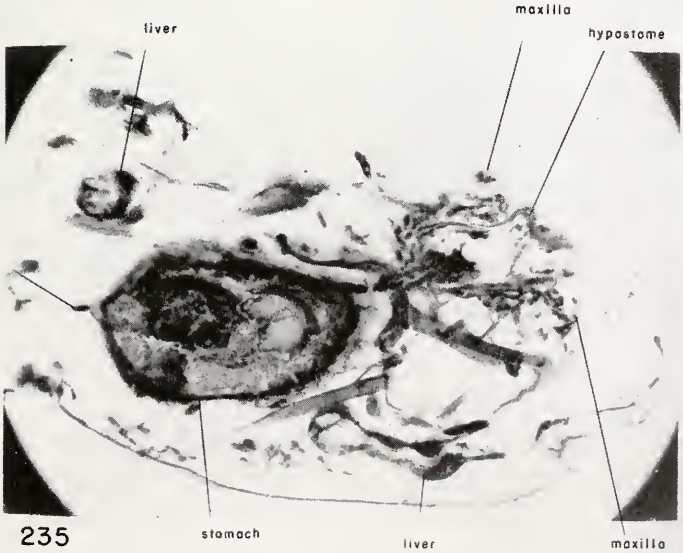
Plate 46

Nos. 234-235. Adult, 10μ transverse sections. These sections follow those shown in Plate 45, and conclude the sequence of transverse sections which began in Plate 40, No. 223.

PLATE 46



234

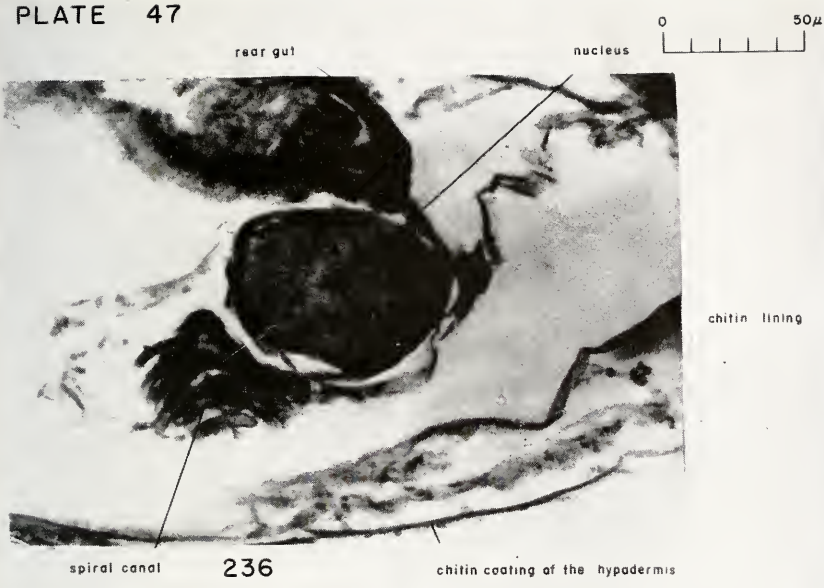


235

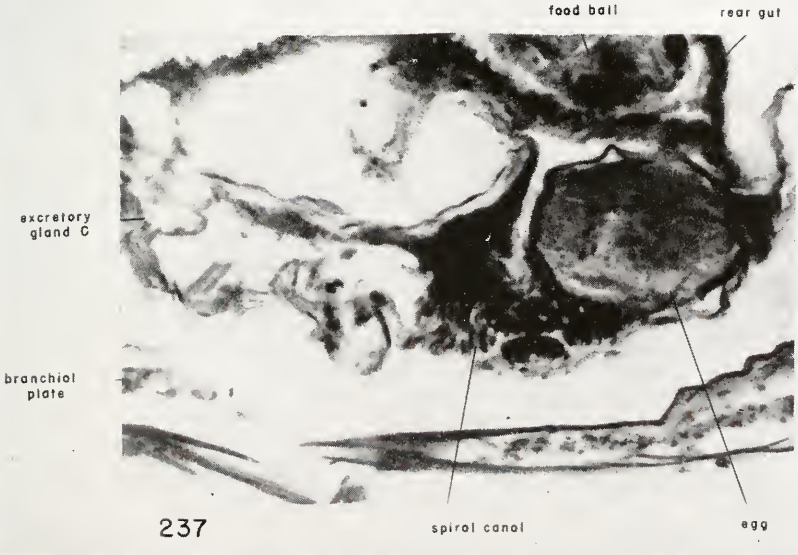
Plate 47

Nos. 236-237. Adult, 10μ sagittal sections through the genital region. The sections progress from left to right.

PLATE 47



236



237

Plate 48

Nos. 238-239. Adult, 10μ sagittal sections. These sections follow those shown in Plate 47.

PLATE 48

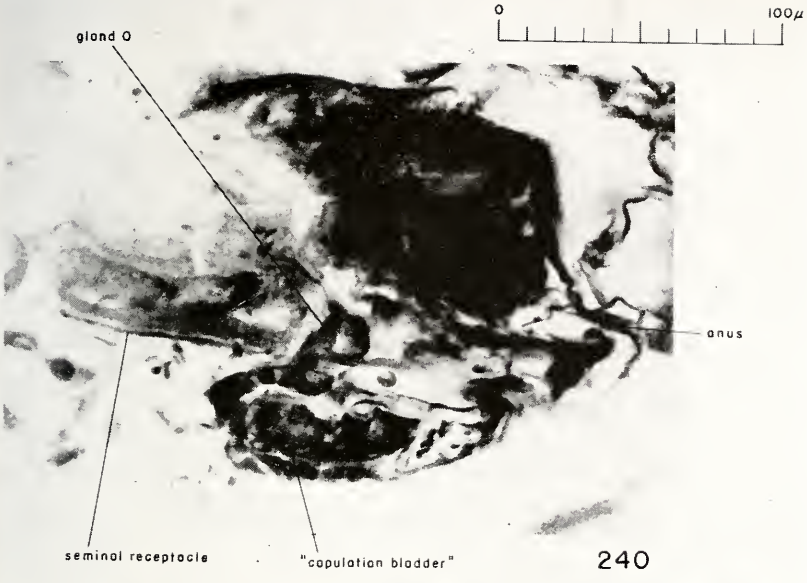
238

239

Plate 49

Nos. 240-241. Adult, 10μ sagittal sections. These sections follow those shown in Plate 48.

PLATE 49



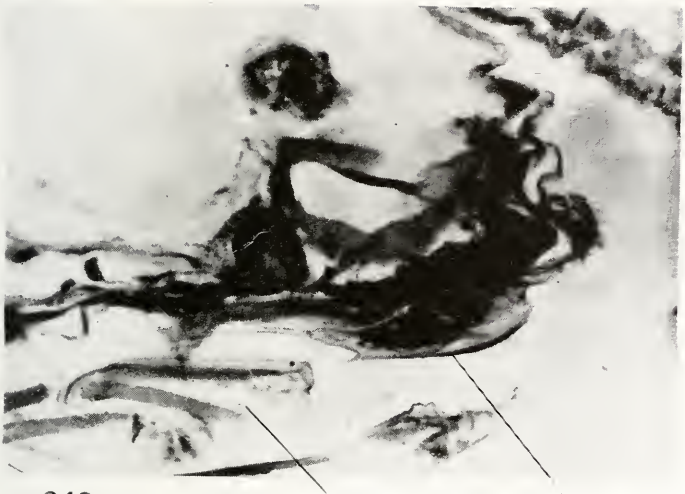
240

241

Plate 50

Nos. 242-243. Adult, 10μ sagittal sections. These sections follow those shown in Plate 49.

PLATE 50


242
2nd thoracic leg
furca

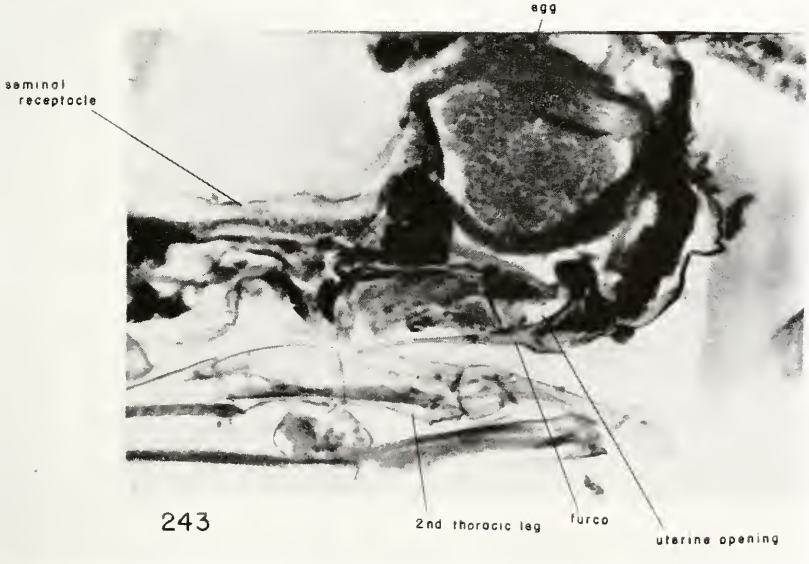
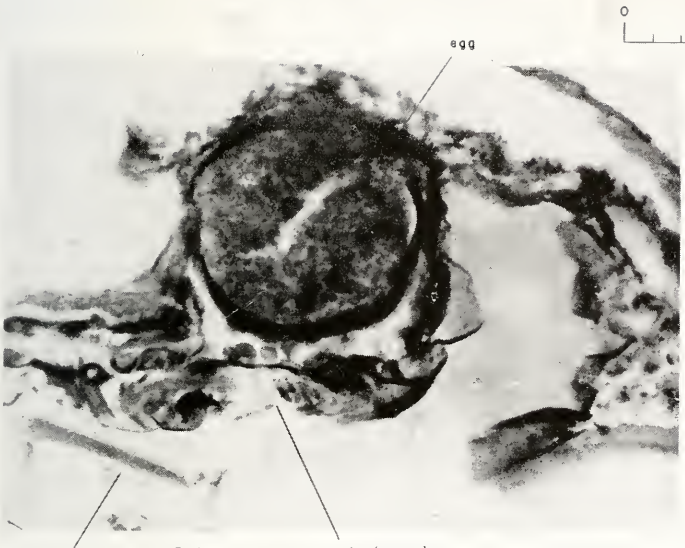

egg
seminal receptacle
243
2nd thoracic leg
furca
uterine opening

Plate 51

Nos. 244-245. Adult, 10μ sagittal sections. These sections follow those shown in Plate 50.

PLATE 51

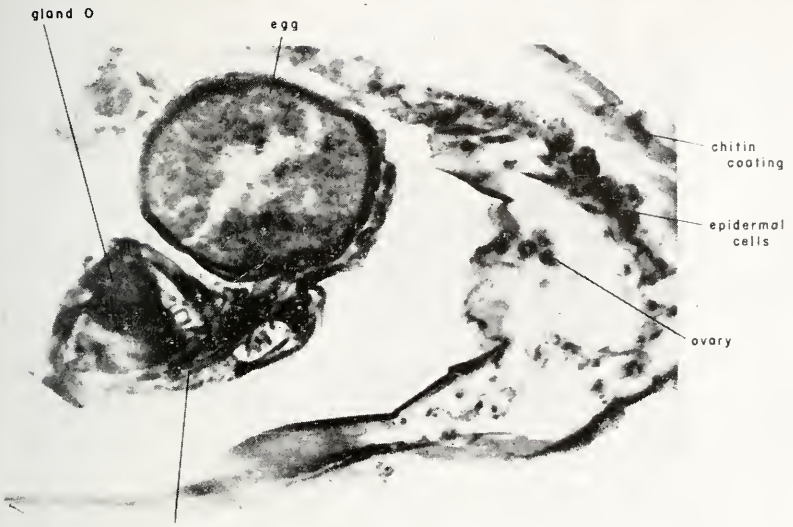

0
50μ
egg
2nd leg
244
vaginal opening


nucleus
gland O
"copulation bladder"
chitin "stick"
genital lobe
245

Plate 52

Nos. 246-247. Adult, 10μ sagittal sections. These sections follow those shown in Plate 51.

PLATE 52



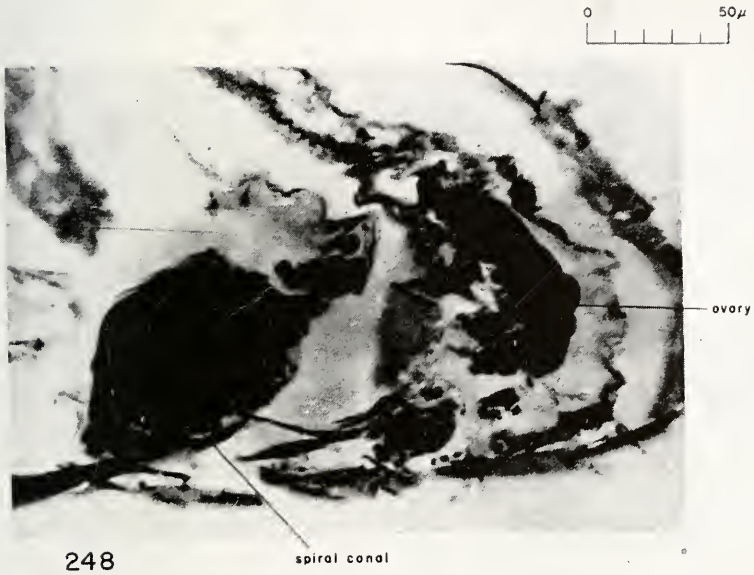
246

247

Plate 53

No. 248. Adult, 10μ sagittal section. This section follows those shown in Plate 52, and concludes the sequence of sagittal sections which began in Plate 47.
No. 249. Adult, 20μ sagittal section through the soft parts of the valve.

PLATE 53



248

249

Plate 54

No. 250. Adult, needle dissection. The antennules as seen from below. The eye is also seen in position.

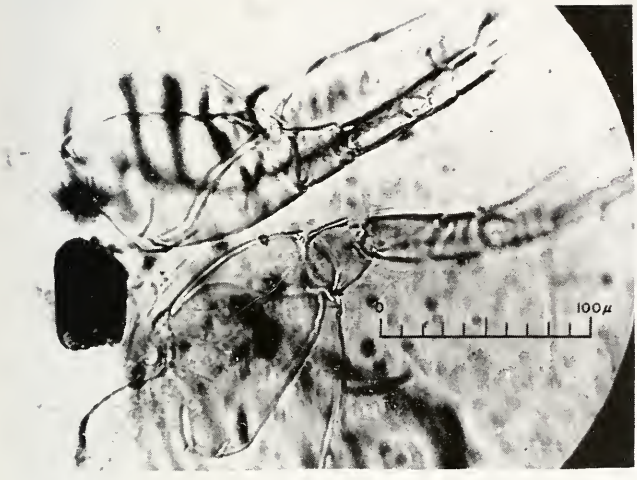
No. 251. Inner face of the left antennule.

No. 252. Terminal podomeres of the right antennule. The bases of some of the natatory setae are shown.

No. 253. A distal portion of the right antennule.

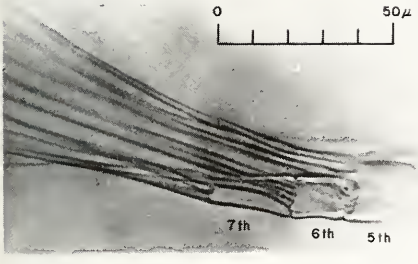
No. 254. The second and third podomeres of the antennule.

PLATE 54

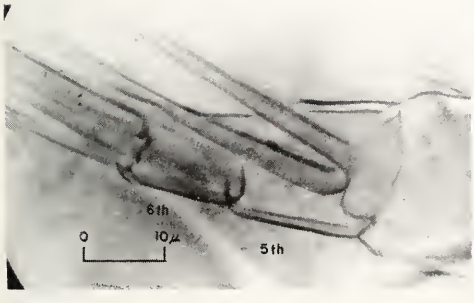


250

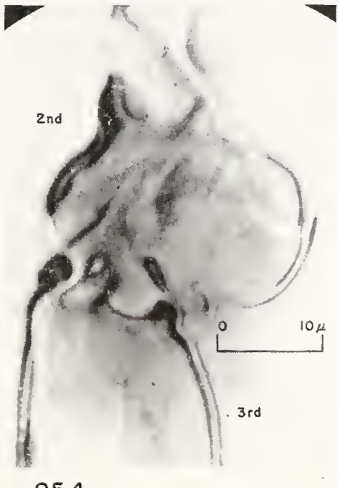
251



252



253



254

Plate 55

No. 255. Adult, needle dissection. Inner face of the left antennule showing the attachment to the forehead.

No. 256. Portion of the proximal podomere of the left antennule.

No. 257. Distal end of the left antennule.

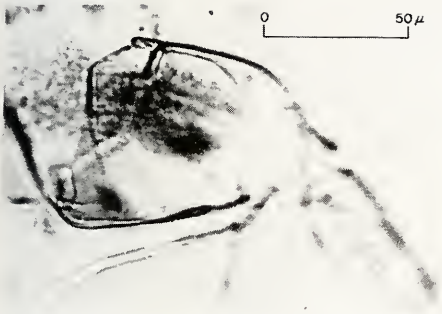
No. 258. Basal podomere of the right antenna. Anterior is at the top, ventral at the left of the photograph.

No. 259. Inner face of the left antenna.

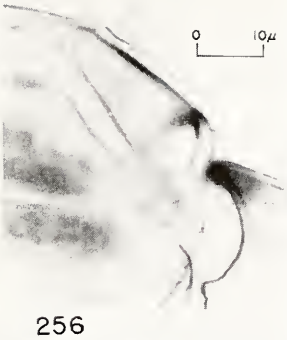
No. 260. First podomere of the endopodite of the left antenna, showing the "sense organ" and the natatory setae.

No. 261. Distal end of the left antenna, showing the attachment of the terminal claws.

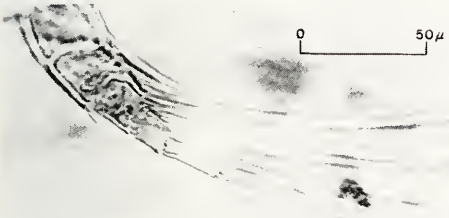
PLATE 55



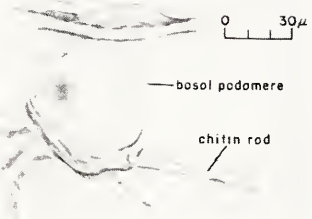
255



256

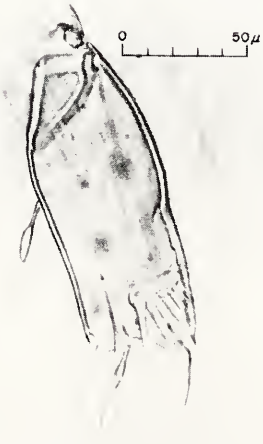


257



258

259



260

261

Plate 56

No. 262. Inner faces of the left antenna and mandible, showing their respective positions.

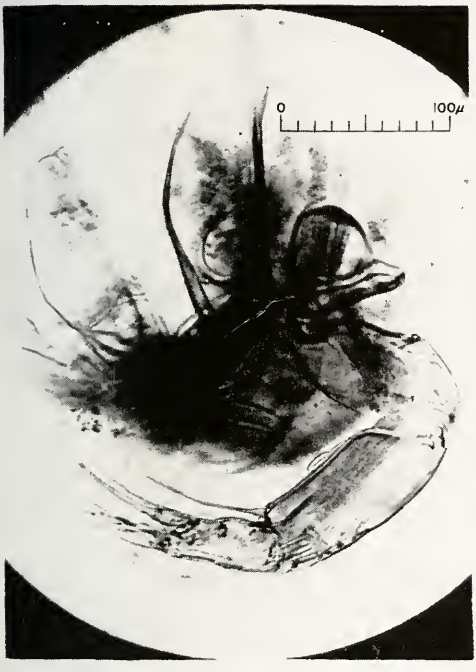
No. 263. Terminal claws of the antenna.

No. 264. Endopodite plate of the mandible.

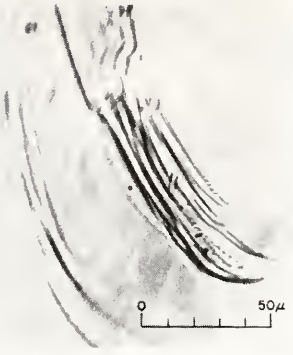
No. 265. Antennae.

No. 266. Branchial plate of the right maxilla.

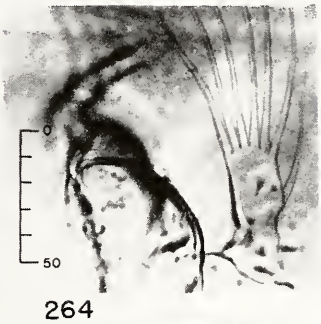
PLATE 56



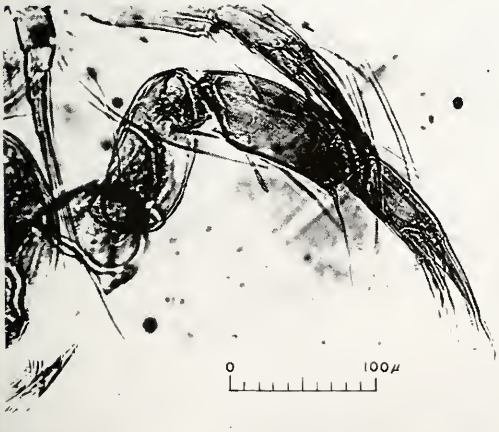
262



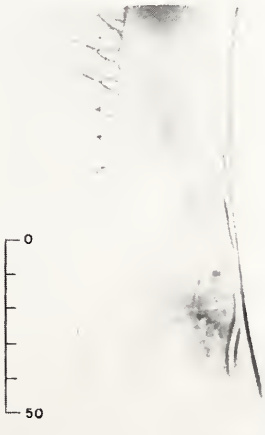
263



264



265

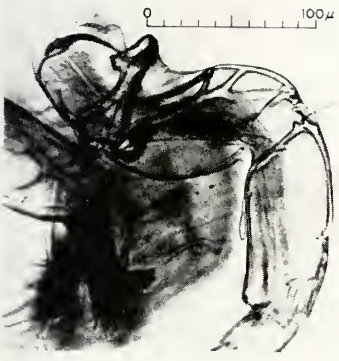


266

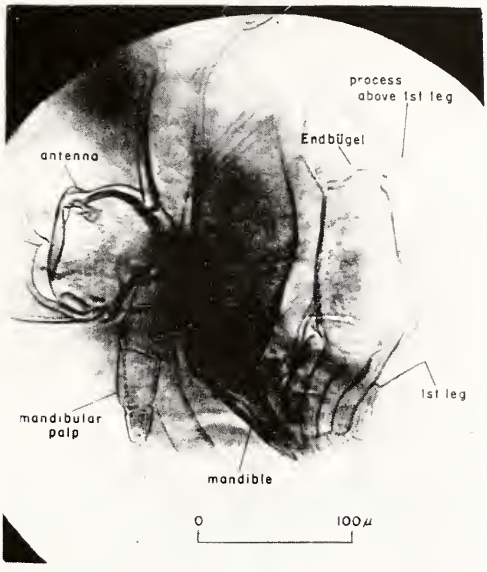
Plate 57

No. 267. Inner face of the left antenna.
No. 268. Anterior portion of the body in needle dissection.
No. 269. Distal teeth of the mandible.
No. 270. Anterior portion of the body as seen from below.

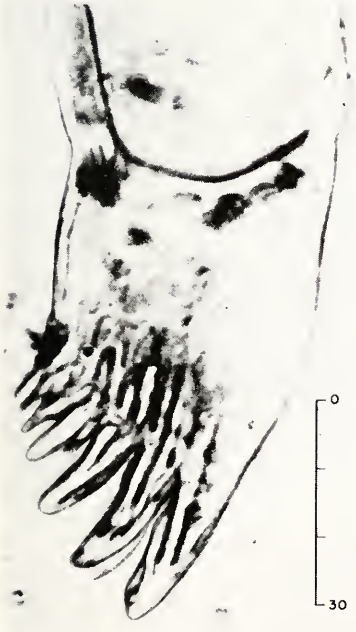
PLATE 57



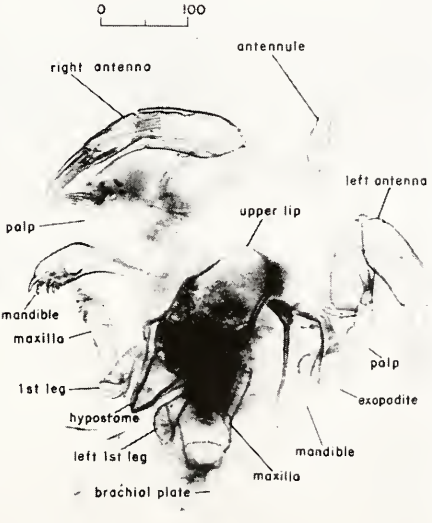
267



268



269



270

Plate 58

No. 271. Inner face of the left mandible.

PLATE 58


100μ
50
0
claws
palp (endapodite)
exopodite plate
setae of exopodite
teeth
base
muscle scars

271

Plate 59

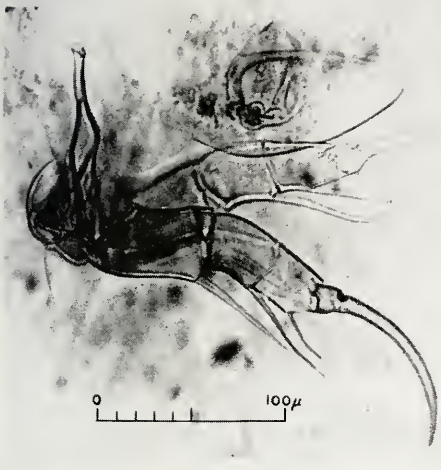
No. 272. Second thoracic legs and genital lobes.

No. 273. Terminal claw of second thoracic leg.

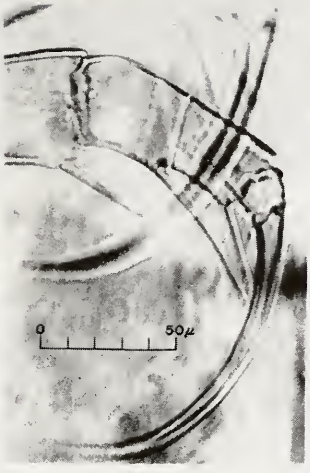
No. 274. Mandible, maxilla, and first thoracic leg in position.

No. 275. First thoracic leg. Anterior is at the top, and ventral at the right of the photograph.

PLATE 59

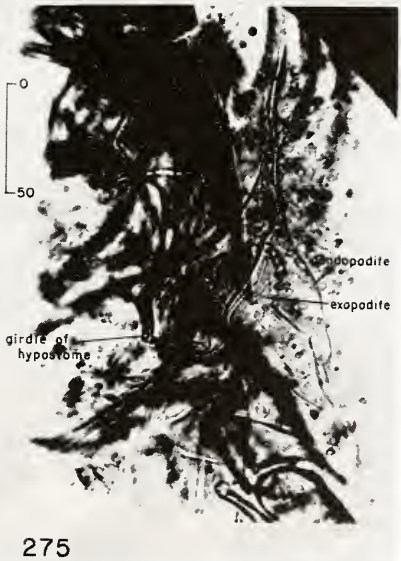


272



273

274



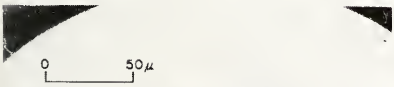
275

Plate 60

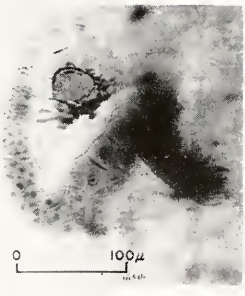
No. 276. Outer face of right mandible, maxilla, and first thoracic leg.
No. 277. Third thoracic leg.
No. 278. Ovary.
No. 279. Genital lobes as seen from below.
No. 280. Mandibular teeth.

PLATE 60

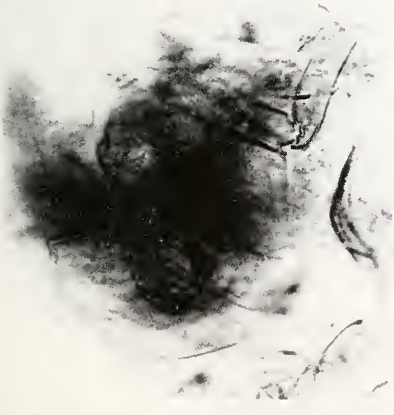
276



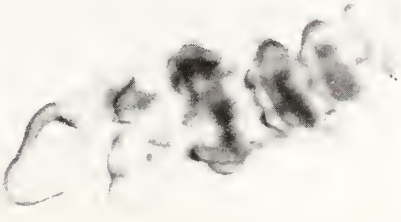
277



278



279

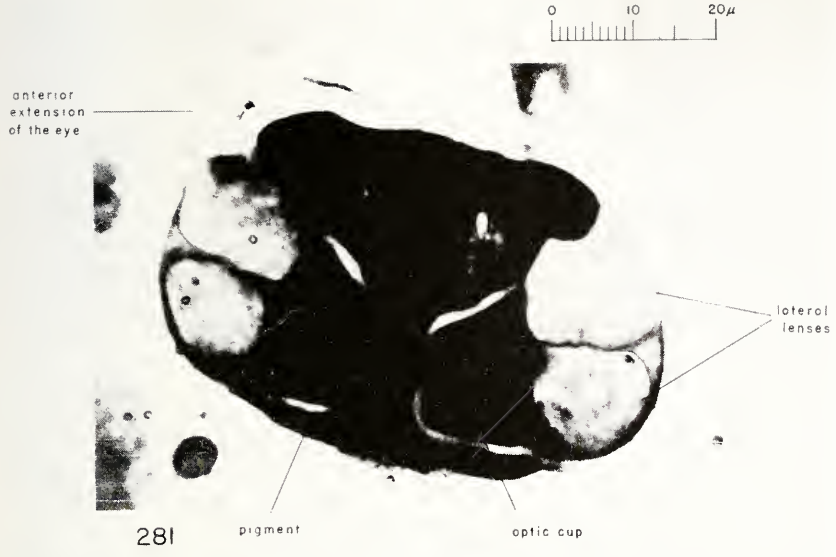


280

Plate 61

Nos. 281-282. Adult, 10μ frontal sections through the eye. The sections progress from dorsal to ventral.

PLATE 61



281

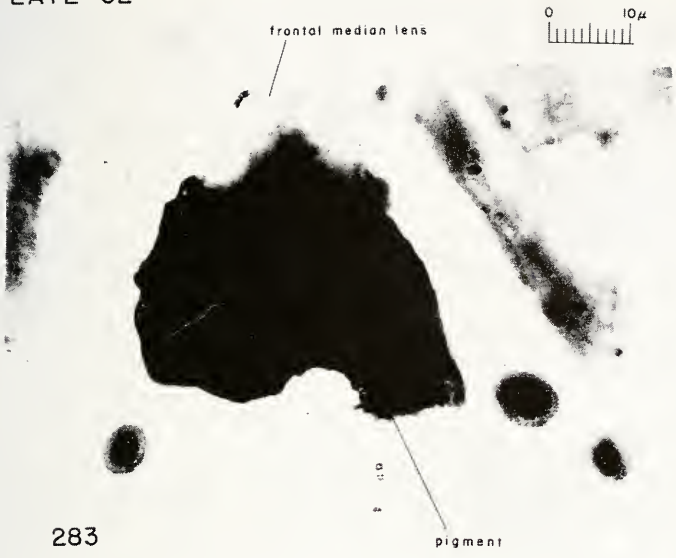
282

Plate 62

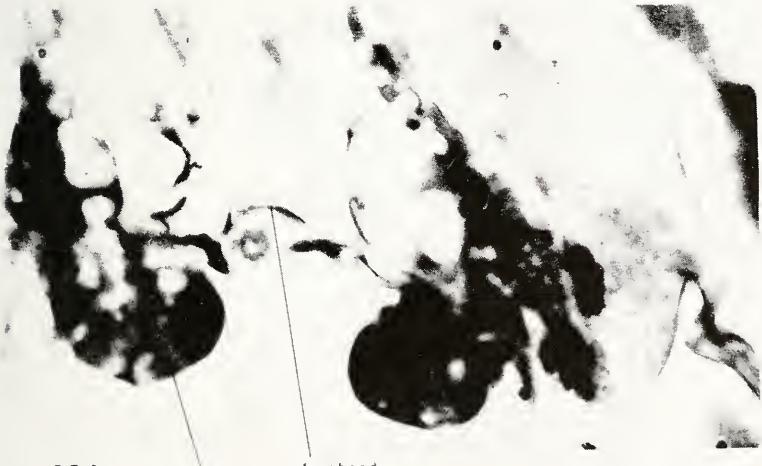
No. 283. 10μ frontal section through the eye, following the sections shown in Plate 61.

No. 284. 10μ frontal section through the bases of the antennules.

PLATE 62



283



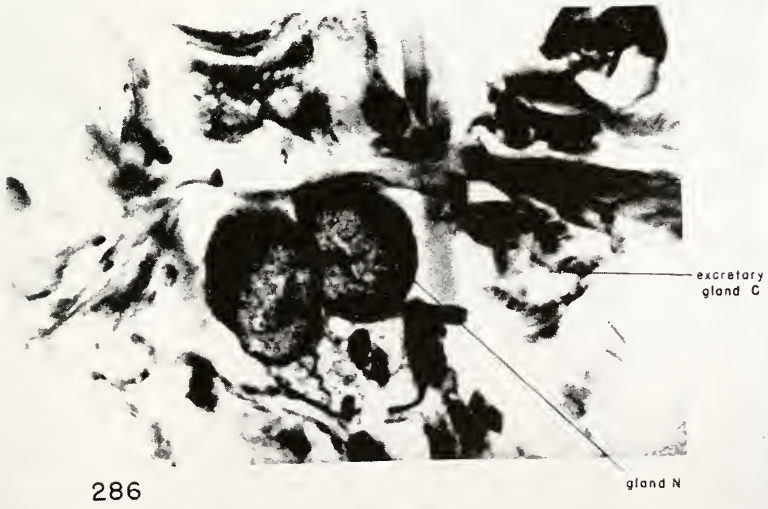
284

Plate 63

Nos. 285-286. Adult, 10μ frontal sections through the middle of the body. The sections progress from dorsal to ventral.

PLATE 63

285



286

Plate 64

Nos. 287-288. Adult, 10μ frontal sections through the middle of the body. These sections follow those shown in Plate 63.

PLATE 64

287

288

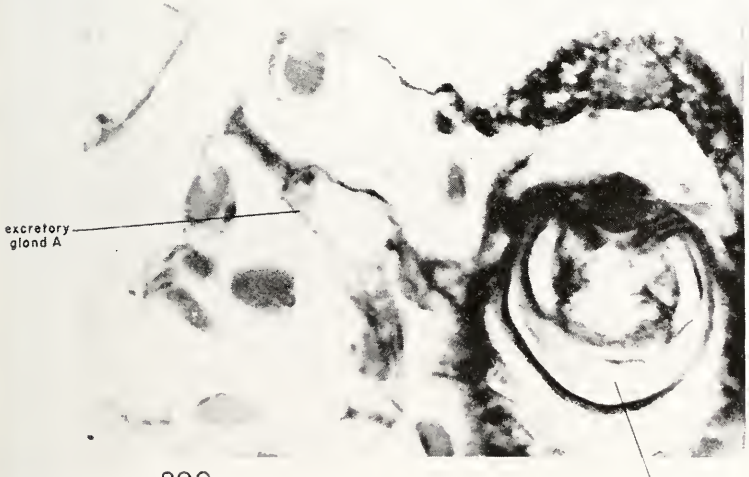
Plate 65

No. 289. Adult, 10μ frontal sections through the middle of the body. These sections follow those shown in Plate 64.

No. 290. Adult, 10μ frontal section through the cerebrum, excretory gland A, and dorsal wulst.

PLATE 65

289



290

Plate 66

No. 291. Inner face of the right valve.

PLATE 66

291

Plate 67

No. 292. Right valve seen with transmitted light.

Nos 293-296. Left valve seen with double polarized light in successive positions.

No. 297. Adult, 10μ frontal section through the cerebrum.

PLATE 67

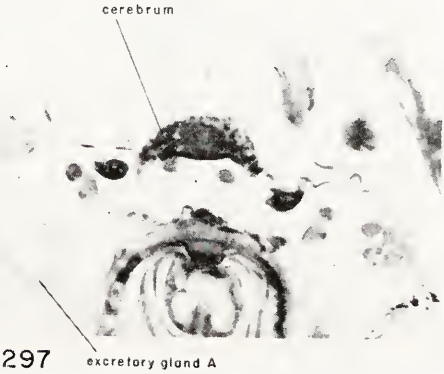
292

293

294

295

296



297

Plate 68

Nos. 298-301. Adult, 10μ frontal sections through the central nervous system. The sections progress from dorsal to ventral.

PLATE 68

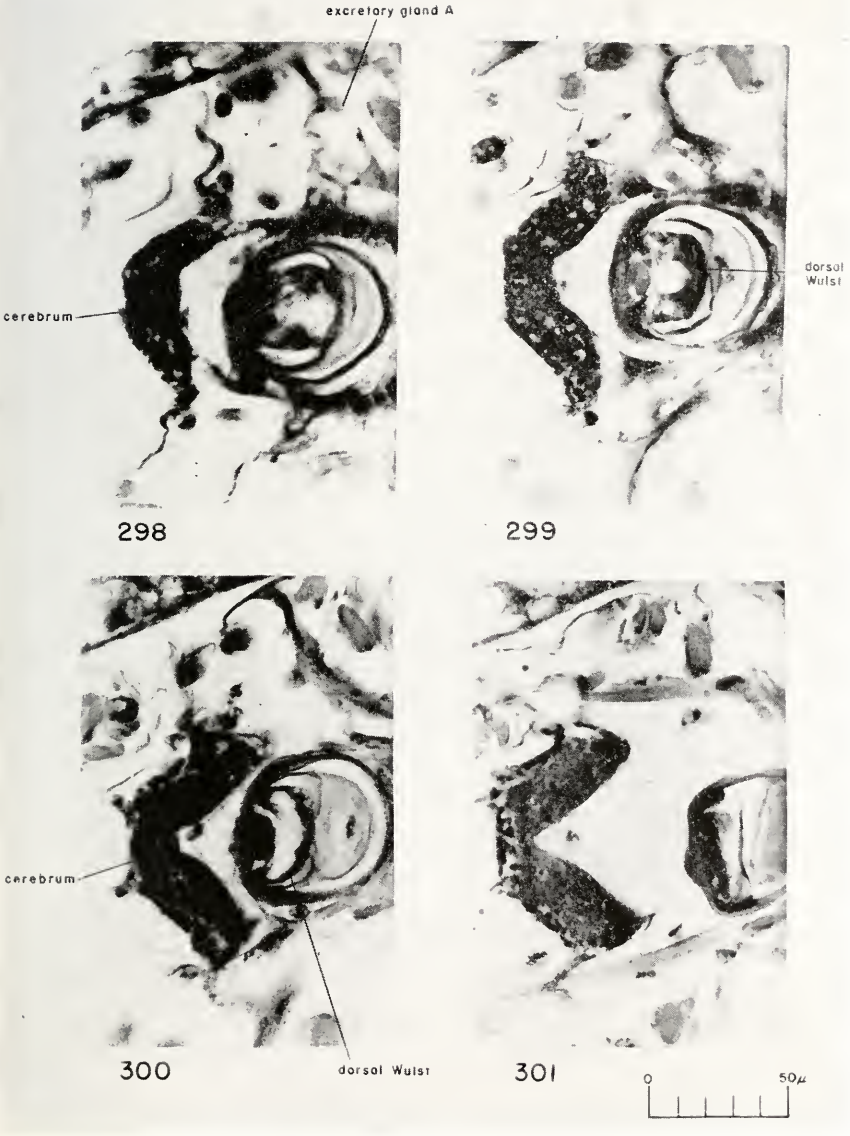

excretory gland A
cerebrum
dorsal Wulst
298
299
cerebrum
dorsal Wulst
300
301
0
50μ

Plate 69

Nos. 302-305. Adult, 10μ frontal sections through the central nervous system. These sections follow those shown in Plate 68.

PLATE 69

302

303

304

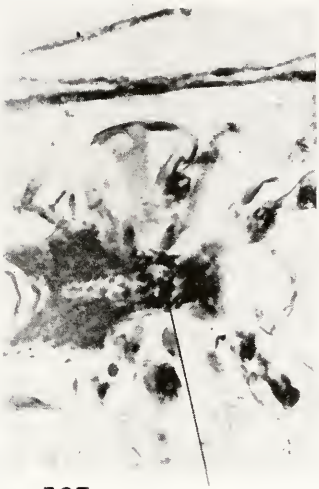
305

Plate 70

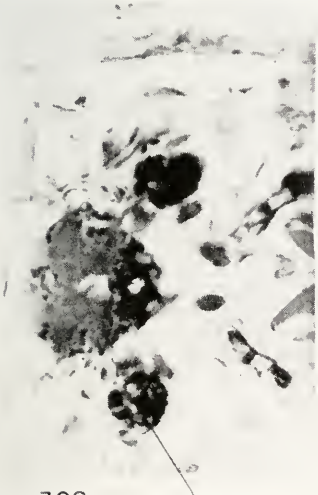
Nos. 306-309. Adult, 10μ frontal sections through the central nervous system. These sections follow those shown in Plate 69.

PLATE 70

306



307



308

309

Plate 71

Nos. 310-312. Adult, 10μ sagittal sections through the left first thoracic leg. These sections progress from the left to the right side.

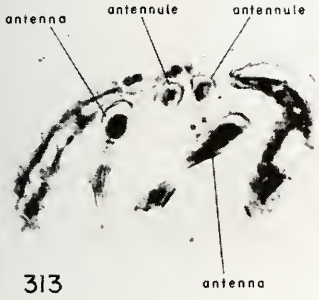
PLATE 71


exopodite plate
muscles of the mandible
masticatory process of maxilla
muscles of the mandible
protopodite
310
endopodite palp
masticatory process of first thoracic leg
3rd leg
endopodite palp
311
masticatory process
3rd leg
muscles of the mandible
ganglion of the maxilla
0
50
100μ
312
endopodite palp
masticatory process

Plate 72

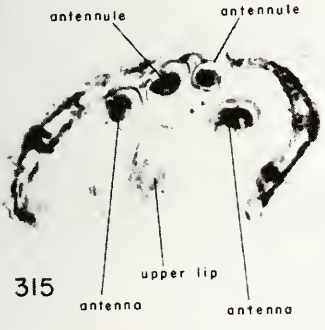
Nos. 313-318. Eighth instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from anterior to posterior.

PLATE 72

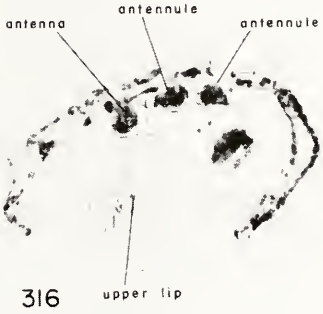


313

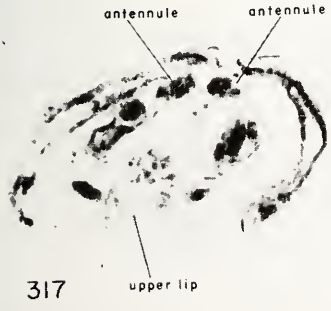
314



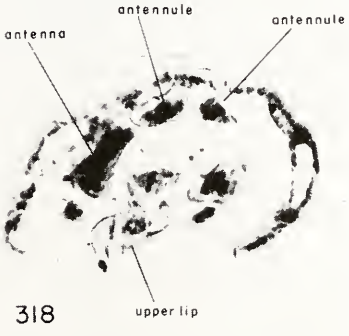
315



316



317



318

Plate 73

Nos. 319-322. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 72.

PLATE 73

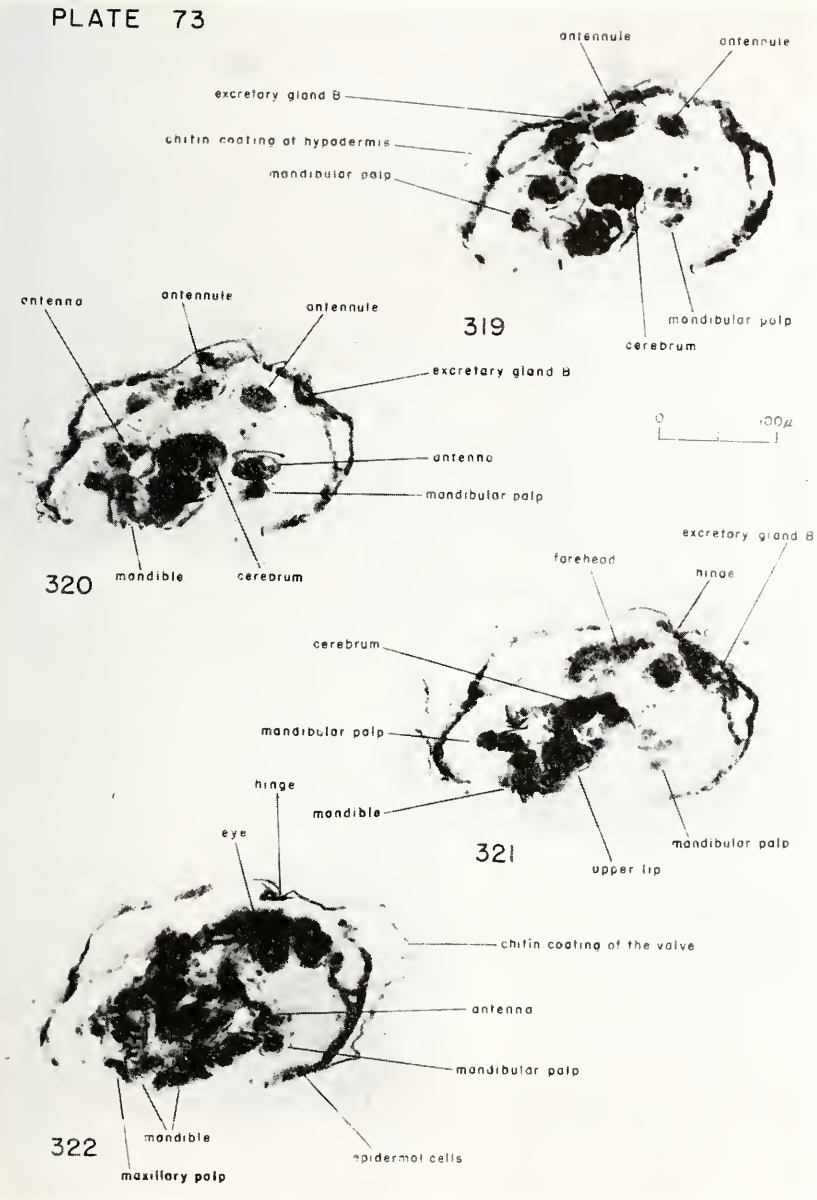

antennule
antennule
excretory gland B
chitin coating of hypodermis
mandibular palp
mandibular palp
cerebrum
319
antenna
antennule
antennule
excretory gland B
0
100μ
antenna
mandibular palp
320
mandible
cerebrum
excretory gland B
forehead
hinge
cerebrum
mandibular palp
hinge
mandible
321
mandibular palp
upper lip
eye
chitin coating of the valve
antenna
mandibular palp
322
mandible
maxillary palp
epidermal cells

Plate 74

Nos. 323-326. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 73.

PLATE 74

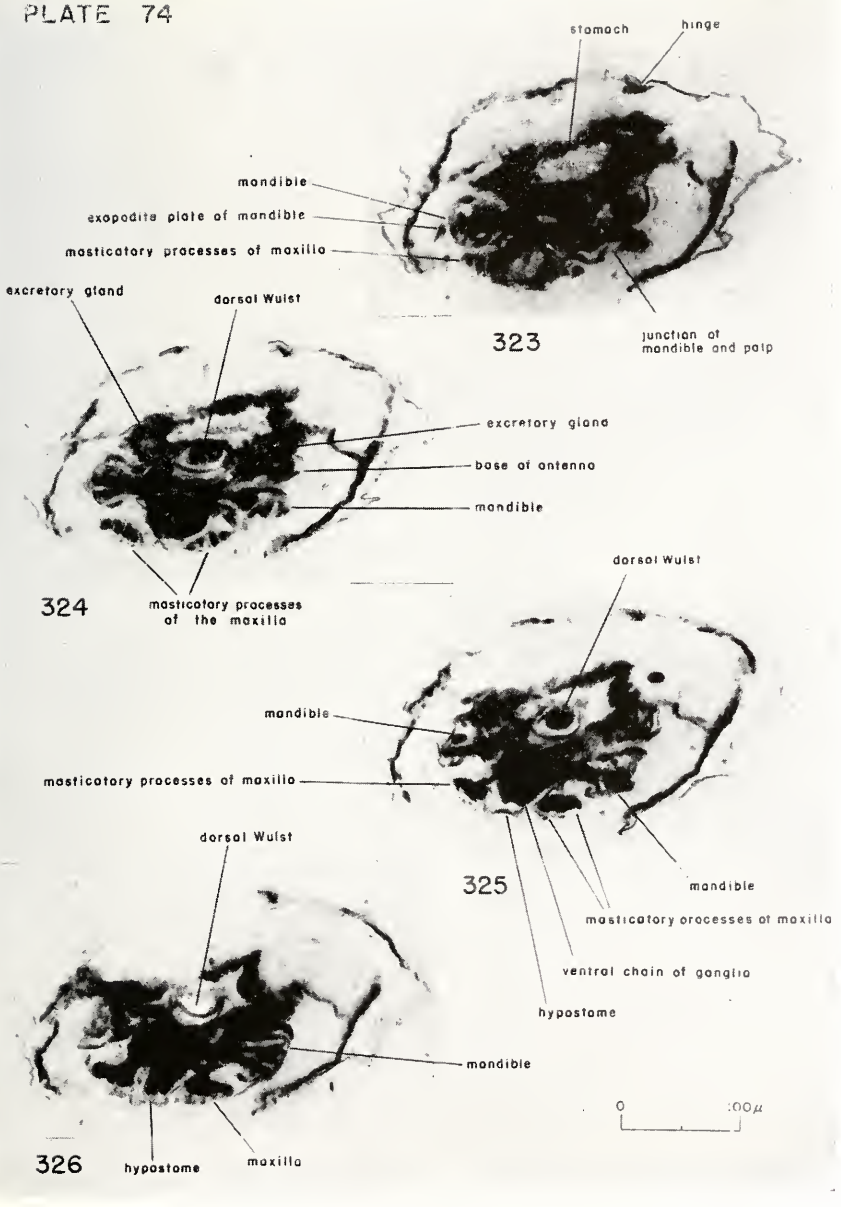

stomach
hinge
mandible
exopodite plate of mandible
masticatory processes of maxilla
excretory gland
dorsal Wulst
323
junction of mandible and palp
excretory gland
base of antenna
mandible
324
masticatory processes of the maxilla
dorsal Wulst
mandible
masticatory processes of maxilla
325
mandible
masticatory processes of maxilla
ventral chain of ganglia
hypostome
dorsal Wulst
mandible
0
100μ
326
hypostome
maxilla

Plate 75

Nos. 327-330. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 74.

PLATE 75

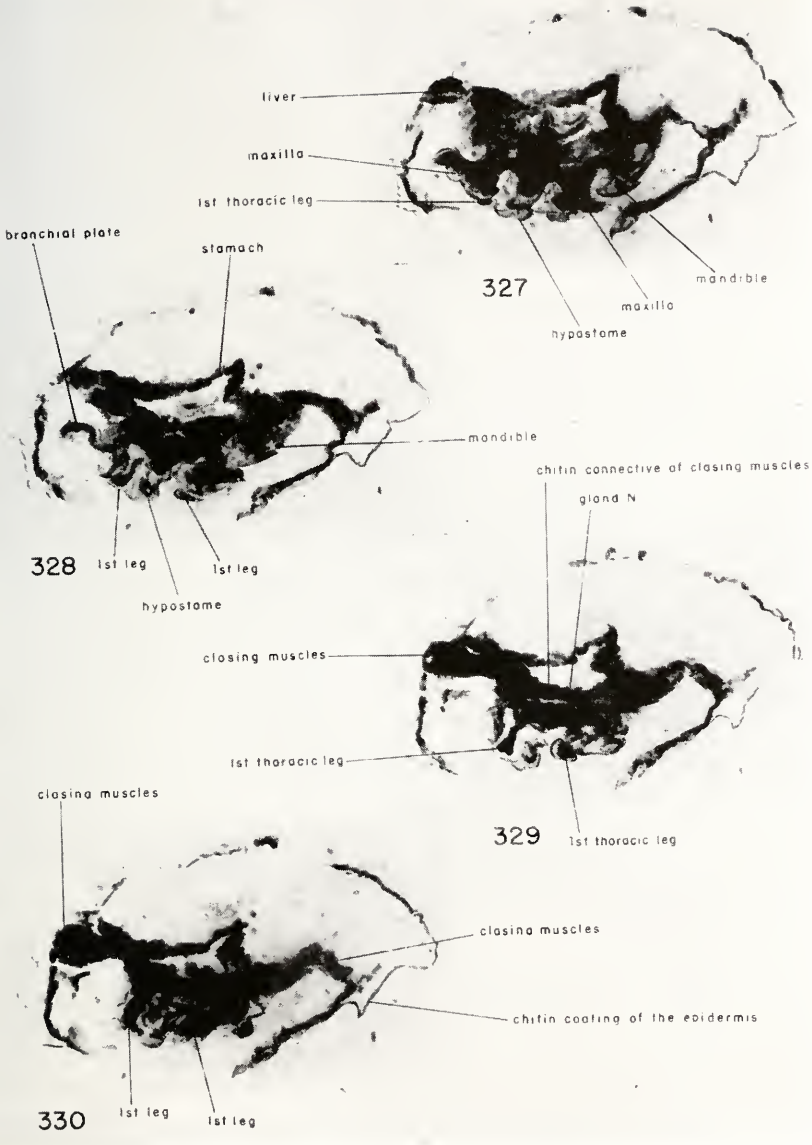

liver
maxilla
1st thoracic leg
mandible
maxilla
hypostome
327
branchial plate
stomach
mandible
328
1st leg
1st leg
hypostome
chitin connective of closing muscles
gland N
closing muscles
1st thoracic leg
329
1st thoracic leg
closing muscles
closing muscles
chitin coating of the epidermis
330
1st leg
1st leg

Plate 76

Nos. 331-334. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 75.

PLATE 76

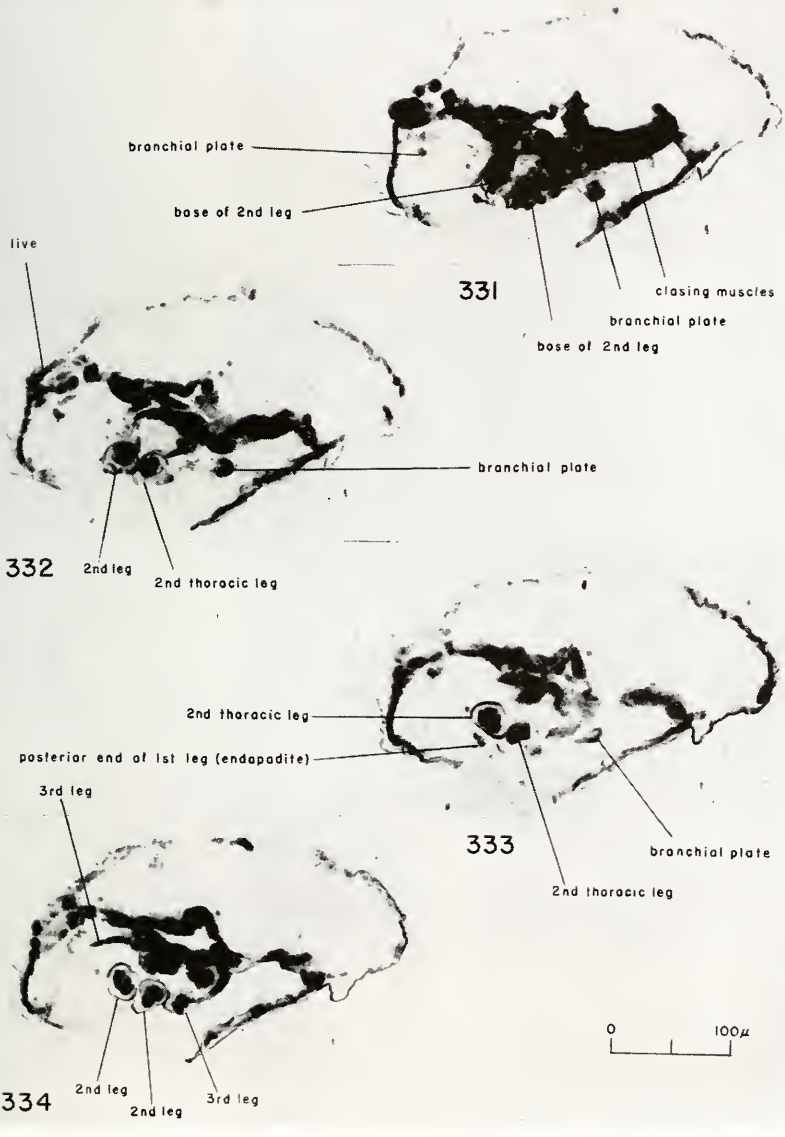

branchial plate
base of 2nd leg
331
closing muscles
branchial plate
base of 2nd leg
live
branchial plate
332
2nd leg
2nd thoracic leg
2nd thoracic leg
posterior end of 1st leg (endapadite)
3rd leg
333
branchial plate
2nd thoracic leg
0
100μ
334
2nd leg
2nd leg
3rd leg

Plate 77

Nos. 335-338. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 76.

PLATE 77

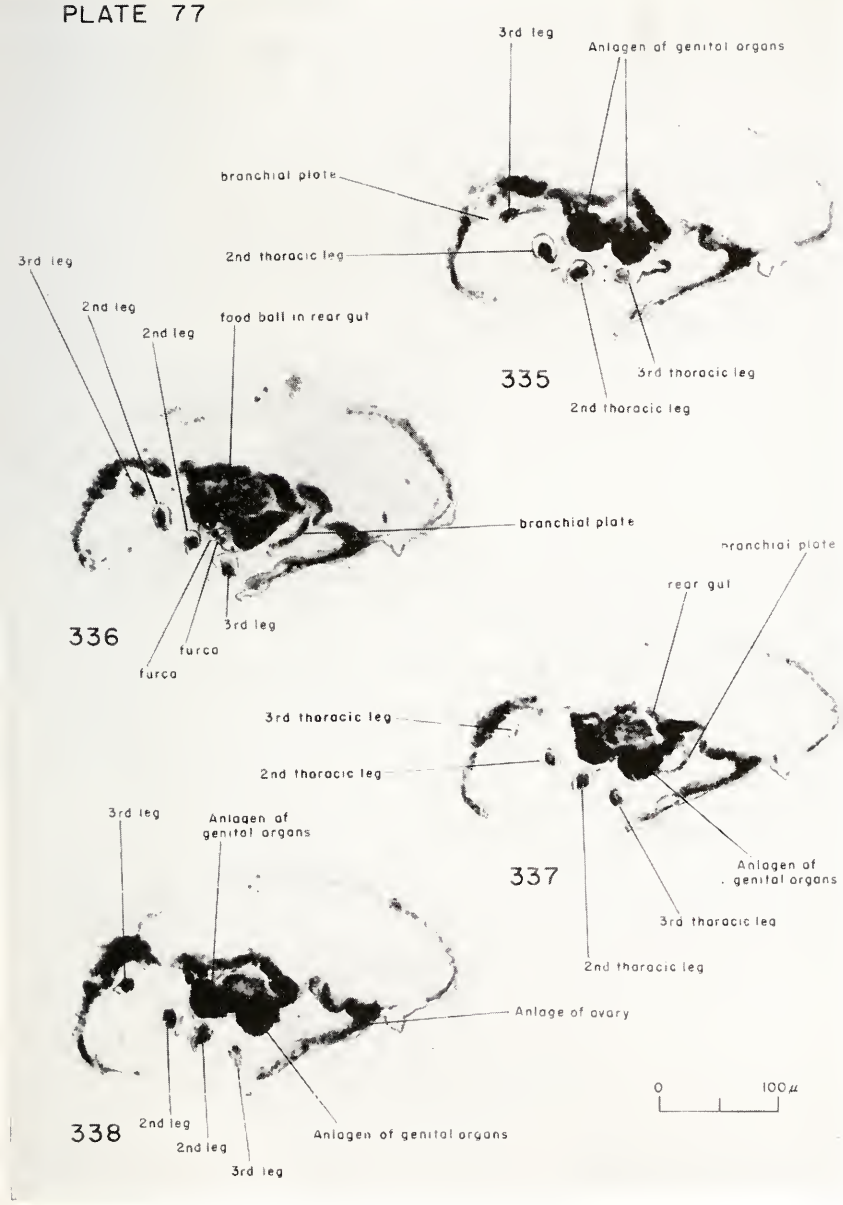

3rd leg
Anlagen of genital organs
branchial plate
2nd thoracic leg
335
3rd thoracic leg
2nd thoracic leg
3rd leg
2nd leg
2nd leg
food ball in rear gut
branchial plate
336
3rd leg
furca
furca
branchial plate
rear gut
3rd thoracic leg
2nd thoracic leg
337
Anlagen of genital organs
3rd thoracic leg
2nd thoracic leg
3rd leg
Anlagen of genital organs
Anlage of ovary
0
100 μ
338
2nd leg
2nd leg
3rd leg
Anlagen of genital organs

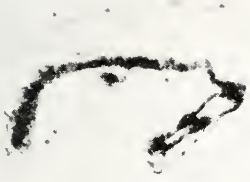
Plate 78

Nos. 339-349. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 77. This ends the sequence of transverse sections starting on Plate 72.

PLATE 78

339

340



341

342

343

344

345

346

347

348

349

Plate 79

Nos. 350-353. Eighth instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. Sections progress from anterior to posterior.

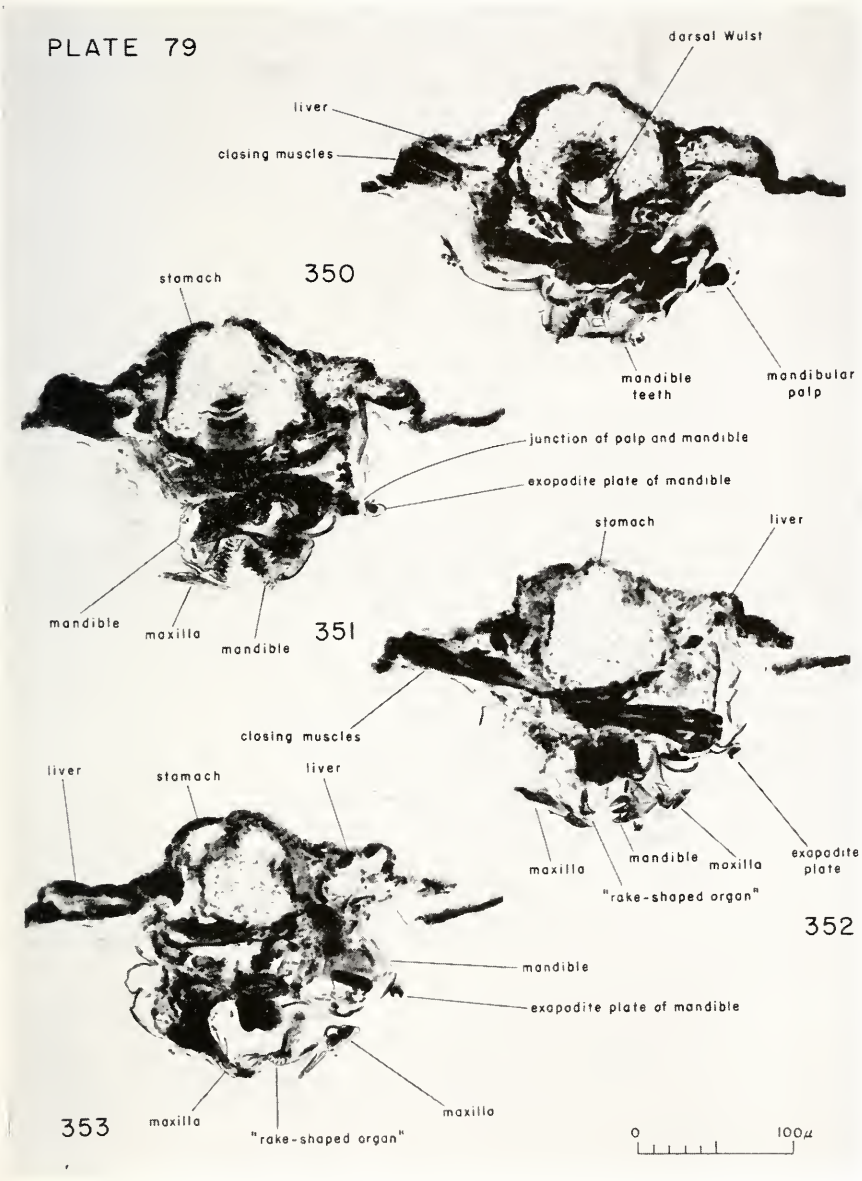


PLATE 79
dorsal Wulst
liver
closing muscles
350
stomach
mandible teeth
mandibular palp
junction of palp and mandible
exopodite plate of mandible
mandible
maxilla
mandible
351
stomach
liver
closing muscles
maxilla
mandible
maxilla
exopodite plate
"rake-shaped organ"
352
liver
stomach
liver
mandible
exopodite plate of mandible
353
maxilla
"rake-shaped organ"
maxilla
0
100μ

Plate 80

Nos. 354-357. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 79.

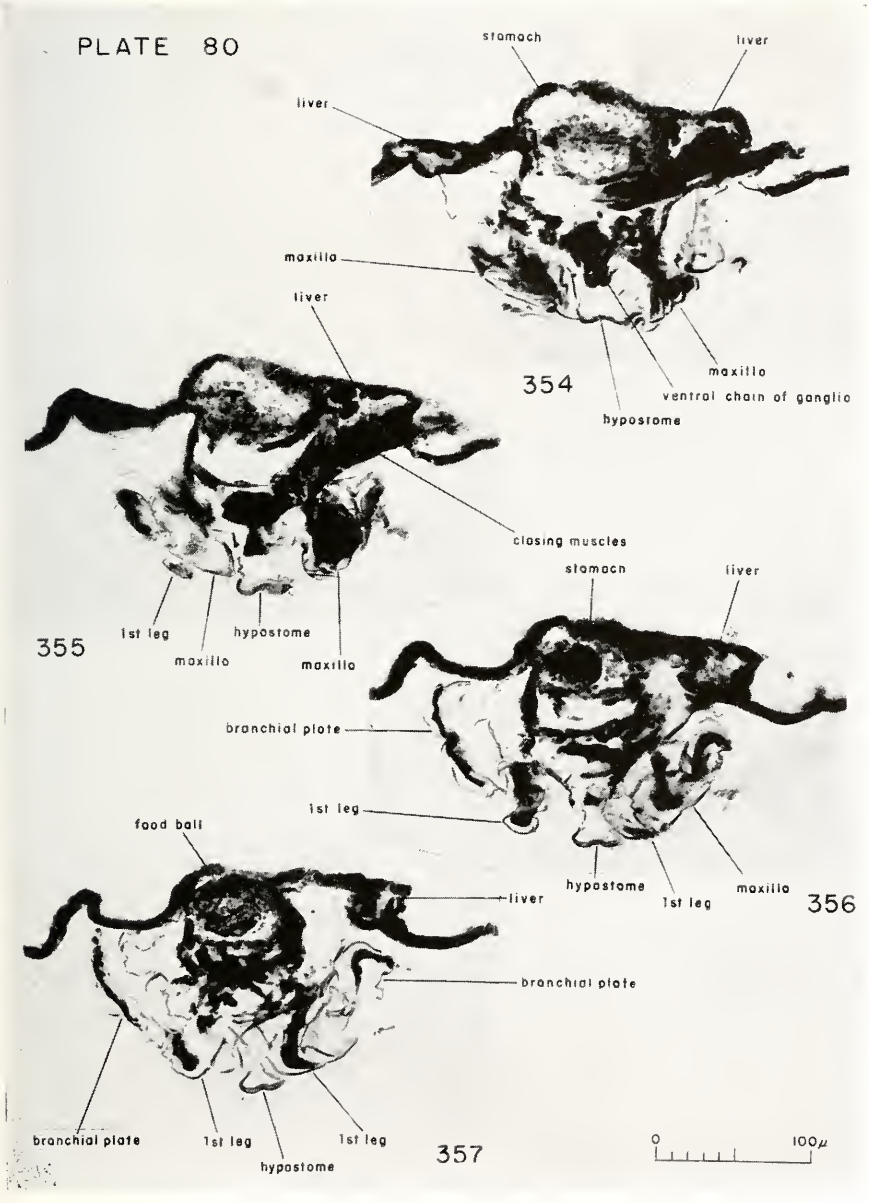


PLATE 80
stomach
liver
liver
maxilla
liver
maxilla
354
ventral chain of ganglia
hypostome
closing muscles
1st leg
hypostome
355
maxilla
maxilla
stomach
liver
branchial plate
1st leg
food ball
hypostome
maxilla
liver
1st leg
356
branchial plate
branchial plate
1st leg
1st leg
hypostome
357
0
100μ

Plate 81

Nos. 358-361. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 80.

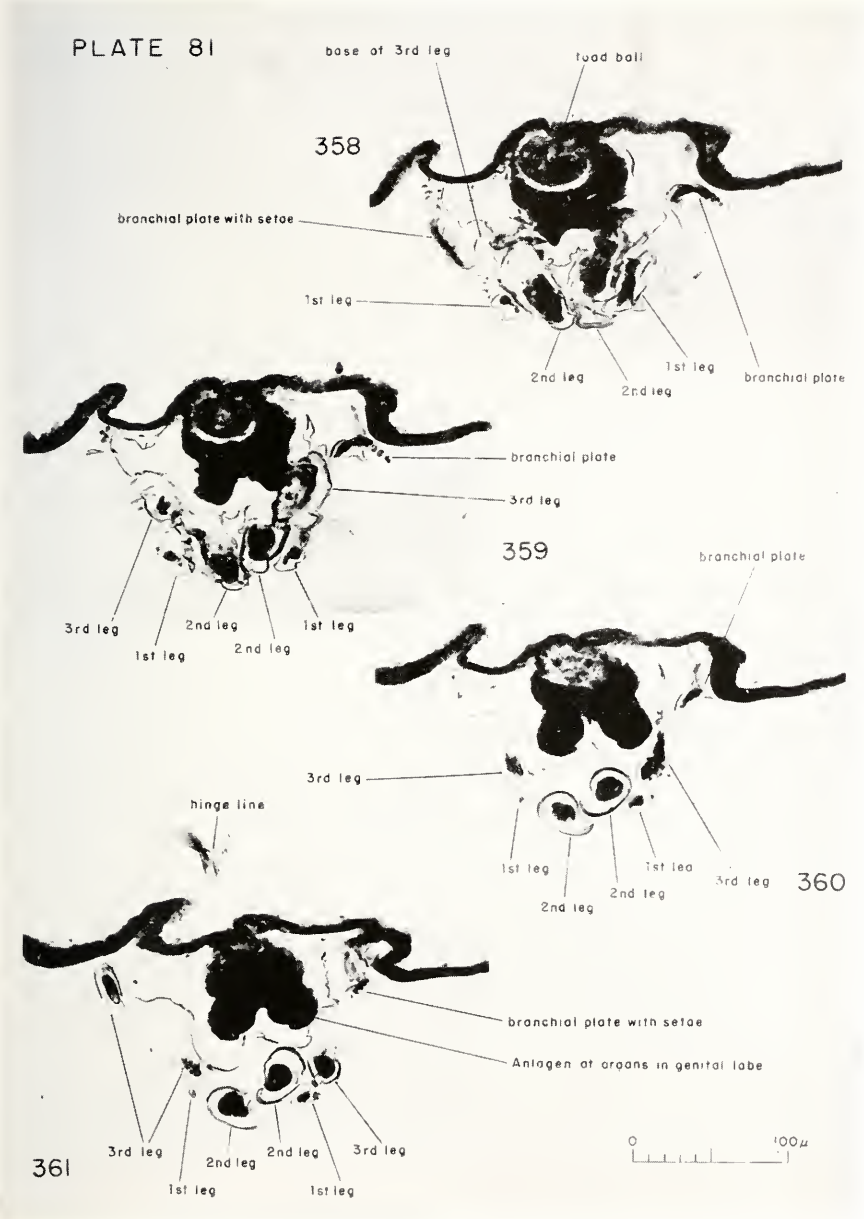


PLATE 81
base of 3rd leg
food ball
358
branchial plate with setae
1st leg
2nd leg
2nd leg
1st leg
branchial plate
branchial plate
3rd leg
359
3rd leg
1st leg
2nd leg
2nd leg
1st leg
branchial plate
3rd leg
hinge line
1st leg
2nd leg
2nd leg
1st leg
3rd leg
360
branchial plate with setae
Anlagen of organs in genital lobe
3rd leg
2nd leg
2nd leg
3rd leg
361
1st leg
1st leg
0
100μ

Plate 82

Nos. 362-365. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 81. This concludes the sequence of transverse sections beginning on Plate 79.

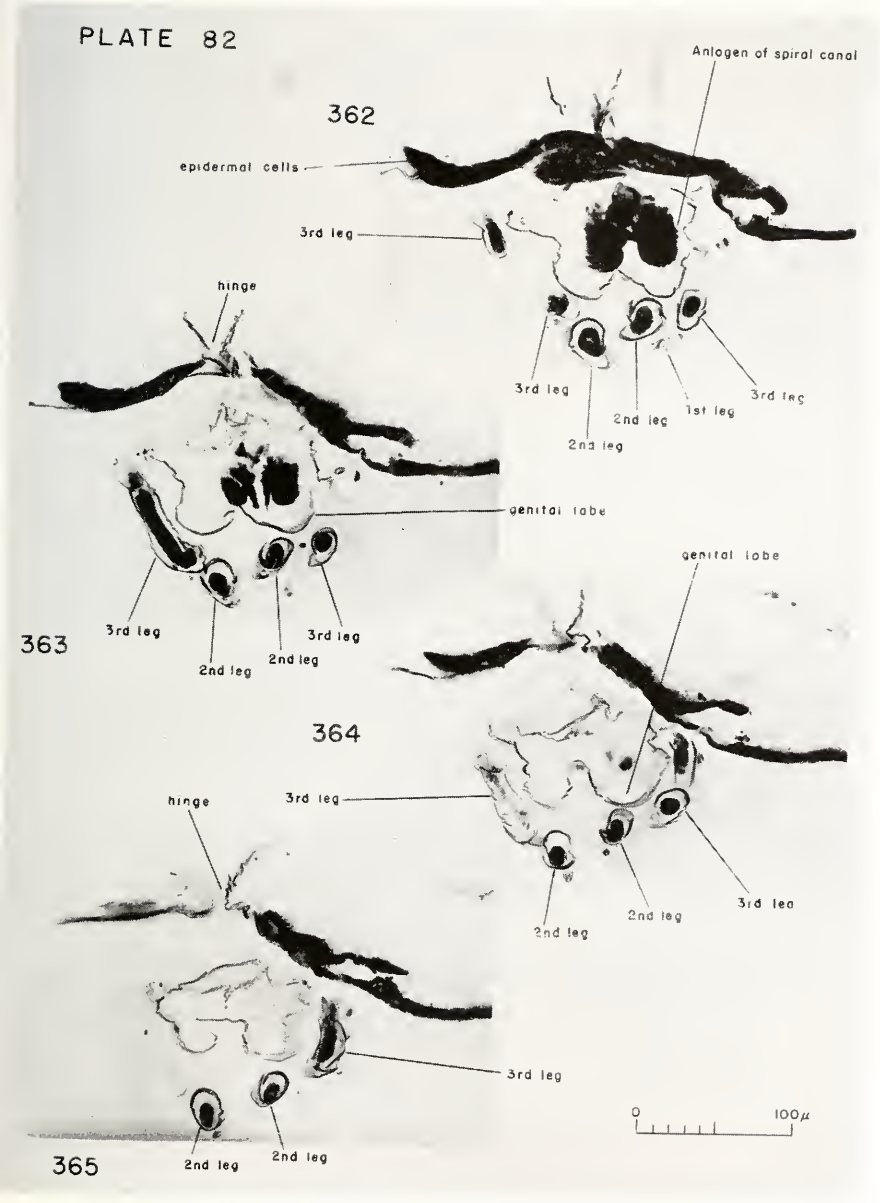


PLATE 82
362
Anlagen of spiral canal
epidermal cells
3rd leg
3rd leg
2nd leg
2nd leg
1st leg
3rd leg
hinge
genital lobe
3rd leg
2nd leg
2nd leg
3rd leg
363
genital lobe
364
hinge
3rd leg
2nd leg
2nd leg
3rd leg
3rd leg
0
100μ
365
2nd leg
2nd leg

Plate 83

Nos. 366-368. Eighth instar, 10μ transverse sections. Sections progress from anterior to posterior.

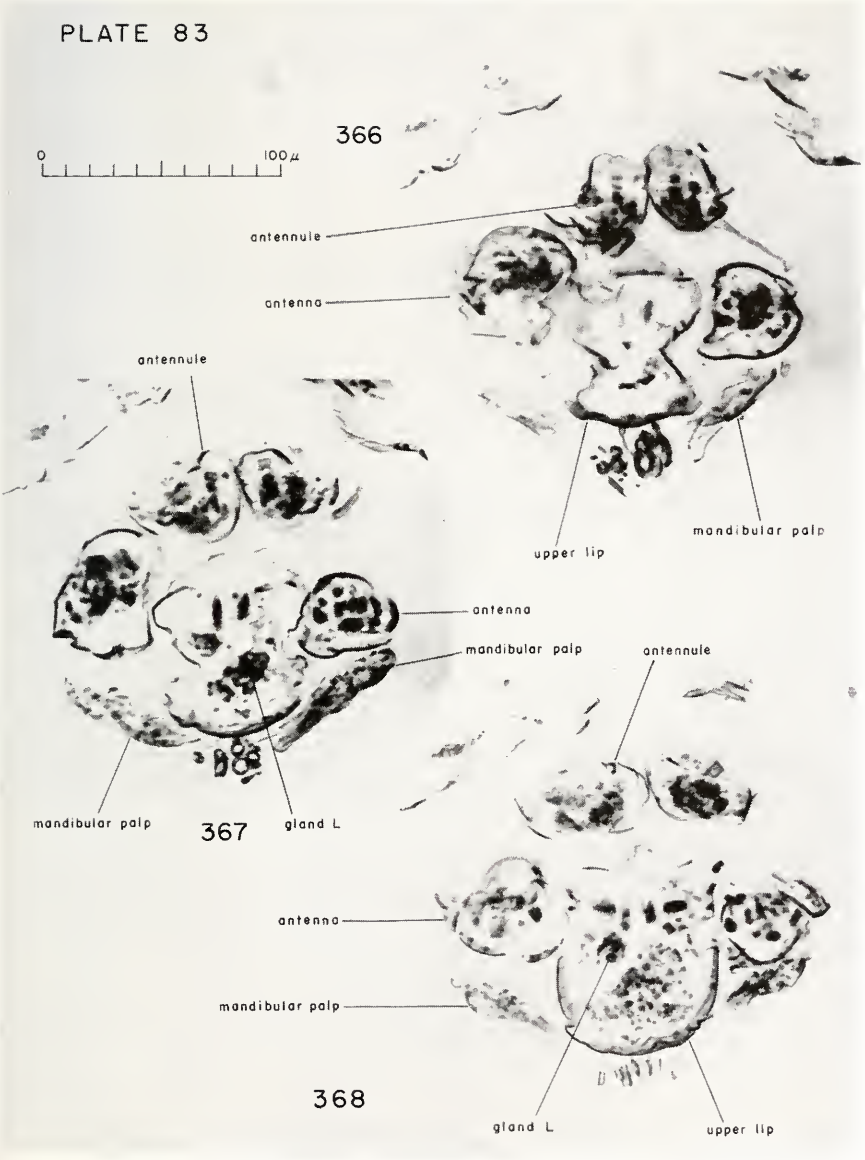


PLATE 83
0
100 μ
366
antennule
antenna
upper lip
mandibular palp
antennule
antenna
mandibular palp
mandibular palp
367
gland L
antennule
antenna
mandibular palp
368
gland L
upper lip

Plate 84

Nos. 369-371. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 83.

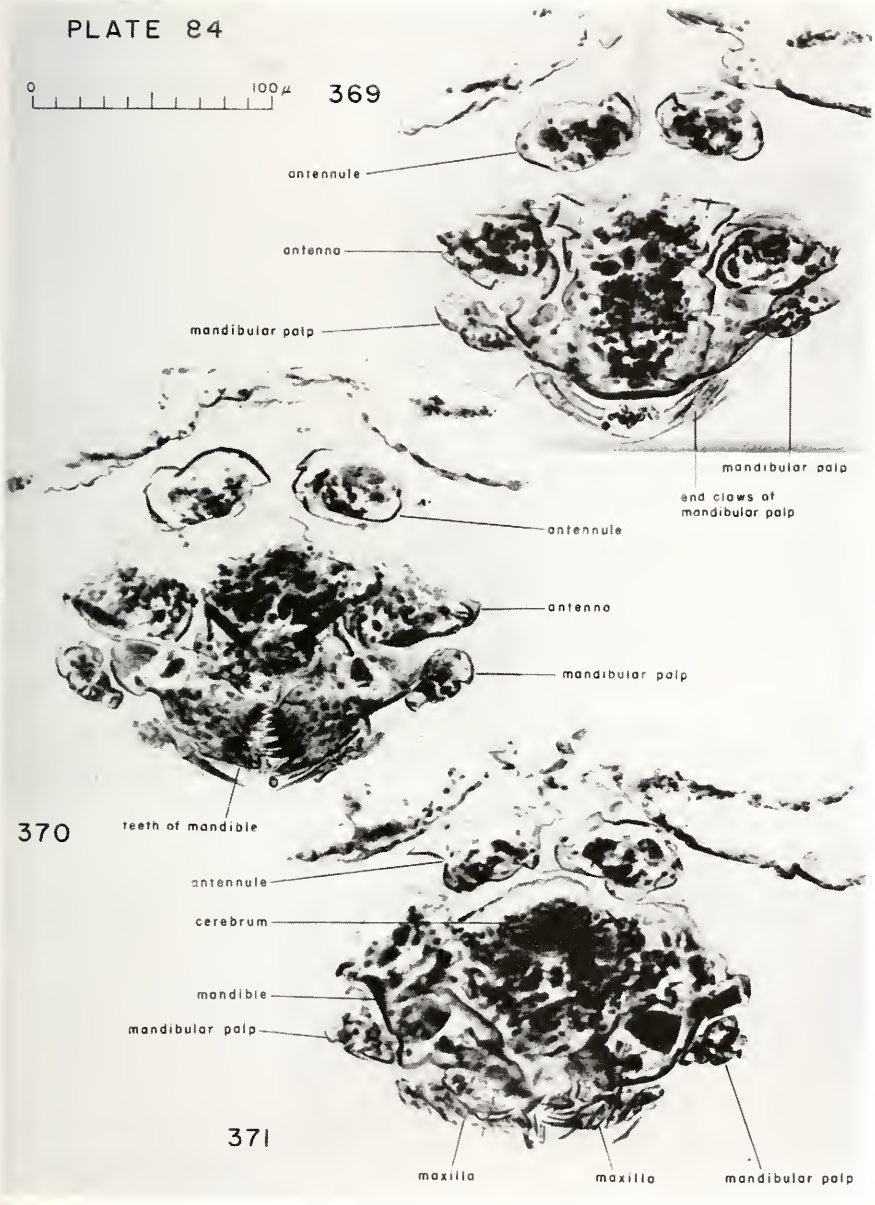


PLATE 84
0
100μ
369
antennule
antenna
mandibular palp
mandibular palp
end claws of mandibular palp
antennule
antenna
mandibular palp
370
teeth of mandible
antennule
cerebrum
mandible
mandibular palp
371
maxilla
maxilla
mandibular palp

Plate 85

Nos. 372-373. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 84.

PLATE 85

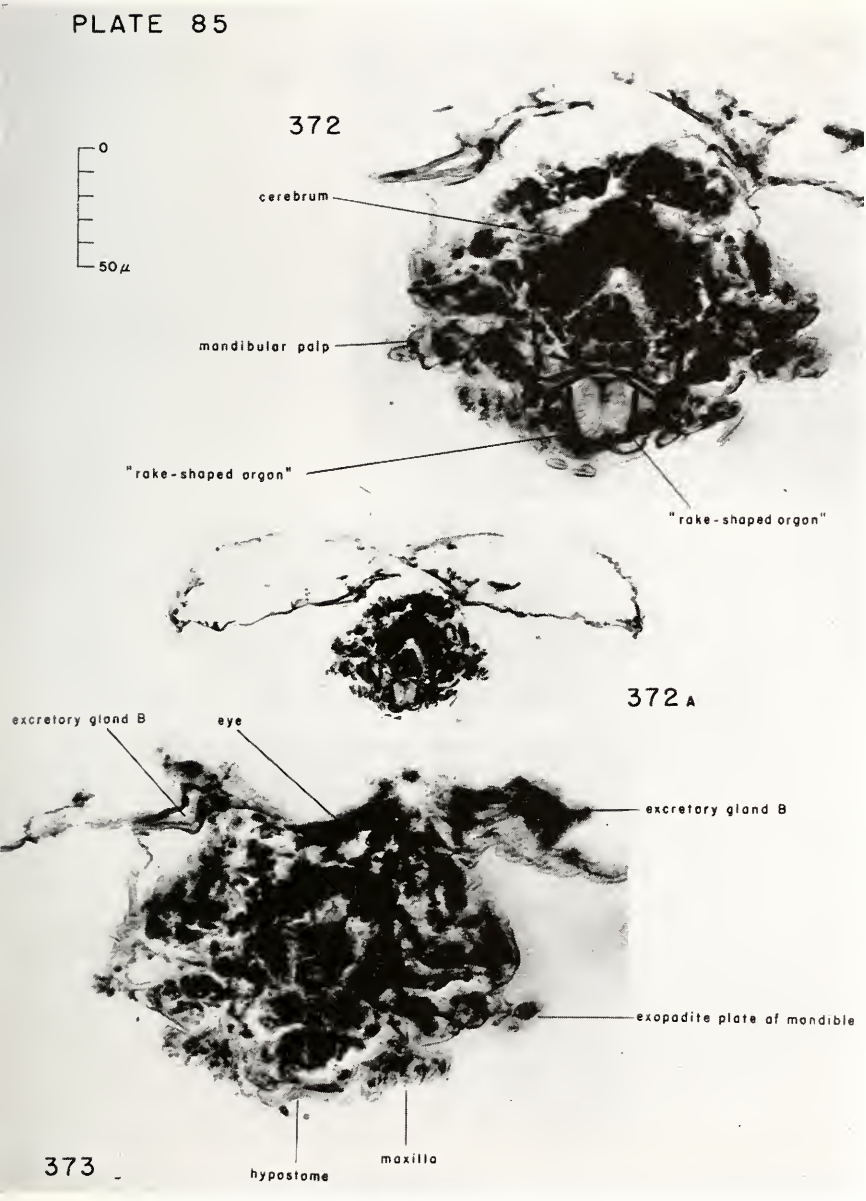

372
0
50μ
cerebrum
mandibular palp
"rake-shaped organ"
"rake-shaped organ"
372 A
excretory gland B
eye
excretory gland B
exopodite plate of mandible
373
hypostome
maxilla

Plate 86

Nos. 374-376. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 85.

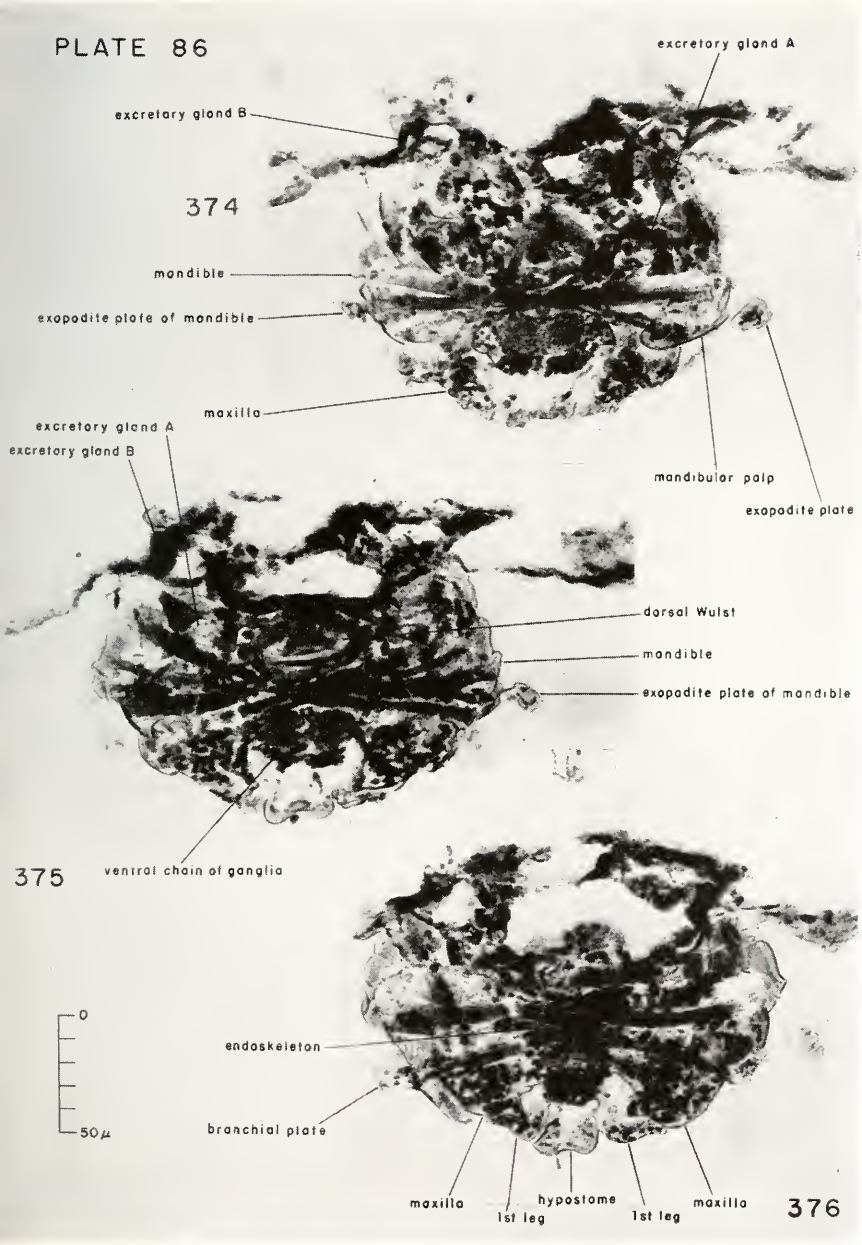


PLATE 86
excretory gland A
excretory gland B
374
mandible
exopodite plate of mandible
maxilla
mandibular palp
exopodite plate
excretory gland A
excretory gland B
dorsal Wulst
mandible
exopodite plate of mandible
375
ventral chain of ganglia
0
50μ
endoskeleton
branchial plate
maxilla
1st leg
hypostome
1st leg
maxilla
376

Plate 87

Nos. 377-379. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 86.

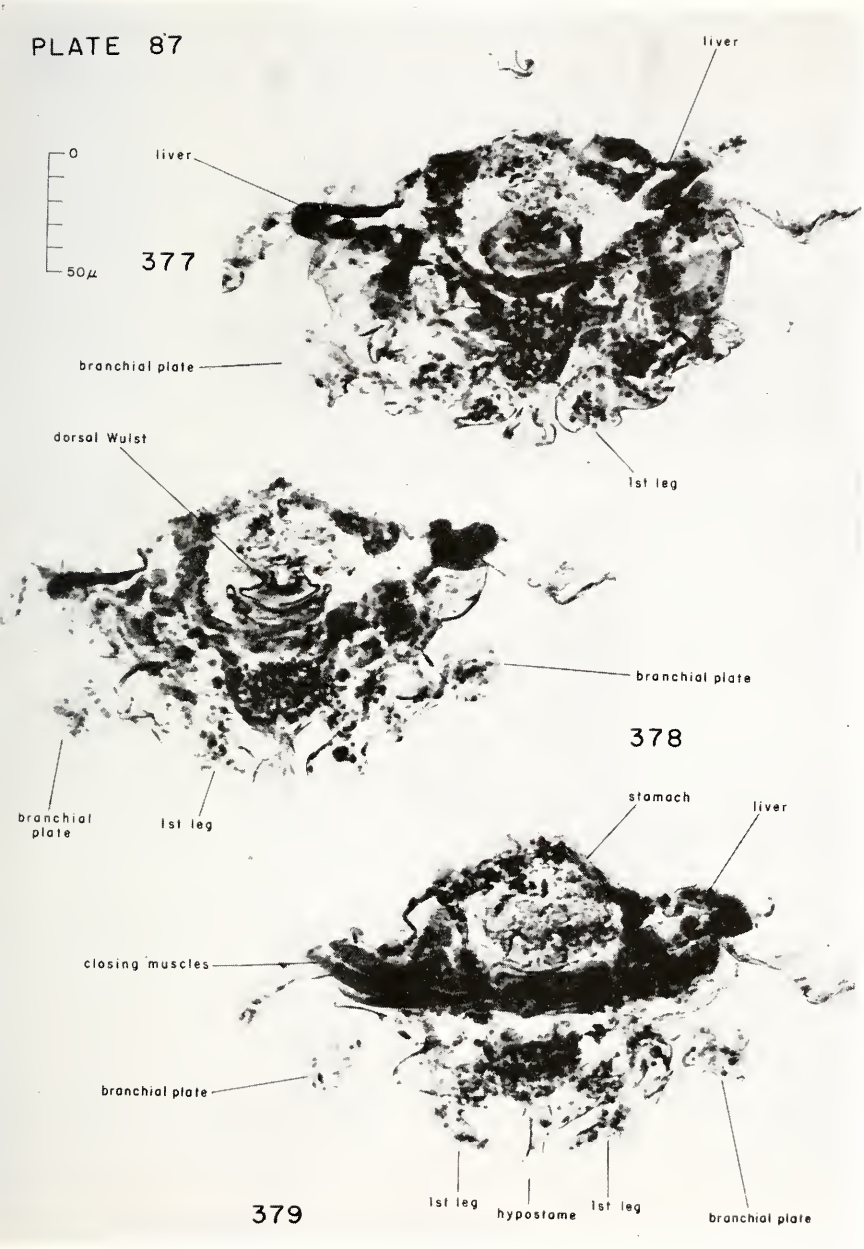
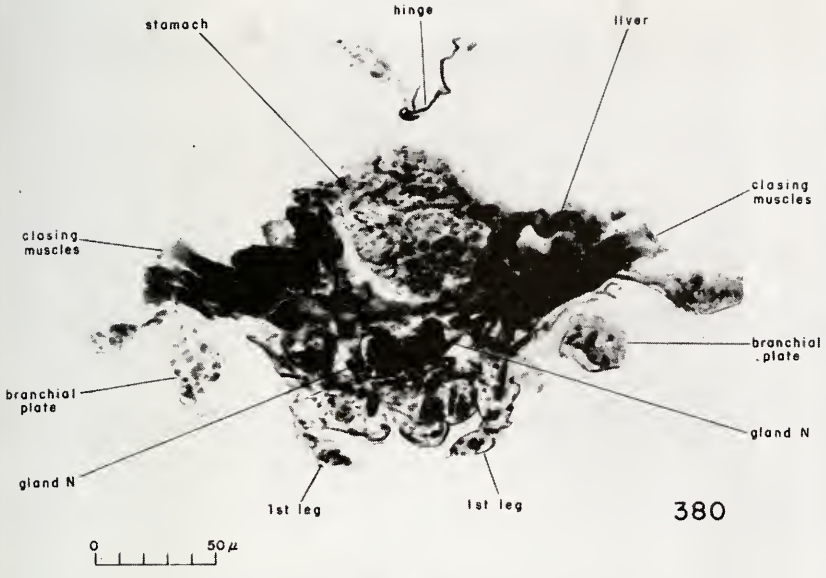


PLATE 87
0
50μ
377
liver
liver
branchial plate
dorsal Wulst
1st leg
branchial plate
378
branchial plate
1st leg
stomach
liver
closing muscles
branchial plate
1st leg
hypostome
1st leg
branchial plate
379

Plate 88

Nos. 380-381. Eighth instar, 10μ transverse sections. These sections follow those shown in Plate 87.

PLATE 88


stomach
hinge
liver
closing muscles
closing muscles
branchial plate
branchial plate
gland N
gland N
1st leg
1st leg
380
0
50 μ

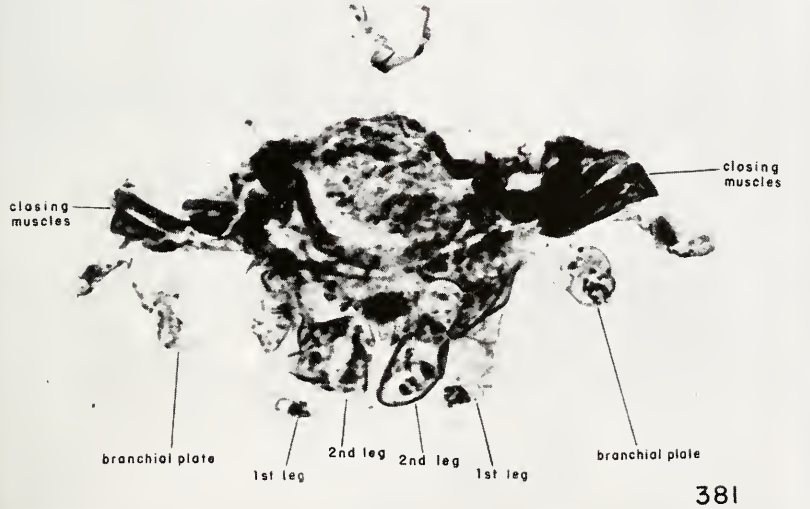

closing muscles
closing muscles
branchial plate
1st leg
2nd leg
2nd leg
1st leg
branchial plate
381

Plate 89

Nos. 382-385. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from anterior to posterior.

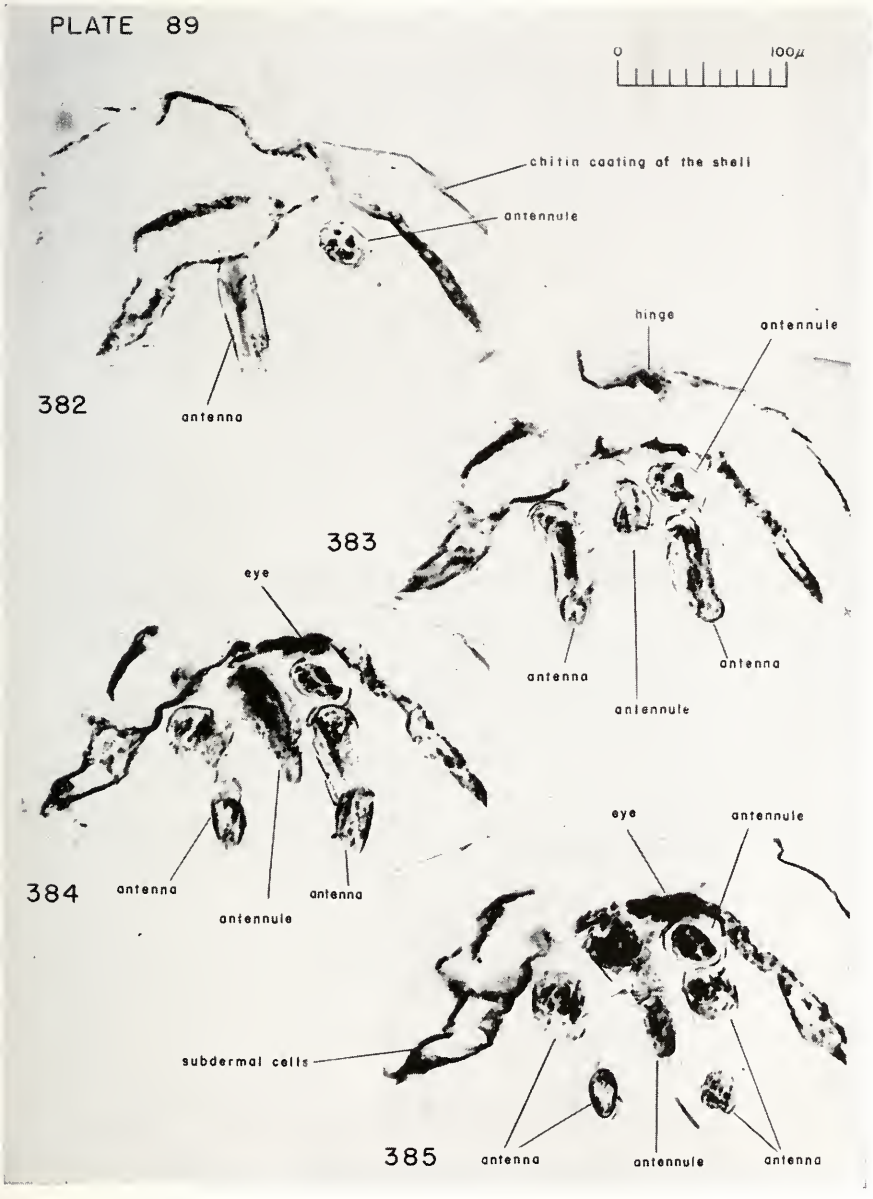


PLATE 89
0
100μ
chitin coating of the shell
antennule
382
antenna
hinge
antennule
383
antenna
antenna
antennule
eye
384
antenna
antennule
antenna
eye
antennule
subdermal cells
385
antenna
antennule
antenna

Plate 90

Nos. 386-389. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. These sections follow those shown in Plate 89.

PLATE 90


base of antennule
antenna
386
antenna
antennule
excretory gland B
antenna
387
claws of antenna
upper lip
claws of antenna
excretory gland B
antenna
388
antenna
claws of antenna
upper lip
stomach
cerebrum
389
base of antenna
upper lip
antenna

Plate 91

Nos. 390-393. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. These sections follow those shown in Plate 90.

PLATE 91

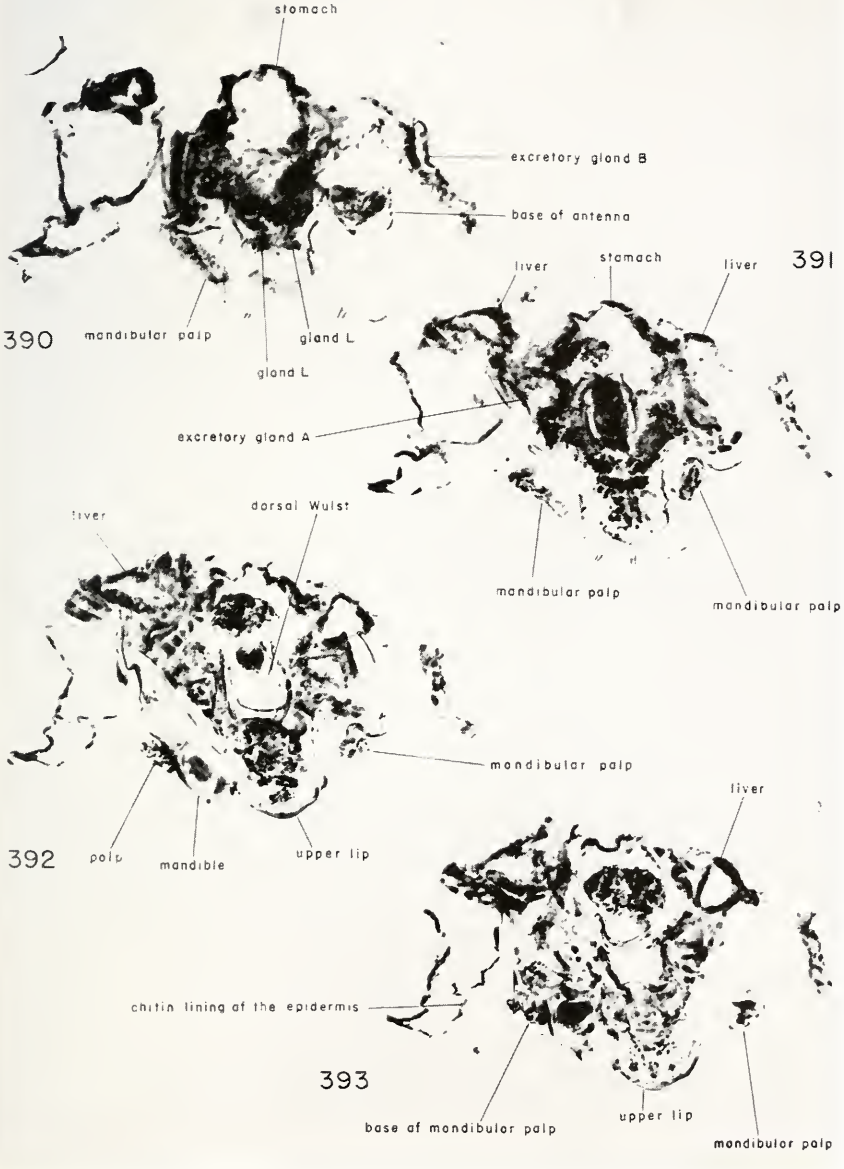

stomach
excretory gland B
base of antenna
390
mandibular palp
gland L
gland L
liver
stomach
liver
391
excretory gland A
mandibular palp
mandibular palp
liver
dorsal Wulst
mandibular palp
392
palp
mandible
upper lip
liver
chitin lining of the epidermis
393
base of mandibular palp
upper lip
mandibular palp

Plate 92

Nos. 394-397. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. These sections follow those shown in Plate 91.

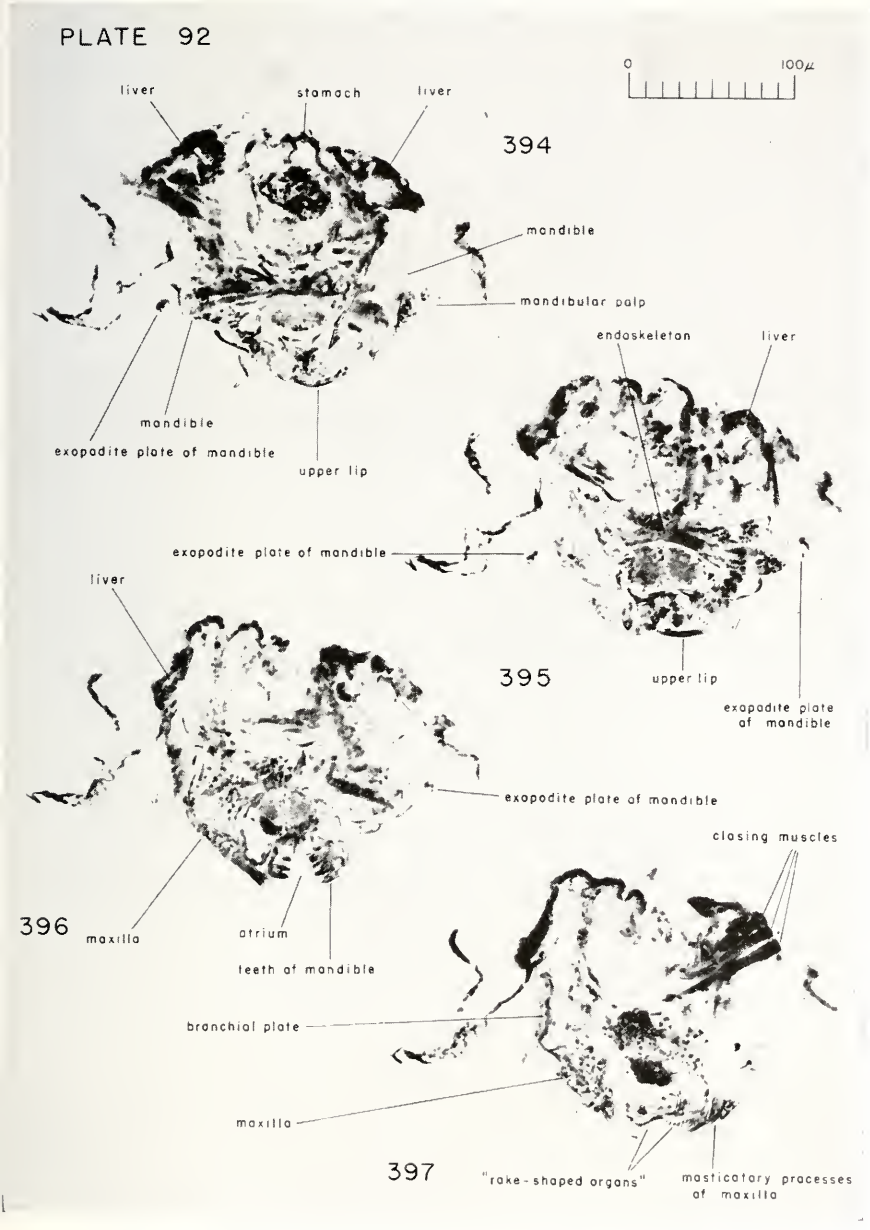


PLATE 92
0
100μ
liver
stomach
liver
394
mandible
mandibular palp
mandible
exopodite plate of mandible
upper lip
endoskeleton
liver
exopodite plate of mandible
395
upper lip
exopodite plate of mandible
liver
exopodite plate of mandible
closing muscles
396
maxilla
atrium
teeth of mandible
branchial plate
maxilla
397
"rake-shaped organs"
masticatory processes of maxilla

Plate 93

Nos. 398-401. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. These sections follow those shown in Plate 92.

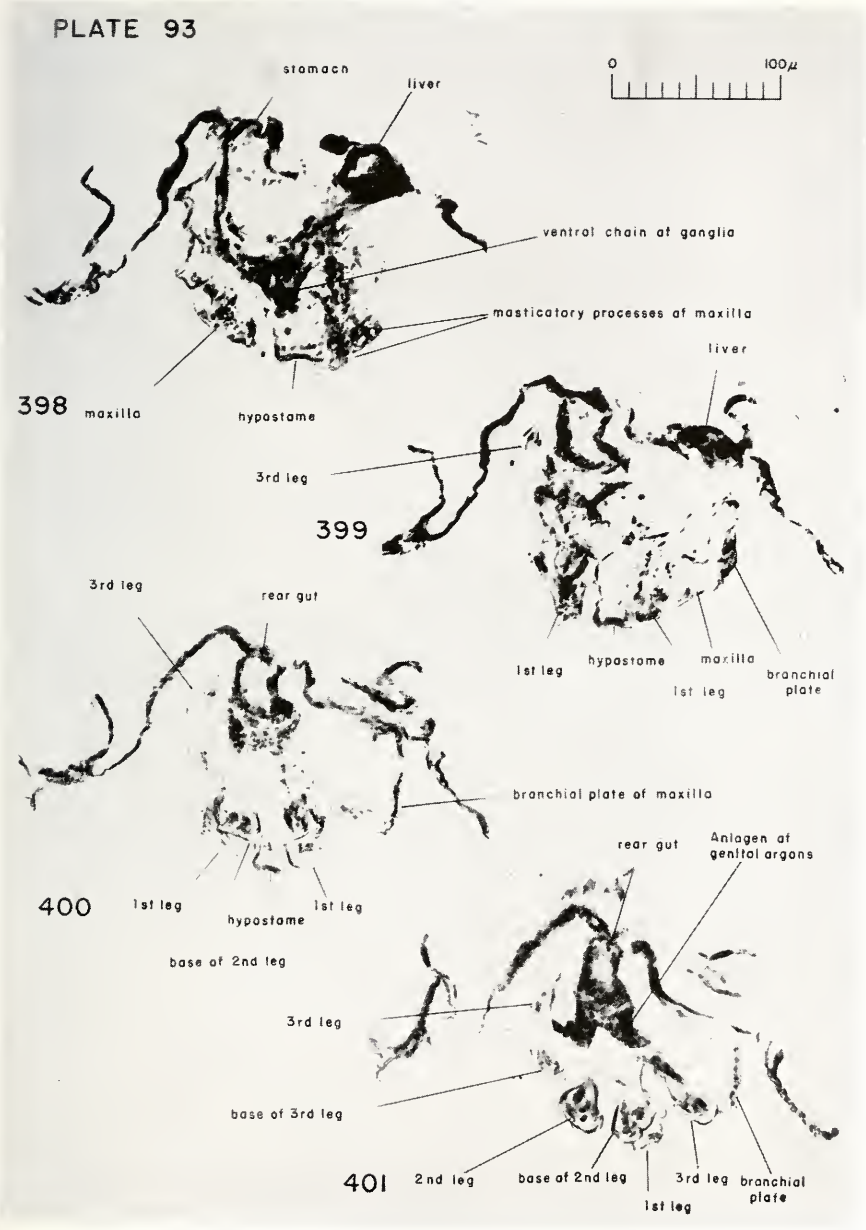


PLATE 93
0
100μ
stomach
liver
ventral chain of ganglia
masticatory processes of maxilla
398
maxilla
hypostome
liver
3rd leg
399
1st leg
hypostome
maxilla
branchial plate
1st leg
3rd leg
rear gut
branchial plate of maxilla
400
1st leg
hypostome
1st leg
base of 2nd leg
rear gut
Anlagen of genital organs
3rd leg
base of 3rd leg
401
2nd leg
base of 2nd leg
3rd leg
branchial plate
1st leg

Plate 94

Nos. 402-405. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. These sections follow those shown in Plate 93. This concludes the sequence of transverse sections which began on Plate 89.

PLATE 94

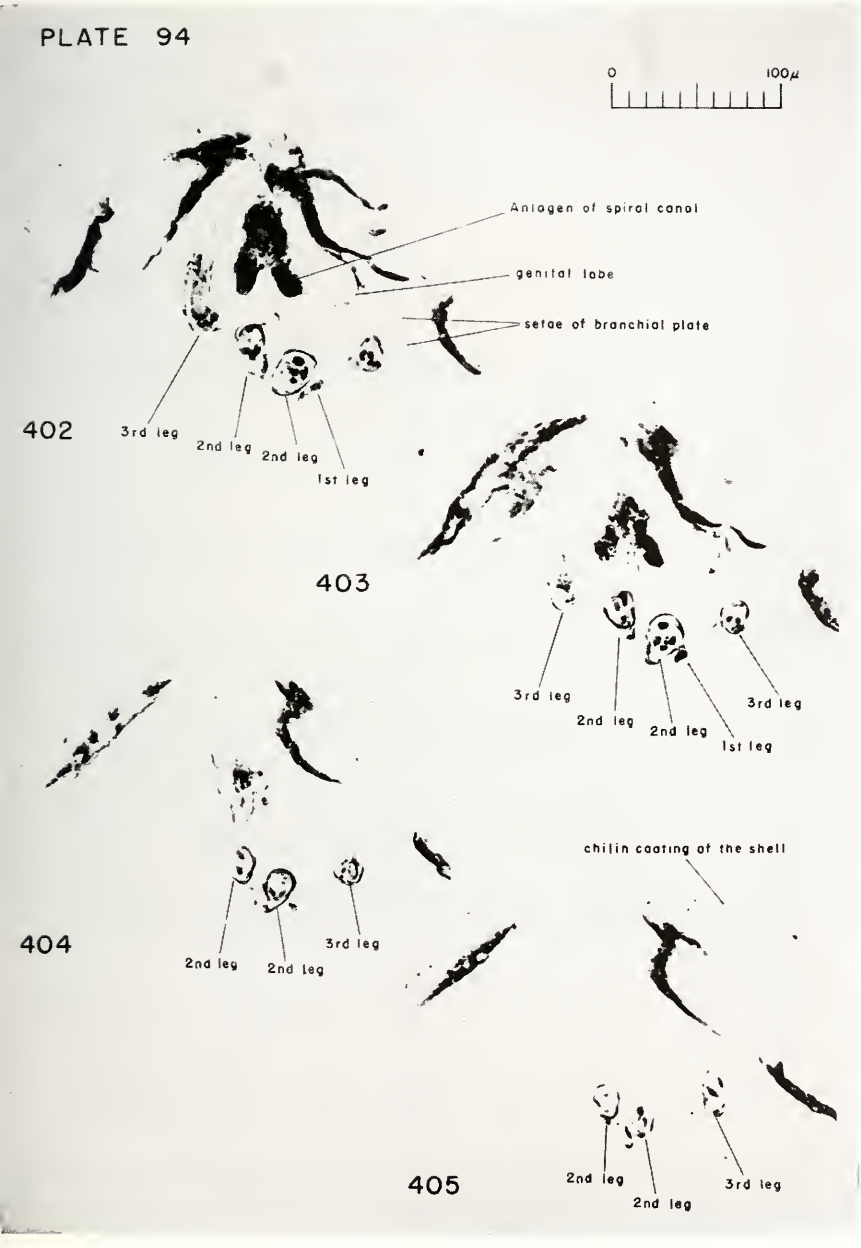

0
100μ
Anlagen of spiral canal
genital lobe
setae of branchial plate
402
3rd leg
2nd leg
2nd leg
1st leg
403
3rd leg
2nd leg
2nd leg
1st leg
3rd leg
404
2nd leg
2nd leg
3rd leg
chitin coating of the shell
405
2nd leg
2nd leg
3rd leg

Plate 95

Nos. 406-413. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. The sections progress from anterior to posterior.

PLATE 95

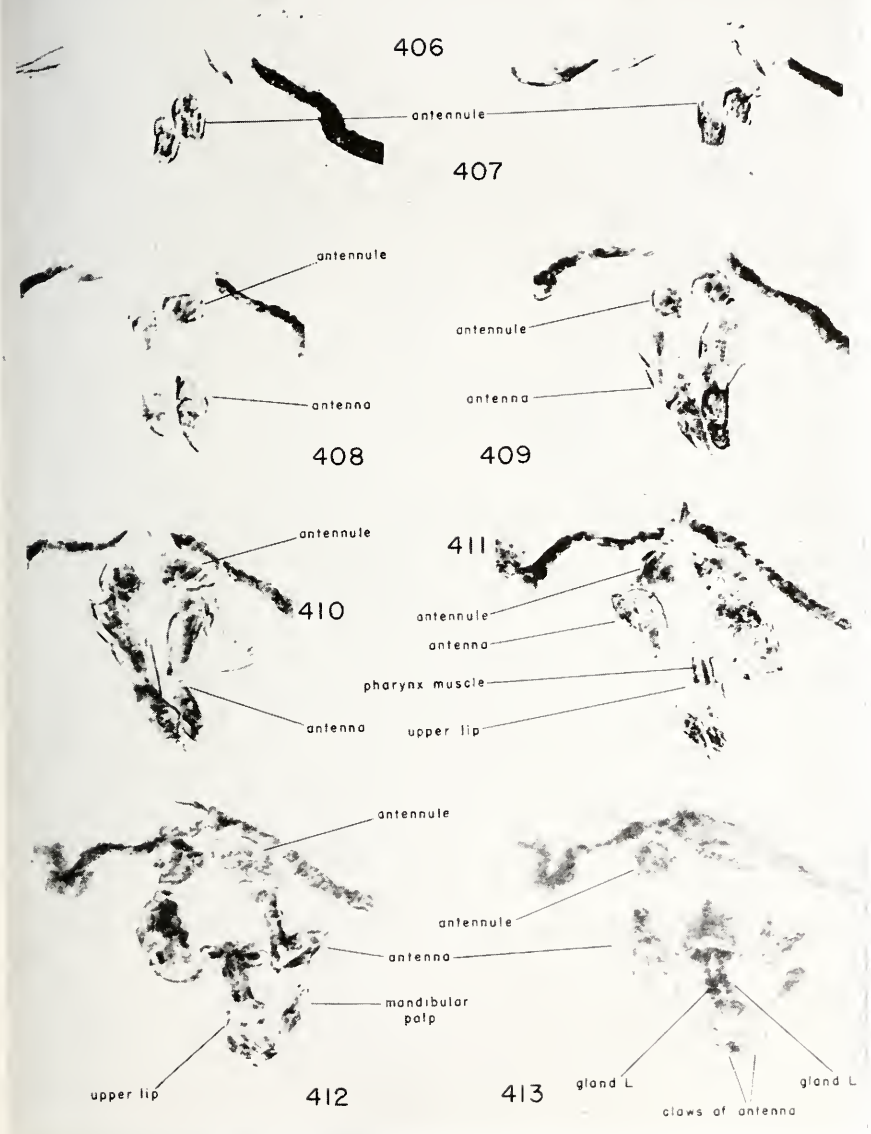
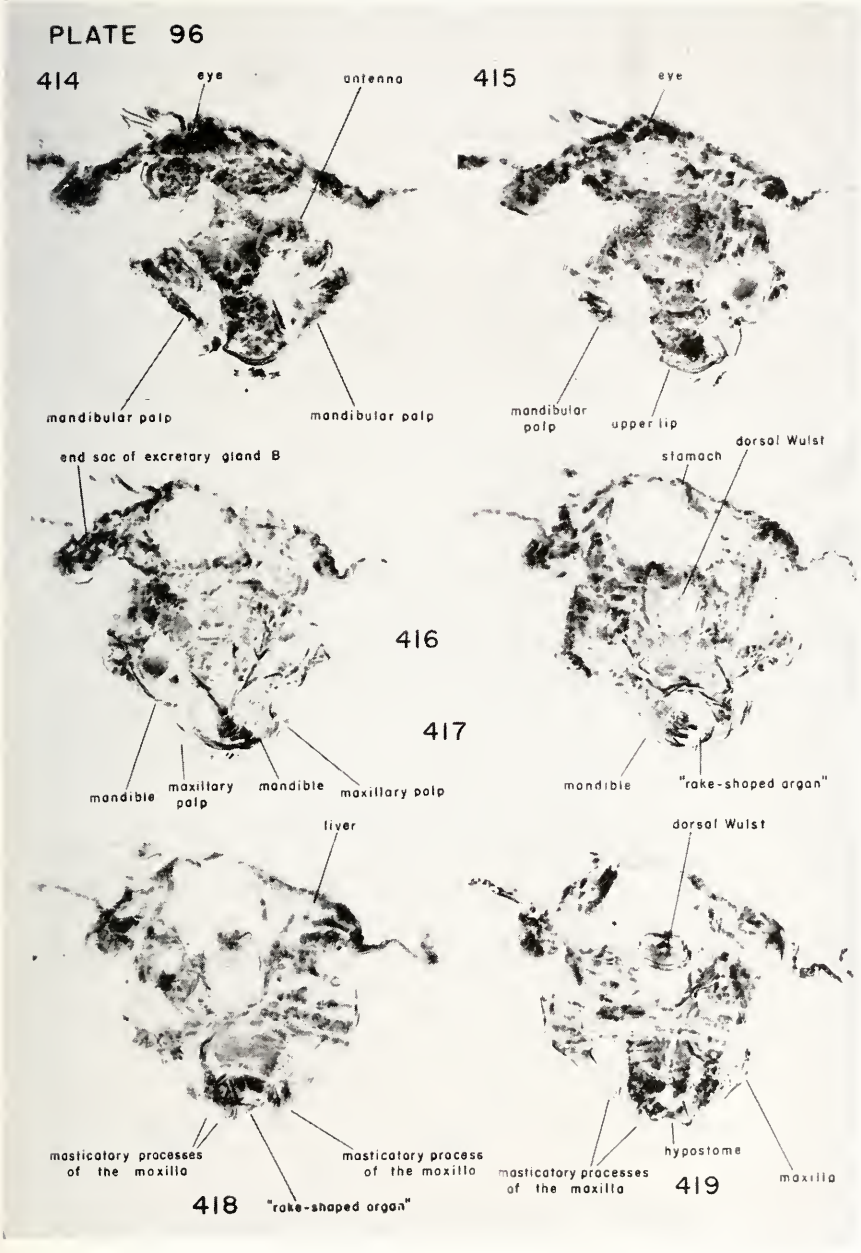

406
antennule
407
antennule
antenna
408
antennule
antenna
409
antennule
411
antennule
antenna
pharynx muscle
upper lip
410
antennule
antenna
antennule
antenna
mandibular palp
upper lip
412
antennule
gland L
gland L
claws of antenna
413

Plate 96

Nos. 414-419. Seventh instar, 10μ transverse sections, stained with Ehrlich's haematoxylin and eosin. These sections follow those shown in Plate 95, and conclude the sequence of transverse sections.

PLATE 96


414
eye
antenna
mandibular palp
mandibular palp
415
eye
mandibular palp
upper lip
end sac of excretory gland B
416
mandible
maxillary palp
mandible
maxillary palp
stomach
dorsal Wulst
417
mandible
"rake-shaped organ"
liver
masticatory processes of the maxilla
masticatory process of the maxilla
418
"rake-shaped organ"
dorsal Wulst
hypostome
masticatory processes of the maxilla
419
maxilla

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