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COPULATORY ADAPTATIONS IN OSTRACODS  
PART I. HEMIPENES OF *CANDONA*

BY

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7. Systematics and faunal analysis of a Lower Pliocene vertebrate assemblage from Trego County, Kansas, by Richard L. Wilson. Pages 75–126, with 17 text-figures.
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10. *Archaeosperma arnoldii*—a cupulate seed from the Upper Devonian of North America, by John M. Pettitt and Charles B. Beck. Pages 139–154, with 6 plates and 3 text-figures.
11. *Ameliacrinus benderi*, a new dicyclic camerate crinoid from the Middle Devonian Silica Formation in northwestern Ohio, by Robert V. Kesling. Pages 155–162, with 3 plates and 2 text-figures.
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# COPULATORY ADAPTATIONS IN OSTRACODS PART I. HEMIPENES OF *CANDONA*<sup>1</sup>

DON L. MCGREGOR<sup>2</sup> and ROBERT V. KESLING

**ABSTRACT**—Hemipenes of the living freshwater cypridid ostracod *Candona* consist of numerous elements, which are identified and described from dissections and microtome sections. In the relaxed position, the elements intricately fit together; in erection, they rotate and unfold to enable the male to copulate with the female in a posterodorsal mating position. Morphology of hemipenes and dimorphism of carapace are strongly interrelated. Dimorphism in *Candona* involves an enlarged posteroventral region in the male (to house the voluminous hemipenes) and a truncated posterodorsal region in the female (to facilitate mating). The same kind of dimorphism exists in fossil species of *Candona*, suggesting that form of sex organs and mating procedure, similar to that in extant species, developed early in the history of the genus and persisted during its evolution.

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## INTRODUCTION

ONLY THROUGH UNDERSTANDING THE BIOLOGY of their living descendants can many fossils be properly interpreted and correctly classified. This is true for Ostracoda, particularly the freshwater cypridids, such as *Candona*. In numerous species, the dimorphism is so strong that it masks taxonomic differences. The female may have a carapace that differs far more from that of the male in its species than from those of females in other species. Because dimorphism of the carapace has persisted through a long span of geologic time, paleontologists as well as zoologists seek to understand this feature in relation to the anatomy of the enclosed parts of the animal.

Investigation of living ostracods shows only minor sexual differences in appendages, nervous system, digestive tract, and glands. The dominant difference lies in the complicated sex systems of these small crustaceans.

Dimorphism of the carapace in *Candona* is directly related to that of the sex organs. The carapace is a protective armor for the whole

animal, closing around all organs and retracted appendages. The carapace of the male is larger than that of the female in the posteroventral region because it must accommodate the huge pair of hemipenes. In turn, the hemipenes must be of exceptional size and complexity because of the difficulty of copulation with a female whose organs are likewise set well within the enclosure of a bivalved carapace.

It seems to us, therefore, that investigation of dimorphism in fossil ostracods must start with a clear understanding of the hemipenes in living species, their functional morphology, and their operation. Furthermore, the heavily sclerotized elements of the hemipenes appear well suited for fossilization. Indeed, they may be present in washed residues from geologic strata, but discarded because they are not recognized.

Of the multitude of kinds of male genitalia in the animal kingdom, those of the cypridid ostracods must rank among the most complex. No zoologist has yet published an accurate description of these paired hemipenes. The state of our knowledge is demonstrated by the avail-

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able illustrations, most of which are clusters of twisted lines. Many drawings of the male ostracod show the hemipenes upside down.

Our poor understanding of these structures is not the product of perfunctory approach nor mediocre research. Rather, it stems from the nature of the organs themselves. Most cypridid adults are about one millimeter long. Although the male copulatory organs may constitute as much as one-tenth of the whole animal, they are still so small that dissection is difficult. In the relaxed position the organs lie entirely within the bivalved carapace. Even when the valves are opened for feeding, swimming, or walking, the genitalia are scarcely visible through the narrow gape. In the erect position assumed for copulation the elements of the hemipenes rotate and unfold at critical pivot points to extend forward to the paired vaginae of the female. The hemipenes are then obscured by the overlapping valves of male and female. Thus, the zoologist has little opportunity to observe the organs in living male cypridid ostracods.

Even when a hemipenis is cleanly excised and properly mounted, details are hard to discern. Completely void of muscles, the organ consists of a covering of chitinous elements and a filling of various kinds of connective tissues. The chitinous elements vary greatly in thickness, some tapering to a thin edge, and in the normal non-erect condition of the hemipenis they lie folded inside and alongside one another. The extent of soft tissues is also difficult to determine, since they have variable thickness as well as density. Hence, the hemipenes of *Candona* offer a special challenge in studies of functional morphology.

Inasmuch as *Candona* is one of the most successful of living ostracods, both from the number of species and from widespread abundance, we wish to study it intensively. Independently, we worked on the biology and anatomy of this genus for many years; together, we concentrated our efforts during the last year. We hope that other ostracods can receive the same attention in the near future, so that the degree and extent of copulatory adaptations can be more accurately assessed.

In part II of this series, we will review what is known of copulatory adaptations in living ostracods and draw some generalizations on the carapace-copulation relationships. Part III, the final in the series, will attempt to interpret the functional adaptations in carapaces of certain extinct Paleozoic ostracods having strong dimorphism. The ultimate goal of such endeavors is to interpret fossil ostracods morphologically and taxonomically.

#### ACKNOWLEDGMENTS

We thank Mr. Harold L. Allen for translating portions of the paper by Jensen (1904). Work by the senior author was supported in part by a National Institute of Health predoctoral fellowship (1-F1-GM-22, 970-01 and 02) from the Institute of General Medical Sciences. We appreciate very much the efforts of Mrs. Helen Mysyk in typing and Mr. Karoly Kutasi in photography. Professor E. C. Stumm and Professor C. A. Arnold critically reviewed the manuscript.

#### PREVIOUS WORK

Literature on the genus *Candona* is far too voluminous for comprehensive review in this study. Several studies cited below exemplify the terms formerly used for male genitalia and the taxonomic emphasis on certain internal elements of the hemipenis. Many ostracod specialists have studied and illustrated the complicated genitalia of male *Candona* and many terms have been used to describe various anatomical structures. Ironically, no author has yet presented an accurate detailed description of the paired hemipenes of *Candona*, even though the hemipenis frequently has been used as an important taxonomic character at the species level.

As early as 1870, Brady & Robertson discussed the "oblong lamina," "hook-shaped process," and "outer tortuous and spinous or hook-like appendages" in the "copulative organs" of *Candona hyalina* Brady & Robertson. Later, Vávra (1891) described the male genitalia of *Candona* and *Notodromas* and discussed (p. 24) the capsule containing a basal part and two wing-formed appendages with hook-like structures and chitinous outgrowths. Turner (1895) referred to the "copulative organ" of *Candona* and *Notodromas*; both Vávra and Turner stated that the "copulative organ" of *Notodromas* was more complicated than that of *Candona*. Hartwig (1900) employed the term "penis" in reference to *Candona brevis* G. W. Müller (= *C. lobipes* Hartwig).

Jensen (1904) reviewed several earlier studies on the genitalia of male and female cypridid ostracods but merely noted the complicated and little understood structure of the "copulationsorganet." In 1909, Vávra illustrated the "penis" of *Candona neglecta* Sars in the relaxed, non-copulatory position, showing the seminal tract of the hemipenis, and the outer, middle, and inner lobes.

Müller (1912) used the term "penis" and emphasized the outer, middle, and inner lobes as characters of taxonomic significance. Alm

(1916) however, stressed the outer process ("äusseren Fortsatz") of the "Copulationsorgan" and the prehensile palps of the first pair of legs in differentiating living species. Sars (1925) discussed the "terminal lappet extending upwards at almost a right angle to the axis of the copulative appendage" of several *Candona* species; this "terminal lappet" presumably is the "outer" or "lateral" lobe of most authors. Sars also illustrated, though sometimes erroneously, the seminal tract of the hemipenis.

In 1926, Klie illustrated the internal elements of the hemipenis of *Candona reducta* Alm by a series of twisted lines. In subsequent (1933, 1938, 1939) works, however, he identified the "innerer," "mittlerer," and "äusseren Fortsatz" in the "Kopulationsorgan," in his drawings of which the duct and middle lobe (see our text-fig. 10) are often difficult to discern as separate structures. Klie attributed great taxonomic value to the three lobes of the hemipenis and the palps of the first pair of legs.

Considerable internal anatomical detail was figured by Furtos (1933) in the original illustration of the hemipenis of *Candona ohioensis* Furtos. The sperm duct and glans (see our text-fig. 16) were incompletely shown for *C. ohioensis* and the terms "terminal and lateral" were substituted for "outer," "middle," and "inner" lobes. As we understand her statements, Furtos (1935) employed the term "base" to include what we call the inner proximal, outer proximal, and distal shield areas.

Hoff (1942) continued the usage of the terms outer, middle, and inner lobes, but did not illustrate adequately other details of the seminal tract. He used the term "penis" to refer to one or both hemipenes. Bronstein (1947) usually avoided illustrating the complex internal structure of the hemipenis, but frequently figured an outline of the hemipenis showing a portion of each of the three lobes.

Kesling (1956, p. 93) used the term "penis" and remarked: "The male penis is strongly modified in the ostracod carapace. . . . Each of the penes has lateral chitinous shields and three lobes inside. Only the front end is joined to the body." Later, Kesling (1957) studied the paired Zenker's organ in *Candona suburbana* Hoff and again used the term "penis." In the latter study, illustrations of the hemipenis, reconstructed from microtome sections in which the hemipenis was accidentally rotated 180°, were figured upside down. The terms "penis" and "penes" were also used somewhat interchangeably in a later study (Kesling, 1965).

Petkovski (1958 to 1962) relied heavily on the genital lobes of females and the hemipenes and prehensile palps of males in describing new

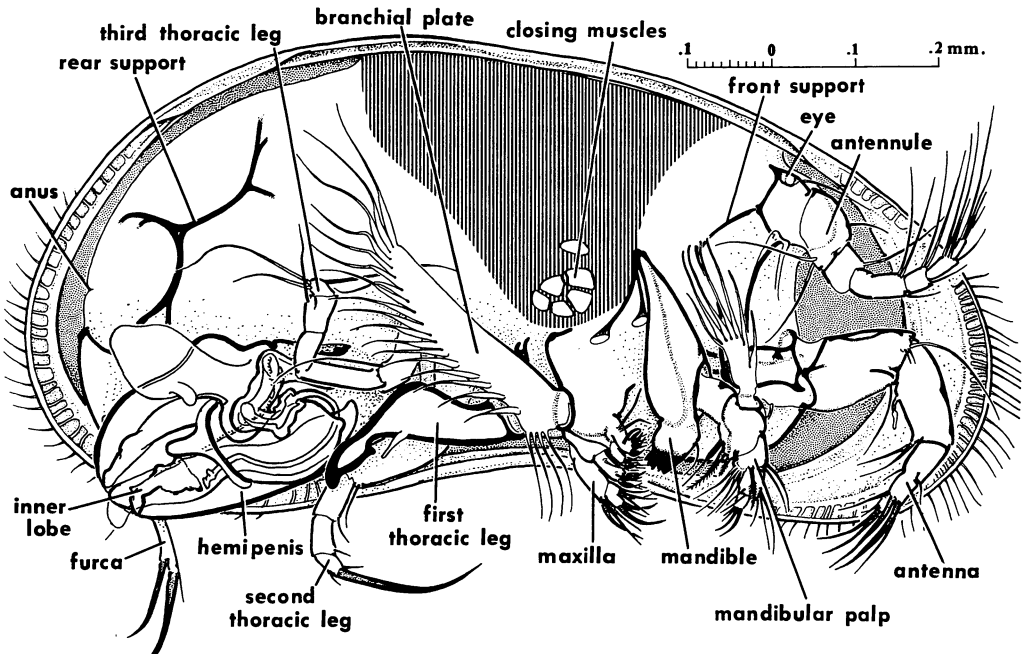
species of *Candona*. Taxonomic emphasis was placed on the middle lobe, especially the distal shank (refer to our text-fig. 14). Petkovski carefully illustrated variations in the distal shank of numerous *Candona* species; all three lobes general were figured in some detail. Fox (1966) recently commented on "the external process of the penis" in *Candona protzi* Hartwig, presumably in reference to the outer lobe.

Kesling (1965) summarized current information concerning the morphology, and presumed function and operation of the hemipenes of *Candona suburbana* Hoff. He noted (1965, p. 34) the absence of muscle scars on the valves associated with the "copulation muscles." In addition, Kesling (1965, p. 38) recognized the thick-walled enlargements of the seminal tract (sleeves A, B, and C; see our text-fig. 16), but did not discover their functions. The middle and outer lobes were suggested to be possible sensory structures functioning to insure insertion of the "inner-lobe" into the vagina of the female. Further consideration of the latter study is presented in subsequent sections of this paper.

#### GENERAL MALE AND FEMALE ANATOMY IN *CANDONA*

For discussion here, only a brief sketch of anatomy is necessary. More complete description is given by Kesling (1965, p. 4-38). From the top of the bivalved carapace, the body hangs down as a chitin-covered sac. Some rigidity is imparted by the front and rear supports (text-figs. 1, 2), frameworks of embedded chitin rods. In front and behind the mouth are two strong chitinous structures, the fixed upper lip and the movable hypostome. Both are reinforced with chitin rods. Through the middle of the soft parts, closing muscles extend from one valve to the other. Around and above these muscles, a flap of tissue extends out and down on either side as the hypodermis, lining the valves.

To the body are attached seven pairs of appendages, a pair of furcae, and the genitalia. Appendages can be divided into cephalic and thoracic groups. The cephalic group includes the antennules (directed forward from the forehead), antennae (directed forward from the upper lip), mandibles (vertical, set on either side of the mouth), and maxillae (directed down and forward along sides of the hypostome). The uniramous antennules are sensory balancing organs in *Candona*. The antennae are walking appendages. The protopod of the mandible has masticating teeth at the end and the endopod forms a mandibular palp for raking food to the mouth (text-fig. 1). The



TEXT-FIG. 1.—*Candona suburbana* Hoff. Labeled sketch of male with right valve removed to expose appendages and hemipenis of right side. Strongly sclerotized parts of appendages shown in solid black. Vertically-striped area represents approximately the section through the soft tissues connecting hypodermis of right valve to body. Right hemipenis in normal retracted, non-copulatory position. Secondary setae on antennules and branchial plate of maxilla not shown. Maxilla turned slightly toward the rear and mandible slightly toward the front in order to show their essential features. Scale in upper right corner.

setiferous endites of the maxilla gather food and shove it forward into the mouth, but the branchial plate (exopod) beats alongside the body for respiration (text-fig. 2).

The thoracic appendages are three pairs of legs attached to the lower part of the body in the posteroventral region. Highly specialized, each pair is designed for a particular function: the first thoracic legs are accessory feeding structures, the second are walking legs, and the third are supple cleaning devices. At the posteroventral end of the body, just below the anus, the paired furcae pivot on a process of the rear support. Each bears two claws, but the uses of these structures needs further investigation. It would seem that the furcae aid in locomotion, keep the region clear of debris, and perhaps play a role in copulation. The genitalia lie between the furcae and the thoracic legs.

**Male appendages.**—Aside from minor differences in proportions and size, the antennules, mandibles, maxillae, second thoracic legs, third thoracic legs, and furcae are alike in male and female. The antennae and first thoracic legs are dimorphic. The male antenna has the second podomere of the endopod nearly divided by an indentation at the rear and an articulation at the front. On the middle of the inner

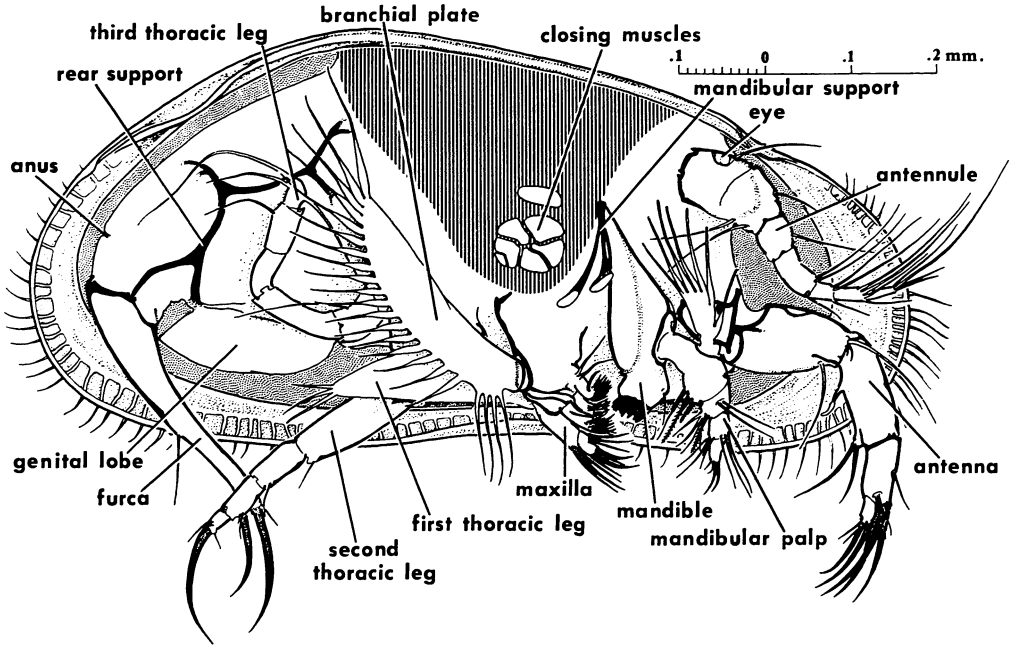
face, this podomere bears two large club-shaped setae, the so-called "male setae" (see text-fig. 3).

The endopod of the first thoracic leg in the male forms a clasping organ. It appears to seize hold of the rear edge of the female valve in copulation. In all species of *Candona*, the left and right endopods differ (compare text-figs. 1 and 3).

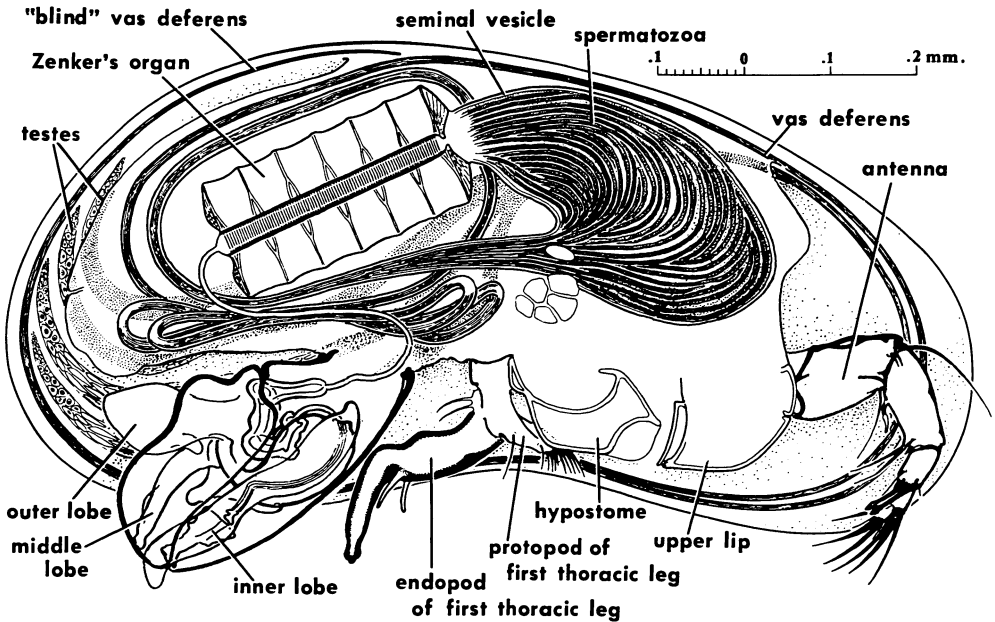
**Female appendages.**—The female antenna shows no constriction or tendency to divide in the second podomere of endopod. In place of the male setae, the female has a scale with four thin setae.

The endopod of the first thoracic leg in the female is developed as a long, thin-walled, sausage-shaped process with three setae extending from the tapered distal end (text-fig. 2). Its use is unknown.

**Male sex system.**—The sex system of the male *Candona* consists of two halves, each complete in itself. Right and left halves are not connected. Sperm originating on the right side are ejected through the right hemipenis. Each half of the system contains four elongate testes, winding vas deferens, a distended seminal vesicle, a voluminous Zenker's organ, and an enormous, complicated hemipenis (text-fig. 3).



TEXT-FIG. 2—*Candona suburbana* Hoff. Labeled sketch of female with right valve removed to show appendages and genital lobe of right side. Strongly sclerotized parts of appendages shown in solid black. Vertically-striped area represents approximately the section through the soft tissues connecting hypodermis of right valve to body. Secondary setae on antennules and branchial plate of maxilla not shown. Maxilla turned slightly toward the rear and mandible slightly toward the front in order to show their essential features. Scale in upper right corner.



TEXT-FIG. 3—*Candona suburbana* Hoff. Labeled sketch of male with right valve and most appendages removed to show sex system. Inner face of left hemipenis, left half of Zenker's organ and left palp of first pair of legs shown. Hemipenis in relaxed, non-copulatory position, and lowered slightly from normal retracted position. Scale in upper right corner.

The four testes on each side are embedded in the hypodermis. Even after the hypodermis is pulled out, traces of the testes can be seen through the valve. The four are subparallel, curving downward along the posterior margin of the valve and thence forward and upward to a junction above the closing muscles (text-fig. 3). Developing sex cells can be traced through the course of each testis, beginning in the syncytium as irregular bodies and becoming nucleated, discrete, polygonal bodies. These change into elongate thread-like sperm, which increase in diameter to the junction of the testes.

The vas deferens is formed by the union of the four testes. Soon after entering the body, this conduit re-enters the hypodermis in the anterodorsal region. Then it extends ventrally parallel to the border of the hypodermis, around the posterior end, and terminates in the posterodorsal region. It passes alongside the testes, for which reason some investigators early reported five testes. This is the so-called "blind section" of the vas deferens (text-fig. 3). In reality, this section is not blind, for it has an exit back along the ventral part in a Y-shaped junction, from whence it extends forward and up to re-enter the body in the anterodorsal region. The spermatozoa of ostracods are among the largest known in the animal kingdom by actual size, each longer than the carapace of the animal, and it has been suggested that the "blind section" of the vas deferens permits them to change direction. This remains to be determined.

The vas deferens extends then along the

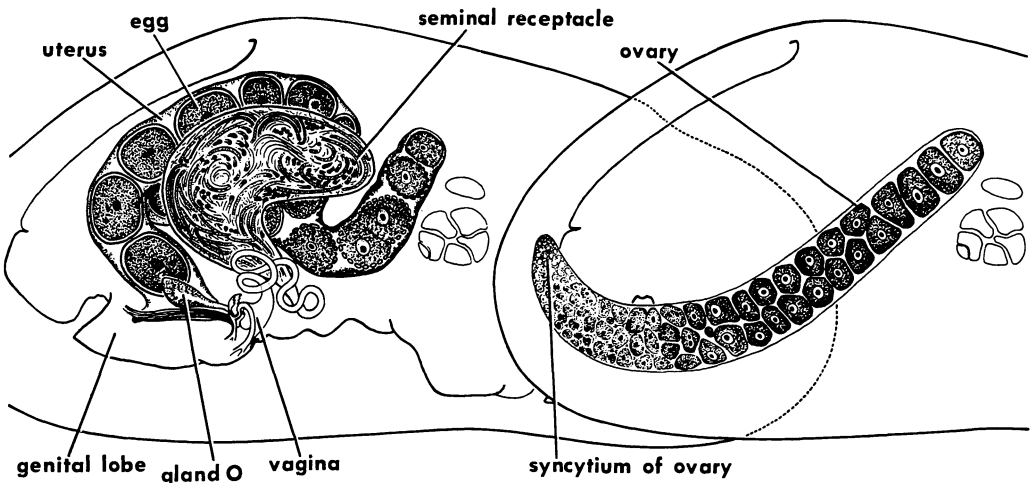
dorsal border, encircles the Zenker's organ, loops back and forth in the ventral part of the body, and enlarges rapidly to form the seminal vesicle.

The paired seminal vesicles nearly fill the anterodorsal region of the body, distended with many spermatozoa. The large lunate vesicle goes anteriorly nearly to the forehead before recurving to empty into the Zenker's organ. Spermatozoa lie in some disarray, but generally follow the outer wall of the seminal vesicle.

Huge seminal pumps, the paired Zenker's organs, fill most of the posterodorsal part of the body. In *Candona*, each of these complex organs is normally composed of seven wreaths of chitinous spines, although a specimen with eight was discovered (Kesling, 1957, p. 175-182). These wreaths are visible through the carapace. Each wreath has numerous spines directed radially. Through the middle of Zenker's organ passes the central tube. A multitude of tiny muscles lace the chitin spines together and by their contractions produce a pulsation to pump spermatozoa through the central tube. The posterior end of Zenker's organ is connected by a narrow tube which curves down and forward to the hemipenis.

Measurements in *Candona suburbana* by Kesling (1965, p. 41) reveal that the male sex system occupies about one-third the volume of all the soft parts of the animal.

*Female sex system.*—Like that of the male, the female sex system consists of two unconnected halves. Each half consists of an ovary, uterus, genital lobe, uterine opening, vagina, and seminal receptacle (text-fig. 4).



TEXT-FIG. 4.—*Candona suburbana* Hoff. Labeled sketch of female with appendages and other organs removed to show essential features of sex system. Right overlay shows right ovary within hypodermis. Left sketch shows left half of sex system as seen from right side. Outlines of closing muscles shown slightly anterior of sex organs on each sketch (compare with text-fig. 2).



The ovary lies in the hypodermis, in nearly the same position as the testes in the male. Progressive stages of oogenesis can be traced from the syncytium to the uterus. Oocytes in the syncytium are irregular cells. After acquiring nuclei, some cells atrophy and finally disappear. These so-called nurse cells are thought to supply vitelline content to the successful eggs. From angular bodies, the eggs assume a more or less rounded shape by the time they enter the uterus.

The uterus is a large duct for reception and development of the eggs pushed forward from the ovary. The terminal section of the uterus is a large tube curving backward and down to the uterine opening. It is in this section that the eggs acquire a cuticular shell.

The genital lobes are the external genitalia. Each is a soft-walled ellipsoidal body set under the body between the furca and the thoracic legs. The uterine opening lies near the inner middle of the lobe and the vagina near the front. Each vagina has a complex chitin rim and muscles to shift its angle. Internally, the vagina tapers to a winding canal leading into the seminal receptacle.

In bred females, the seminal receptacles are filled with spermatozoa. No connection has been discovered between the receptacle and the uterus. Apparently, the receptacle ends blindly, and spermatozoa pass back through the vagina and into the uterine opening. How this is accomplished remains unknown.

In *Candona suburbana* Hoff, the female sex system occupies only about half as much space as the male system (Kesling, 1965, p. 41).

#### PROCEDURES AND TECHNIQUES

Microtome sections of *Candona suburbana* Hoff and needle dissections of *Candona ohioensis* Furtos were used in examining male and female genitalia. These preparations provided a reference basis for identifying anatomical structures whose function and operation were revealed by other techniques.

Frontal, sagittal, and transverse microtome sections 10  $\mu$  thick and stained with Ehrlich's haematoxylin and eosin, permitted detailed examination of muscle attachment and sclerotization of male genitalia. However, hemipenis orientation and certain anatomical features occasionally were distorted by the sectioning process, making anatomical reconstruction difficult.

Dissection of the excised hemipenes of *Candona ohioensis* and *Candona rawsoni* Tressler yielded morphological information which complemented that gained through microtome sections of *C. suburbana*. As a result, some of our

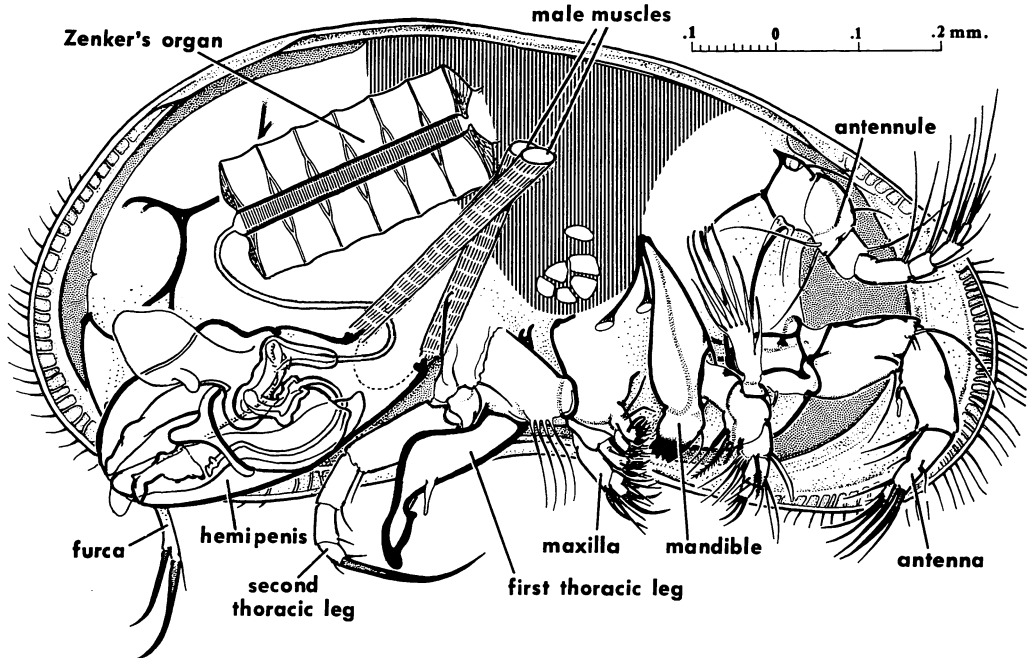
earlier interpretations of the function and operation of various elements were modified extensively. Component parts of the non-erect hemipenis were excised under highest (120 $\times$ ) magnification of a dissection microscope, using minute needles mounted on long wooden rods. All dissections, excluding muscles, were made in glycerine, in both transmitted and reflected light. Male copulatory muscles were excised in alcohol fixatives. Specimens treated with 1-5 percent sodium hypochlorite solutions allowed observation of muscles through the transparent carapace. Temporary glycerine mounts and permanent mounts in Turtox CMC-S stain-mountant and Canada balsam were examined under a compound microscope and photographed for viewing in two dimensions and stereoscopic pairs (pls. 1-3).

Laboratory cultures of *Candona ohioensis* and *C. rawsoni* were maintained for direct observation of mating behavior. Unfortunately, little opportunity was afforded for viewing the process of hemipenis erection and retraction through microscope observation of mating pairs.

A simple technique was developed for inducing erection of the hemipenis in animals under microscopic examination. This technique provided a convenient means of relating structure to function and facilitated removal of the internal elements of the hemipenis. Dissection of the non-erect hemipenis proved a difficult and arduous task.

Physical manipulation of the male copulatory muscles in partially anesthetized individuals stimulated those muscles to contract and usually resulted in hemipenis erection. Dilute solutions of Tricaine Methanesulfonate (MS-222) or alcohol were added to the culture media to relax the adductor muscles which close the valves. Dissecting needles then were inserted between the ostracod valves for gentle teasing of the male muscles. Manipulation of the muscles near their junction with the hemipenis was most often successful in effecting erection.

Induced erection of the hemipenis often was followed by rapid retraction before detailed observations of the organ could be made. The difficulty was remedied by inducing erection of the hemipenes before the organs were rotated 180 degrees to the pre-copulatory position. The hemipenes thus were forced to unfold in a posterior direction rather than anteriorly and were maintained in the erect state by forcibly closing the valves or by rapid addition of an excess of anesthetics and preservatives. Progressive stages of hemipenis erection, from relaxed to fully erected organs, were studied with the above techniques. Physical manipulation and



TEXT-FIG. 5—*Candona suburbana* Hoff. Labeled sketch of male with right valve removed to expose appendages, genitalia, and male muscles of right side. Third thoracic leg, and branchial plate of maxilla of right side not shown. Male muscle separation exaggerated for clarity. Hemipenis in non-erect, non-copulatory position. Scale in upper right corner.

dissection of the major internal elements in the erected hemipenis provided additional information concerning critical pivotal points and the mechanism of erection.

Mating ostracods occasionally were preserved in the original copulatory posture through rapid introduction of hot water, strong preservatives, or excess anesthetics to the culture media.

#### ELEMENTS OF HEMIPENIS

*swivel*—highly flexible junction of the hemipenes with the body, acting as a pivot in erection (text-figs. 3, 5, 7, 9–11; pl. 1, fig. 3; pl. 2, fig. 4; pl. 3, figs. 2, 5). In bringing the hemipenes from the rear to the front, this section can be twisted through 180 degrees by the action of the male muscles.

*proximal shield*—inner and outer protective

sheaths around the proximal part of each hemipenis, joined along their ventral edges (text-figs. 10–12; pl. 3, fig. 5). The inner proximal shields of the two hemipenes meet along a median suture in their proximal section. In the outer proximal shield, the proximal half is reinforced by a frame of sclerotized rods, but the distal half is thin and highly flexible. The inner proximal shield has a frame of variously sclerotized rods and forms a pivot with the distal shield.

*distal shield*—a movable, sclerotized sheath pivoted to the inner proximal shield (text-figs. 10, 14; pl. 1, fig. 2; pl. 2, figs. 1, 5; pl. 3, fig. 5). The outward-facing surface of the distal shield bears sclerotized rods outlining a main longitudinal groove, which appears to guide the shank of the middle lobe. In

#### EXPLANATION OF PLATE 1

Figure 1,  $\times 80$ ; figures 2 and 3,  $\times 100$

FIGS. 1–3—*Candona ohioensis* Furtos. Specimens in glycerine as seen by transmitted light. 1, male with right valve removed; hemipenis rotated to opposite side, but in retracted, pre-copulatory position. 2, 3, fully erect excised hemipenes (rotated to opposite sides of body) as seen posteroventrally, with focus on outer and inner lobes (near side of specimen) and on male muscles and shank of middle lobe (far side); anterior is downward; compare with outer lateral view of left hemipenis shown in text-figure 10 (lower); glans extruded beyond distal margin of shields.

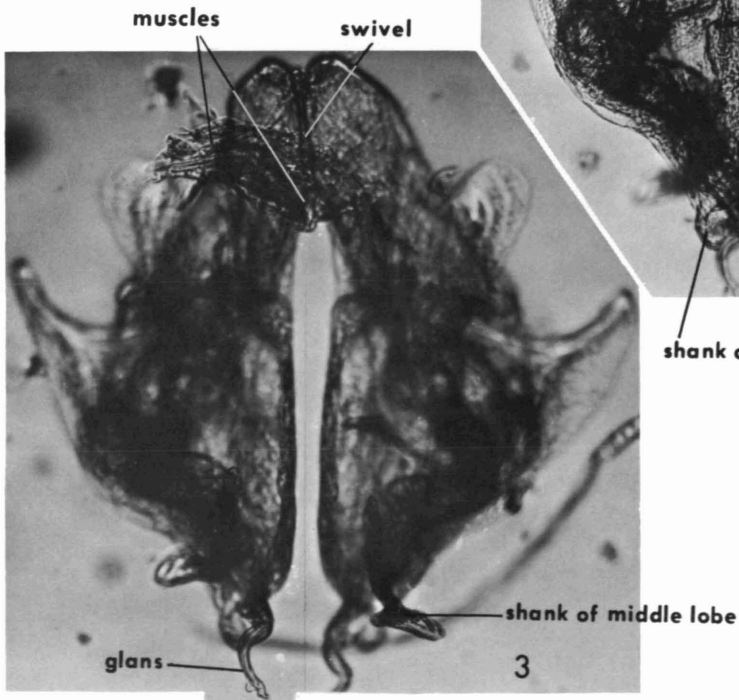
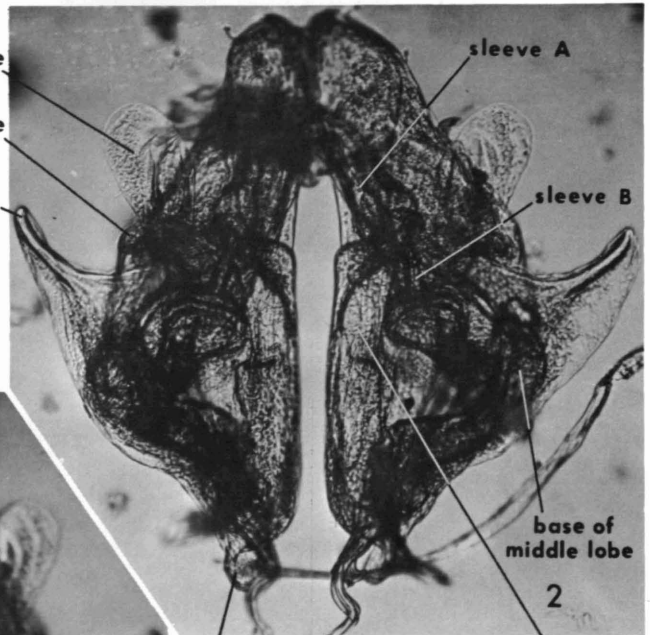
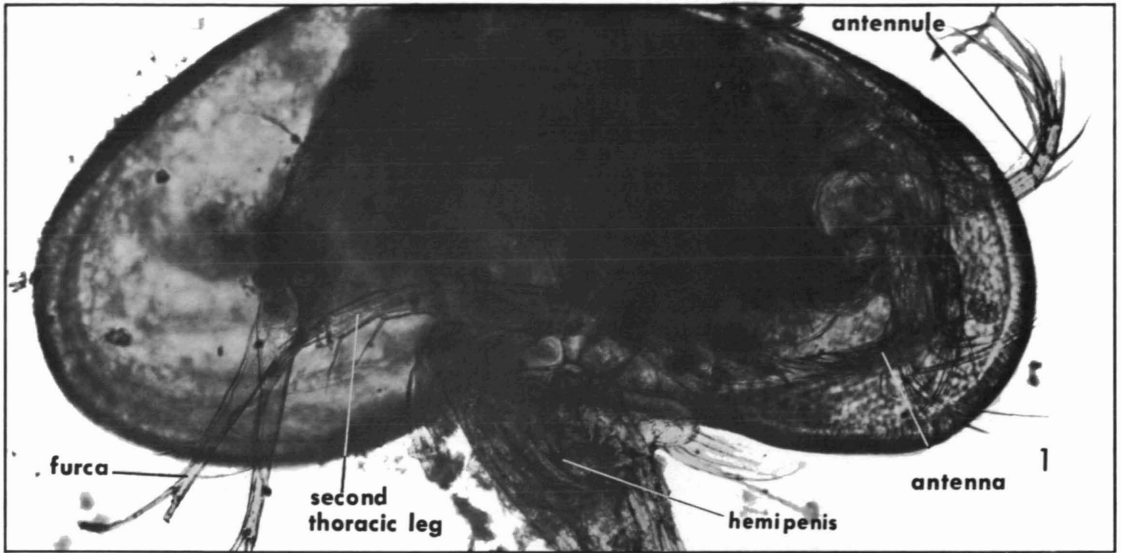


PLATE 1

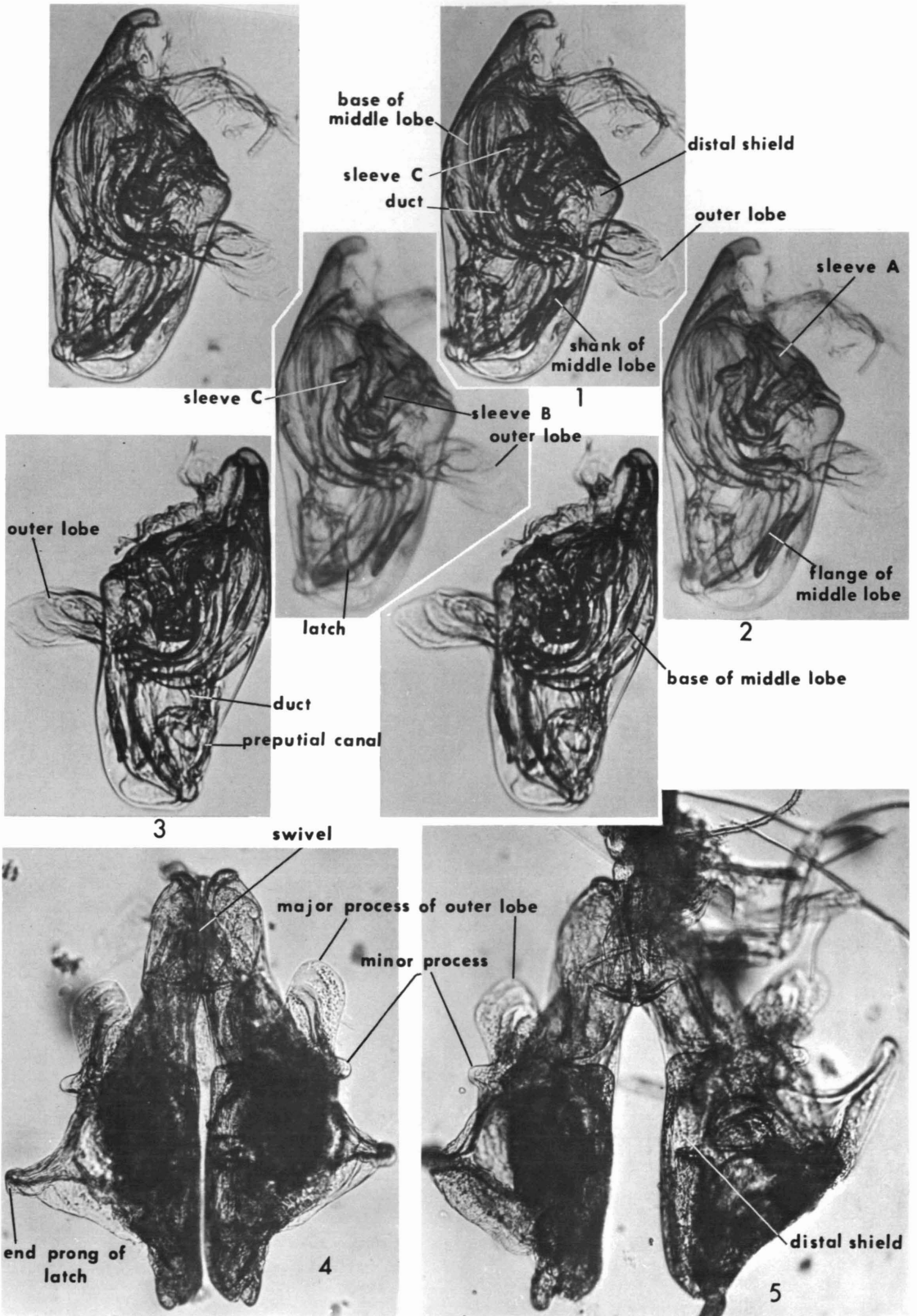


PLATE 2

erection, this shield swings forward to allow extension of the middle and inner lobes and protrusion of the glans.

*latch*—an unusual elastic Y-shaped structure which serves to fasten the lobes in place in the relaxed position and to release the lobes in the erect position (text-figs. 10, 13; pl. 1, fig. 2; pl. 2, figs. 2, 4; pl. 3, figs. 3–4). The two proximal prongs are strong and springy. The dorsal prong merges with the edge of the outer proximal shield; the middle of this prong is connected by a short flexible band of chitin (text-fig. 13; pl. 1, fig. 2) to the minor process of the outer lobe. The ventral prong of the latch is pivoted to the ventral edge of the base of the middle lobe. In the relaxed position the end prong is directed distally in each hemipenis, but in erection it flips over to point outward and proximo-ventral.

*outer lobe*—a large lobe of uncertain function, covered by thin chitin and connected only at its base, which rotates nearly 180 degrees in erection (text-figs. 3, 8, 10, 13; pl. 1, fig. 3; pl. 2, figs. 1–5; pl. 3, fig. 2). Of the three lobes in each hemipenis, this one is “outer” in the sense of being farthest from the midplane of the animal; in the relaxed position, it is the closest lobe to the venter of the body. The outer lobe has the shape of a mitten, in which the major process corresponds to the “hand,” the minor process to the “thumb,” and the base to the “wrist.” In the relaxed position the major process is directed dorsally and the base lies in a pocket between the two proximal shields, being inside the confluence of the dorsal prong of the latch and the edge of the outer proximal shield (text-fig. 13). In erection the minor process of the outer lobe is pulled by its attachment to the dorsal prong of the latch. The base acts as a hinge and the lobe is swung 180 degrees, so that the major process is directed ventrally and the base lies outside the margin of the outer prox-

imal shield. Possibly, the outer lobe is a sensory structure, but its function has not been proved.

*middle lobe*—a lobate structure consisting of a tapering linguiform base and a subcylindrical shank (text-figs. 10, 14; pl. 1, figs. 2, 3; pl. 2, figs. 1, 3; pl. 3, figs. 1–3, 5) and playing an important role in the erection process. The large, broad, flattened proximal part of the base lies in the ventral part of the hemipenis, tangent to the junction of the two proximal shields; the distal part of the base tapers and curves dorsally. The shank joins the base at a right angle and lies in a groove on the inner surface of the distal shield. The shape of the middle lobe is little altered in erection, but the position is much affected. As the hemipenis is unfolded, the shank retains its relationship to the distal shield and the base slides distally along the junction of the two proximal shields. The ventral prong of the latch, pivoted to the leading edge of the base of the middle lobe, is forced distally and brought under strong tension until finally it flips over. In the erect position, the base of the middle lobe, lying across the hemipenis, seems to serve as a prop to keep the distal shield extended (text-fig. 8). The shank bears a flange, more strongly developed in some species than in others, which in the relaxed position appears to act as a stop for the dorsal edge of the outer proximal shield.

*inner lobe*—a long, distally bifurcated lobe which contains the terminus of the seminal tract (text-figs. 10, 15; pl. 1, fig. 2; pl. 3, figs. 2, 4, 5). Distally the lobe divides into a shank and a distal process. In the relaxed position (text-fig. 1) the distal process lies outside the shank, but in the erect position (text-fig. 8) it swings upward away from the shank. The tapering base of the inner lobe lies between the somewhat larger base of the middle lobe and the inner proximal

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EXPLANATION OF PLATE 2

All figures  $\times 100$

FIGS. 1–5—*Candona ohioensis* Furtos. 1–3, stereograms of left and right hemipenes stained and mounted in Turttox CMC-S medium; 4–5, views of two pairs of hemipenes unstained in glycerine; all viewed by transmitted light. 1–2, outer face of relaxed left hemipenis with focus on outer lobe (middle of specimen) and on latch (near side); anterior is upward and ventral is left. 3, outer face of relaxed right hemipenis; anterior is upward and ventral is right. 4, 5, nearly erect hemipenes (glans not fully everted) as seen posteroventrally, showing connection of outer lobe to dorsal prong of latch; anterior is ventral.

shield (text-fig. 10). It is elongate and not as heavily sclerotized as the middle lobe. The seminal duct and preputial canal pass through the base and distal process of the inner lobe. The glans is retracted in the inner lobe in the relaxed condition and extruded from it in the erect position.

*sleeves A, B, and C*—strongly sclerotized structures around the proximal part of the seminal tract in the hemipenis (text-fig. 16; pl. 1, fig. 2; pl. 2, figs. 1, 2; pl. 3, figs. 2, 4). The three sleeves are joined in series. Sleeve A is subcylindrical, distally expanded. Sleeve B is cylindrical. Sleeve C is geniculate, expanded in its distal part. Sleeve A is innermost, lying close to the inner proximal shield; sleeve B is median; and sleeve C is outermost, its distal border overlapping the base of the middle lobe. In the relaxed position, sleeve A lies diagonal across the proximal part of the hemipenis; sleeve B forms a right angle with sleeve A; and sleeve C joins sleeve B at a right angle and bends back so that its distal part is parallel to sleeve B and directed toward the swivel (text-fig. 10). In erection, sleeves A and B form a straight passage and sleeve C is turned somewhat distally. The three sleeves seem to shove the shank of the middle lobe distally and to push the duct into the inner lobe, thereby forcing the glans out from the preputial canal.

*duct*—narrow seminal tube from sleeve C to the glans (text-fig. 16; pl. 2, figs. 1, 3). The distal part of the tube lies in a preputial canal in which it can be retracted or extended.

*glans*—sclerotized tip of the seminal tract, retracted in the inner lobe when relaxed or extruded from it in erection (text-fig. 16; pl. 1, figs. 2, 3; pl. 3, fig. 5). Not enough species have been studied in detail to discover if the form of the glans is a specific character.

*preputial canal*—tubular passageway in the inner lobe permitting the duct to freely retract or extrude (text-fig. 16; pl. 2, fig. 3; fig. 4). In the relaxed position, the glans lies inside the preputial canal.

#### ERECTION AND RETRACTION

*Erection*.—Erection of the hemipenis in *Candona* was reviewed recently by Kesling (1965). He emphasized the important role of the male muscles (text-fig. 5) in the erection process and suggested (1965, p. 38) that the chitinous hemipenes are "intricately hinged" so that erection results from pressure caused by contraction of the "copulation muscles." As the name implies, the paired male muscles are present only in males of *Candona* and unfortunately leave no muscle scar trace on the valves. These muscles were formerly referred to as "ventral muscles" (Kesling, 1956, p. 92, 115) and "copulation muscles" (Kesling, 1965, p. 34).

The male muscles control most of the action of the hemipenes during copulation. Knowledge of the location and operation of these muscles is, therefore, of great importance in understanding the mechanism of erection. A pair of these large, powerful muscles are attached to each valve at a point slightly posterior and dorsal to the closing muscles. They pass posteroventrally from the valves in the form of an inverted "V" (shown exaggerated in text-fig. 5 for clarity) and connect through fine thread-like extensions to the highly flexible chitin at the proximal end of the hemipenis. When the hemipenis is in the relaxed or non-copulatory position (as in text-fig. 5), one muscle is attached to the proximoanterior part of the swivel and the other to the proximoposterior part. Although these muscles are always attached at the same point on the hemipenis, their directional orientation changes as the hemipenis is rotated 180 degrees to the copulatory position. Because both hemipenes rotate as a unit, further contraction of the two muscles produces

#### EXPLANATION OF PLATE 3

All figures  $\times 100$

FIGS. 1-5—*Candona ohioensis* Furtos. Stereograms of specimens stained and mounted in Turttox CMC-S medium. 1, excised middle lobe of right hemipenis from right side; anterior is upward and ventral is right. 2, outer face of relaxed right hemipenis with focus on near side; compare with plate 2, figure 3, with focus near middle of specimen; anterior is upward and ventral is right. 3-5, outer face of nearly erect left hemipenis (glans not fully everted), with focus on successive (near to far) levels of the specimen; anterior is downward and ventral is left; 3, focus on end prong of latch; 4, focus on sleeves and middle lobe; 5, focus on distal shield.

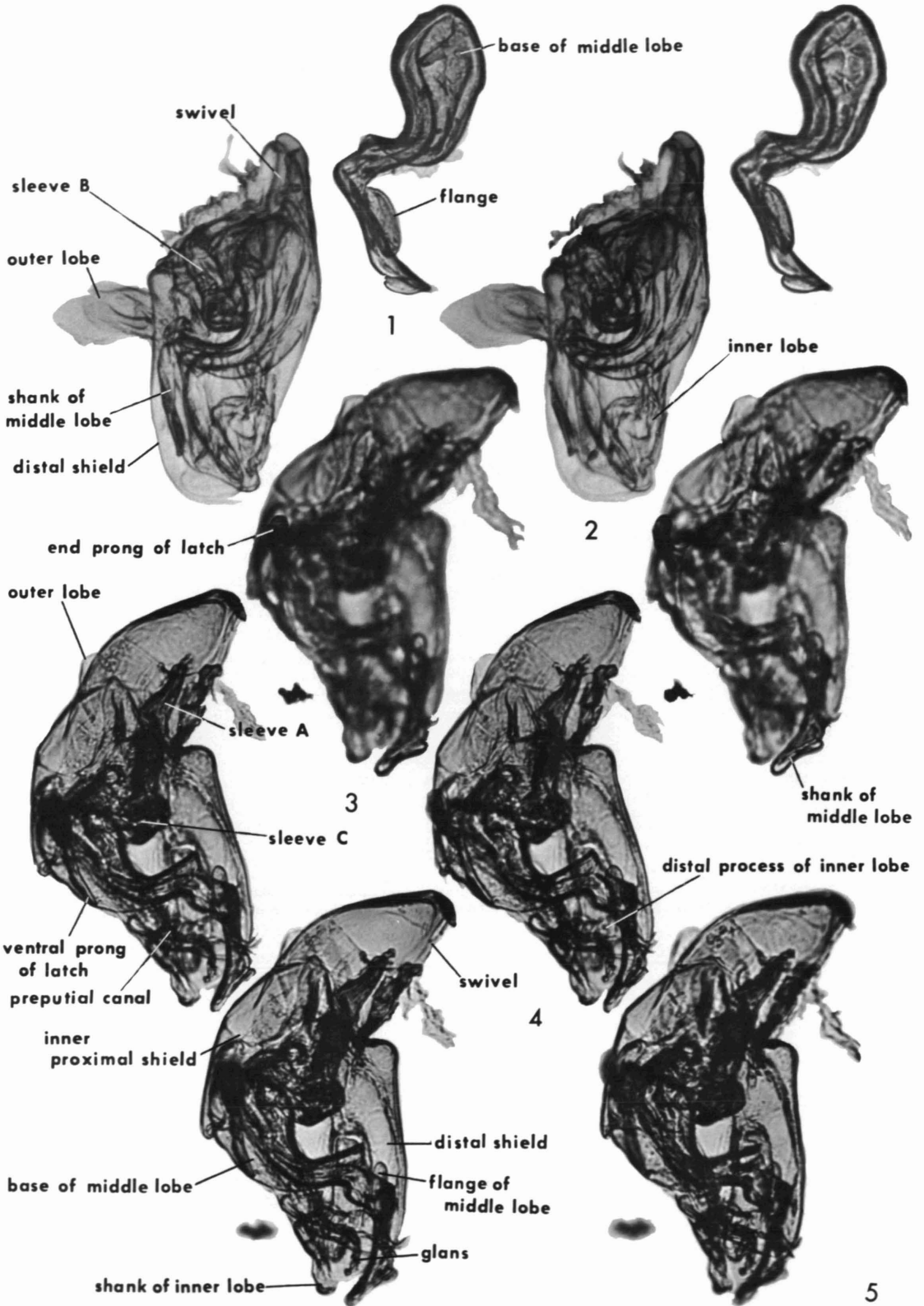
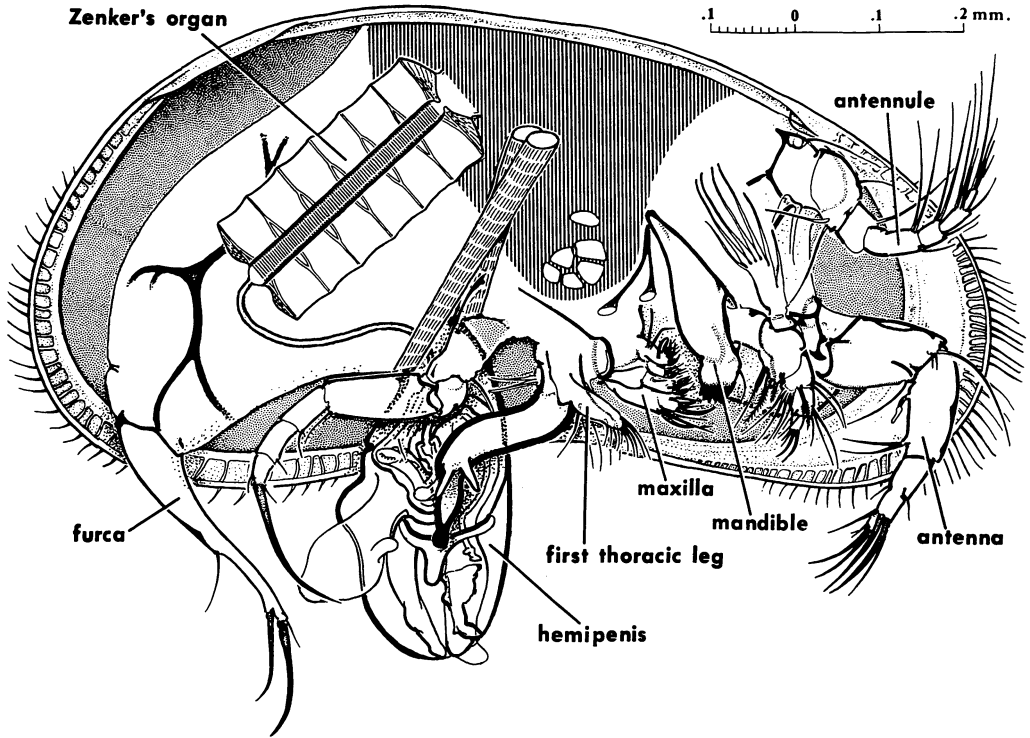


PLATE 3



TEXT-FIG. 6.—*Candona suburbana* Hoff. Labeled sketch of male with right valve removed to show position of right hemipenis following contraction of anterior male muscle on right side. Hemipenis in non-erect, non-copulatory position prior to 180 degree rotation. Appendages similar to those shown in text-figs. 1, 3, 5. Third leg and branchial plate of the maxilla on right side not shown. Scale in upper right corner.

tension on the hemipenis which in rotation is drawn to the opposite side of the body.

Each of the two muscles on one side of the body performs a given function during copulation and works in harmony with the corresponding muscle of the pair on the opposite side of the body. Stages in the operation and functional role of the male muscles are shown in text-figures 5-7.

The male muscles shown in text-figure 5 represent the pair on the right side of the body attached to the proximal end of the right hemipenis in its normal relaxed and non-copulatory position. The right valve has been removed, exposing the convex outer face of the right hemipenis, whose distal margin is directed posteriorly. The distal margin of the outer lobe (text-fig. 3) points posterodorsally.

When the muscle attached to the anterior section of the hemipenis contracts, the hemipenis is shifted to a vertical position (text-fig. 6). Contraction of the other muscle then rotates the hemipenis 180 degrees (text-fig. 7). As noted above, both hemipenes are rigidly joined

in the proximal region and, thus, rotate together. After rotation, the convex outer face of the left hemipenis faces outward on the right side of the body and the anterior muscle shifts to lie behind the other male muscle of the left side. At this stage, the two muscles on the left control the action of the left hemipenis, which has rotated to the opposite side of the body. Further contraction of these muscles swings the hemipenis anteriorly to a pre-copulatory position and tension on crucial pivotal points inside the hemipenis forces it to unfold and erect.

Erection of the hemipenis is accompanied by a marked constriction of the posterior region of the body and the rotation of the Zenker's organ to an almost vertical position (text-fig. 7). Contraction of other muscles in the posterior region presumably assists in constricting the body. When the hemipenis is thrust anteriorly, tension on the seminal duct connecting the Zenker's organ to the hemipenis appears to aid in pulling the posterior end of the Zenker's organ downward. The furca sometimes assists in rotating the hemipenis before or following



copulation and may be pressed against the posterior margin of the hemipenis during copulation.

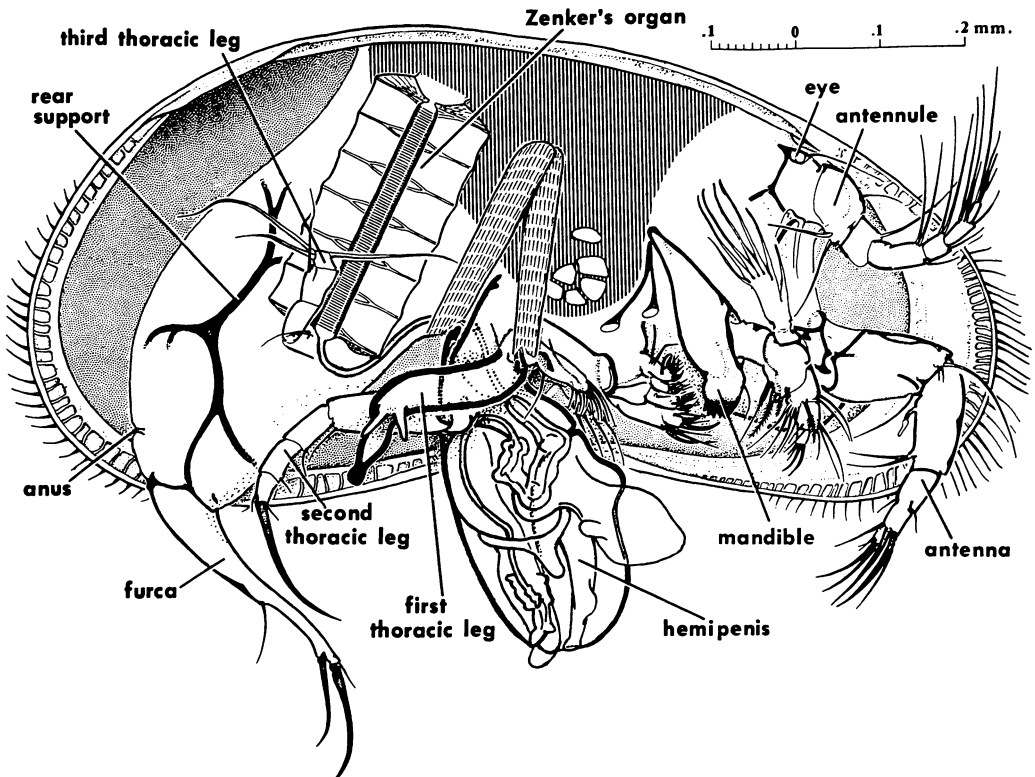
Rotation of the hemipenes and Zenker's organs, and the constriction of the body may easily be observed in mating *Candona*. However, erection and retraction of the hemipenes proceeds so rapidly that little opportunity is afforded for observing the action of most internal elements. The techniques described above provided a means for studying the progressive stages of hemipenis erection and retraction in *Candona ohioensis* Furtos (text-fig. 9) and provided details necessary in reconstructing the erection process in *Candona suburbana* Hoff (text-figs. 5-8).

No muscles are present within the hemipenis. Contraction of the male muscles and tension on the duct passing from the Zenker's organ to the hemipenes operate critical pivotal points within the hemipenis which forces the

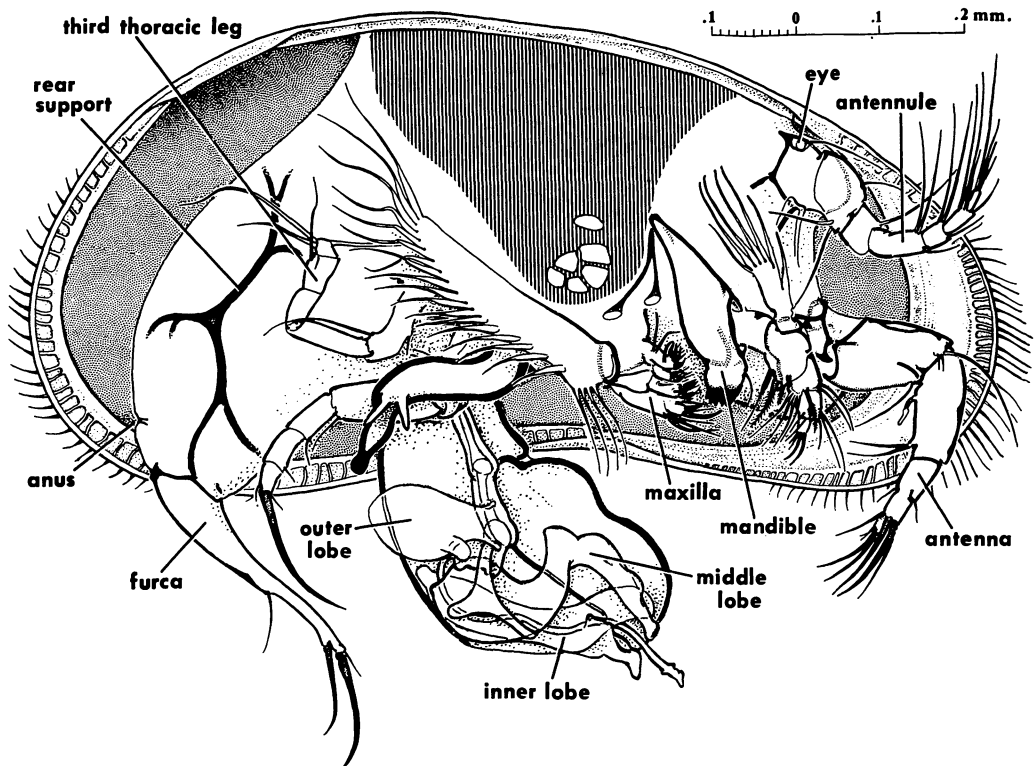
organ to unfold with a spring-like action. Further discussion of the erection process will be limited to that illustrated for *Candona ohioensis* (text-figs. 9-16).

Most of the internal elements of the hemipenis are strongly sclerotized and are articulated in such a fashion that they maintain the same orientation to one another, similar to that in the non-erect hemipenis, when removed from the enclosing sclerotized sheaths. Sleeves A, B, and C, for example, may be stretched out to positions like those in the erect hemipenis, but will spring back to their former relaxed positions when the tension is released (text-fig. 16). The seminal duct leading from sleeve C to the glans is joined proximally to the base of the middle lobe by a narrow, elastic band of chitin. If the middle lobe and this duct are excised intact, this elastic band returns them to their original orientation after manipulation.

When the male muscles contract, the hemi-



TEXT-FIG. 7—*Candona suburbana* Hoff. Labeled sketch of male with right valve removed to show orientation of left hemipenis and left Zenker's organ. Left Zenker's organ has been rotated almost 90 degrees in a vertical plane. The left hemipenis has been rotated 180° so that it lies on the right side and its outer face is exposed. It is shown in the non-erect but pre-copulatory position. The left pair of male muscles and left Zenker's organ are shown controlling the action of the left hemipenis following rotation. Attachment of anterior male muscle to hemipenis has shifted behind the posterior male muscle (compare with text-figs. 5, 6). The second leg and palp of the first thoracic leg are shown posterior to their true positions, with the palp turned to clasp the edge of the female valve. Note constriction of posterior region of body. Scale in upper right corner.



TEXT-FIG. 8.—*Candona suburbana* Hoff. Labeled sketch of male with right valve removed to expose fully erect rotated left hemipenis in copulatory position. Outer face of hemipenis exposed to show the three lobes. (Compare with text-figs. 6, 7). Posterior part of body constricted. Second leg and palp of first leg on right side are shown posterior to their position during copulation. Scale in upper right corner.

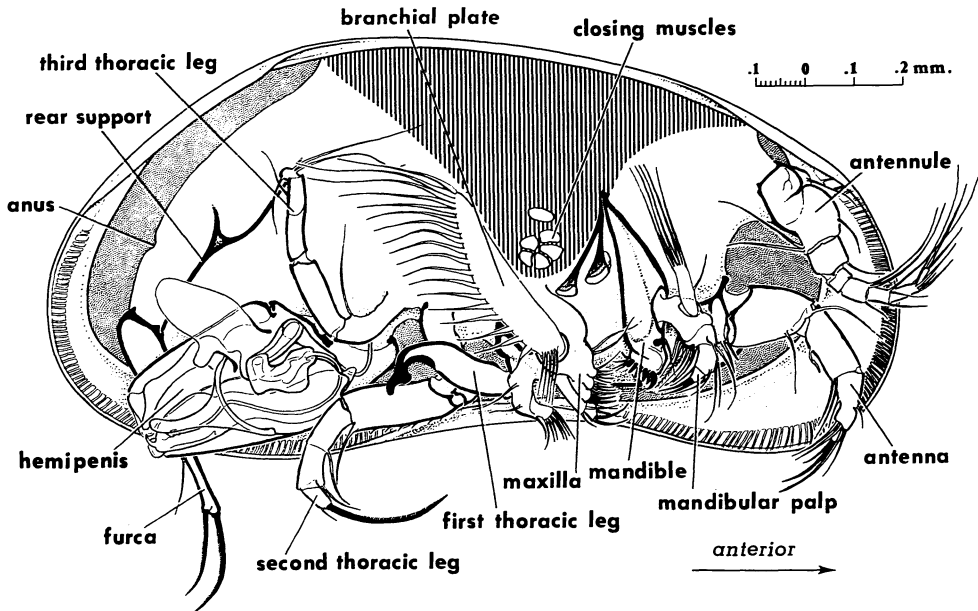
penis is forced beyond the edge of the carapace, rotated 180 degrees, and swung forward. Sleeve A, its proximal end near the convex outer face (outer proximal shield) and its distal part adjacent to the inner proximal shield, lies diagonally across the hemipenis and forms a right angle with sleeve B (text-fig. 10). As the rotated hemipenis swings anteriorly, tension increases on the seminal duct leading from the Zenker's organ on the opposite side of the body. At some point in the forward motion of the hemipenis, the tension on sleeve A becomes great enough to pull its proximal end dorsally and toward the inner proximal shield. As a consequence of this movement of sleeve A, the proximal end of sleeve B is shifted ventrally and its distal end is forced slightly dorsal from its former position. In turn, sleeve C is pushed anteriorly and dorsally, exerting pressure on the base of the middle lobe (text-fig. 10).

The dorsal prong of the latch merges with the anterodorsal margin of the outer proximal shield and is connected to the minor process of the outer lobe by a flexible band of chitin (text-fig. 13; pl. 2, figs. 4-5). The ventral prong of the latch is pivoted to the ventral margin of

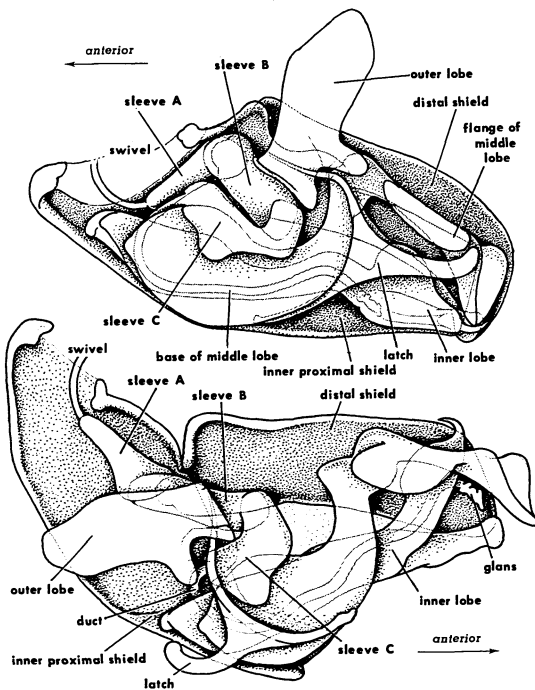
the base of the middle lobe. When sleeves A and B begin to straighten, pressure from sleeve C and the proximal end of the duct forces the base of the middle lobe to move anteriorly; this, in turn, creates tension on the ventral pivot of the latch. As sleeves A and B continue to straighten, the base of the middle lobe shifts forward until tension on the dorsal and ventral prongs of the latch surpasses a critical value. Thereupon, the end prong of the latch springs outward and over to a point proximoventral to its original position (text-figs. 10, 13).

The outer lobe, pivoted to sleeve B and connected to the dorsal prong of the latch, is flipped outward and posteroventrally almost 180 degrees. Sleeve B presses against the base of the outer lobe and the dorsal prong of the latch pulls the minor process outward and ventrally (text-figs. 10, 13).

The shank of the middle lobe glides along a longitudinal groove in the distal shield when the base of this lobe is forced anteriorly. The tapered distal portion of the hemipenis cannot accommodate both the large base and the shank because the latter joins the base at a right angle. By movement of the middle lobe, the



TEXT-FIG. 9—*Candona ohioensis* Furto. Labeled sketch of male with right valve removed to expose appendages and right hemipenis. Strongly sclerotized parts of appendages shown in solid black. Vertically-striped area represents approximately the section through the soft tissues connecting hypodermis of right valve to body. Hemipenis in normal retracted, non-copulatory position. Maxilla turned slightly toward the rear and mandible slightly toward the front in order to show their essential features. Scale in upper right corner.



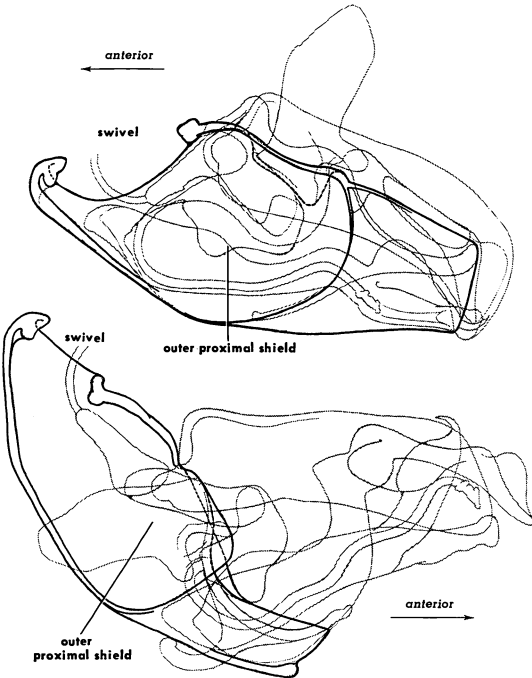
TEXT-FIG. 10—Hemipenis of *Candona ohioensis* Furto. *Upper*. Labeled sketch showing major internal elements of left hemipenis as seen from the left. Hemipenis in retracted, non-

distal shield is forced anteriorly and rotates its distal margin dorsally, pivoting on its connection with the dorsal part of the inner proximal shield (text-fig. 14). The distal process of the inner lobe, connected by chitin supports to the distal shield, is shifted dorsally by the anterodorsal rotation of the distal shield (text-fig. 10). The middle lobe, therefore, separates the distal shield from the latch and the distal process of the inner lobe comes to a position which allows extrusion of the glans from the preputial canal. By the actions of the distal shield and middle lobe, the base and shank of the inner lobe move anterodorsally.

The glans is extruded well beyond the distal margin of the inner lobe and distal shield during erection (pl. 1, figs. 2, 3). A rhythmic

rotated position. Note attitude of hemipenis in relation to body orientation, shown by arrow in upper left corner (compare with text-figs. 9, 11-16).

*Lower*. Labeled sketch showing positions of principal internal elements of rotated, erect hemipenis as seen from the right; the same hemipenis as that shown in upper sketch following 180 degree rotation. Note directional orientation of body shown by arrow in lower right corner indicating that hemipenis now lies on the right side of the body (compare with text-figs. 11-16).



TEXT-FIG. 11—Hemipenis of *Candona ohioensis* Furtos. *Upper.* Position of outer proximal shield in non-rotated, retracted left hemipenis as seen from the left. *Lower.* Position of outer proximal shield in erect left hemipenis after rotation to the right side. Directional orientation of body shown by arrow.

anterior-posterior movement of the glans accompanies the discharge of spermatozoa and may possibly reflect the tension exerted on the duct by pulsations of the Zenker's organ. Spermatozoa observed being discharged from the glans were, in every instance, ejected singly.

*Retraction.*—Retraction of the hemipenis usually occurs immediately after withdrawal of the glans from the vagina of the female. Relaxation of the muscles holding the hemipenis in the copulatory position releases the tension on the proximal end of sleeve A. Sleeves A, B, and C then spring back to their normal relaxed position. Sleeve C no longer presses on the base of the middle lobe, but instead pulls it posteriorly by the flexible band of chitin connected to the duct. The duct and glans are drawn into the preputial canal.

Each of the other elements springs back to its former position as withdrawal of the middle lobe eases the tension on the critical pivotal areas indicated above. Fully retracted, the hemipenis is again enclosed proximally by the sclerotized shields. The flange of the middle lobe rests against the dorsal edge of the outer

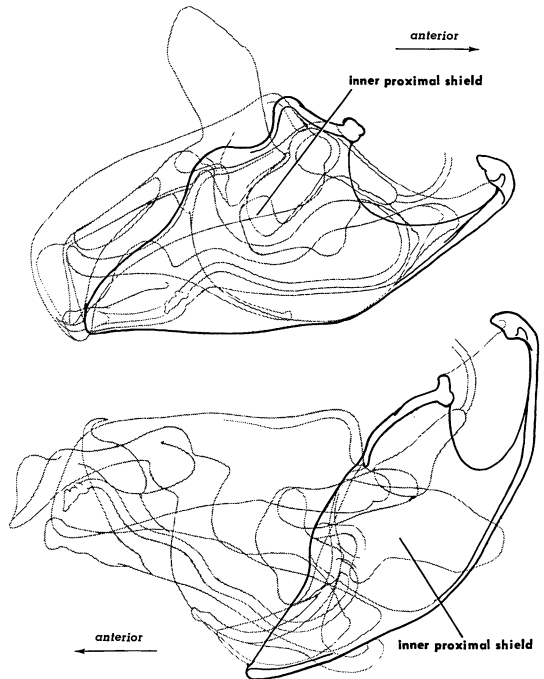
proximal shield, making the hemipenis appear as though the internal elements are completely enclosed by a single protective sheath.

Contraction of the appropriate pair of male muscles rotates the hemipenis 180 degrees and brings it to the normal non-copulatory position within the carapace.

#### CARAPACE DIMORPHISM

*Range of genus.*—More definitive work must be done before the history of dimorphism in *Candona* can be said to be established. A few examples will suffice to show that even the range of the genus is not known with any degree of certainty.

According to Bassler & Kellett in 1934 (p. 236) four Paleozoic species had been assigned to *Candona* at that time (two of them with question). Of the four, two were Carboniferous and two were Permian. In 1862, Professor T. Rupert Jones named, described, and figured (p. 122, pl. 5, fig. 13–14) *Candona* (?) *salteriana* from the Four-foot Coal at Bradford Pit near Manchester, England, and (p. 123, pl. 5, fig. 15) *Candona* (?) *tateana* from the Moun-

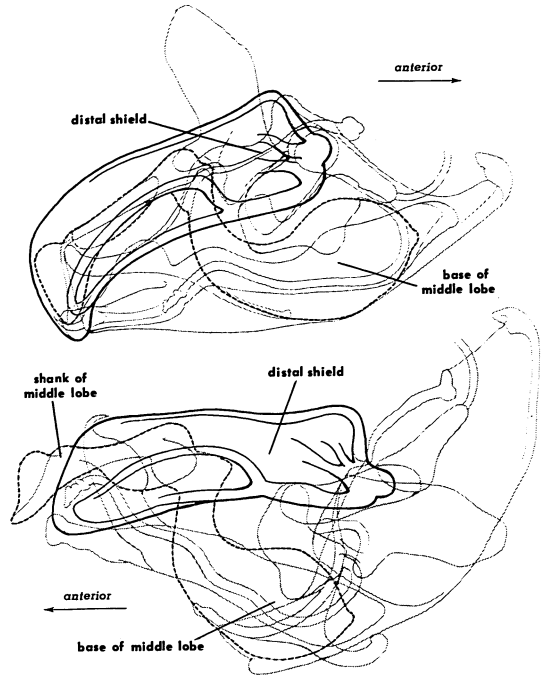


TEXT-FIG. 12—Hemipenis of *Candona ohioensis* Furtos. *Upper.* Position of inner proximal shield in retracted, non-rotated left hemipenis as seen from the right. *Lower.* Position of inner proximal shield in erect left hemipenis as seen from the left. Directional orientation of body shown by arrow.

tain Limestone at Berwickshire, Scotland. In the same publication, Jones named, described, and figured ostracods from the "Lower Mesozoic shales" of Pennsylvania, Virginia, and North Carolina, including (p. 124, pl. 5, figs. 20-22) *Candona* (?) *rogersii* and (p. 125, text-fig. 12) *Candona* (?) *emmonsii*.

Scott & Summerson (1943, p. 672, pl. 1, fig. 18) described *Candona kentuckyensis* from the Pennsylvanian Hance Formation in Harlan County, Kentucky. Tasch (1963, p. 1249, pl. 174, figs. 9-12) assigned a species from Permian freshwater strata in Kansas to his new *Candona paleostraca*.

In a review of Cretaceous Ostracoda in 1958 (p. 104-108) Howe & Laurovich discovered that eleven Cretaceous species had been assigned to the genus *Candona*, only one of them with question. The first Cretaceous *Candona* to appear in literature was by Professor Jones, who described (1888, p. 535, figs. 2a,b) *Candona mantelli* from the Weald Clay of England. The last to come to our attention is by Tetsuro Hanai, who described (1951, p. 425-427, pl. 2, figs. 4-5, 10-12) three species from the Cretaceous deposits of Manchuria.

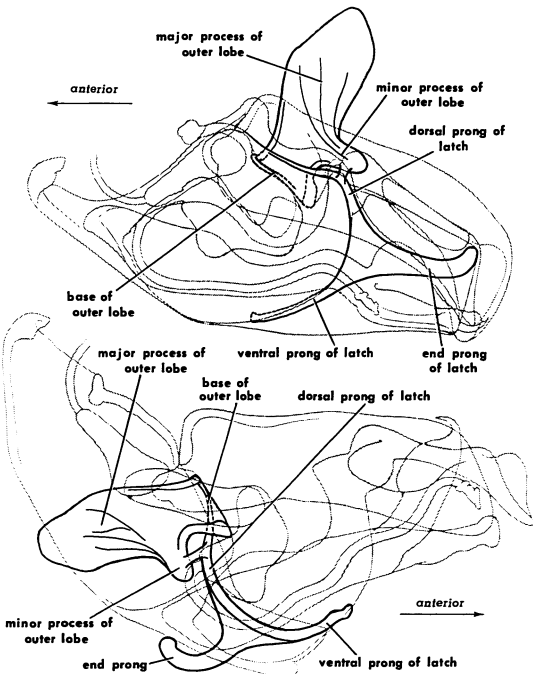


TEXT-FIG. 14—Hemipenis of *Candona ohioensis* Furtos. Upper. Labeled sketch showing positions of distal shield and middle lobe in retracted, non-rotated left hemipenis as seen from the right.

Lower. Labeled sketch showing positions of distal shield and middle lobe in erect left hemipenis from the left. Directional orientation of body shown by arrow.

Several investigators have described Tertiary species of *Candona*. Scott & Smith (1951, p. 327-353, pl. 52, 3 text-figs.) made a detailed study of their *Candona whitei* from Eocene outcrops in the Bridger Basin of Wyoming. Gerta Schneider of the Russian VNIGRI Institute (1949, p. 118-119) reported *Candona* in the Miocene Karagan Group of the Caucasus and Crimea. More recently, Mandelstam & Schneider (1963, p. 143-159) described Russian species of *Candona*, most of them new, including 6 from the Miocene, 24 from the Pliocene, and 5 from post-Pliocene beds. Gutentag & Benson (1962, p. 32-35) found *Candona* in Plio-Pleistocene deposits of the central High Plains region of the United States.

Staplin (1963, p. 762-791, pls. 91-94) described and figured numerous species of *Candona* from the Pleistocene of Illinois. In the same publication, Swain (1963, p. 802-805, pls. 95-96) dealt with late Pleistocene *Candona* in Alaska. Last year, Benson (1967, p. 211-241) published his studies of some Pleistocene ostracods including *Candona*. There also numerous references to postglacial fossil species.



TEXT-FIG. 13—Hemipenis of *Candona ohioensis* Furtos. Upper. Labeled sketch showing positions of outer lobe and latch in retracted, non-rotated left hemipenis as seen from the left. Lower. Labeled sketch showing positions of outer lobe and latch in erect left hemipenis after rotation to the right side. Directional orientation of body shown by arrow.

This is not intended to be an exhaustive review of the genus, and numerous other citations of the genus could be found. The uncertainty of its range can be demonstrated by some published ages: "Carboniferous to Recent" (Hanai, 1951, p. 407), "? Permian, Triassic-Recent" (Swain, 1963, p. 802), Permian-Recent (Pokorný, 1954, p. 419), "Cretaceous (?) to Recent" (Staplin, 1963, p. 762), and Tertiary-Recent (Grekoff, 1953, p. 282). Undoubtedly, much of the confusion around *Candona* could be cleared by carefully study of muscle scars, especially using the method explained by Benson (1967, p. 219-229, figs. 3-8), which could lead to recognition of dimorphs in each species.

**Range of dimorphism.**—Of all authors on Pleistocene and older species of *Candona*, only Staplin (1963) and Benson (1967) have described dimorphism in their ostracods. Illustrations by other writers strongly suggest to us that some of their species were based on males and some on females. Hence, there are questions not only of how far back in time *Candona* extends but also of the antiquity of its dimor-

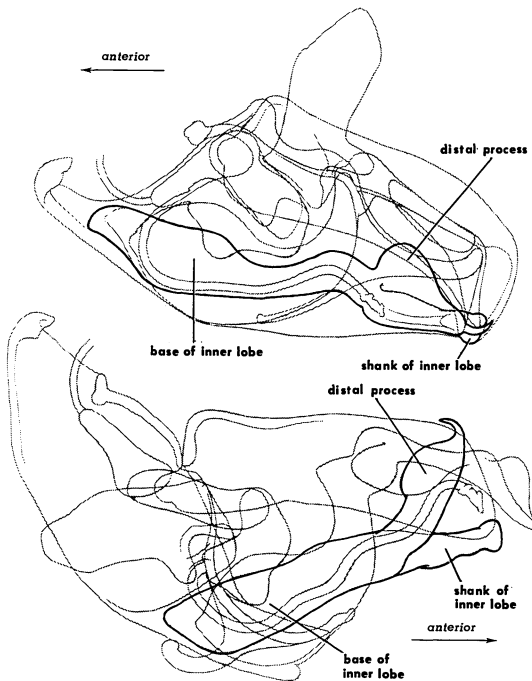
phism. Literature is not a convincing basis for an opinion. From our review we believe that *Candona* has existed at least from Cretaceous time and that it has always been dimorphic.

**Variation between dimorphs.**—Table 1 lists 38 Pleistocene and Recent species of *Candona* in which dimorphic carapaces have been described and illustrated. Many others could have been added, since there are nearly 200 species known from the Recent alone. In this study, the length and area in lateral view were measured for each dimorph. Then the areas were converted to square units of length to eliminate differences in length between the dimorphs, using the formula

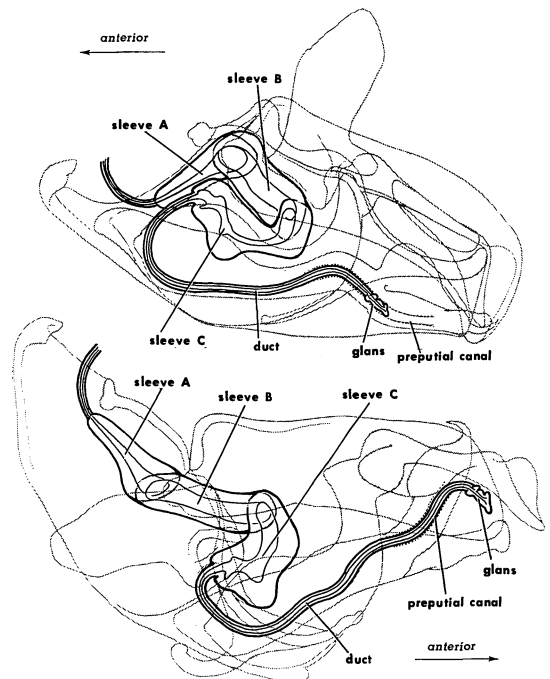
$$\text{Converted area} = \text{Area}/\text{Length}^2.$$

The converted area serves two purposes. First, for dimorphs of a species it differentiates between areal differences due to length differences and those due to shape differences. Second, it offers a basis for comparison between species, inasmuch as it has the effect of enlarging or reducing each specimen to unit length.

From this table, one can readily see that the



TEXT-FIG. 15—Hemipenis of *Candona ohioensis* Furtos. *Upper.* Labeled sketch showing position of inner lobe in retracted, non-rotated left hemipenis as seen from the left. *Lower.* Labeled sketch showing position of inner lobe in erect left hemipenis after rotation to the right side. Directional orientation of body shown by arrow.



TEXT-FIG. 16—Hemipenis of *Candona ohioensis* Furtos. *Upper.* Labeled sketch showing seminal tract in retracted non-rotated left hemipenis as seen from the left. *Lower.* Labeled sketch showing seminal tract in erect left hemipenis after rotation to the right side. Directional orientation of body shown by arrow.

TABLE 1—*CANDONA* SPECIES: LENGTH AND AREA IN LATERAL VIEW OF EQUIVALENT VALVES IN ADULT DIMORPHS IN SELECTED SPECIES. Based on illustrations in Klie (1938), Staplin (1963), Benson & MacDonald (1963), and Benson (1967).

Species	Male		Female		Age <sup>1</sup>	Converted Areas <sup>2</sup>	
	Length (mm)	Area (mm <sup>2</sup> )	Length (mm)	Area (mm <sup>2</sup> )		Male	Female
<i>insueta</i> Klie	0.46	0.081	0.46	0.078	Rec.	.383	.369
<i>schellenbergi</i> Klie	.50	.109	.48	.100	Rec.	.436	.435
<i>thomasi</i> Staplin	.74	.248	.76	.246	Pleist.	.450	.430
<i>elliptica alta</i> Staplin	.85	.285	.93	.316	Pleist.	.399	.370
<i>sucki</i> Hartwig	.90	.337	.89	.336	Rec.	.416	.424
<i>zschokkei</i> Wolf	.90	.353	.80	.292	Rec.	.436	.456
<i>willmani</i> Staplin	.97	.413	.74	.257	Pleist.	.441	.470
<i>illinoiensis</i> Staplin	.97	.415	.87	.344	Pleist.	.439	.450
<i>poseyensis</i> Staplin	.99	.416	.92	.330	Pleist.	.423	.394
<i>leightoni</i> Staplin	1.00	.452	1.01	.441	Pleist.	.452	.429
<i>pearlensis</i> Staplin	1.01	.480	.97	.421	Pleist.	.470	.445
<i>havanaensis</i> Staplin	1.02	.403	.90	.307	Pleist.	.391	.380
<i>distincta</i> Furtos	1.04 <sup>3</sup>	.429	1.05	.458	Pleist.	.394	.416
	1.29 <sup>4</sup>	.717	1.21	.611	Pleist.	.431	.418
<i>muelleri</i> Hartwig	1.06	.687	1.03	.671	Rec.	.611	.632
<i>shawneensis</i> Staplin	1.07	.520	.84	.292	Pleist.	.454	.416
<i>truncata</i> Furtos	1.09	.550	1.04	.469	Pleist.	.462	.436
	1.13	.597	1.06	.517	Pleist.	.471	.459
<i>candida</i> (O. F. Müller)	1.10	.555	1.11	.547	Rec.	.459	.444
<i>faba</i> Benson & MacDonald	1.11	.496	1.04	.420	Rec.	.402	.389
<i>wabashensis</i> Staplin	1.12	.531	1.00	.408	Pleist.	.421	.409
<i>paraohioensis</i> Staplin	1.15	.508	1.06	.463	Pleist.	.385	.415
<i>swaini</i> Staplin	1.18	.632	1.19	.599	Pleist.	.457	.425
<i>weltneri</i> Hartwig	1.19	.674	1.19	.660	Rec.	.476	.466
<i>scopulosa</i> Furtos	1.20	.586	1.00	.394	Pleist.	.406	.394
<i>eriensis</i> Furtos	1.23	.598	1.24	.600	Pleist.	.395	.393
<i>renoensis</i> Gutentag & Benson	1.28	.745	1.08	.569	Pleist.	.455	.488
<i>fragilis</i> Hartwig	1.29	.637	1.20	.518	Rec.	.383	.360
<i>fabaeformis</i> Fischer	1.30	.663	1.16	.515	Rec.	.392	.383
<i>acuta</i> Hoff	1.30	.669	1.13	.498	Pleist.	.397	.393
<i>croghaniana</i> Turner	1.32	.710	1.43	.772	Pleist.	.410	.379
	1.55	.964	1.51	.866	Pleist.	.402	.382
<i>nyensis</i> Gutentag & Benson	1.35	.845	1.20	.649	Rec.	.464	.451
<i>novacaudata</i> Benson & MacDonald	1.36	.713	1.27	.604	Rec.	.385	.374
<i>caudata</i> Kaufmann	1.36	.728	1.22	.545	Rec.	.394	.366
<i>swaini sappaensis</i> Staplin	1.38	.841	1.10	.563	Pleist.	.442	.462
<i>neglecta</i> Sars	1.39	.888	1.19	.618	Rec.	.460	.437
<i>hyalina</i> Brady & Robertson	1.44	.810	1.41	.810	Rec.	.391	.408
<i>acuminata</i> Fischer	1.50	.931	1.54	.892	Rec.	.414	.376
<i>angulata</i> G. W. Müller	1.56	1.088	1.49	.943	Rec.	.447	.425
<i>ohioensis</i> Furtos	1.87	1.328	1.81	1.108	Pleist.	.380	.338

<sup>1</sup> Age listed as given for specimens measured. Many Pleistocene entries have Recent representatives, and many listed as Recent are fossil rather than living.<sup>2</sup> For converted area, the area in lateral view is enlarged or reduced so that the length = 1 unit; measurements are in (unit length)<sup>2</sup>.<sup>3</sup> Based on Staplin, 1963, pl. 93, figs. 5–6.<sup>4</sup> Based on Benson, 1967, fig. 6, nos. 2, 4; marked size difference from those assigned to the species by Staplin.

female valves are (with rare exceptions) actually smaller than the male valves. It is also apparent from the converted areas that in most species the female valves are less plicate than the male valves. There are a few exceptions. These species deserve special attention, to discover if the male valves really are smaller. They might seem smaller because of individual variations in the specimens selected for illustration, because of inaccuracies in drawing, or because of improper orientation under the camera or camera lucida. If the males are actually smaller, their sex organs probably differ from those of other *Candona* species. It should be pointed out that in the larger species measured, all males are more plicate than the females.

*Variation between species.*—Table 1 also shows that, irrespective of length, some species are more plicate than others. The average converted area for males is 0.429 and for females 0.419. The medium-size *Candona muelleri* has a female with converted area of 0.632, whereas the very small *C. insueta* has 0.369 and the very large *C. ohioensis* has 0.338. Hence, shape of valves is completely independent of size in *Candona*; some species are high and broad, whereas others are low and narrow.

*Variation in time.*—The measurements in table 1 are far from conclusive because of individual variation within each species. No investigator has come close to adequately measuring a significant sample of a population of *Candona*. In converted areas, averages for Pleistocene species are 0.426 for males and 0.416 for females; averages for Recent species are 0.432 for males and 0.423 for females. Hence, insofar as these measurements are concerned, dimorphism was just as pronounced in Pleistocene as it is in Recent species of *Candona*. Furthermore, the Pleistocene dimorphism was of the same kind as the Recent, with female valves beveled posterodorsally and male valves rounded posteriorly and posteroventrally. To some extent dimorphism in *Candona* is a persistent character.

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