COPULATORY ADAPTATIONS IN OSTRACODS
PART II. ADAPTATIONS IN LIVING OSTRACODS

BY

DON L. McGREGOR   and   ROBERT V. KESLING

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Director: ROBERT V. KESLING

VOLUME 22

COPULATORY ADAPTATIONS IN OSTRACODS
PART II. ADAPTATIONS IN LIVING OSTRACODS[1]

DON L. McGREGOR[2] and ROBERT V. KESLING

ABSTRACT—Literature on living ostracods contains only scattered and incomplete information on the genitalia and mating behavior. Most observations are directed more toward form than toward function; many are based on dissected, unoriented, and distorted material. A review of current knowledge reveals several adaptations for copulation, from which generalizations can be made on the relationship of the mode of copulation to carapace morphology. These generalizations may prove useful in interpreting similar features of extinct ostracods.

CONTENTS

INTRODUCTION

ONLY VERY RECENTLY have zoologists directed their attention toward studies of functional morphology and behavior in living ostracods. In particular this applies to genitalia and mating procedures, about which nothing is known in the majority of ostracod families. A few investigations now under way have not appeared in print.

Carapace dimorphism appears to us to be directly related to the accommodation of sex organs and facilitation of mating. Because dimorphism of the carapace is a factor in taxonomy of both living and fossil ostracods, study of copulatory adaptations takes on special significance. When representative species have been investigated, the distribution of genitalia types and mating modes can be more effectively evaluated in relation to configuration and dimorphic features of the carapace.

Except for those species which reproduce parthenogenetically, the male does copulate with the female. Whatever the shape of the valves and whatever the degree of carapace dimorphism, copulation is always possible. In different groups, however, it is accomplished in different ways, suggesting that morphological adaptations developed in separate lineages.

Whether carapace shape or mode of copulation has been the stronger influence in evolution may be difficult or impossible to establish. We can be sure, however, that both have always been closely integrated in any particular species..

The next, and concluding, part of this series will apply the generalizations from living ostracods to certain of the strongly dimorphic Paleozoic ostracods. From our study of copulatory adaptations in living forms, we find some correlations between configuration of the carapace and mating procedures which seem applicable to interpretation of extinct groups.

ACKNOWLEDGMENTS

Mysyk and Mrs. Geraldine McGregor in typing and Mr. Karoly Kutasi in photography are gratefully acknowledged. Professor E. C. Stumm and Professor C. A. Arnold critically reviewed the manuscript.

PREVIOUS WORK

Genitalia.—The genitalia of marine and freshwater ostracods have been studied by a large number of investigators over the past 100 years. Most of these studies were concerned with the structure and taxonomic significance of reproductive organs rather than with the functional morphology of male and female genitalia or mating behavior in living animals.

Many authors (Zenker, 1854; Brady & Robertson, 1870; Stuhlmann, 1886; Vávra, 1891; Müller, 1894; Turner, 1895; Jensen, 1904; Hirschmann, 1912; Skogsberg, 1920, 1928; Sars, 1922–28; Klie, 1926, 1938; Hard-ing & Sylvester-Bradley, 1953; Van Morkhoven, 1962; Kesling, 1965; Danielopol, 1968; Hart & Hart, 1968; McGregor & Kesling, 1968) have stressed the anatomical complexity of the male genitalia in various ostracod groups. Yet, these and other workers (Alm, 1916; Blake, 1931; Furtos, 1933, 1935; de Vos, 1957; Hartmann, 1959, 1964; Petkovski, 1959; Reys, 1964; Hulings, 1967) have recognized and described many taxonomically important features of ostracod genitalia.

In referring to similar anatomical features, authors have used many diverse terms. This problem in terminology developed both from actual differences in kinds of genitalia and from personal interpretations of the authors. Some of the early workers (Zenker, 1854; Nordquist, 1885; Stuhlmann, 1886; Schwartz, 1888; Vávra, 1891; Müller, 1900; Jensen, 1904) were engaged mostly in identifying and suggesting
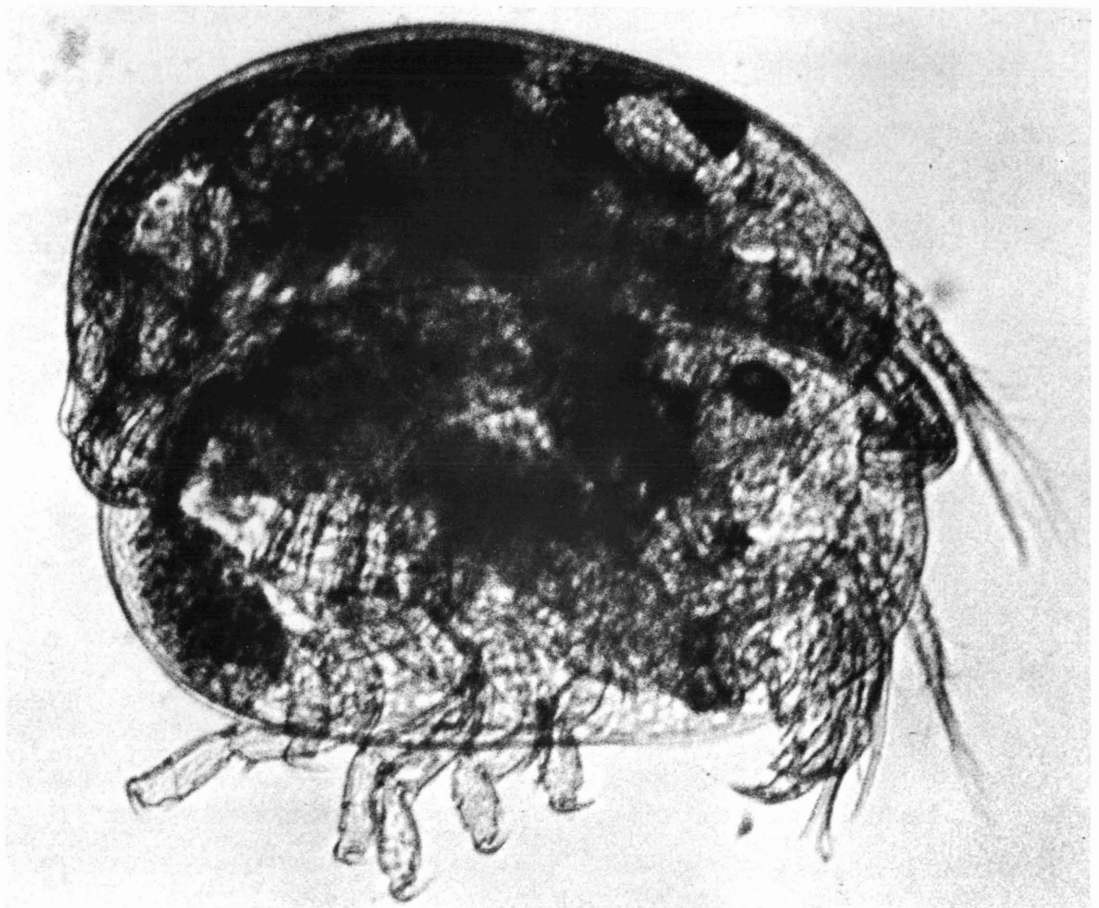
TEXT-FIG. *1—Entocythere* sp. [Podocopida, Podocopina, Cytheracea]. Pair in mating position, the male atop the dorsal side of the female. Hemipenes of male lowered, rotated, and inserted in the posterior gape between female valves. Other views of these specimens in text-figure 2. Female carapace 0.328 mm long.
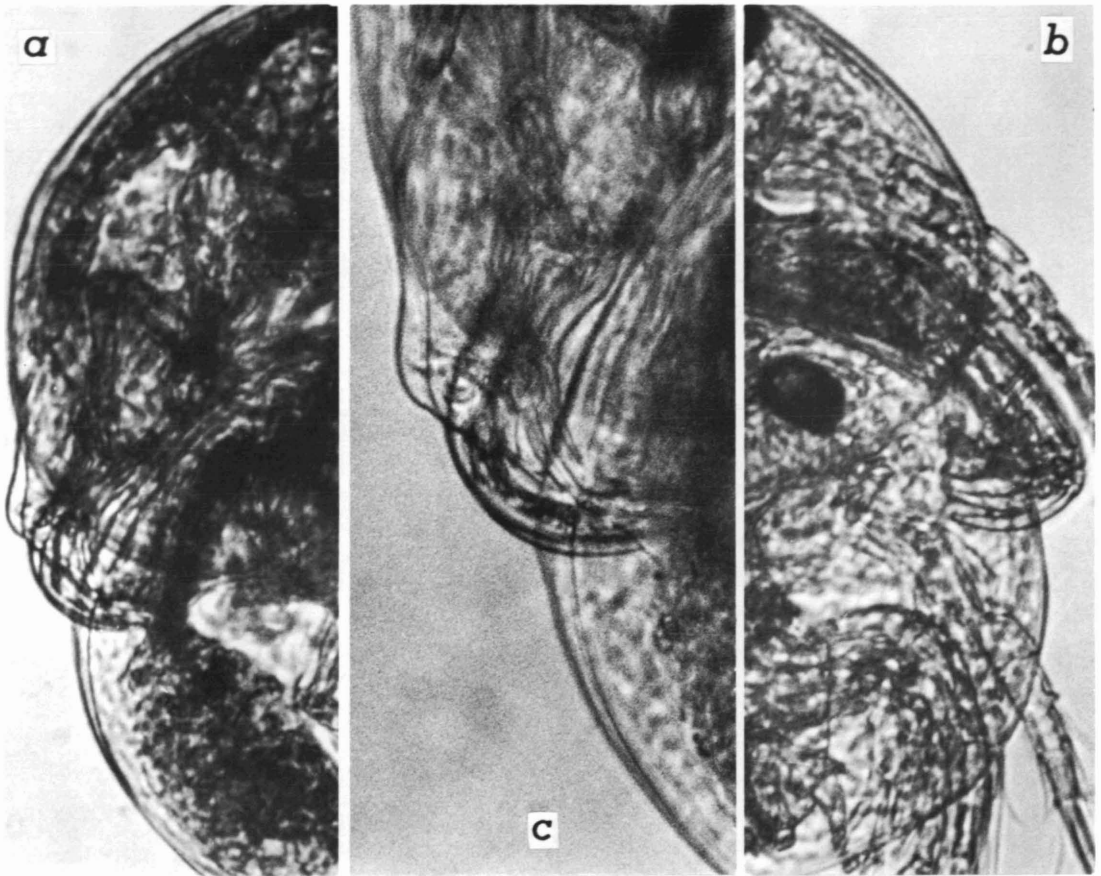
TEXT-FIG. 2—*Entocythere* sp. Same specimens as shown in text-figure 1. *a,* posterior end of mating pair. *b,* anterior end of mating pair, showing male with antennal claws holding to front end of female carapace. *c,* enlargement of hemipenes.

the functions of various male and female reproductive organs. These and other authors often used different terms for the same anatomical structure based upon the known or supposed structural-functional relationships.

Professor Tage Skogsberg, one of the foremost early authorities on marine ostracods, discussed (1920, p. 59) the necessity of defining and amplifying the terminology of the copulatory apparatus ("penis") of male cypridinid ostracods and remarked:

> The complicated structure of this organ needs a very thorough and comprehensive examination, a piece of work that probably needs a special treatise.

The genitalia of male cypridinid ostracods consist of an unpaired medial papilla-like swelling with a lateral, sometimes distally bifurcated, projection on each side. These lateral "appendages" do not contain the spermatic ducts but, according to Skogsberg (1920, p. 58), they

were called "penes" by C. Claus and G. W. Müller, "penes or genital limbs" by Ramsch (1906), and "zampe sessuali" by Garbini (1887). Skogsberg, however, used the term "penis" for the small medial papilla on which the spermatic ducts emerge. He (p. 95–96) also noted that the most primitive type of genital structures in living ostracods appeared to be those of the cypridinids such as *Philomedes* and *Asterope*. Van Morkhoven (1962, p. 25) stated that the copulatory organ of cytherid ostracods is usually less complex than that of cypridids, but more heavily chitinized.

In subsequent studies of the genus *Cythereis,* Skogsberg (1928, p. 16) again stressed the need for study of the reproductive organs of male ostracods and expressed what perhaps were his strongest sentiments:

> Especially the structure of the penis appears to be significant. Indeed, just as in several other groups of Arthropods, this organ appears
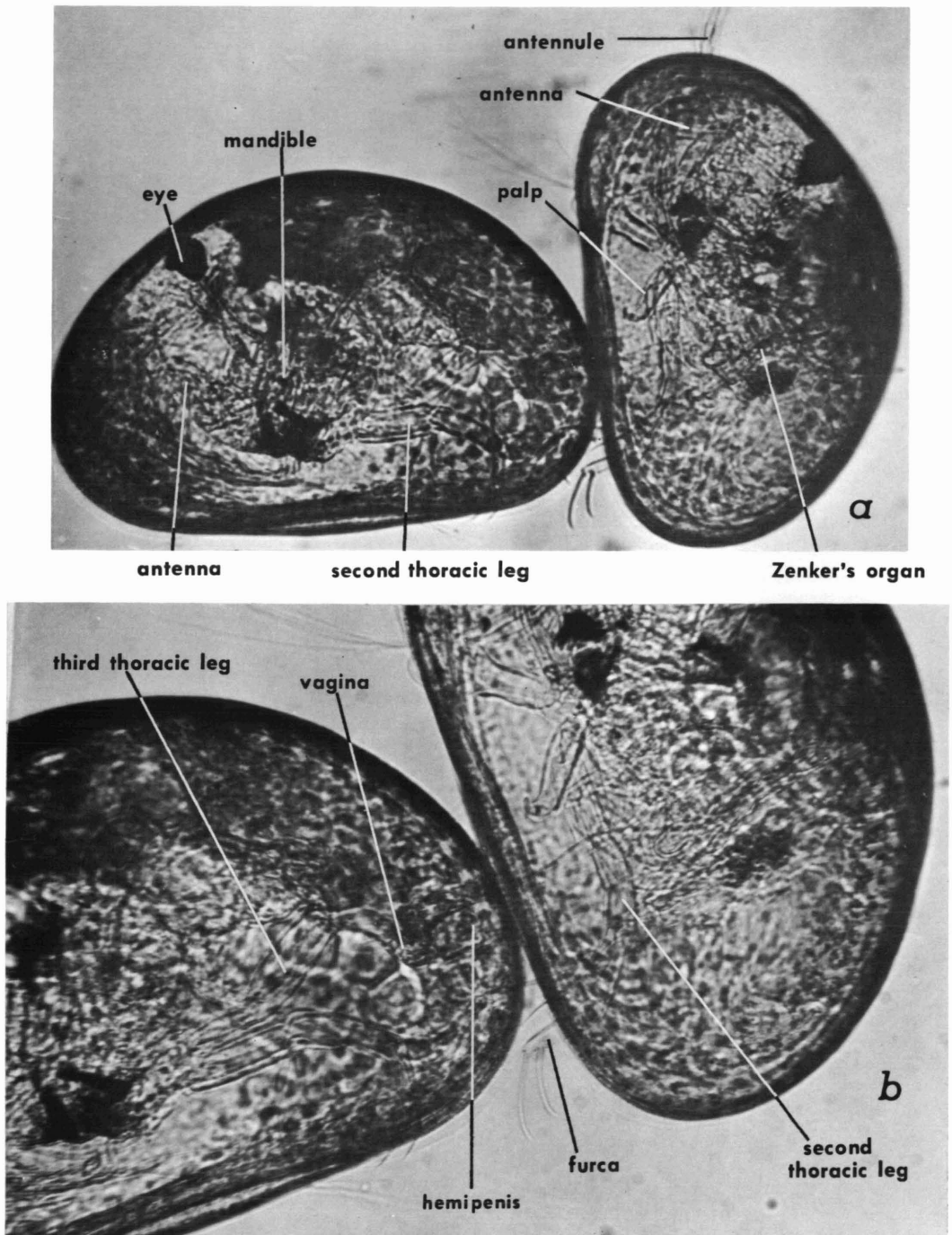
TEXT-FIG. 3—*Cypria turneri* Hoff. *a,* pair in copula; as specimens were killed, palps or clasping organs of male first thoracic legs released their hold on edges of the female valves, permitting the male carapace to slip and rotate very slightly down on the female carapace; Zenker's organs turned to vertical in erection, *b,* enlargement showing glans of male hemipenes still engaged in vagina of the female; part of ovary can be distinguished in hypodermis of one valve, appearing as a series of subquadrate nucleated eggs. Female 0.656 mm long, male 0.600 mm long.

to have been the seat of initial morphological changes leading to speciation. Unfortunately, the morphological complexities of this organ is still uncertain. To carry out the homologies of its different parts will probably prove the most fascinating and fruitful morphological problem that the Ostracod group has to offer.

The complex genitalia of male ostracods recently have received attention by Howe *et al.* (1961), Van Morkhoven (1962), and Kesling (1965). Van Morkhoven (1962, p. 25) stated the problem generally applicable to most groups of ostracods in reference to the hemipenis:

> The mechanism and function of each part is often extremely difficult to explain or even to guess.

Kesling (1965, p. 38) also noted that the "extremely complicated penes have never been fully understood" in the freshwater genus *Candona.* Recent work by Danielopol (1968), Hart & Hart (1968), and Part I of this series detail the functional morphology of the hemipenes of certain freshwater ostracods.

The copulatory complex of male entocytherids has received intensive study (notably, Hobbs & Walton, 1963; Hobbs & Hart, 1966; Hart, 1962; Hart & Hart, 1967, 1968) compared to most other groups. Hart & Hart (1968) recently reviewed and proposed a standardized terminology for the copulatory apparatus of entocytherids and suggested possible homologs in a hemicytherid ostracod. The latter authors used the term "penis" for the sclerotized portion of the "peniferum" of entocytherids which corresponds, at least functionally, to the "glans" in *Candona* (McGregor & Kesling, 1968). The long established terminology for certain elements of the hemipenes of *Candona* and difficulty in homologizing internal structures of the hemipenis of the latter with those of entocytherids make detailed comparisons of their respective genitalia beyond the scope of this report.

As noted above and discussed in Part I of this series, carapace dimorphism often appears to be related directly to the accommodation of sex organs. As reported by Kesling (1957), Claus (1893) was one of the earlier workers to comment on this relationship in the freshwater genus *Candona.* Van Morkhoven (1962) made a similar observation for certain species of *Semicytherura.* Later, Sandberg (1964, p. 47) discussed sexual dimorphism in the cytherid *Cyprideis* and stated:

> The differences between the genital organs themselves account for most of the sexual dimorphism in the soft parts of *Cyprideis.* In

addition, it is those same genital structures (particularly of the male) and functions associated with reproduction which give rise to strong sexual dimorphism in the shell of that genus.

Sandberg (p. 47–48) also found this same relationship in other cytherid genera, *Cytheromorpha* and *Perissocytheridea,* which have large male genitalia.

Copulation.—The earliest recorded observation of ostracod copulation mentioned by Klie (1926, p. 33–34) was that of Lilljeborg, who had described in 1854 the ventral position used by *Notodromas monacha* (O. F. Müller). However, in a rare volume on the wonders of microscopy, Martin Frobenius Ledermüller in 1761 (p. 140–141, pl. 73) noted and illustrated some freshwater creatures which he called "eine besondere Art von Schaalenthierchens im Wasser; oder die nierenförmige Pücerons." His "special kind of aquatic shelledanimalcules, or kidney-shaped aphids" were undoubtedly Ostracoda, although we would not venture to guess as to the species. Ledermüller depicted (pl. 73, fig. d) a pair copulating in a posterior-to-posterior position.

Little is known about the mating behavior and mode of copulation in most ostracod families. According to Jensen (1904, p. 11) male ostracods were described first by Zenker in 1850. Most subsequent early workers were involved more with studies of reproductive structures than with reproductive behavior. In 1880, Weismann recorded his observations of sexual and parthenogenetic reproduction in several genera of freshwater ostracods and commented on the frequency of spermatozoa in the seminal receptacle of female *Candona* and other genera. Jensen (1904) later summarized some of the work on mating behavior prior to 1900 and presented one of the most detailed descriptions of copulation in the genus *Candona.* The structure and function of the male hemipenis and the mechanism of erection and retraction were at that time unknown.

Copulation in cypridid ostracods has been observed and described, or briefly noted in: *Cyprinotus dentato-marginatus* (Sars) by Sars (1889, in Jensen, 1904); *Notodromas monacha* (O. F. Müller) by Vávra (1891), Jensen (1904), and Klie (1926); *Cyprois marginata* (Straus) by Jensen (1904) and Klie (1926); *Cyprinotus incongruens* (Ramdohr) by Wohlgemuth (1914); *Candonopsis kingsleii* (Brady & Robertson) [=*Candona Kingsleyi*] by Jensen (1904); *Candona fabaeformis* Fischer and *C. rostrata* Brady & Norman by Jensen (1904); and *Potamocypris smaragdina* (Váv-
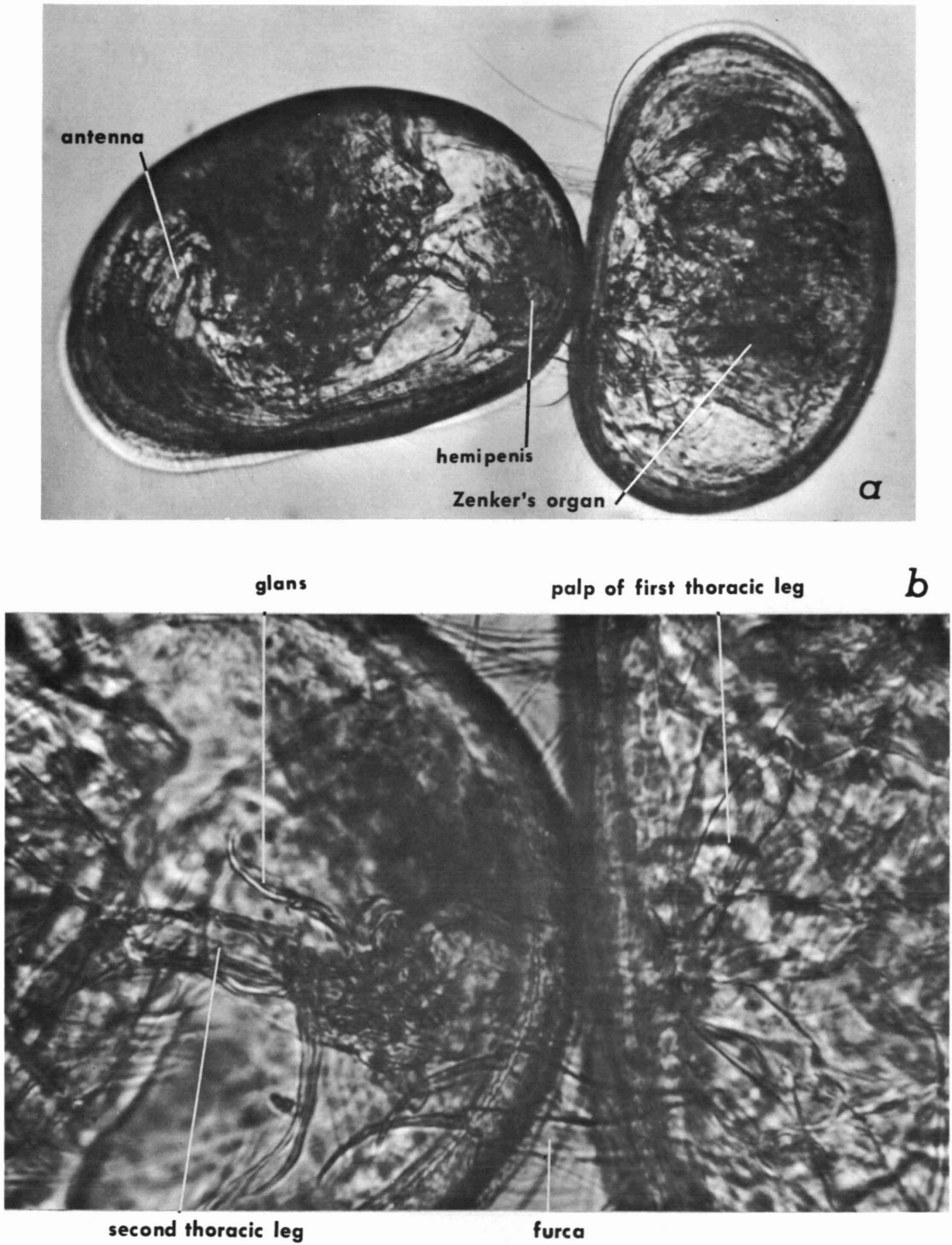
TEXT-FIG. 4—*Physocypria pustulosa* (Sharpe). *a*, pair in copula; as specimens were killed, palps of male first thoracic legs released their hold on edges of female valves, whereupon the male slipped and rotated slightly down on the female carapace; Zenker's organs turned to vertical position in erection. *b*, enlargement showing the hemipenes still inserted deep within the female carapace, the glans of one clearly defined. Female 0.600 mm long, male 0.544 mm long.

ra) by Ferguson (1944). Among the Cytheracea, copulation has been briefly described for *Entocythere heterodonta* Rioja [=*Ankylocythere heterodonta* (Rioja) Hart 1962] by Rioja (1940); *Leucocythere mirabilis* Kaufmann by Kaufmann (1892), and Klie (1926); and *Metacypris cordata* Brady & Robertson by Paris (in Klie, 1926). Elofson (1941, p. 359) recorded the copulatory positions for *Cythere lutea* O. F. Müller, *Leptocythere* spp., *Cythereis tuberculata* Sars, "*C. dunelmensis* Norman," *Cytherura nigrescens* (Baird), *C. undata* Sars, *Cytheropteron cellulosum* (Norman), *Hirschmannia viridis* (O. F. Müller), *Xestoleberis aurantia* (Baird), *X. pusilla* (Elofson), and *Paradoxostoma* spp.

Kaufmann (1892) observed the 180 degree rotation of the hemipenes and the posterodorsal attitude of the male in *Leucocythere mirabilis* Kaufmann. Later (1896, p. 375–376), he again described the posterodorsal position and speed of consummation in the same species:

> . . . die Männchen auf den Rücken der weiblichen Schale kletterte, welche es mit den Klauen der zweiten Antenne festhielt, wobei sich die Schläge der Branchialplatten stark vermehrten. Hierauf wurde das Copulationsorgan wie an einem elastischen Band weit aus der Schale herausgeschleudert, der ganze Apparat gedreht, so dass die Wölbung nach unten zu liegen kam, derselbe rasch in die Schale des Weibchens eingeführt, um nach kurzem wieder die ursprüngliche Lage einzunehmen.

Still later (1900, p. 261), Kaufmann remarked that in *Cyprois marginata*, as in the Cytheridae, the entire male apparatus in copulation was thrust forward and contorted ("vorgeschoben und gedreht").

Jensen (1904, p. 18–19) and Klie (1926, p. 22–23) also studied the copulatory behavior of *Cyprois marginata*. Jensen noted the rotation of the hemipenis and the posterodorsal mating position; Klie carefully illustrated (1926, figs. 29, 30) the position of the male both before and during copulation.

According to Jensen (1904), Sars (1889) observed the mating behavior of *Cyprinotus dentato-marginatus* and stated that the male grasped the female with the palps of the first pair of legs. Jensen questioned the validity of Sars' observation and discussed the important function of the specialized setae of the male second antennae in *Candona, Cyclocypris, Cypris, Cyprois,* and *Notodromas.* Alm (1916, p. 11) also maintained that the palps of the first pair of legs were not suited for grasping and holding the female.

Wohlgemuth (1914, p. 44) recorded that in *Cyprinotus incongruens* the male approached the female from the rear, assumed a posterodorsal position at about a 75° angle, inserted the copulatory organs from the rear and below, and accomplished fertilization in a few seconds. For *Cyclocypris laevis* (O. F. Müller), Wohlgemuth stated that the short duration and the movements of male and female made it impossible to get a clear understanding of the operation of the complicated penis apparatus.

In 1904, Jensen presented one of the first detailed descriptions of the mating behavior of a freshwater ostracod, *Candona fabaeformis.* He also noted the similarity of the copulatory act of the latter to that of *C. rostrata, Candonopsis kingsleii,* and *Cyprois marginata.* Of *Candona,* Klie stated (1938, p. 14–15) that the male employed a posterodorsal approach and completed copulation with quick entry and retraction.

Ferguson (1944, p. 717) described a posterodorsal mating posture in *Potamocypris smaragdina* and stated further:

> The ventral concavity of the male shell was firmly appressed to the convex surface of the posterodorsal part of the female shell and the valves of the latter were kept open by the long curved claw of the 2nd thoracic appendage which was used as a wedge.

Among the freshwater Cypridacea only *Notodromas monacha* is known to mate in other than a posterodorsal position (Kesling, 1961a, p. 18). According to Jensen (1904, p. 17), and Klie (1926, p. 38), the venter-to-venter mating position is not accompanied by the 180 degree rotation of the hemipenes. Consequently, spermatozoa pass from the right testicle and hemipenis of the male to the left vagina and seminal receptacle of the female, as in other cypridid genera. In a subsequent publication on German Ostracoda, Klie said (1938, p. 15) of *Notodromas monacha* that:

> . . . bei dieser Art liegen die unteren Schalenränder der Tiere der Länge nach einander, und die Drehung des Kopulationsorgans unterbleibt; ähnlich werden sich vermutlich die meisten Cytheridae verhalten.

Klie's (1938) statement that in most cytherids the "Kopulationsorgans" are not rotated was confirmed by Elofson (1941, p. 358–360) for those species he observed. Elofson described the mating positions of several marine cytherids including species of *Cythere, Leptocythere, Cythereis, Cytherura, Cytheropteron, Hirschmannia, Xestoleberis,* and *Paradoxostoma.* These ostracods mate in a venter-to-

TEXT-FIG. 5—*Candona suburbana* Hoff. Pair in copula, drawn with right valves removed to expose append-
    ages and genitalia. Palp of right first leg shown withdrawn from proper position on female cara-
    pace for clarity of illustration. Compare with text-figure 6.

venter position but form a wide angle to one
another. He stated (1941, p. 359):

> Während der Paarung wenden alle von mir
> studierten Arten die Ventralseiten gegeneinan-
> der, wobei diese jedoch einen weiten Winkel
> miteinander bilden, der gewöhnlich 50°–120°
> beträgt.

In the species he observed, the "penis" is
erected in such a fashion that the distal end
assists in forcing the female valves apart
(Elofson, p. 359).

According to Klie (1926, p. 33) in his re-
view of previous contributions, Paris reported
a ventral copulatory position for the fresh-
water cytherid *Metacypris cordata,* but no in-
formation regarding rotation of hemipenes in
this species was given.

In the detailed study of his *Entocythere
heterodonta,* Rioja (1940, p. 603–604) de-
scribed the anatomy of the male copulatory
apparatus. He also noted the role played by the
male antenna and thoracic legs in grasping the
female, and suggested that the copulatory po-
sition was maintained by contraction of the
male's closing muscles. He stated (1940, p.
606):

> Entre los numerosos ejemplares observados
> hemos podido ver algunos durante el momento

de la cópula. En este momento parece es de
importancia el funcionamiento de la segunda
antena del macho, que sujeta las valvas de la
hembra de modo que el borde de ellas pasa
entre la uña terminal externa y la mediana, así
una y otras la sujetan por sus dos superficies.
Entre las valvas entreabiertas se introduce en
la partie posterior el órgano copulador que se
dirige al encuentro del oroficio femenino. Los
tres pares de patas del macho contribuyen a
fijarle sobre el caparazón de la hembra. Las
dos valvas del macho se abren para dar lugar
a que entre ellas se coloque el cuerpo del in-
dividuo del otro sexo. Los músculos de la
concha del macho, al contraerse, favorecen se-
guramente la unión de los individuos que cop-
ulan.

His sketch (1940, pl. 3, fig. 1) of a mating
pair corresponds remarkably to our photograph
(text-fig. 1).

Hart & Hart (1968) described and illus-
trated the relaxed and erect positions of hemi-
penes in entocytherids and noted the 180 de-
gree rotation which occurs before the organs
are inserted between the valves of the female.
The rotation of the "copulatory complex" of
entocytherids apparently involves each half
independently rather than both halves together
as occurs in *Candona.*

Jensen (1904, p. 17), Klie (1926, p. 33), and Elofson (1941, p. 360) noted that individuals of both sexes may mate with many partners over intervals of a few minutes in densely populated cultures. Elofson also stated that under both high light intensity and increased temperature the frequency of mating increases.

Jensen (1904, p. 15) observed that copulation in *Candona fabaeformis* lasted about 15 seconds. Klie (1926, p. 33) reported *Cyprois marginata* in copula for periods of a few seconds and stated that 50 seconds was maximal for those he observed. In marine species, Elofson (1941, p. 360) found that the copulation act often lasts from one-half to several minutes

TEXT-FIG. 7—*Notodromas monacha* (O. F. Müller) [Podocopida, Podocopina, Cypridacea]. *a, b*, lateral and ventral views of female carapace, showing dimorphic ventral indentation. *c*, lateral view of male carapace. [From T.I.P., pt. Q, 1961, fig. 180, *1*.]

TEXT-FIG. 6—*Candona* [Podocopida, Podocopina, Cypridacea]. *a, b*, diagrams of male and female animals as seen with left valves removed; hemipenes inverted in error. *c, d*, male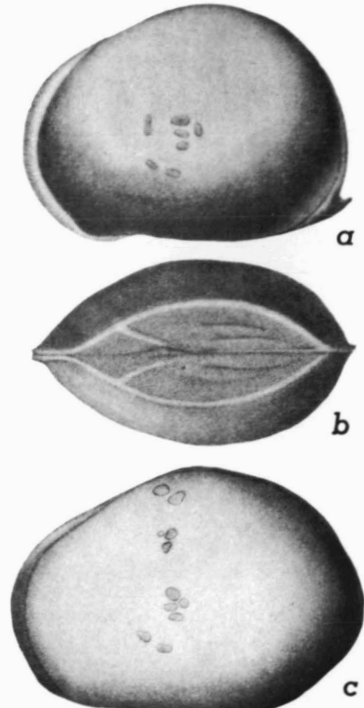 left first thoracic leg and palp (endopod) of right first thoracic leg. *e, f*, inner faces of ends of male and female right antennae; note "male setae." [From Kesling *in* Howe, Kesling, & Scott, 1961, fig. 6.]

and, rarely, for five minutes. He also (p. 360) reported copulation involving a male *Cythereis villosa* Sars and female *Cythere lutea*.

Both Weismann (1880, p. 83) and Elofson (1941, p. 360) noted the presence of spermatozoa in almost all sexually reproducing female ostracods examined. Theisen (1966, p. 258, 261) stated that copulation occurs soon after the last molt and often several times in the life span of *Cytherura gibba* (O. F. Müller), *Loxoconcha elliptica* Brady, and *Elofsonia baltica* (Hirschmann).

OBSERVATIONS

Our observations of mating in *Candona suburbana* Hoff, *C. ohioensis* Furtos, *C. rawsoni* Tressler, and *C inopinata* Furtos correspond closely to those of Jensen (1904). The mating pattern in *Candona* varies slightly among species but generally is similar to that of *Candona suburbana* (text-fig. 5). In brief, the male grasps the female by a specialized pair of setae on the second antennae and maneuvers his body to a posterodorsal position on the female carapace. Once this position is attained, the palps

of the first pair of legs (second maxilla, Jensen) are inserted inside the valves of the female and turned to assist in forcing and holding the valves apart for intromission of the voluminous hemipenes. The second pair of legs also appear to stimulate the female to spread her valves. The latter appendages often come in contact with the female carapace and body before the hemipenes are thrust through the gape of the female valves.

The paired "male muscles" (McGregor & Kesling, 1968, text-figs. 5–7), passing from the valves of the male to the hemipenes, contract to bring the hemipenes downward and out of the carapace. The hemipenes then are rotated as one unit through 180 degrees, swung forward between the valves of the female, unfolded in erection, and the glans inserted into

the paired vaginae. Rotation of the hemipenes thus results in contact and transfer of sperm from the male left and right testicles and hemipenes to the right and left vaginae and seminal receptacles, respectively, of the female. Erection of the hemipenes is accompanied by a nearly vertical rotation of the paired Zenker's organs and marked constriction of the posterior region of the body.

After copulation, the hemipenes are withdrawn from the female carapace, rotated 180 degrees, retracted, and returned to their original posterocentral position within the male carapace. The palps of the first pair of legs are withdrawn from the female valves shortly before the male releases the female. The functional morphology of the hemipenes of *Candona* and the process of erection and retraction are discussed in greater detail by Danielopol (1968) and McGregor & Kesling (1968).

In free-swimming ostracods [i.e., *Physocypria pustulosa* (Sharpe), *Cypria turneri* Hoff, *Cyclocypris ampla* Furtos, and *Cyprinotus glaucus* Furtos] the male assumes a posterodorsal position on the female carapace. However, the body of the male is pulled toward the female posterior as the hemipenes are everted and rests with the long axis of the carapace perpendicular, or nearly so, to that of the female (text-figs. 3, 4). As in *Candona* the antennae serve to grasp and hold the female whereas the palps of the first pair of legs function to hold the female valves apart and to pull the carapace and body of the male and female against one another. The second pair of legs of the male often assist in pulling and holding his carapace firmly against that of the female. The female usually remains passive during copulation; in strong light or as the temperature of the medium increases, the male may copulate with the female while the latter is swimming, walking, or lying on her side. Often, the male may be carried about by the female for several minutes before copulation occurs.

Rotation of the hemipenes is very difficult to observe in the above free-swimming species because of the extremely rapid introduction of these organs between the female valves. In *Physocypria*, for example, the hemipenes are usually rotated before extrusion from the carapace. The copulation act, including rotation, erection, intromission, retraction, and rotation of the hemipenes to their original position, may be completed in less than four seconds.

In freshwater ostracods we have studied, individuals of both sexes may mate repeatedly with several partners over intervals of about five minutes in densely populated cultures.
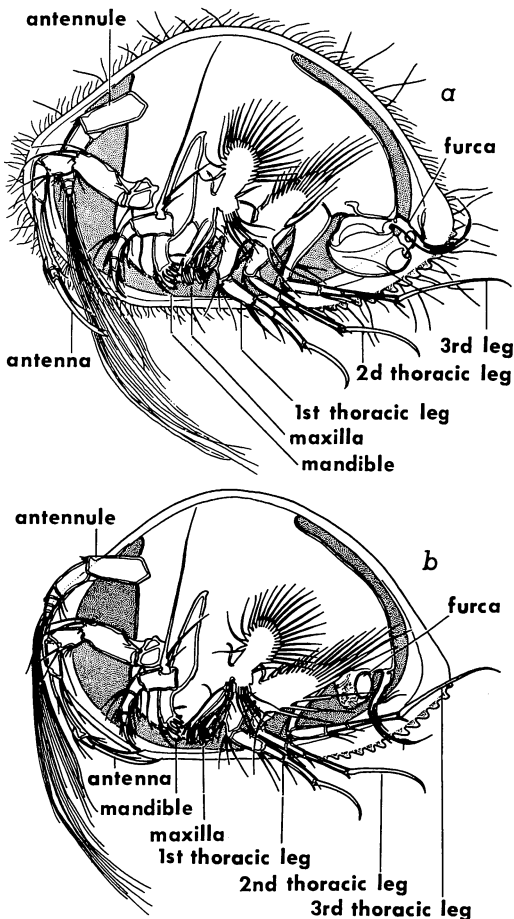
TEXT-FIG. 8—*Bairdia* [Podocopida, Podocopina, Bairdiacea]. *a, b,* diagrams of male and female animals with left valves removed. [From Kesling *in* Howe, Kesling, & Scott, 1961, figs. 10, 11.]
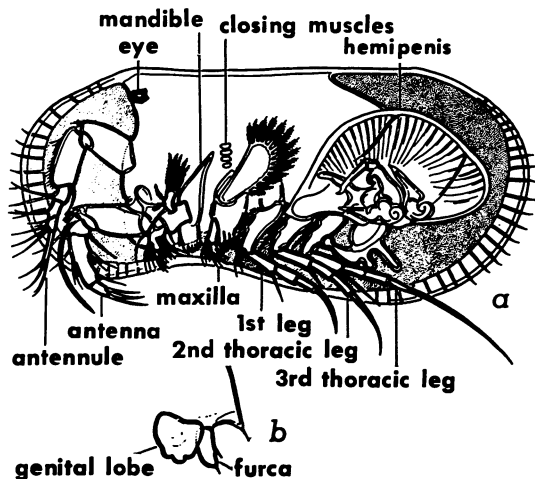
Among species of *Candona,* copulation generally lasts from 10 to 25 seconds but occasionally may last up to two minutes. Mating in *Physocypria pustulosa* and *Cypria turneri* is usually completed within a few seconds but in rare instances lasts up to one minute. In addition, the male often copulates with the female two or more times before releasing her. *Cyclocypris ampla* and *Cyprinotus glaucus* generally remain in copula for periods of 15–20 seconds and often longer than one minute.

In densely populated cultures, males often attempt to copulate with other males and occasionally with females of other species. Sexual discrimination is decidedly poor when the animals are subjected to intense light, even for brief intervals. We have observed male *Cyprinotus glaucus* mate with females of the parthenogenetic ostracod *Cypridopsis vidua* (O. F. Müller). Attempted copulation between different species of *Candona* is common.

ADAPTATIONS

Living ostracods seem to be adapted for copulation in several ways: mating position, location of genitalia, general shape and dimorphism of carapace, extensible hemipenes, protrusible posterior section of the body, and clasping organs. Most ostracods exhibit a combination of two or more of these features.

Mating position.—The known positions assumed by the male are dorsal, posterodorsal, and ventral on the female carapace. Unfortunately, most genera have not been observed in copulation, so that other positions may exist.

Entocythere exemplifies the dorsal position (text-figs. 1, 2). It is a small ostracod commonly commensal on crayfish. This genus belongs in the order Podocopida, suborder Podocopina, superfamily Cytheracea, and family Entocytheridae. Its carapace is oval to subelliptical, laterally compressed. The hemipenes are hinged to a process in the posterodorsal part of the animal in such a manner that they can be lowered straight down, much as from a crane, and then independently rotated (Hart & Hart, 1968). Although the hemipenis does not unfold for greater length, the glans ("penis") everts

TEXT-FIG. 9—*Limnocythere* [Podocopida, Podocopina, Cytheracea]. *a,* diagram of male animal with left valve removed. *b,* female furca and genital lobe. [From Kesling *in* Howe, Kesling, & Scott, 1961, fig. 7.]
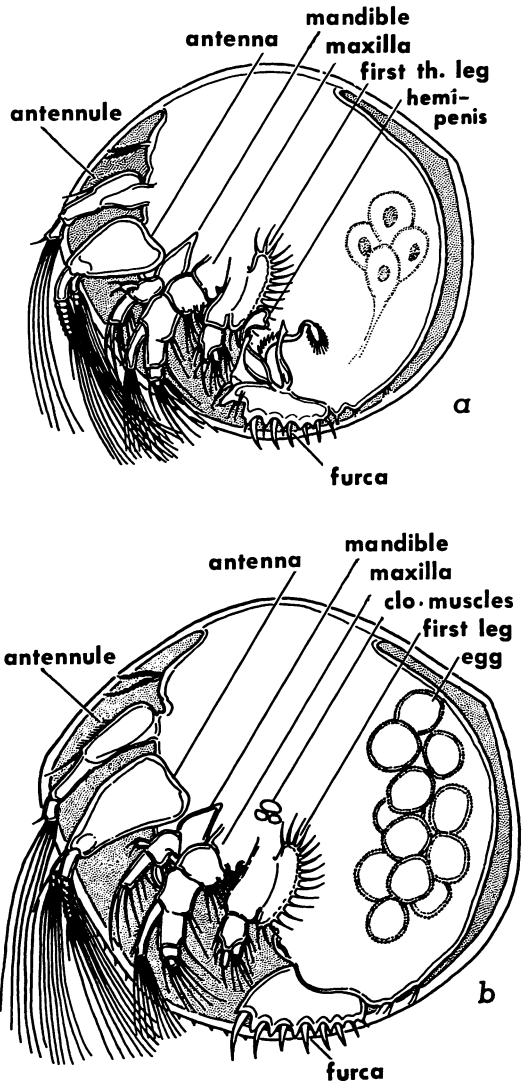
TEXT-FIG. 10—*Polycope* [Myodocopida, Cladocopina, Polycopidae]. *a, b,* diagrams of male and female animals with left valves removed. [From Kesling *in* Howe, Kesling, & Scott, 1961, fig. 4.]

in copulation. The two hemipenes and their supports are rather voluminous. By lowering and rotation, each hemipenis can be extended into the valves of the female immediately below through the posterior gape in her opened carapace (text-fig. 2a). Part of the hemipenis structure forms a clasping device (text-fig. 2c). The male holds to the front end of the female valves with his antennal claws (text-fig. 2b).

Ostracods of the superfamily Cypridacea are practitioners of the posterodorsal position. We have observed *Cypria turneri, Physocypria pustulosa,* and several species of *Candona* in copula. The copulation act is so quickly accomplished that it can scarcely be photographed. Preserving a pair in copula is difficult. Sedation is too slow, and killing with boiling water usually results in the male releasing his hold with the clasping organs and slipping down on the female carapace (text-figs. 3a, 4a). For *Cypria turneri* (text-fig. 3a,b) we were able to kill, fix, and clear a pair while the hemipenes were still engaged in the vaginae of the female, and for *Physocypria pustulosa* (text-fig. 4a,b) while the glans of the hemipenes were still inserted deep within the female carapace. We were not so successful with pairs of *Candona,* and the copulation position is drawn from a series of rapid sketches (text-fig. 5).

As described in Part I of this series, *Candona* shows notable dimorphism on the posterodorsal region of the carapace, the female being strongly beveled (text-figs. 5, 6b). In erection, the male hemipenes rotate 180 degrees, unfold, and extend to about half the length of the carapace (text-fig. 5). The posterior section of the body, to which the hemipenes are attached, can also be lowered slightly to aid in protrusion of the organs.

Several genera of the superfamily Cytheracea are known to use the ventral position, as reported by Elofson (1941, p. 359). Their common character is a straight to very slightly concave ventral border. In general, *Leptocythere, Xestoleberis,* and *Paradoxostoma* species are elongate, whereas *Cythere* and *Hirschmannia* are more reniform. *Cytheropteron,* characterized by a flat venter and large ventrolateral wing processes extending outward to form a flat surface, appears well suited for the ventral position. According to Elofson (1941, p. 359), marine ostracods he observed in copulation lay venter-to-venter, their posteroventral borders in contact, and their bodies forming an angle, usually 50 to 120 degrees. More observations are needed to discover if the initial phase of copulation is made with the partners subparallel (as we suspect) or at different angles according to the species involved.

One ostracod of the superfamily Cypridacea is known to mate in the ventral position. It is *Notodromas,* a specialized freshwater ostracod that spends its life upside down scooting along just under the surface film of standing water (text-fig. 7). The male *Notodromas* has a robust, inflated carapace with a beveled posteroventral corner. The female, however, has a rounded posteroventral edge provided with a short spine; she also has a special flat or concave lanceolate venter bordered by low keels, apparently designed to accommodate the ventral edges of the male valves in copulation.

Location of genitalia.—The second adaptation to facilitate mating is location of the genitalia. For each living species that has been studied, the copulatory organs are attached at about the same part of the body in the male as in the female. In some species, such as *Entocythere,* the organs are posterior to posterodorsal. In others, such as *Bairdia* (text-fig. 8) and *Limnocythere* (text-fig. 9), the furca is much reduced and the genitalia lie near the posteroventral end of the body. In *Candona,* they are on the ventral side of the body in a posterocentral position. In the subcircular *Polycope* (text-fig. 10) they are nearly ventral because of the concentration of appendages in the front half of the carapace.

Insofar as known, hemipenes are functional from a particular location. It would appear impossible for the large hemipenes of *Candona,* for example, to be retracted to a posterior position or to function from a posteroventral attachment. Similarly, the hemipenes of *Entocythere* would be useless in the dorsal mating position if fastened to the posterocentral part of the body.

General shape of carapace.—Shape of the carapace has received special attention in taxonomy but very little in functional analysis. Aside from such dimorphic features of the carapace as the posteroventral enlargement in male *Candona,* necessary to house the voluminous protrusible hemipenes (text-fig. 6a), most carapace dimorphism appears to be directly related to the copulation act. Even the general shape of the carapace seems to be a significant factor in the feasible modes of copulation in a species.

In text-figure 11, five generalized carapace shapes are shown in the three copulatory positions. The posterodorsal, posteroventral, and posterocentral locations of genitalia are indicated by symbols. In these models we assume that the body of the male occupies at least one
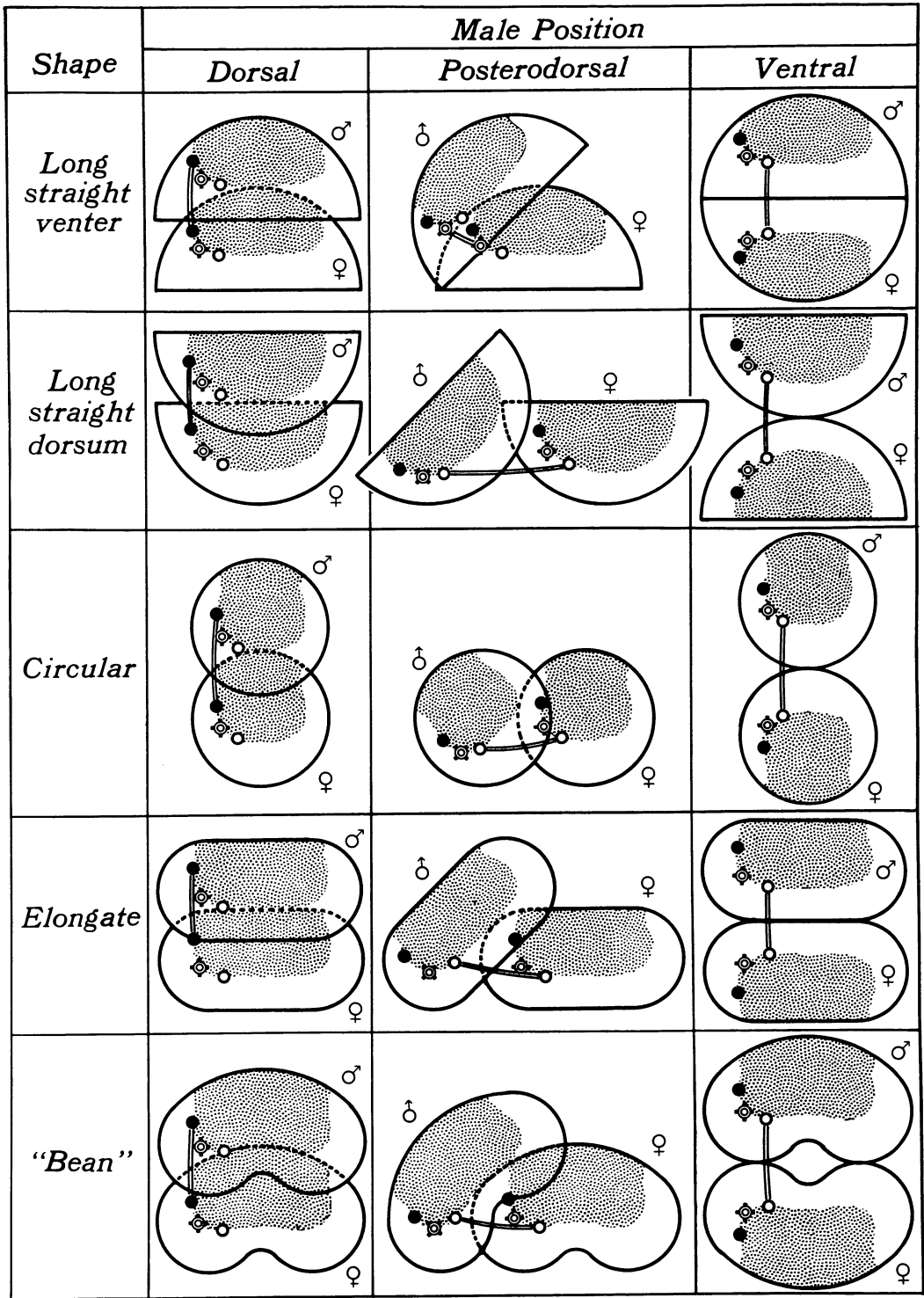
TEXT-FIG. *11*—Generalized shapes of carapaces and copulatory positions. Three possible locations of genitalia are indicated by symbols.
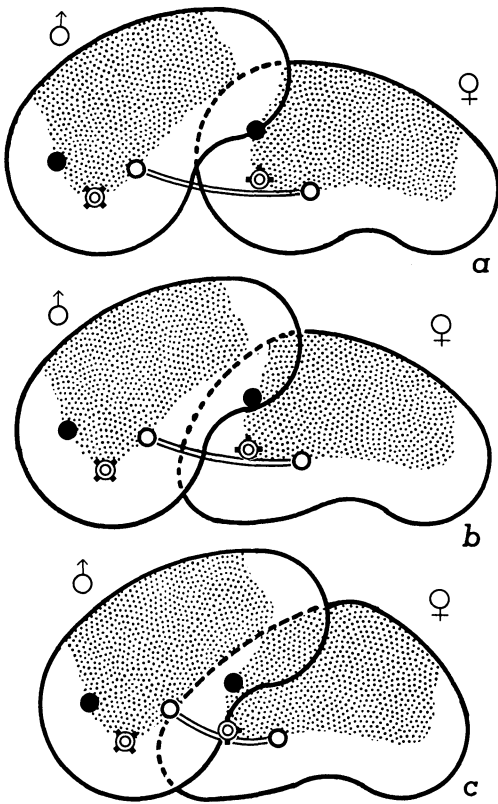
TEXT-FIG. *12*—Generalized sketch of "bean-shaped" ostracods showing effect of progressive modification of female carapace upon mating in the posterodorsal position.

half of height and length, that his body marks the limit of his overlap of the female carapace, and that the posterodorsal position of the male involves an inclination of 45 degrees and posteroventral contact with the substrate. These assumptions seem to be in reasonable agreement with observations of various living species. In reality, modifications of the copulatory position and location of genitalia may be discovered in future studies. Nevertheless, these drawings indicate that certain positions and locations would require less length and complexity of hemipenes for ostracods of a given shape.

Contrary to what one might expect, the circular shape is not ideal. Actually, a long ventral border combined with posterodorsal position and posteroventral genitalia involves relatively short hemipenes. By the nature of their geometry, ostracods with long straight dorsal borders, such as the multitude of Paleozoic palaeocopes, would appear to have needed extremely long, extensible hemipenes in any except the dorsal position. In the text-figure, the

dorsal position and elongate shape correspond closely to the copulatory plan of *Entocythere* and the posterodorsal position and "bean" shape to *Candona*.

Dimorphism of carapace.—In *Candona*, the beveled posterodorsal border in the female probably evolved concomitantly with the posterodorsal copulatory position and the posterocentral extensible hemipenis in the male. There is a practical limit (text-fig. 12) of female
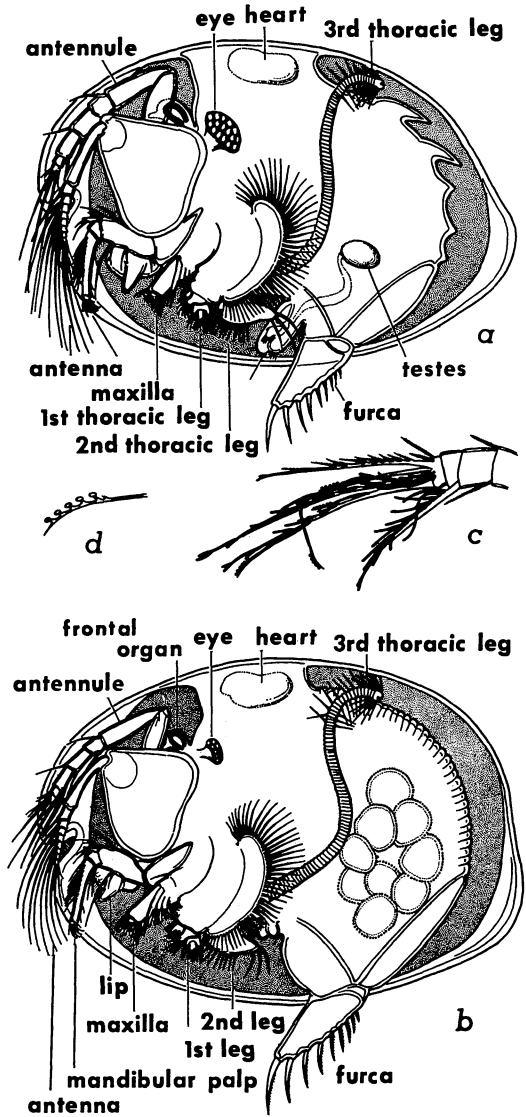
TEXT-FIG. *13*—*Cypridina* [Myodocopida, Myodocopina, Cypridinacea]. *a, b,* diagrams of male and female animals with left valves removed. *c, d,* distal end of male antennule and enlarged suctorial structures. [From Kesling *in* Howe, Kesling, & Scott, 1961, figs. 1–2.]

modification beyond which little copulatory advantage accrues. Indeed, extreme dimorphism in *Candona* would appear to be disadvantageous both for copulation and for accommodation of female body and appendages. As mentioned above, ventral indentations in the female carapace of *Notodromas* (text-fig. 7) fit the edges of the male valves in the ventral position of mating.

Extensible hemipenes.—Genitalia of male and female are separated by a considerable distance in some kinds of ostracods. The copulation problem apparently was not solved for all ostracods by optimum position of the male or favorable location of genitalia. Some species achieved union by extensible hemipenes, others by a protrusible posterior part of the body. In fact, one or the other arrangement seems to exist, to some degree, in all living, sexually reproductive ostracods that have been thoroughly studied. Extensible hemipenes are found in *Entocythere* and *Candona* (as representatives of the Cytheracea and Cypridacea), of different structure and mode of operation, and undoubtedly of different evolutionary history.

Protrusible body.—Numerous examples can be cited of protrusible posteriors, in which the rear of the body can be bent down and may be thrust beyond the edges of the valves. In *Cypridina* (text-fig. 13) the body has a very narrow dorsal attachment to the carapace. The rear of the body follows a long curve parallel to the posterodorsal, posterior and posteroventral borders of the carapace, and the furca and genitalia are set forward, not far behind the middle of the ventral border. The same arrangement occurs in the much more elongate *Conchoecia* (text-fig. 14) and in the subcircular *Polycope* (text-fig. 10). In *Cytherella* (text-fig. 15) the posterior part of the body is a discrete structure, approaching in form the abdomen of a crayfish. In these genera and others, the protrusion of the posterior part of the body undoubtedly serves to bring the non-extensible hemipenes into contact with the female vaginae.

Clasping organs.—Clasping organs in the male are functional and the mating position permits them to reach and hold to particular parts of the female carapace. Several kinds of clasping organs have evolved, specialized structures in various appendages. Ostracods of the superfamily Cypridacea have the endopod or palp of the male first thoracic leg modified to form a pincer-like clasper (text-figs. 5, 6c,d). The male uses these claspers to hold fast to the rear part of the female valves in the posterodorsal mating position. Because the same modification exists in males of the Macrocy-

prididae (text-fig. 16), we would classify this family in the superfamily Cypridacea (as done by G. W. Müller and others) rather than in the superfamily Bairdiacea (as in the *Treatise on Invertebrate Paleontology*). Other superfamilies of the suborder Podocopina—the Cytheracea, Darwinulacea, and Bairdiacea—have no clasping organs developed on the first thoracic legs.

In addition, males of certain cypridid ostracods, such as *Candona*, have special "male setae" on the inner sides of the antennae (text-fig. 6e). These are conspicuous tubular setae with expanded tips, attached to the second podomere of the endopod. They are presumed to assist the male in holding to the smooth dorsal margin of the female carapace.

The highly specialized *Entocythere* (text-figs. 1, 2) has adaptations in the male for assuming and maintaining the dorsal mating position. The male uses strong claws on the antenna for holding to the anterior end of the female valve (text-fig. 2c), and probably uses his thoracic legs to cling to the sides of the smooth female valve. Since the hemipenes them-
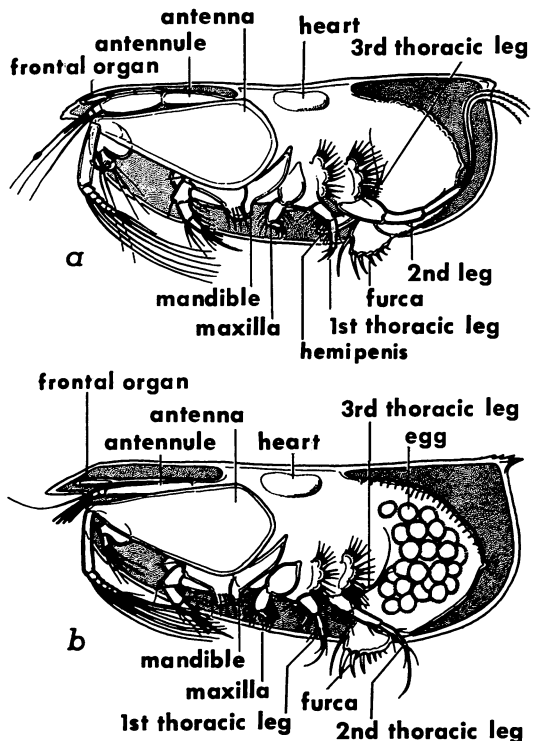
TEXT-FIG. *14—Conchoecia* [Myodocopida, Myodocopina, Halocypridacea]. *a, b,* diagrams of male and female animals with left valves removed. [From Kesling *in* Howe, Kesling, & Scott, 1961, fig. 3.]

selves serve as clasping devices (text-fig. 2b), the male attaches to the dorsal side of the female more or less as tongs, with opposing actions by the antennal claws and the falcate processes of the hemipenes.

In *Cytherella,* a typical deep marine ostracod of the suborder Platycopina and family Cytherellidae, the male has the endopods of both the first and second thoracic legs provided with subdistal articulations to form effective claspers (text-fig. 15c,d). Carapace dimorphism is strong, the male having a thin, parallel-sided shell and the female an expanded posterior section for brood care. Unfortunately, the mating habits of the Cytherellidae are unknown.

In the order Myodocopida, suborder Myodocopina, noted as planktonic ostracods, the clasping organs are located farther forward. In

We suspect that it has a long geologic history and that many extinct cypridaceans were similarly equipped. Probably, the posterodorsal mating position, which makes use of these claspers, evolved at the same time and was employed by extinct ancestral forms.

COPULATION-CARAPACE RELATIONSHIPS

Current knowledge of living species permits a few generalizations regarding the relationship of copulation to carapace. Whether these generalizations will be substantiated or will be modified by additional research, for the present they can serve as working hypotheses for consideration in fossil ostracods.

(1) Male valves can scarcely gape in mating by more than the length of the contracted closing muscles. From observations of some living
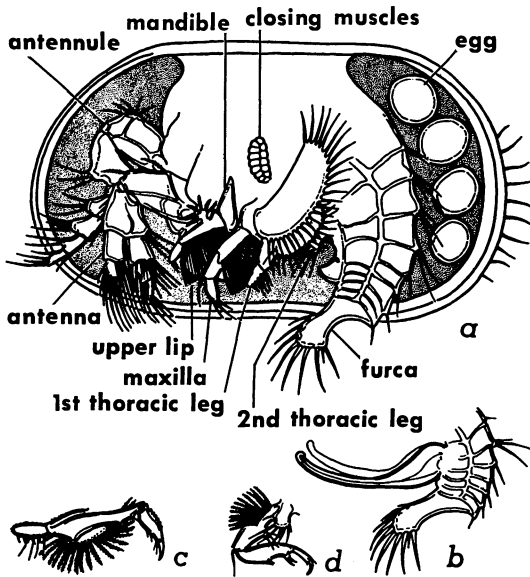
TEXT-FIG. *15—Cytherella* [Podocopida, Platycopina, Cytherellidae]. *a,* diagram of female animal with left valve removed. *b-d,* male furca and hemipenes, left first thoracic leg, and left second thoracic leg. [From Kesling *in* Howe, Kesling, & Scott, 1961, fig. 5.]

Cypridina, the male antennule possesses special suctorial setae for holding to the female (text-fig. 13c,d), and in *Conchoecia* the endopod of the male antenna has a terminal hook-shaped device forming a pincer-like clasper (text-fig. 14a). Observations of the mating of myodocopids are needed.

Of the various kinds of clasping organs developed in Ostracoda, the modification of the male first thoracic leg in the Cypridacea seems to be unique and universal in the superfamily.
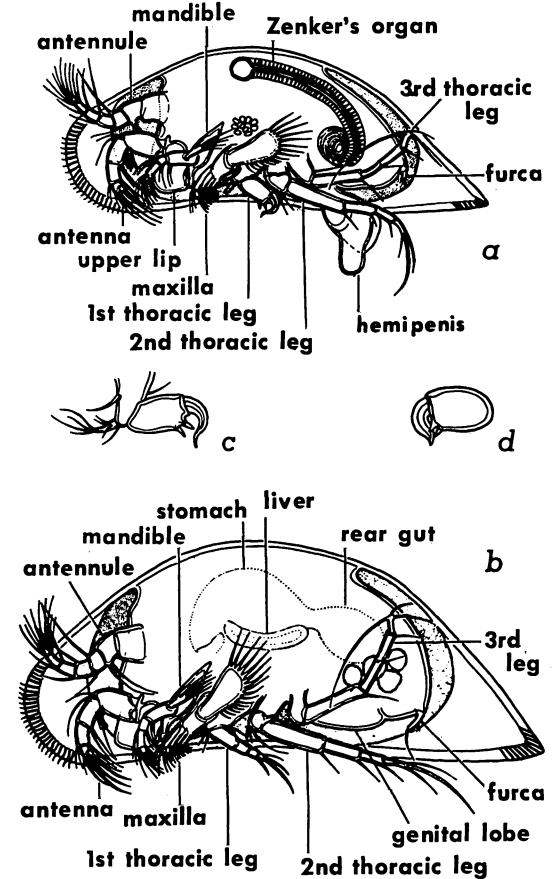
TEXT-FIG. *16—Macrocypris* [Podocopida, Podocopina, Cypridacea]. *a, b,* diagrams of male and female animals with left valves removed. *c, d,* male left first thoracic leg and palp (endopod) of right first thoracic leg. [From Kesling *in* Howe, Kesling, & Scott, 1961, fig. 6.]

freshwater species, we find that the valves seldom gape by as much as the closed width of the domicilium in feeding and locomotion. In mating, however, they appear to open somewhat wider; we base this on the amount of overlap of the female carapace in *Candona* rather than on actual measurements of the angle between the opened valves, since mating lasts only a few minutes at most.

In addition, the geometry of the ostracod makes this hypothesis reasonable. The valves are hinged at their dorsal border, gape widest at their ventral border, and are shut by closing muscles attached near mid-height. In such an arrangement, if the closing muscles expand from their contracted condition by half their length, then the ventral edges of the valves separate by a distance approximating the length of the contracted muscles.

(2) *A female carapace can scarcely be overlapped by the male in mating in any part which in width exceeds the length of the male's contracted closing muscles.* This is a corollary of the first hypothesis. It is especially significant in selecting possible areas of overlap in ostracods with a broad venter, bulbous expansions of the carapace, or dimorphic inflation of the posterior section of the female carapace.

(3) *A male can scarcely overlap a female carapace by more than half the height of his carapace.* Body and appendages occupy at least two-thirds the height of the male carapace in living species (text-figs. 8–10, 13–16), and cannot be much compressed. This is exclusive of the small distal tips of appendages. The protopods of appendages and the ventral wall of head and thorax cannot be displaced dorsally to an appreciable degree. Minor displacements, brought about by contraction of muscles from the dorsal part of the carapace to appendages and endoskeleton, have been described by many workers, but the mass of the body prevents very much contraction and dorsal displacement. In the absence of preserved soft parts, we presume that those of extinct species were as large as those in living ostracods.

(4) *Genitalia of both sexes attach in the posterior one-third of the carapace.* All living ostracods have a pair of maxillae behind the closing muscles. In addition, living Podocopina and Myodocopina have three pairs of thoracic legs, Platycopina have two pairs, and Cladocopina one pair. The sequence of appendages added during ontogeny, in which one pair of post-mandibular appendages is added at each ecdysis until the full set is developed, has an irregularity that indicates the ancestral ostracod probably had an additional pair of maxillae (Kesling, 1961b, p. 20). Hence, between the

closing muscles and the genitalia, Paleozoic Ostracoda may have had four pairs of appendages, possibly five pairs. It seems reasonable to presume that genitalia could not encroach forward beyond the posterior one-third of the carapace. Within the posterior region, however, the genitalia may have been in a posterior, posteroventral, or posterocentral position in a particular lineage.

(5) *Genitalia require some lateral as well as vertical accommodation within the carapace.* The inner space of the carapace, the domicilium, houses the genitalia and other soft parts of the body when the valves close (except for the antennules in the Myodocopina). The volume and requisite maneuverability of hemipenes in living forms show that accommodation and functioning of these organs would not be
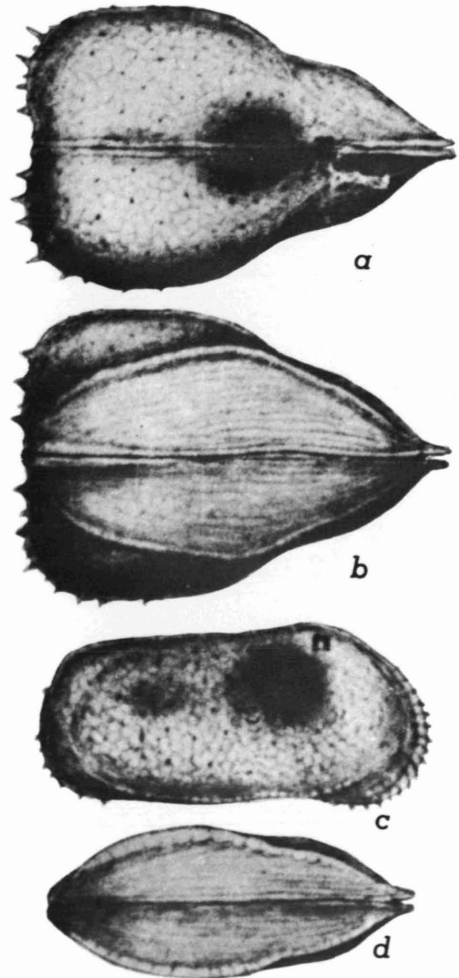
TEXT-FIG. 17—*Gomphocythere expansa* (Sars) [Podocopida, Podocopina, Cytheracea]. *a, b,* dorsal and ventral views of female carapace, *c, d,* lateral and ventral views of male carapace. [From T.I.P., pt. Q, 1961, fig. 236, 2.]

possible in a constricted section of the carapace. Female genitalia are situated at about the same place on the body as those of the male of the species. For extinct ostracods with a deeply indented S3, therefore, the genitalia were most likely confined in L4. Generally, genitalia are associated with lobate rather than sulcate parts of the carapace.

(6) *Dimorphic modification in the female carapace may correlate with the mating position assumed by the male.* This has been shown in *Candona* and in *Notodromas.* As will be discussed in the third part of this series, fossil ostracods exhibit several kinds of dimorphic modifications in the female which seem to be indicative of mating position. The flattened venter in certain benthonic species was termed the fundium by Morris (1958, p. 344), who interpreted it to be an adaptation for stability. It seems to us that this flattening of the part of the carapace in contact with the substrate may serve a dual purpose: it may promote stability in locomotion and also facilitate the ventral position in mating. The flattened venter in *Gomphocythere* (text-fig. 17), for example, would certainly be of value in the ventral mating position. Other Cytheracea, even those which do not have obvious dimorphism of the carapace, if any, could similarly take advantage of the flat ventral area for the two functions.

(7) *Posteroventral enlargement of the male carapace may correlate with large, complicated hemipenes.* This is especially emphasized in *Candona,* although present in some other cypridaceans. It is necessary, however, to distinguish between posterior dimorphic enlargements which are present in the male for accommodation of the sex organs and those in the female which are used to house the eggs and young. This may not be easy to identify in extinct groups.

A few more points could be listed, but they would be based on only a few observations or reports. We anticipate that future functional studies of living forms will lead to substantial and reliable generalizations of carapace-copulation relationships.

LITERATURE CITED

ALM, GUNNAR, 1916, Monographie der Schwedischen Süsswasser-Ostracoden nebst systematischen Besprechungen der Tribus Podocopa: Uppsala Univ. Zool. Bidrag, v. 4, p. 1–247, 95 figs., 1 tab.

BLAKE, C. H., 1931, Two freshwater ostracods from North America: Bull. Mus. Comp. Zool. Harvard, v. 72, no. 7, p. 279–292, 26 text-figs.

BRADY, G. S., & ROBERTSON, D., 1870, The Ostracoda and Foraminifera of tidal rivers. With an analysis and descriptions of the Foraminifera, by H. B. Brady: Ann. Mag. Nat. History, ser. 4, v. 31, p. 1–33.

CLAUS, C., 1893, Beiträge zur Kenntnis der Süsswasser-Ostracoden, I. Über den Körper- und Gliedmassenbau der Cypriden nebst Bemerkungen über einzelne innere Organe derselben: Arb. Zool. Instit. Univ. Wien Zool. Stat. Triest, v. 10, p. 147–216.

DANIELOPOL, D. L., 1968, Recherches sur la morphologie de l'organe copulateur male chez quelques ostracodes du genre *Candona* Baird (Fam. Cyprididae Baird). (Abstract), *in* Symposium on the taxonomy, morphology and ecology of Recent Ostracoda (J. W. Neale, ed.): Oliver and Boyd Publ., Edinburgh. (In Press).

ELOFSON, OLOF, 1941, Zur Kenntnis der marinen Ostracoden Schwedens, mit besonderer Berücksichtigung des Skageraks: Uppsala Univ. Zool. Bidrag, v. 19, p. 215–534, 52 text-figs., 42 charts.

FERGUSON, EDWARD, JR., 1944, Studies of seasonal life history of three species of freshwater Ostracoda: Amer. Midland Naturalist, v. 32, no. 3, p. 713–727, 2 pls., 3 tabs.

FURTOS, N. C., 1933, The Ostracoda of Ohio: Ohio Biol. Survey, Bull. 29, v. 5, no. 6, p. 411–524, 16 pls.

——, 1935, Fresh-water Ostracoda from Massachusetts: Jour. Wash. Acad. Sci., v. 25, no. 12, p. 530–544, 6 figs.

GARBINI, A., 1887, Contribuzione all' anatomia ed alla istiologia delle Cyprinidae: Bull. Soc. Entom. Ital., v. 19, p. 35–51.

HARDING, J.P., & SYLVESTER-BRADLEY, P. C., 1953, The ostracod genus *Trachyleberis:* Bull. British Mus. Nat. Hist., v. 2, no. 1, p. 1–15, 2 pls.

HART, C. W., JR., 1962, A revision of the ostracods of the family Entocytheridae: Proc. Acad. Nat. Sci., Philadelphia, v. 114, no. 3, p. 121–147, 18 figs.

——, & HART, D. G., 1967, The entocytherid ostracods of Australia: *Ibid.,* v. 119, no. 1, p. 1–51, 95 figs.

——, & ——, 1968, The functional morphology of entocytherid ostracod copulatory appendages, with a discussion of possible homologs in other ostracods, *in* Symposium on the taxonomy, morphology, and ecology of Recent Ostracoda. (J. W. Neale, ed.): Oliver and Boyd, Edinburgh. (In Press).

HARTMANN, GERD., 1959, Zur Kenntnis der lotischen Lebensbereiche der pazifischen Küste von El Salvador unter besonderer Berücksichtigung seiner Ostracodenfauna. Beitrag zur Fauna El Salvadors III: Kieler Meeresforschungen, v. 15, no. 2, p. 187–241, 48 pls.

——, 1964, Asiatische Ostracoden. Systematische und zoogeographische Untersuchungen. Nach Material der Sammlung K. Lindberg aus der Türkei, dem Iran, Afghanistan, Indien, Kambodscha und Indonesien mit einem Anhang über Ostracoden aus Madagaskar: Int. Revue ges. Hydrobiol., Systematische B. 3, 155 p., 64 figs., 2 tabs., 3 maps.

HIRSCHMANN, N., 1912, Beitrag zur Kenntnis der Ostracoden-Fauna des Finnischen Meerbusens: Acta Soc. Fauna et Flora Fennica, v. 36, no. 2, p. 3–64, pls. 1–3, 15 text-figs.

HOBBS, H. H., JR., & WALTON, MARGARET, 1963, Four new species of the genus *Donnaldsoncythere* (Ostracoda, Entocytheridae) from Virginia with a key to the species of the genus: Trans. Amer. Microsc. Soc., v. 82, no. 4, p. 363–370, 26 figs.

——, & HART, C. W., JR., 1966, On the entocytherid ostracod genera *Ascetocythere, Plectocythere, Phymocythere* (Gen. Nov.), and *Cymocythere,* with descriptions of new species: Proc. Acad. Nat. Sci., Philadelphia, v. 118, no. 2, p. 35–61, 37 figs.

HOWE, H. V., KESLING, R. V., & SCOTT, H. W., 1961, Morphology of living Ostracoda: *in* Treatise on Invertebrate Paleontology, (R. C. Moore, ed.) v.

Q, Arthropoda 3, Crustacea, Ostracoda, p. Q3–Q17, 12 text-figs.

HULINGS, N. C., 1967, Marine Ostracoda from the Western North Atlantic Ocean: Labrador Sea, Gulf of St. Lawrence and off Nova Scotia: Crustaceana, v. 13, part 3, p. 310–328, 8 figs., 1 pl.

JENSEN, SØREN, 1904, Biologiske og systematiske Undersøgelser over Ferskvands-Ostracoder: Vid. Medd. naturhist. Foren. Kjøbenhavn, 78 p., 3 pls.

KAUFMANN, A., 1892, Über die Gattung *Acanthopus* Vernet und eine neue Süsswassercytheride: Zool. Anz., v. 15, p. 393–395.

——, 1896, Die schweizerischen Cytheriden: Rev. Suisse Zoologie (& Ann. Mus. d'Hist. Nat. Genève), v. 4, no. 2, p. 313–384, pls. 12–15.

——, 1900, Cypriden und Darwinuliden der Schweiz: Rev. Suisse Zoologie, v. 8, p. 209–423.

KESLING, R.V., 1957, Notes on Zenker's organs in the ostracod *Candona*: Amer. Midland Naturalist, v. 5, no. 1, p. 175–182, 9 figs.

——, 1961a, Reproduction of Ostracoda: *in* Treatise on Invertebrate Paleontology, (R. C. Moore, ed.) v. Q, Arthropoda 3, Crustacea, Ostracoda, p. 17–19.

——, 1961b, Ontogeny of Ostracoda: *Ibid.,* p. 19–20, figs. 13–14.

——, 1965, Anatomy and dimorphism of adult *Candona suburbana* Hoff, *in* KESLING, R. V., DARBY, D. G., SMITH, R. N., & HALL, D. D., Four reports of ostracod investigations (NSF Project GB-26), no. 1, iv + 56 p., 13 pls., 15 text-figs., Mus. Paleontol. Univ. Mich., Ann Arbor, Mich.

KLIE, WALTHER, 1926, Ostracoda, Muschelkrebse: Biol. Tiere Deutschlands, v. 22, no. 16, 56 p., 43 figs.

——, 1938, Krebstiere oder Crustacea, III: Ostracoda, Muschelkrebse: Die Tierwelt Deutschlands und der angrenzenden Meeresteile, pt. 34, iv + 230 p., 786 figs.

LEDERMÜLLER, M. F., 1761, Mikroskopische Gemüths- und Augen-Ergötzung, bestehend, in ein Hundert nach der Natur gezeichneten und mit Farben erleuchteten Kupfertafeln, sammt deren Erklärung: xxiv + 202 p., 100 pls. (+ frontispiece and patronymic plate), Christian de Launoy. Bayreuth.

McGREGOR, D. L., & KESLING, R. V., 1968, Copulatory adaptations in ostracods Part I. Hemipenes of *Candona*: Contrib. Mus. Paleontol. Univ. Mich., v. 23, no. 1, p. 1–23, 3 pls., 16 text-figs.

MORRIS, R. W., 1958, A new concept in ostracod taxonomy: Micropaleontology, v. 4, no. 4, p. 341–346, 8 text-figs.

MÜLLER, G. W., 1894, Die Ostracoden des Golfes von Neapel und der angrenzenden Meeres-abschnitte: Naples Sta. Zool., Fauna und Flora des Golfes von Neapel, Monographie, v. 31, viii + 404 p., pls. 1–40.

——, 1900, Deutschlands Süsswasserostracoden: Zoologica, v. 12, no. 30, p. 1–112, pls. 1–21.

NORDQUIST, O., 1885, Geschichtlicher Ueberblick der Untersuchungen ueber die Geschlechtsverhältnisse bei den Cypriden: Acta Soc. Sci. Fennicae, v. 15, p. 129–168, 6 pls.

PETKOVSKI, T. K., 1959, Süsswasserostracoden aus Jugoslavien VI: Acta Mus. Maced. Sci. Nat., v. 6, no. 3, p. 53–75, 70 figs.

RAMSCH, A., 1906, Über die weiblichen Geschlechtsorgane von *Cypridina mediterranea,* eines in Mittelmeer vorkommenden Ostrakoden (Muschelkrebses): Verh. ges. Naturf., Leipzig, v. 77, pt. 2, 204 p.

REYS, S., 1964, Note sur les Ostracodes des Phanérogames marines des cotes de provence: Rec. Trav. St. Mar. End., v. 32, no. 48, p. 183–202, 2 text-figs., 4 tabs.

RIOJA, ENRIQUE, 1940, Estudios carcinologicos. V. Morfologia de un ostracodo epizoario observado sobre *Cambarus (Cambarellus) montezumae* Sauss. de Mexico, *Entocythere heterodonta* n. sp. y descripcion de algunos de estados lavarios: Anales Inst. Biol. Mexico, v. 11, no. 2, p. 593–609, 3 pls.

SANDBERG, P. A., 1964, The ostracod genus *Cyprideis* in the Americas: Stockholm Contr. Geol., v. 12, 178 p., 33 text-figs., 5 tabs., 23 pls.

SARS, G. O., 1889, On some freshwater Ostracoda and Copepoda, raised from dried Australian mud: Förhandl. vidensk. Selskab. Christiania, v. 8, p. 1–79, pls. 1–8.

——, 1922–28, An account of the Crustacea of Norway: Bergen Mus. (Norway), v. 9 (Ostracoda), xii + 277 p., 119 pls.

SCHWARTZ, C. G., 1888, Über die sogenannte Schleimdrüse der männlichen Cypriden: Ber. naturf. Gesell. Frieburg, v. 3, p. 133–158, 2 pls.

SKOGSBERG, TAGE, 1920, Studies on marine ostracods. Part I. (Cypridinids, Halocyprids and Polycopids): Uppsala Univ. Zool. Bidrag, Suppl., no. 1, 784 p., 153 figs.

——, 1928, Studies on marine ostracods. Part II. External morphology of the genus *Cythereis* with descriptions of 21 new species: Occas. Papers California Acad. Sci., no. 15, 155 p., pls. 1–6.

STUHLMANN, F., 1886, Beiträge zur Anatomie der inneren männlichen Geschlechtsorgane und zur Spermatogenese der Cypriden: Zeitschr. Wiss. Zoologie, v. 44, p. 536–569, pl. 32.

THEISEN, B. F., 1966, The life history of seven species of ostracods from a Danish brackish-water locality: Medd. Danm. Fiskeri-og Havunders., N. S., v. 4, no. 8, p. 215–270, 23 text-figs., 7 tabs.

TREATISE ON INVERTEBRATE PALEONTOLOGY, ed. R. C. MOORE, pt. Q, Arthropoda 3, Crustacea, Ostracoda (by R. H. BENSON, J. M. BERDAN, W. A. VAN DEN BOLD, TETSURO HANAI, IVAR HESSLAND, H. V. HOWE, R. V. KESLING, S. A. LEVINSON, R. A. REYMENT, R. C. MOORE, H. W. SCOTT, R. H. SHAVER, I. G. SOHN, L. E. STOVER, F. M. SWAIN, P. C. SYLVESTER-BRADLEY, & JOHN WAINWRIGHT), 1961: xxiii + 442 p., 334 figs., Geol. Soc. Am. & Univ. Kansas Press.

TURNER, C. H., 1895, Freshwater Ostracoda of the United States: Second Rept. State Zool. Minnesota 1895, p. 277–337, pls.

VAN MORKHOVEN, F. P. C. M., 1962, Post-Paleozoic Ostracoda. I. Their morphology, taxonomy, and economic use: Elsevier Pub. Co., New York, vii + 204 p., 79 figs., 8 tabs., 1 enclosure.

VÁVRA, V., 1891, Monographie der Ostracoden Böhmens: Archiv. naturwiss. Landesdurchf. Böhmens (Archiv pro přírodovědecký výzkum Chech.), v. 8, p. 1–116, figs.

VOS, A. P. C. DE, 1957, Lists annotée des Ostracodes marins des environs de Roscoff: Arch. de Zool. Exp. et Gen., v. 95, no. 1, p. 1–74, 29 pls., 1 tab.

WEISMANN, AUGUST, 1880, Parthenogenese bei den Ostracoden: Zool. Anz., v. 3, no. 46, p. 82–84.

WOHLGEMUTH, R., 1914, Beobachtungen und Untersuchungen über die Biologie der Süsswasserostracoden; ihr Vorkommen in Sachsen und Böhmen, ihre Lebensweise und ihre Fortpflanzung: Int. Revue ges. Hydrobiol., Biol. Suppl., no. 6, 72 p., 4 figs.

ZENKER, W., 1854, Monographie der Ostracoden: Archiv. für Naturgeschichte, v. 20, no. 1, p. 1–87, pls. 1–6.