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A STUDY OF
CTENOLOCULINA CICATRICOSA (WARTHIN)

BY

ROBERT V. KESLING



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A STUDY OF *CTENOLOCULINA CICATRICOSA* (WARTHIN)

By
ROBERT V. KESLING

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INTRODUCTION

THE increased use of microscopic fossils in stratigraphic correlations has given additional impetus to the study of ostracods. Ostracods are ideal fossils for determining the age of strata penetrated in drilling wells, because their minute size makes it possible to recover specimens with little or no damage. Frequently, their abundance in a few inches of rock recovered by drilling gives a knowledge of a complete ostracod fauna.

The use of ostracods as index species depends upon two factors, (1) the determination of which particular species are "indices" and (2) the establishment of sound principles for distinguishing a "species." The first of these objectives may be approached by detailed faunal analyses of ostracod-bearing formations throughout the geo-

logic column. The second is more elusive and, hence, more difficult, especially as there is great need for clarity in precisely characterizing an ostracod species.

The nature of the animal itself introduces problems into the taxonomy of fossil specimens. Since the appendages, which are important in the taxonomy of living ostracods, are composed of thin chitin and are not preserved in fossil specimens, species of extinct ostracods necessarily have to be based on the form of the carapace. Another problem arises from the fact that the ostracod is a crustacean and grows by molting the old carapace and secreting a new and larger one. As a result of this externally discontinuous growth habit, the hard parts which are preserved as fossils fall into distinct size groups for each species. While it is possible for a number of specimens to be found which belong to a definite size group, sharply set off from any other group and different in proportions from any described species, yet this number or group of specimens may in reality only constitute one instar of a species based on types representing a different instar. Some of the Paleozoic ostracods present additional difficulties, because the families to which they belong are now extinct. The internal anatomy of these ostracods is unknown and the morphology of their carapaces differs in details from that of living animals. Direct comparison of fossil with living ostracods obviously may not be valid.

Although specimens are abundant in many geologic formations, few detailed studies of species have been made. The paleontologic species, as admitted above, is one based on the form of the carapace alone; the variations, however, occurring in the carapaces need to be examined in detail to determine more exactly what magnitude of variation appears to result from individual differences and what magnitude of variations appears to be consistent and sufficient to be classed as a specific difference.

This paper describes the ostracod *Ctenoloculina cicatricosa* (Warthin), in the fourth to adult instars and discusses the probability of younger instars and their dimensions. Constrictions of the carapace in this species furnish strong evidence for a correct reconstruction and orientation of the soft parts. Measurements of specimens are

analyzed for grouping into instars. Some unusual coefficients of variations are attributed to abnormal individuals, and the known causes of variation in ostracods are listed.

Ctenoloculina cicatricosa is an excellent species for a detailed study, because it has such distinctive shape and exotic decoration that young instars can be recognized without difficulty. The specimens are from the Middle Devonian, Norway Point formation, and were collected from the southwest bank of the Thunder Bay River, one mile below Four Mile Dam, Alpena County, Michigan. The specimens used in this study are deposited and catalogued in the Museum of Paleontology of the University of Michigan. All are topotypes and the numbers are listed in Tables I to XIV.

The author appreciates very much the helpful criticism of this manuscript by Dr. L. B. Kellum, Dr. G. M. Ehlers, and Dr. C. A. Arnold, of the Museum of Paleontology of the University of Michigan.

SYSTEMATIC DESCRIPTION

Order OSTRACODA

Superfamily Beyrichiacea

Family Hollinidae

Ctenoloculina cicatricosa (Warthin)

Tetradella cicatricosa Warthin, Warthin, 1934. p. 209, Pl. I, Figs. 4-6; Coryell and Malkin, 1936, p. 3, Fig. 9.

Ctenoloculina cicatricosa (Warthin), Bassler, 1941, p. 22; Stewart and Hendrix, 1945, p. 102, Pl. 11, Fig. 11; Kesling and McMillan, 1951, p. 49, Pl. IV, Figs. 9-10.

Ctenoloculina acanthophora Swartz and Oriel, Swartz and Oriel, 1948, p. 553, Pl. 79, Figs. 8-14.

Remarks.—The specimens from the Windom beds, illustrated by Swartz and Oriel (1948, Pl. 79, Figs. 8-14), are so highly corroded that the loculi in the females continue into the domicillium. It is logical to suppose that such corrosion would reduce the low papillae ornamenting the lobes of *Ctenoloculina cicatricosa* (Warthin) to the "spinules" described by Swartz and Oriel. Other morphological features described for these Windom specimens are like

those of the Traverse specimens of *C. cicatricosa* from Michigan, and the ostracods described by Swartz and Oriol as *C. acanthophora* are probably actually corroded specimens of *C. cicatricosa* (Warthin).

In addition to the specimens assigned to *Ctenolocolina acanthophora*, from the Windom beds of New York (Swartz and Oriol, 1948), *Ctenolocolina cicatricosa* (Warthin) has been described from the following Devonian formations: the Norway Point formation in the Traverse Group of Michigan (Warthin, 1934); the Bell shale, basal formation of the Traverse Group of Michigan (Kesling and McMillan, 1951); the Olentangy shale of Ohio (Stewart and Hendrix, 1945); and the Widder beds of Ontario (Coryell and Malkin, 1936). The author has also found this species in the Ferron Point formation of the Traverse Group of Michigan.

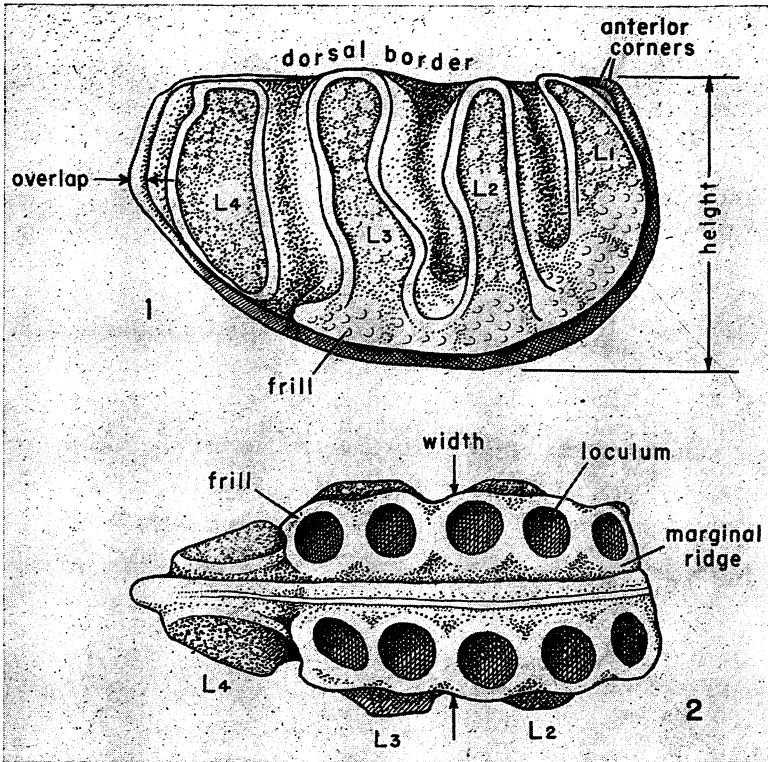
Specimens in each of the instars present are illustrated in Plate I.

Adult female.—Valves subelliptical in lateral view. Hinge line straight. Anterior border subrounded; ventral border gently rounded; posterior border subrounded, in some specimens geniculate near the middle. Left valve overlapping right valve along free edge. (Figs. 1-2).

Each valve distinctly quadrilobate. L1, L2, and L3 narrow, nearly vertical, extending from dorsal border to the frill; their surfaces flat, ornamented with low papillae, and precisely bordered on the anterior, dorsal, and posterior sides by rounded rims, terminating ventrally against the frill. L4 broad; its surface gently convex, ornamented with low rather indistinct papillae, and completely surrounded by a low rim. L1 short, ventrally confluent with the frill, dorsal tip extending slightly above the hinge line. L2 long, slanting a little forward and down from the dorsal border, with a slight posterior increase in width near the middle; its anterior rim straight. L3 long, parallel to L2, constricted near the middle, terminating against the posterior part of the frill. Sulci smooth, with rounded bottoms and sides flaring out to the rims of the lobes. S2 sinuous.

Broad frill from anterior to posteroventral part of each valve. Transverse partitions extending from the frill to the marginal ridge, dividing the space into six cuplike loculi. Frill slightly scalloped on outer surface with convexities corresponding to the loculi. Posterior

(sixth) loculum aligned with posterior part of L3, next (fifth) loculum aligned with anterior part of L3, fourth loculum aligned with posterior part of L2, third loculum aligned with anterior rim of L2, second loculum aligned with S1, and anterior (first) loculum at the



FIGS. 1-2. Right lateral and ventral views of adult female carapace of *Ctenoloculina cicatricosa* (Warthin), with certain morphological features and locations of measurements labeled.

base of L1. Structure of loculi shown in Plates II and III; frill, marginal ridge, and partitions between loculi apparently secreted and extruded from epidermis before the formation of rest of valve.

Anterior cardinal angle approximately 115 to 120 degrees. Posterior cardinal angle not well defined.

Dimensions listed in Tables I and II. Length of left valve, 0.80 to 1.08 mm.; mean, 0.898 mm.; length of right valve, 0.78 to 1.05 mm.; mean, 0.846 mm. Height of left valve, 0.43 to 0.58 mm.; mean, 0.486 mm.; height of right valve, 0.43 to 0.60 mm.; mean, 0.474 mm. Greatest width of valves through L3, but width measured through S2, because of extraneous material usually adhering to the papillae of L3; width of left valve (through S2), 0.16 to 0.23 mm.; mean, 0.197 mm.; width of right valve, 0.19 to 0.24 mm.; mean, 0.211 mm. Length of hinge of left valve, approximately 0.815 mm.; length of hinge of right valve, approximately 0.77 mm. Distance from anterior corner to axis of L2 of left valve measured along dorsal border, 0.20 to 0.26 mm.; mean, 0.219 mm.; distance from anterior corner to axis of L2 of right valve measured along dorsal border, 0.19 to 0.27 mm.; mean, 0.204 mm. Distance from axis of L2 to axis of L3 of left valve measured along dorsal border, 0.20 to 0.26 mm.; mean, 0.229 mm.; distance from axis of L2 to axis of L3 of right valve measured along dorsal border, 0.21 to 0.26 mm.; mean, 0.227 mm. Angle formed by dorsal border and axis of left L2, 72 to 80 degrees, mean, 75.4 degrees; angle formed by dorsal border and axis of right L2, 72 to 90 degrees; mean, 81.3 degrees. With the two valves closed the dorsal end of left L2 slightly posterior to dorsal end of right L2; but because of steeper slant of right L2, the middle of right L2 located opposite to middle of left L2.

Anterior and posterior corners of right valve projecting slightly to fit into socket-like depressions in left valve. Contact margin of left valve rabbeted to fit against edge of right valve. Very delicate fringe of fused curved marginal denticles on posteroventral free edge of some valves, usually broken off.

Adult male.—Valves with same general shape in lateral view as those of adult female. Posterior border more rounded than that of female. Left valve overlapping right valve along free edge. (Fig. 3).

Each valve distinctly quadrilobate. Dorsal half of each valve the same as that of the female. No ventral frill; only slight development of a marginal ridge. L1, L2, and L3 extending beyond the free edge of each valve as spurs. Spur of L1 short and straight; spur of L2 bladelike and curved backward; spur of L3 particularly

well developed and strongly curved backward. Lobes with flat surfaces ornamented by low papillae and surrounded by distinct rounded rims. Sulci smooth with rounded bottoms and flaring sides. S2 slightly sinuous, S3 distinctly sinuous.

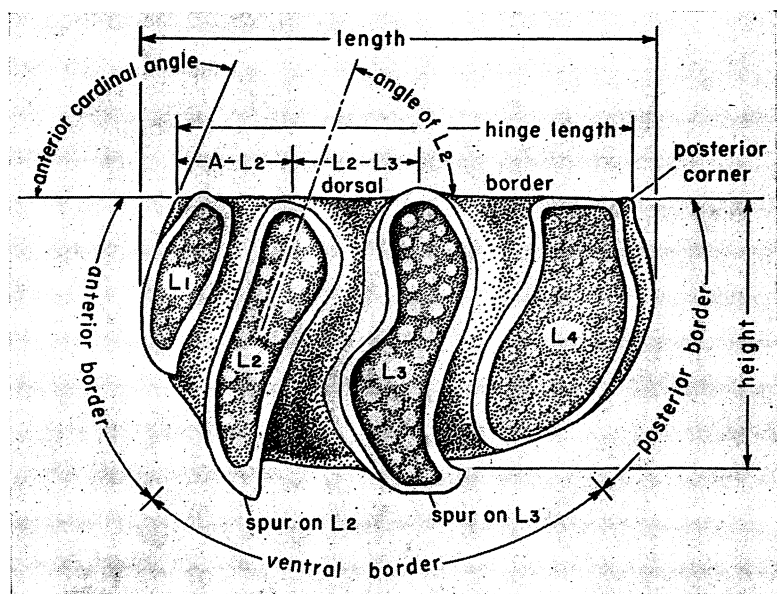


FIG. 3. Left lateral view of adult male carapace of *Ctenoloculina cicatricosa* (Warthin), with certain morphological features and locations of measurements labeled.

Anterior cardinal angle, approximately 120 degrees; posterior cardinal angle, approximately 110 degrees.

Dimensions listed in Tables III and IV. Mean length of left valve, 0.900 mm.; mean length of right valve (based on two specimens), 0.795 mm. Mean height of left valve, 0.475 mm.; mean height of right valve, 0.440 mm. Mean width of left valve (measured through S2), 0.178 mm.; mean width of right valve, 0.180 mm. Mean length of hinge of left valve, approximately 0.81 mm.; mean length of hinge of right valve, approximately 0.73 mm. Distance from anterior corner to axis of L2, measured along dorsal border,

greater in left valve than in right. Angle formed by dorsal border and axis of L2, greater in right valve than in left. With the two valves closed, dorsal end of left L2 slightly posterior to dorsal end of right L2, but middle of right L2 directly opposite to middle of left L2.

Hingement and contact margins same as those of female.

Eighth instar.—Valves with same general shape and form as those of adult male. Left valve overlapping right valve.

Each valve distinctly quadrilobate. Lobes proportionally narrower than those of adult male. L1 projecting below free edge in only a few specimens. L2 and L3 with distinct spurs; spur of L2 slightly curved; spur of L3 distinctly curved backward. Sulci smooth, proportionally wider than those of adult male.

Dimensions listed in Tables V and VI. Mean length of left valve, 0.675 mm.; mean length of right valve, 0.695 mm.; complete carapaces, however, have left valve longer and overlapping right valve. Height of left valve greater than height of right valve. Right valve wider than left. Same relative positions of left L2 and right L2 as given for adult male. Spur of right L2 longer than spur of left L2, with tips of the two spurs equal distances from the hinge line.

Seventh instar.—Valves with same general shape and form as those of eighth instar. Flat surfaces of lobes proportionally narrower than those of eighth instar. Ornamentation of lobes indistinct. Sulci wide, with bottoms gently rounded.

Dimensions listed in Tables VII and VIII. Left and right valves showing same relations of length, height, width, distance from anterior corner to axis of L2, angle from dorsal border to axis of L2, and length of spur on L2 as those of adult male and eighth instar valves.

Sixth instar.—Valves with same general shape and form as those of other immature instars and the adult male. Flat surfaces of lobes very narrow, about the same width as the surrounding rims. Sulci wide and shallow.

Dimensions listed in Tables IX and X. Left and right valves showing same relations of the various measurements as those of the seventh instar. Spur of right L2 long and only slightly curved.

Fifth instar.—Valves with same general shape and form as those of other immature instars. Flat surfaces of lobes very narrow and indistinct. Sulci wide and shallow.

Dimensions listed in Tables XI and XII. Left and right valves showing same relations of length, height, and width as those of other immature instars and the adult male.

Fourth instar.—Valves with same general shape and form as those of other immature instars. L1, L2, and L3 narrow, with no distinct flat areas; L4 not developed. Sulci wide, shallow, with very gently rounded bottoms.

Dimensions listed in Tables XIII and XIV. Only one specimen of the left valve found for this instar.

Summary.—The means of the measurements for the valves of each instar, as listed on Table XV, show certain trends in the ontogeny and certain consistent differences between the left and right valves. With few exceptions, the per cent of height increases with growth, the per cent of width and the ratio of width/length decrease (except in the adult female), and the per cent of length is nearly constant. In all instars measured, the left valve has the greater length, height, per cent of length, and distance from the anterior corner to the axis of L2; on the other hand, the right valve has the greater width, per cent of width, ratio of width/length, and angle between the dorsal border and the axis of L2. The per cent of height, the ratio of height/length, and the distance between the axes of L2 and L3 are nearly the same for both valves.

PROBABILITY OF YOUNGER INSTARS AND THEIR COMPUTED DIMENSIONS

The smallest specimens of *Ctenoloculina cicatricosa* obtained were those whose measurements are listed in Tables XIII and XIV. It is problematical whether these are the youngest instars of the species, for the ontogeny of living ostracods indicates that three younger instars may have existed in *C. cicatricosa*.

In living ostracods the number of immature instars varies. Of the seven families of ostracods as classified by Elofson (1941, pp. 232-355), little or nothing is known about the development of the Asteropidae, Polycopidae, or Cytherellidae. It is particularly unfortunate that information is lacking on the Polycopidae and Cythe-

rellidae, because the ostracods of these families reach maturity with fewer than the seven pairs of appendages present in all other ostracods. The species of Cypridinidae which were investigated by Elofson (1941, pp. 369-70) have only five immature instars. The Conchoeciidae, according to Claus (1894, p. 5) and G. W. Müller (1894, p. 183), have six larval instars. The Cytheridae and Cypridae have been investigated by Claus (1868, pp. 151-66), Müller-Calé (1913, pp. 113-70), Schreiber (1922, pp. 511-28), Scheerer-Ostermeyer (1940, pp. 349-70), and Elofson (1941, p. 370); these workers reported eight immature instars in species of these families with the exception of three of the species of *Xestoleberis* (Cytheridae), which have only seven larval instars according to Elofson (1941, p. 370).

A comparison of the descriptions of the larval instars of various ostracods reveals a most remarkable relationship. The Cypridae, which have eight larval instars, are characterized by only three pairs of appendages in the first instar, but increase this number by primordia (anlagen) and development of additional appendages in a regular order toward the posterior in successive instars. In the three species of *Xestoleberis* which have only seven immature instars, individuals hatch with the same appendage development as that typical in other Cytheridae at the second instar, and in the successive instars follow the pattern for other genera of the family (Elofson, 1941, p. 371). In *Cypridina mediterranea* Costa of the family Cypridinidae, which has only five immature instars, the young hatch with the same appendage development as that typical in the Cypridae and Cytheridae at the fourth instar and appear to follow the pattern of development for those families in the successive instars (Müller, 1894, p. 185). If the appendage developments and arrangements of a series of instars of the Cypridae are used as a standard for reference, the three species of *Xestoleberis* would begin their ontogeny in the second instar of the series, and species of the Cypridinidae in the fourth instar. This demonstrates that, as far as is known, decreases in the number of instars is the result not of paedogenesis but of advanced embryonic development in the egg. Some ostracods pass through certain developmental stages prior to hatching which others attain only after

one or more molts. Of the families of living ostracods, the Cypridae have the longest geologic history and, until there is evidence to the contrary, Paleozoic species of this family may be regarded as characterized by eight immature instars. Cooper (1945, pp. 368-75) reported eight immature instars in *Ectodemites plummeri* Cooper, a Pennsylvania species of the superfamily Beyrichiacea, but it is possible that certain families of the Paleozoic Beyrichiacea had less than eight instars, just as certain families of recent Cypracea have a smaller number.

(An assumption that extinct ostracods also increased at specific rates throughout their ontogeny, as do living forms, is just as tenable as the assumption that fossil ostracods had the same internal anatomical structures as those found in living specimens.)

Fowler (1909, p. 224) suggested a principle to express the relationship between the sizes of the various instars: "During early growth, each stage increases at each moult by a fixed percentage of its length, which is approximately constant for the species and sex." He termed this Brooks' Law in honor of W. K. Brooks, who had suggested the same principle for the stomatopods. Brooks' Law can be expressed as a formula:

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

where L_n is the length of instar n , L_{n+1} is the length of the succeeding instar, and k is the constant percentage for the species. The author found this formula to be close to observed lengths for the youngest six instars of a living fresh-water species, *Cypridopsis vidua* (O. F. Müller). When this formula is tried for the fourth instar through the adult of *Ctenoloculina cicatricosa* (Warthin) an average value of k is found to be 0.26. This value is used to calculate the probable lengths of the youngest three instars, assuming that such existed, and the results are listed in Table XVI.

Julian S. Huxley (1924, p. 895) proposed a constant differential growth-ratio formula for comparison of relative growth rates.

$$y = Cx^k,$$

where y is the size of an organ, x is the size of the rest of the body, C is a constant, and k is the constant differential growth-ratio. This

formula can be used to compute the probable heights of the youngest three instars of *C. cicatricosa*, if it is expressed as a relationship between height (h) and length (l),

$$h = Cl^k.$$

The results of these computations are listed in Table XVII. The computed length and height of the first instar are seen to be .139 and .075 mm.

ACCOMMODATION OF SOFT PARTS AND ITS
BEARING ON ORIENTATION

The oldest fossil-ostracod remains show that even in the early periods of the Paleozoic this highly specialized animal had developed the characteristic bivalved carapace. Studies of living ostracods establish that the form of the carapace bears a definite relationship to that of the appendages and soft parts of the animal. Modification of the internal anatomy has eliminated all traces of segmentation so that the head and thorax have arbitrary boundaries and the internal organs do not reveal close affinities with those of the higher Crustacea. Because of the sharp constrictions of the interior space by the deep sulci, *Ctenoloculina cicatricosa* (Warthin) must have been even more specialized than any species living today. These constrictions may be seen in the frontal sections illustrated in Plates II and III. An ostracod animal once lived within this restricted space and performed all the necessary functions of life—locomotion, nutrition, reproduction, respiration, and excretion.

To reconstruct the *Ctenoloculina cicatricosa* animal, assuming that it had the same type of appendages and organs as modern ostracods, one must fit these organs and appendages into the available space in the carapace, the larger by necessity into the enlargements which constitute the lobes. The larger organs and appendages for which lateral accommodation is required are the antennae, mandibles, maxillae, genital lobes, and stomach; also the livers, ovaries (or testes), and a pair of excreting and secreting glands (labeled "gland B" in Fig. 5) contained within the left and right epidermal layers. The adductor muscles extend from one valve to the other, at a point slightly anterior to the middle of the valves; Bonnema (1933, p. 33)

and others have found that the adductor-muscle scars of quadrilobate Beyrichiacea are in S2. If the point of attachment of the adductor muscles is the middle of S2, the esophagus, since it is always in front of the adductor muscles, would be anterior to S2. The left and right mandibles meet in the mouth, the opening of the esophagus, and lie behind the strong antennae. Thus, there are two pairs of appendages

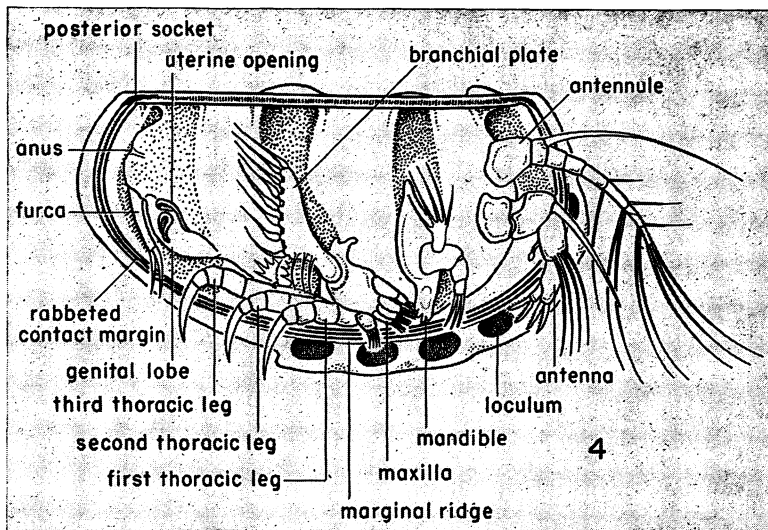


FIG. 4. Left valve of adult female *Ctenoloculina cicatricosa* (Warthin), with proposed reconstruction of appendages and genital lobe based on the locations possible in the constricted space. Details of the appendages are hypothetical, and are illustrated only to show their probable relations. Shaded areas are the internal depressions of the valve corresponding to the external lobes.

requiring great lateral accommodation which lie in front of S2, the mandibles and the antennae; the mandibles probably occupied L2 and the antennae L1 (see Fig. 4). Only one other pair of appendages has great lateral expanse, that is, the maxillae, which have large branchial plates; since these always lie behind the adductor muscles, they were probably in L3. The wide genital lobes are in the posterior part of the carapace, well behind the maxillae, and were probably

in L4, as were the small furcae, which are attached to the body behind the genital lobes. The thoracic legs, between the maxillae and genital lobes, are narrow and close together, and could readily have functioned in S3. The stomach is dorsal to the mouth and was in the same lobe as the mandibles, probably L2. The antennules are in front of the stomach and above the antennae, and would have been in L1. From anterior to posterior, the three large organs located

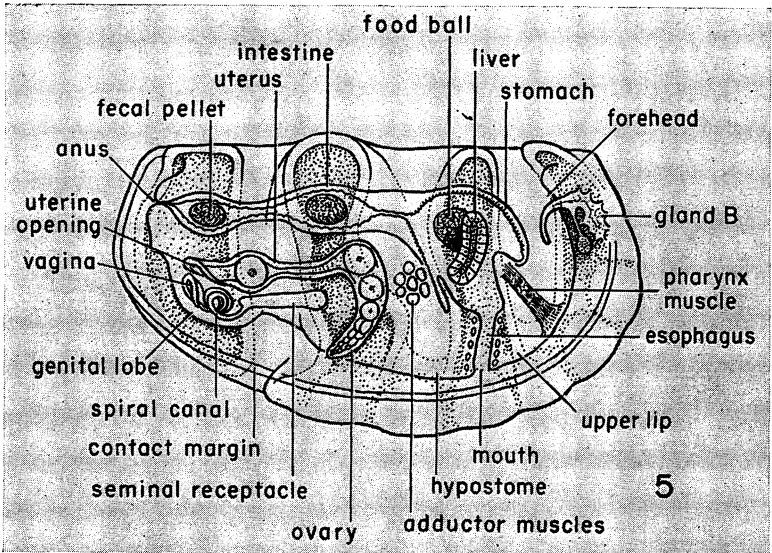


FIG. 5. Right valve of adult female *Ctenoloculina cicatricosa* (Warthin), with proposed reconstruction of the larger internal organs; details are hypothetical. Shaded areas are the flat areas of the lobes.

in each half of the epidermis are (1) an excreting and secreting gland; (2) the liver; and (3) the ovary or testes (male organs always multiple, never one to a valve). The gland empties near the base of the antennule and would, therefore, be in L1. The liver empties into the stomach and would be in L2, (Fig. 5); its normal posterior extent, however, would be blocked by S2 so as to modify the direction of its long dimension to a more vertical position. The

ovary (or testes), located behind the liver, would be in L3 or L4. Such a suggested internal anatomy may be verified, at some future date, by some unusual preservation or by the discovery of a selective stain which will outline the former position of the ovaries, livers, and glands.

Certain characteristics of the carapace in *Ctenoloculina cicatricosa* give additional evidence concerning the orientation of this Devonian species. The smallest specimens which were found belong to the fourth instar, that is, if it is assumed that there were eight immature instars. Without evidence to the contrary, it may be postulated that the individuals in the fourth instar in *C. cicatricosa* had the same appendages and morphology as those of living ostracods in that instar. Living ostracods in the fourth instar have antennules, antennae, mandibles, maxillae, and the primordia of the first thoracic legs and furcae. In successive instars are added, first as primordia and then as definite organs and appendages, the second thoracic legs, the third thoracic legs, the ovaries and testes, and the genital organs. With the exception of the small furcae, the appendages and organs are added from the anterior to the posterior. There is good evidence that the addition of new appendages and organs is accompanied by corresponding changes in the carapace. The strongest growth gradient of the carapace throughout the ontogeny is in the posterior part, to accommodate the new appendages as they appear. Table XVIII reveals that the relative position of L3 in *C. cicatricosa* shifts forward progressively from the fourth instar to the adult; in other words, during the ontogeny the carapace has its greatest growth in that part behind L3, the part which, in the light of observations on the ontogeny of living ostracods, should be regarded as posterior. This is in complete agreement with the author's orientation of the Hollinidae.

GROUPING OF SPECIMENS INTO INSTARS

Although many specimens of a species are more valuable than a few, because they represent the population of the species more accurately, it is difficult for an investigator to summarize satisfactorily the accumulation of measurements and observations on a large num-

ber of specimens. Certain statistical formulas have been designed, therefore, to facilitate the summarization of data for a large number of specimens and give the worker a complete view of the group under study.

The mean of a series of measurements is obtained from the formula

$$m = \frac{\sum x}{N},$$

where m is the mean, x is the variable being measured, and N is the number of specimens. The standard deviation is determined from another formula

$$\sigma = \sqrt{\frac{\sum (d^2)}{N}},$$

where σ is the standard deviation, d is the arithmetic difference between the variable and the mean, and N is the number of specimens. The standard deviation has particular significance for the population, because it can be shown that in a normal distribution: $m \pm 1\sigma$ includes 68 per cent of the population; $m \pm 2\sigma$, 95 per cent; $m \pm 3\sigma$, 99.7 per cent; $m \pm 4\sigma$, 99.994 per cent; $m \pm 5\sigma$, 99.9997 per cent and so on.

The coefficient of variation (v) is derived simply by

$$v = 100 \times \frac{\sigma}{m}$$

expressed as a percentage.

Standard deviations, means, and coefficients of variations for length, height, and width in several instars are listed in Table XIX.

An inspection of the distribution of length and of height for all specimens of *Ctenoloculina cicatricosa* reveals that about 84 per cent of the population fits into distinct instar categories by length, and about 84 per cent of the population fits into distinct instar categories by height (Table XX). These figures are derived from tables of the probability of occurrence of deviations, which is based on the fact that the boundaries of length and height for each instar extend to the mean ± 1.4 times the standard deviation.

HEIGHT VS. LENGTH FOR *CTENOLOCULINA CICATRICOSA* (WARTHIN)

WITH DRAWINGS OF SOME SPECIMENS

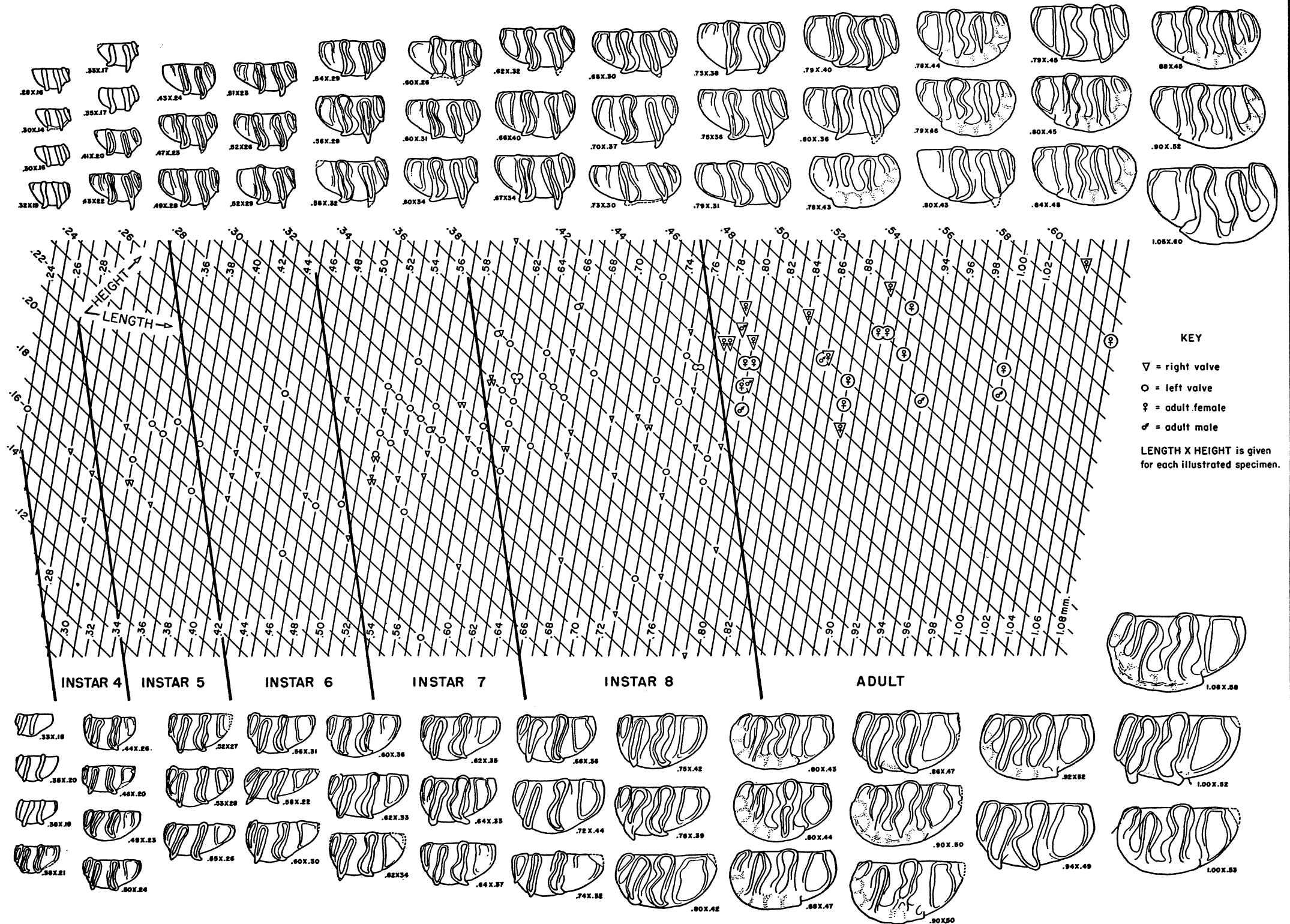


CHART 1

Of the 16 per cent of the population which does not fit into distinct instar categories by length, some specimens fit into distinct instar categories on the basis of their height; and of the 16 per cent which does not fit into categories by height, some specimens fit into categories on the basis of their length. As shown in Chart 1, however, there are not distinct boundaries to each instar group; some specimens are so elongate that they might be considered as distinct subspecies, if there were not other specimens of intermediate elongation.

COEFFICIENTS OF VARIATIONS AND THEIR SIGNIFICANCE

The coefficients of variation for length and height are not the same for left and right valves, as may be seen from Table XXI, but appear to follow a trend for the three advanced instars. Differences in these coefficients for the two valves may prove to be characteristics of a species. There are no other studies of variation in ostracod valves for comparison at this time. It is to be hoped that additional studies will determine if such variations are different for each species or if they follow the same trend for all ostracods.

Tables XIX and XXI also show that the length, height, and width have only slight differences in coefficients of variation for the seventh, eighth, and adult instars. However, the figures for the ratios of height/length show a markedly different situation, since the coefficients of variation for adult valves are only about one-third the value of those for the seventh- and eighth-instar valves. The same relationship exists, to a lesser degree, for the ratios of width/length; the coefficients of variation for adult valves are approximately one-half the value of those for seventh- and eighth-instar valves. These factors reveal that the proportions of the adult vary much less than those of the younger instars, although dimensions vary to the same degree for all instars.

The size of an ostracod depends upon three dimensions, the length, the height, and the width. Chart 2 has values for length, height, and width, which are prorated for specimens used in this study on the basis of 100 per cent total for the three factors. Several specimens plotted on this chart are outside the general range of the

prorated values. Those specimens which show large percentages of length are proportionally elongate in both lateral and dorsal views, because of low percentages of height and width; those which show large percentages of width are proportionally wide in both dorsal and end views, because of low percentages of length and height. Chart 2 emphasizes the general shape for each specimen and plots its variations from the average of the specimens studied.

When an unusually elongate specimen occurs in Instar 7, the height and length portrayed on Chart 1 show its differences from the other specimens of this instar. For example, a height of only .22 mm. differs from the median of the group by 3.14 σ , and a table of the probability of occurrence of deviations reveals that such a height has a probable occurrence of 0.171 per cent and that the odds against such a measurement are 584 to 1. The ratio of height/length is even more exceptional; a ratio of 37.9 per cent from the mean by 3.44 σ and has a probable occurrence of 0.590 per cent, with the odds against such a ratio 1694 to 1.

In none of the scientific literature in this field is there any indication that an individual ostracod is able to alter its proportions from one instar to another except by following a certain trend which is characteristic for the species. It appears certain that among ostracods of the eighth instar, the elongate individual after molting will be a proportionately elongate adult, the thick individual will be a thick adult, and the high individual will be a high adult. In a group of three adults of approximately the same proportions, is it possible in their eighth instars for one to have been unusually elongate, another unusually thick, and a third unusually thin? The author believes not.

If relative proportions do remain the same for an individual from one instar to another, then the large coefficients of variation for height/length and for width/length in specimens in the eighth instar need to be explained. The author studied *Cypridopsis vidua* (O. F. Müller), a living fresh-water parthenogenetic ostracod. Table XXII gives the variations of height/length for valves collected from a culture of thriving *C. vidua*. The coefficients of variation for length, height, and height/length are nearly the same for the adult and

100% THREE FACTOR DIAGRAM OF LENGTH, HEIGHT, AND WIDTH

OF VALVES OF *CTENOLOCULINA CICATRICOSA* (WARTHIN) FROM SIXTH INSTAR TO ADULT

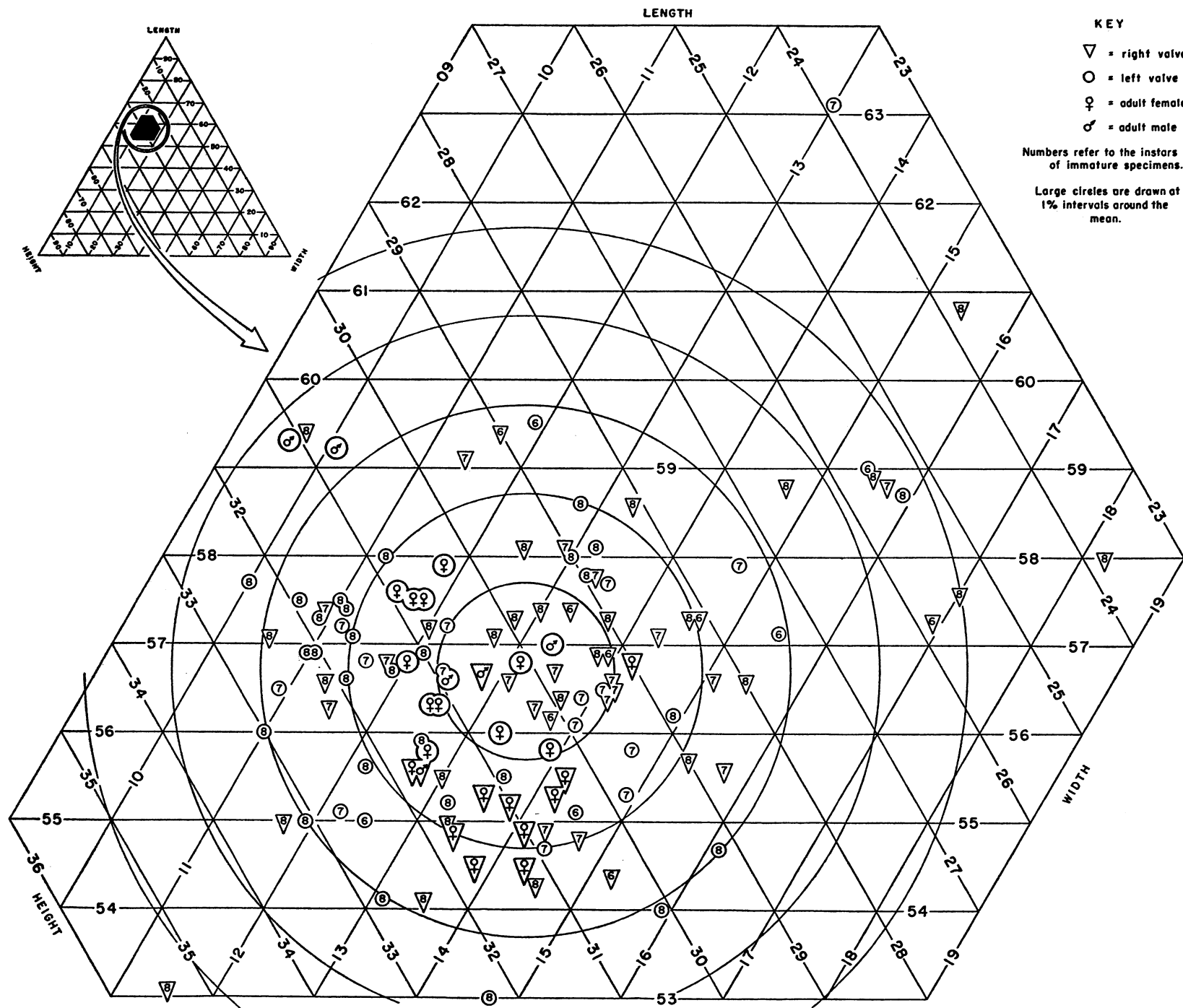


CHART 2

younger instars. Continuity of variation of proportions through different instars appears to be normal for healthy populations of a species having no abnormal members.

Some of the elongate specimens of *Ctenoloculina cicatricosa*, shown in Chart 1, probably were abnormal individuals during their lifetime and could not have survived to maturity under any circumstance. The process of molting is a critical one for the animal. To become an adult, the ostracod must be able to form sex organs and secrete a carapace to accommodate them. Elongate specimens of *C. cicatricosa* may have belonged to animals which died because they were unable to shed the abnormal carapace, because their metabolism precluded the formation of sex glands and organs, or because the shape of their carapaces, after they had formed sex glands, prevented such vital functions as respiration, nutrition, excretion, and locomotion.

FUNCTION OF THE LOCULI

The loculi are deep cuplike pits present in the adult female valves between the frills and the marginal ridges. Warthin (1934, p. 209) referred to them as "brood pits." These unusual morphological features do not occur in any living species.

Literature on Paleozoic ostracods contains much discussion of the possible utilization of certain spaces in the females as brood pouches for the care of the young. Certain living marine species carry the young in the posterodorsal part of the carapace, but there are no instances reported of brood care in special ventral structures. As illustrated in Plate II, Figures 1-9, the loculi are only about .12 mm. deep and slightly less than .1 mm. in diameter at the openings. The computed measurements of the first instar, assuming eight immature instars, are .139 mm., in length, and .075 mm., in height; young of this size would protrude from the loculi. Furthermore, it is difficult to imagine that an ostracod with appendages like those of living forms could transfer eggs forward from the uterine openings and out of the carapace, and lodge them firmly in the loculi. These important considerations are against the use of loculi for brood care. The partitions between loculi extend from the frill to the marginal

ridge and appear to strengthen the structure of the frill by acting as buttresses. It is, therefore, plausible that the loculi are only incidental spaces between these partitions, whose function was to give rigidity to the frill.

Sars (1922, p. 13) wrote of the living marine species *Philomedes globosa* (Lilljeborg) that "the males are very active, swimming about with great speed, and in some cases ascending to the very surface of the sea, the adult females are constantly bound to the bottom, dragging themselves slowly through the loose mud." This statement seems to be only partly true. The work of G. W. Müller (1898, pp. 42-44), later confirmed by Skogsberg (1920, pp. 352-68), reveals a strange adult life for females of *P. globosa*. The females enter adulthood with natatory setae, and soar upward for planktonic copulation with the males; after mating they return to the bottom and lose their natatory setae, probably biting them off and by this act of self-mutilation resigning themselves to egg-laying, brood care, and a creeping existence. In Paleozoic species the two sexes may also have lived for the most part in different biotopes, with the females benthonic and the males pelagic. Hessland (1949, p. 128) suggested that velate structures may have served to prevent the animal from sinking into the soft bottom sediments. The frills of the female of *Ctenoloculina cicatricosa* (Warthin), it is logical to suppose, may have functioned as sled runners with the partitions between loculi increasing the effective bottom area of the carapace.

CAUSES OF VARIATION IN OSTRACOD CARAPACES

There are several causes of variations in ostracod carapaces, many of them interrelated. During the life of an ostracod, the size and shape of the carapace are related to: (1) the instar or growth stage; (2) sex of the adult; (3) individual variations; (4) diet; and (5) parasitism. In addition, fossil ostracods may show variations in size and shape as a result of two further factors: (6) noncontemporaneity of specimens (the time factor) and (7) deformation of the fossil remains.

Ostracods have not been thoroughly studied, particularly with regard to their ontogeny. Claus (1868) was the first to study vari-

ations in instars of the same species, but his work was qualitative. Additional descriptions of instars were made by G. W. Müller (1912), Skogsberg (1920), Schreiber (1922), Scheerer-Ostermeyer (1940), Elofson (1941), Le Roy (1945), C. L. Cooper (1945, 1946), and Sohn (1950*a*, 1950*b*). The works of Skogsberg, Scheerer-Ostermeyer, Le Roy, Cooper, and Sohn were quantitative in part. At the present time it appears more likely that the variations within an instar are less than those between the instars, so that generally no question arises in assigning a specimen to a particular instar of its species.

There is no clear case of dimorphism in immature ostracods. Among adult specimens, the dimorphism in living Cypracea is extremely variable. Some species have no dimorphism; some show very little difference in the carapaces of the two sexes; some have larger male carapaces, some have larger female carapaces; and in only a few marine species is dimorphism of the carapaces pronounced. In the Paleozoic ostracods, on the other hand, dimorphism is pronounced for many species of the Beyrichiacea. Ostracods of the family Beyrichiidae are characterized by internal anteroventral pouches in one of the sexes; those of the family Hollinidae are characterized by large incurved frills in one; and those of the family Kloedenellidae have posterior inflation of the carapace in one. Because no soft parts have been found preserved in fossils of these families, it is not positively known which dimorphic form is male and which is female; tentatively, the forms possessing internal pouches, incurved frills, and posterior inflations are called females. On the basis of this tentative assignment, the immature instars resemble the adult males rather than the adult females.

Too insufficient a number of species has been studied quantitatively to know whether the degree of individual variation has any relation to the taxonomic position. The results obtained by the author indicate that the degree of variation in a species is a specific character, and that some species have greater variations in their instars than other species. Individual variations are superimposed on other types of variation, and only the marked variations caused by diet and parasitism can be recognized.

The effects of diet on ostracods has not been thoroughly investi-

gated and no conclusive statements can be made on certain phases of the problem. Schreiber (1922) noted that not all ostracods of one species molted in the same period of time. The author, who studied *Cypridopsis vidua* (O. F. Müller), a fresh-water parthenogenetic ostracod, in considerable detail, could find no gland corresponding to the gland which causes molting in the Malacostraca. In his opinion the deficiencies in the diet of an immature ostracod merely prolong the period of time until molting and do not cause a dwarfing of the animal. The kind of food available, however, has been described as producing two distinct effects on ostracods. First, Fassbinder (1912, p. 563) proved that altering the diet of *Cypris pubera* O. F. Müller, normally a smooth species, from plants to crushed snails (rich in calcium carbonate) produces secondary thickening of the shells, marked by conspicuous anterior and posterior protuberances. Wohlgemuth (1914, p. 21) fed *Cyprinotus incongruens* Ramdohr on a near-starvation diet, and discovered that they developed saddle-shaped indentations in the posterior dorsal border. Such effects are of critical importance to taxonomy, since lobation is one of the chief characteristics used in description and classification of fossil ostracods. The second effect of diet may be to change the type of reproduction. Wohlgemuth (1914, pp. 62-63), in his series of experiments with *Cyprinotus incongruens* Ramdohr, first isolated females in a culture; the females thereupon began to reproduce parthenogenetically instead of syngamically.¹ He then fed the parthenogenetic females on excrement and algal residue, and they returned to syngamic reproduction. This experiment indicates that in some instances diet may control the type of reproduction and, hence, determine whether or not the species will be dimorphic.

Parasites have been described as producing pathologic variations of the carapace. Rome (1947, pp. 3-4) found that about 1 per cent of the specimens of *Candona candida* O. F. Müller from a pond in Belgium contained cysticerci of the cestode *Hymenolepis gracilis* Krabbe, the adult of which parasitizes the domestic black duck *Anas*

¹ *Cyprinotus incongruens* Ramdohr in nature occurs as both sexes in central Germany, Hungary, and North Africa, but only as females in western and northern Europe and central United States.

boschas domestica. Ducks were being raised on the pond. In the ostracod, the cysticerci occurred in the ovaries, generally at the place where they empty into the uteri. The parasite produces a complete atrophy of the ovaries and a marked hypertrophy of the carapace. The width of the infected specimens is much greater than that of normal adults, and the length is slightly more; in dorsal view the carapaces are more globular, and in lateral view they are shorter in height.

The author believes that pathologic effects on the carapace can result only if the parasitic infection takes place before the last molting. The shell is formed immediately after molting; first, the chitin coating is secreted, then the layer of calcite, and finally the calcite is sealed off from the epidermis by another layer of chitin. No instances of an ostracod dissolving any part of the shell and secreting new material has ever been found, and it appears that changes in shape of the carapace can be accomplished only by complete molting.

Other types of internal parasites may also produce hypertrophy of the carapace, but additional observations are needed to complete the study of parasitism and its effect on form. Ostracods are beset by a variety of internal parasites. Mrázek (1890, pp. 226-48) reported fresh-water ostracods which were inhabited by cercocysts of a cestode which reaches its adult stage in aquatic birds; Ward (1940, pp. 327-47) another fresh-water ostracod which served as the first intermediate host of an acanthocephalan, the adult of which parasitizes the largemouthed black bass. G. W. Müller (Klie, 1926, p. 53) found certain marine ostracods which were badly damaged by undetermined nematodes. Monod (1932, pp. 1-8) discovered another marine ostracod which acts as host for two different parasites, a copepod larva and an isopod. G. O. Sars (1882, p. 13; 1899, pp. 235-36) reported an isopod, *Cyproniscus cypridinae* (Sars), living inside the carapace of the ostracod *Cypridina norvegica* Baird. This parasitic isopod was only found as a sexually mature animal in the adult female ostracod, where it occupied the place in which the eggs and nauplii of the ostracod would have been carried, otherwise, during their development; individuals of this parasite found in the male ostracods had never reached sexual maturity.

The female isopod upon reaching maturity in the ostracod buries her head in the flesh of her female host and sheds the larval carapace; she becomes greatly modified, the neck constricts into a stringlike attachment and the body is converted into an inert capsule filled with eggs. The male isopod does not attach and crawls actively over the bodies of the ostracod and the female isopod. The female isopod reaches a length of 2.10 mm., and the male a length of 0.90 mm.; the length of the carapace of the host, as given by Skogsberg (1920, p. 248), is only 3.3 to 3.65 mm. The size of the parasite shoves the entire body of the ostracod toward the anterior, as shown by Sars (1899, Pl. 96). Elofson (1941, pp. 232-33, 235) also reported this isopod in the brood space of the adult female of *Cypridina norvegica* Baird, and in one occurrence both ostracod eggs and two young parasites in the brood space. Elofson also discovered this same parasitic isopod in the ostracod *Philomedes globosa* (Lilljeborg). Because *P. globosa* is only 2.3 to 3.1 mm. in length (Skogsberg, 1920, p. 382), the displacement of the body of the host by the parasite must be even more remarkable than in *Cypridina norvegica* Baird. Such parasites must greatly affect the living processes of the ostracod host.

In addition to the above factors, which can cause variations during the life of the animal, the carapaces of fossil ostracods may exhibit variations arising from differences in the time when the specimens lived. It is very difficult to collect specimens which all lived at the same time; samples collected through only a small vertical distance may represent a time interval of many thousands of years. During such a time interval the ostracods may have experienced several evolutionary changes affecting the shape of the carapace. Again, after fossil ostracods are buried in the sediments and the sediments are compacted into rocks, differential forces acting on the rocks may contort the fossils into shapes and proportions very different from those that existed during the life time of the animals.

TABLE I

MEASUREMENTS OF ADULT FEMALE LEFT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN)

L =length; H =height; W =width; per cent of L , per cent of H , and per cent of W =pro-rated percentages of length, height, and width, respectively, based on a total of 100 per cent; $A-L_2$ =distance from anterior corner to axis of L_2 measured along the dorsal border; L_2-L_3 =distance from axis of L_2 to the axis of L_3 measured along the dorsal border; H/L =ratio of height to length; W/L =ratio of width to length; and angle=angle formed by dorsal border and the axis of L_2 .

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	$A-L_2$ (in mm.)	L_2-L_3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degr.)
27790	.80	.43	.16	57	31	12	.20	.20	54	20	75
27791	.80	.44	.17	57	31	12	.20	.20	55	21	75
27792	.80	.44	.19	56	31	13	.20	.20	55	24	80
27793	.88	.46	.18	58	30	12	.21	.22	52	20	77
27794	.88	.47	.18	57	31	12	.20	.24	53	20	72
27795	.90	.50	.20	56	31	13	.22	.22	56	22	77
27796	.90	.50	.20	56	31	13	.22	.24	56	22	75
27797	.92	.50	.23	56	30	14	.22	.24	54	25	76
27798	.92	.52	.21	56	31	13	.24	.25	57	23	75
27799	1.00	.53	.23	57	30	13	.24	.25	53	23	76
27800	1.08	.58	.22	57	31	12	.26	.26	54	20	70
Mean	.898	.486	.197	56.6	30.7	12.6	.219	.229	54.5	21.8	75.4

TABLE II

MEASUREMENTS OF ADULT FEMALE RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN)

Abbreviations are the same as those in Table I.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	$A-L_2$ (in mm.)	L_2-L_3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degr.)
27801	.78	.43	.20	55	31	14	.20	.21	55	26	90
27802	.78	.44	.19	55	31	14	.19	.21	56	24	83
27803	.78	.44	.20	55	31	14	.19	.21	56	26	84
27804	.79	.46	.20	54	32	14	.20	.22	58	25	80
27805	.80	.45	.20	55	31	14	.19	.23	56	25	80
27806	.84	.48	.22	55	31	14	.20	.23	57	26	82
27807	.86	.47	.22	55	31	14	.20	.23	55	26	82
27808	.88	.45	.22	57	29	14	.20	.22	51	25	72
27809	.90	.52	.22	55	32	13	.20	.26	58	24	80
27810	1.05	.60	.24	55	32	13	.27	.25	57	23	80
Mean	.846	.474	.211	55.1	31.1	13.8	.204	.227	55.9	25.0	81.3

TABLE III

MEASUREMENTS OF ADULT MALE LEFT VALVES *Ctenoloculina cicatricosa* (WARTHIN)

Abbreviations are the same as those for Tables I-II, except that "spur" refers to the length of the spur projection at the end of L2, which is designated as *s*=short, *s-m*=short to medium, *m*=medium, *m-l*=medium to long, *l*=long, *ll*=very long, and *lll*=extremely long.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27811	.80	.42	.13	59	31	10	.20	.20	53	16	72	<i>l</i>
27812	.86	.47	.19	57	31	12	.22	.24	55	22	71	<i>m-l</i>
27813	.94	.49	.22	57	30	13	.24	.24	52	23	73	<i>m-l</i>
27814	1.00	.52	.17	59	31	10	.23	.25	52	17	70	<i>ll</i>
Mean	.900	.475	.178	58.0	30.8	11.3	.223	.233	53.0	19.5	71.5	

TABLE IV

MEASUREMENTS OF ADULT MALE RIGHT VALVES of *Ctenoloculina cicatricosa* (WARTHIN)

Abbreviations are the same as those for Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27815	.79	.45	.18	55	32	13	.19	.23	57	23	80	<i>l</i>
27816	.80	.43	.18	57	30	13	.18	.22	54	23	75	<i>m</i>
Mean	.795	.440	.180	56.0	31.0	13.0	.185	.225	55.5	23.0	77.5	

TABLE V

MEASUREMENTS OF LEFT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN EIGHTH INSTAR
Abbreviations are the same as those for Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27817	.60	.36	.13	55	33	12	.18	.18	60	22	72	s
27818	.61	.34	.15	55	31	14	.16	.20	56	25	72	...
27819	.61	.36	.12	56	33	11	.16	.17	59	20	71	m-l
27820	.62	.31	.14	58	29	13	.17	.16	50	23	75	m-l
27821	.62	.33	.12	58	31	11	.17	.19	53	19	73	l
27822	.62	.34	.12	57	32	11	.17	.20	55	19	71	l
27823	.62	.35	.12	57	32	11	.16	.17	56	19	72	m-l
27824	.62	.35	.12	57	32	11	.17	.19	57	19	73	l
27825	.62	.35	.14	56	31	13	.16	.18	60	23	75	m
27826	.63	.35	.12	57	32	11	.16	.19	56	19	74	l
27827	.63	.36	.15	55	32	13	.14	.17	57	24	70	m
27828	.64	.33	.17	56	29	15	.19	.17	52	27	72	ll
27829	.64	.36	.13	57	32	11	.17	.18	56	20	78	s
27830	.64	.37	.14	56	32	12	.19	.19	58	22	82	m
27831	.65	.36	.12	57	32	11	.19	.19	55	18	73	m
27832	.66	.36	.14	57	31	12	.17	.18	55	21	72	l
27833	.66	.40	.16	54	33	13	.18	.20	61	24	72	s
27834	.68	.38	.20	54	30	16	.17	.19	56	29	74	m-l
27835	.72	.44	.20	53	32	15	.18	.19	61	28	68	s-m
27836	.73	.40	.14	58	31	11	.19	.19	55	19	75	m
27837	.74	.32	.20	59	25	16	.22	.20	44	27	72	m
27838	.75	.37	.17	58	29	13	.21	.20	49	23	72	l
27839	.75	.40	.22	55	29	16	.23	.20	53	29	77	m
27840	.75	.42	.13	58	32	10	.20	.20	56	17	74	m
27841	.76	.42	.15	57	32	11	.20	.20	55	20	69	m
27842	.76	.42	.16	57	31	12	.20	.20	55	21	73	m
27843	.78	.38	.17	59	28	13	.14	.20	49	22	67	m-l
27844	.78	.39	.18	58	29	13	.20	.20	50	23	70	l
Mean	.675	.369	.150	56.6	30.9	12.5	.180	.188	55.0	22.2	72.8	

TABLE VI
 MEASUREMENTS OF RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN EIGHTH INSTAR
 Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27845	.60	.34	.11	57	33	10	.14	.19	57	18	76	ll
27846	.60	.34	.12	57	32	11	.16	.18	57	20	75	l
27847	.60	.34	.14	56	31	13	.13	.17	57	23	75	m
27848	.60	.36	.15	54	32	14	.14	.18	60	25	77	m
27849	.60	.40	.13	53	35	12	.21	.22	67	22	80	l
27850	.62	.32	.14	57	30	13	.15	.18	52	23	80	l
27851	.62	.32	.15	57	29	14	.15	.18	52	24	79	m
27852	.66	.38	.16	55	32	13	.15	.18	58	24	78	l
27853	.66	.40	.14	55	33	12	.15	.21	61	21	77	m
27854	.67	.34	.16	57	29	14	.17	.20	51	24	77	lll
27855	.67	.35	.15	57	30	13	.16	.18	52	22	77	l
27856	.68	.30	.20	58	25	17	.18	.19	44	29	73	l
27857	.70	.37	.17	56	30	14	.18	.20	53	24	78	ll
27858	.71	.35	.18	57	28	15	49	25	84	m-l
27859	.72	.38	.16	57	30	13	.15	.21	53	22	72	m
27860	.73	.30	.23	58	24	18	.18	.20	41	32	64	m-l
27861	.73	.38	.12	59	31	10	.19	.21	52	16	71	l
27862	.73	.38	.20	56	29	15	.19	.23	52	27	81	m-l
27863	.75	.36	.17	59	28	13	.22	.22	48	23	74	ll
27864	.75	.43	.20	54	31	15	.19	.21	57	27	82	m
27865	.76	.33	.20	59	26	15	.19	.19	43	26	84	m
27866	.76	.41	.16	57	31	12	.18	.23	54	21	80	l
27867	.77	.38	.21	57	28	15	49	27
27868	.79	.31	.20	61	24	15	.18	.22	39	25	64	l
27869	.79	.40	.17	58	29	13	.17	.19	51	22	78	m-l
27870	.80	.36	.20	59	26	15	.20	.20	45	25	75	m-l
Mean	.695	.359	.166	57.0	29.5	13.6	.171	.199	52.1	23.7	76.4	

TABLE VII

MEASUREMENTS OF LEFT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN SEVENTH INSTAR
Abbreviations are the same as those in Table III.

Topotype Number	<i>L</i> (in mm.)	<i>H</i> (in mm.)	<i>W</i> (in mm.)	Per Cent of <i>L</i>	Per Cent of <i>H</i>	Per Cent of <i>W</i>	A-L2 (in mm.)	L2-L3 (in mm.)	<i>H/L</i> (in Per Cent)	<i>W/L</i> (in Per Cent)	Angle (in Degs.)	Spur
27871	.52	.27	.13	57	29	14	.16	.14	52	25	75	<i>m-l</i>
27872	.52	.28	.14	55	30	15	.13	.16	54	35	71	...
27873	.52	.30	.10	57	32	11	.15	.14	58	19	74	<i>s</i>
27874	.53	.28	.14	56	29	15	.15	.15	53	26	78	<i>l</i>
27875	.53	.30	.14	55	31	14	.14	.16	57	26	77	<i>l</i>
27876	.54	.30	.11	57	31	12	.16	.18	56	20	78	<i>m</i>
27877	.54	.32	.12	55	33	12	.12	.16	59	22	71	<i>m</i>
27878	.55	.26	.14	58	27	15	.15	.13	47	25	70	<i>l</i>
27879	.55	.30	.12	57	31	12	.15	.17	55	22	78	<i>l</i>
27880	.56	.30	.12	57	31	12	.16	.16	54	21	74	<i>l</i>
27881	.56	.31	.11	57	32	11	.15	.16	55	20	76	<i>m</i>
27882	.57	.30	.14	56	30	14	.14	.18	53	25	77	...
27883	.58	.22	.12	63	24	13	.13	.15	38	20	58	<i>ll</i>
27884	.60	.30	.14	58	29	13	.14	.17	50	23	73	<i>m</i>
27885	.60	.32	.15	56	30	14	.17	.18	53	25	74	<i>m-l</i>
Mean	.551	.291	.128	56.9	29.9	13.1	.147	.159	52.9	23.6	73.6	

TABLE VIII

MEASUREMENTS OF RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN SEVENTH INSTAR
Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27886	.49	.28	.10	56	32	12	.13	.16	57	20	78	<i>l</i>
27887	.50	.28	.13	55	31	14	.13	.18	56	26	79	<i>s</i>
27888	.52	.26	.10	59	30	11	.12	.17	50	19	75	<i>ll</i>
27889	.52	.26	.12	58	29	13	.12	.17	50	23	80	<i>l</i>
27890	.52	.26	.13	57	29	14	.13	.16	50	25	79	<i>m-l</i>
27891	.52	.27	.13	57	29	14	.16	.14	52	25	75	<i>m-l</i>
27892	.52	.29	.14	55	30	15	.13	.15	56	27	75	<i>ll</i>
27893	.54	.27	.12	58	29	13	.13	.16	50	22	78	<i>l</i>
27894	.54	.29	.13	56	30	14	.12	.17	54	24	82	<i>l</i>
27895	.52	.27	.13	57	29	14	.13	.15	52	25	75	<i>l</i>
27896	.56	.28	.15	57	28	15	.14	.16	50	27	76	<i>l</i>
27897	.56	.29	.14	57	29	14	.15	.17	52	25	80	<i>ll</i>
27898	.56	.30	.13	57	30	13	.14	.17	54	23	75	<i>l</i>
27899	.58	.32	.11	57	32	11	.14	.19	55	19	75	<i>m-l</i>
27900	.58	.32	.12	57	31	12	.13	.17	55	21	77	<i>l</i>
27901	.59	.31	.14	57	30	13	.15	.17	53	24	71	<i>m-l</i>
27902	.60	.26	.16	59	25	16	.15	.19	43	27	75	...
27903	.60	.31	.17	55	29	16	.17	.17	52	28	78	<i>l</i>
Mean	.546	.284	.131	56.9	29.6	13.6	.137	.167	52.3	23.9	76.8	

TABLE IX

MEASUREMENTS OF LEFT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN SIXTH INSTAR
Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27904	.38	.21	.10	55	30	15	.11	.11	55	26	77	<i>m</i>
27905	.44	.26	.10	55	37	13	.12	.14	59	23	74	<i>m</i>
27906	.46	.20	.12	59	26	15	.11	.13	44	26	77	<i>l</i>
27907	.48	.23	.13	57	28	15	.13	.15	48	27	70	<i>s</i>
27908	.50	.24	.10	59	29	12	.12	.13	48	20	75	<i>m-l</i>
Mean	.452	.228	.110	57.0	30.0	14.0	.118	.132	50.8	24.4	74.6	

TABLE X

MEASUREMENTS OF RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN SIXTH INSTAR
Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27909	.41	.20	.08	59	29	12	.13	.13	49	20	79	<i>l</i>
27910	.41	.21	.10	57	29	14	.11	.12	51	24	70	<i>m-l</i>
27911	.41	.22	.10	56	30	14	.11	.14	54	24	80	<i>m</i>
27912	.43	.22	.10	58	29	13	.11	.14	51	23	73	<i>ll</i>
27913	.43	.24	.12	55	30	15	.10	.12	56	28	81	<i>l</i>
27914	.47	.23	.12	57	28	15	.12	.14	49	26	78	<i>ll</i>
27915	.51	.23	.15	57	26	17	.12	.14	45	29	70	<i>ll</i>
Mean	.440	.221	.110	57.0	28.7	14.3	.114	.133	50.7	25.0	76.0	

TABLE XI

MEASUREMENTS OF LEFT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN FIFTH INSTAR
Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27916	.33	.18	.08	56	31	13	.07	.10	55	24	73	<i>m-l</i>
27917	.34	.20	.07	56	33	11	.09	.10	59	21	74	<i>m-l</i>
27918	.35	.20	.06	57	33	10	.10	.11	57	17	76	<i>m-l</i>
27919	.36	.21	.09	54	32	14	.08	.11	58	25	80	...
27920	.38	.19	.08	59	29	12	.09	.11	50	21	77	<i>l</i>
Mean	.352	.196	.076	56.4	31.6	12.0	.086	.106	55.8	21.6	76.0	

TABLE XII

MEASUREMENTS OF RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN FIFTH INSTAR

Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27921	.32	.19	.08	54	32	14	.09	.11	59	25	81	<i>m</i>
27922	.33	.17	.08	57	29	14	.09	.10	52	24	80	<i>ll</i>
27923	.33	.17	.09	56	29	15	.09	.11	52	27	77	<i>l</i>
27924	.35	.17	.09	57	28	15	.11	.10	49	26	78	<i>m</i>
Mean	.333	.175	.085	56.0	29.5	14.5	.095	.105	53.0	25.5	79.0	

TABLE XIII

MEASUREMENTS OF LEFT VALVE OF *Ctenoloculina cicatricosa* (WARTHIN) IN FOURTH INSTAR

Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27925	.24	.16	.09	49	33	18	.05	.07	67	38	73	<i>m</i>

TABLE XIV

MEASUREMENTS OF RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN) IN FOURTH INSTAR

Abbreviations are the same as those in Table III.

Topotype Number	L (in mm.)	H (in mm.)	W (in mm.)	Per Cent of L	Per Cent of H	Per Cent of W	A-L2 (in mm.)	L2-L3 (in mm.)	H/L (in Per Cent)	W/L (in Per Cent)	Angle (in Degs.)	Spur
27926	.28	.16	.08	54	31	15	.08	.10	57	29	79	<i>l</i>
27927	.30	.14	.08	58	27	15	.09	.09	47	27	75	<i>ll</i>
27928	.30	.16	.08	56	29	15	.07	.10	53	27	75	<i>s</i>
Mean	.293	.153	.08	56.0	29.0	15.0	.08	.097	52.3	27.7	76.3	

TABLE XV
 MEAN DIMENSIONS OF *Ctenoloculina cicatricosa* (WARTHIN) BY VALVES
 Abbreviations are the same as those in Table I.

Measurement	Valve	Instar						Adult Male	Adult Female
		4	5	6	7	8			
Number of Specimens	{ Left	1	5	5	15	28	4	11	
	{ Right	3	4	7	18	26	2	10	
Length (mm.)	{ Left	.24	.352	.452	.551	.675	.900	.898	
	{ Right	.293	.333	.440	.546	.695	.795	.846	
Height (mm.)	{ Left	.16	.196	.228	.291	.369	.475	.486	
	{ Right	.153	.175	.221	.284	.359	.440	.474	
Width (mm.)	{ Left	.09	.076	.110	.128	.150	.178	.197	
	{ Right	.08	.085	.110	.131	.166	.180	.211	
Per cent of <i>L</i>	{ Left	49.	56.4	57.0	56.9	56.6	58.0	56.6	
	{ Right	56.0	56.0	57.0	56.9	57.0	56.0	55.1	
Per cent of <i>H</i>	{ Left	33.	31.6	30.0	29.9	30.9	30.8	30.7	
	{ Right	29.0	29.5	28.7	29.6	29.5	31.0	31.1	
Per cent of <i>W</i>	{ Left	18.	12.0	14.0	13.1	12.5	11.3	12.6	
	{ Right	15.0	14.5	14.3	13.6	13.6	13.0	13.8	
A-L2 (mm.)	{ Left	.05	.086	.118	.147	.180	.223	.219	
	{ Right	.080	.095	.114	.137	.171	.185	.204	
L2-L3 (mm.)	{ Left	.07	.106	.132	.159	.188	.233	.229	
	{ Right	.097	.105	.133	.167	.199	.225	.227	
<i>H/L</i> × 100	{ Left	67.	55.8	50.8	52.9	55.0	53.0	54.5	
	{ Right	52.3	53.0	50.7	52.3	52.1	55.5	55.9	
<i>W/L</i> × 100	{ Left	38.	21.6	24.4	23.6	22.2	19.5	21.8	
	{ Right	27.7	25.5	25.0	23.9	23.7	23.0	25.0	
Angle L2 (degrees)	{ Left	73.	76.0	74.6	73.6	72.8	71.5	75.4	
	{ Right	76.3	79.0	76.0	76.8	76.4	77.5	81.3	

TABLE XVI
 LENGTHS OF INSTARS OF *Ctenoloculina cicatricosa* (WARTHIN)
 The computed values of length of all instars are based on the formula
 $L_{n+1} = L_n (0.26 + 1)$.

Instar	Left Valves		Right Valves	
	Observed <i>L</i> (in mm.)	Computed <i>L</i> (in mm.)	Observed <i>L</i> (in mm.)	Computed <i>L</i> (in mm.)
1139133
2175167
3221210
424	.279	.293	.264
5352	.352	.333	.333
6452	.444	.440	.420
7551	.559	.546	.530
8675	.704	.695	.667
Adult Male900	.887	.795	.840
Adult Female898		.846	

TABLE XVII
 HEIGHTS OF INSTARS OF *Ctenoloculina cicatricosa* (WARTHIN)

Heights of instars are computed from the formula: Height = C (length)^{*k*}, where $C=0.54$ for the left valves, $C=0.52$ for the right valves, and $k=1$ for both valves.

Instar	Left Valves			Right Valves		
	Length (in mm.)	Observed <i>H</i> (in mm.)	Computed <i>H</i> (in mm.)	Length (in mm.)	Observed <i>H</i> (in mm.)	Computed <i>H</i> (in mm.)
1139*075	.133*069
2175*095	.167*087
3221*119	.210*109
4279*151	.264*137
5352	.196	.190	.333	.175	.173
6452	.228	.244	.440	.221	.229
7551	.291	.297	.546	.284	.284
8675	.369	.364	.695	.359	.361
Adult900	.475	.486	.795	.440	.413

* Computed lengths from Table XVI.

TABLE XVIII

MEANS OF SELECTED MEASUREMENTS OF *Ctenoloculina cicatricosa* (WARTHIN) AND THEIR RATIOS
 A-L3=distance from anterior corner to the axis of L3 measured along the dorsal border.

Measurement	Instar					Adult Male
	4	5	6	7	8	
A-L3 (in mm.)	.177	.200	.247	.304	.370	.410
Length (in mm.)	.293	.333	.440	.546	.695	.795
A-L3/Length in per cent	.605	.601	.561	.554	.532	.516

TABLE XIX

COEFFICIENTS OF VARIATION OF VALVES OF *Ctenoloculina cicatricosa* (WARTHIN)

Measurement	Sixth Instar	Seventh Instar	Eighth Instar	All Adults	Adult Males	Adult Females
Number of Specimens	18	49	89	38	11	27
Length {						
σ0361	.0336	.0595	.0793	.0731	.0812 mm.
m4411	.5406	.6855	.8742	.855	.882 mm.
v	8.19	6.22	8.68	9.08	8.55	9.21 %
Height {						
σ0174	.0215	.0345	.0411	.0321	.0425 mm.
m2350	.2876	.3689	.4739	.458	.4804 mm.
v	7.41	7.47	9.36	8.68	7.01	8.85 %
H/L {						
σ0463	.0518	.0237
m5380	.5419	.5437
v	8.60	9.56	4.36%
Number of Specimens	12	33	54	27		
Width {						
σ0177	.0164	.0307	.0244 mm.
m1083	.1297	.1580	.1981 mm.
v	16.35	12.65	19.42	12.32 %

TABLE XX
COMPUTED RANGES IN SIZE WITHIN INSTARS FOR 83.85 PER CENT OF A POPULATION OF
Ctenoloculina cicatricosa (WARTHIN) WITH NORMAL DISTRIBUTION

Instar	Length			Height		
	$m-1.4\sigma$	m	$m+1.4\sigma$	$m-1.4\sigma$	m	$m+1.4\sigma$
97642	.87424163	.4739
86022	.6855	.7688	.3206	.3689	.4172
74936	.5406	.5876	.2575	.2876	.3177
64411	.49162350	.2593

TABLE XXI
COEFFICIENTS OF VARIATION OF LEFT AND RIGHT VALVES OF *Ctenoloculina cicatricosa* (WARTHIN)

Measurement	Seventh Instar		Eighth Instar		Adult Females		
	Left Valve	Right Valve	Left Valve	Right Valve	Left Valve	Right Valve	
Number of Specimens	15	18	28	26	11	10	
Length	σ0260	.0334	.0608	.0662	.0647	.0802 mm.
	m551	.546	.675	.695	.898	.846 mm.
	v	4.7	6.1	9.0	9.5	7.2	9.5 %
Height	σ0249	.0201	.0332	.0339	.0435	.0486 mm.
	m291	.284	.369	.359	.486	.474 mm.
	v	8.6	7.1	9.0	9.4	9.0	10.3 %
$H/L \times 100$	σ	4.94	3.20	3.88	6.30	1.44	1.92
	m	52.9	52.3	55.0	52.1	54.5	55.9
	v	9.3	6.1	7.1	12.1	2.6	3.4 %
$W/L \times 100$	σ	3.84	2.71	3.34	3.25	1.70	1.00
	m	23.6	23.9	22.2	23.7	21.8	25.0
	v	16.3	11.3	15.0	13.7	7.8	4.0 %

TABLE XXII
 COEFFICIENTS OF VARIATION OF VALVES OF *Cypridopsis vidua* (O. F. MÜLLER)

Instar	1	2	3	4	5	6	7	8	Adult
Number of Specimens	41	68	65	53	49	72	77	60	15
Length	σ .00444	.00694	.00624	.00709	.00766	.0151	.0178	.0242	.0191 mm.
	m .1322	.1555	.1882	.2268	.2698	.3334	.4180	.5280	.6170 mm.
	v 3.36	4.46	3.32	3.13	2.84	4.53	4.26	4.59	3.10 %
Height	σ .00563	.00556	.00524	.00714	.00573	.00943	.0112	.0123	.0250 mm.
	m .0920	.1060	.1238	.1456	.1697	.2308	.2505	.3162	.3730 mm.
	v 6.12	5.24	4.23	4.90	3.38	4.62	4.47	3.89	6.72 %
H/L	σ 3.47	2.74	2.14	2.73	1.97	1.96	2.19	2.41	3.38 %
	m 69.44	68.41	65.88	64.13	63.04	61.08	60.00	59.95	60.33 %
	v 5.00	4.01	3.24	4.26	3.12	3.21	3.65	4.02	5.61 %

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PLATES

EXPLANATION OF PLATE I

(All figures $\times 40$)

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FIGS. 1-3. Fourth instar. Lateral views of two right valves, topotypes Nos. 27926-7; and left lateral view of carapace, topotype No. 27925.

FIGS. 4-5. Fifth instar. Lateral view of right valve, topotype No. 27923; and left lateral view of carapace, topotype No. 27929.

FIGS. 6-9. Sixth instar. Lateral views of right valve, topotype No. 27912; left valve, topotype No. 27905; and right valve, topotype No. 27914; and left lateral view of carapace, topotype No. 27930.

FIGS. 10-13. Seventh instar. Lateral views of right valve, topotype No. 27888; left valve, topotype No. 27881; right valve, topotype No. 27891; and left valve, topotype No. 27880.

FIGS. 14-19. Eighth instar. Lateral views of right valve, topotype No. 27845, and left valve, topotype No. 27834; right lateral and ventral views of carapace, topotype No. 27938; and lateral views of left valve, topotype No. 27835; and right valve, topotype No. 27854.

FIGS. 20-29. Adult. Lateral and ventral views of female left valve, topotype No. 27792; right lateral and ventral views of female carapace, topotype No. 27936; lateral views of female left valve, topotype No. 27798, male left valve, topotype No. 27813, male right valve, topotype No. 27932, and female right valve, topotype No. 27810; and lateral and ventral views of female left valve, topotype No. 27800.

PLATE I

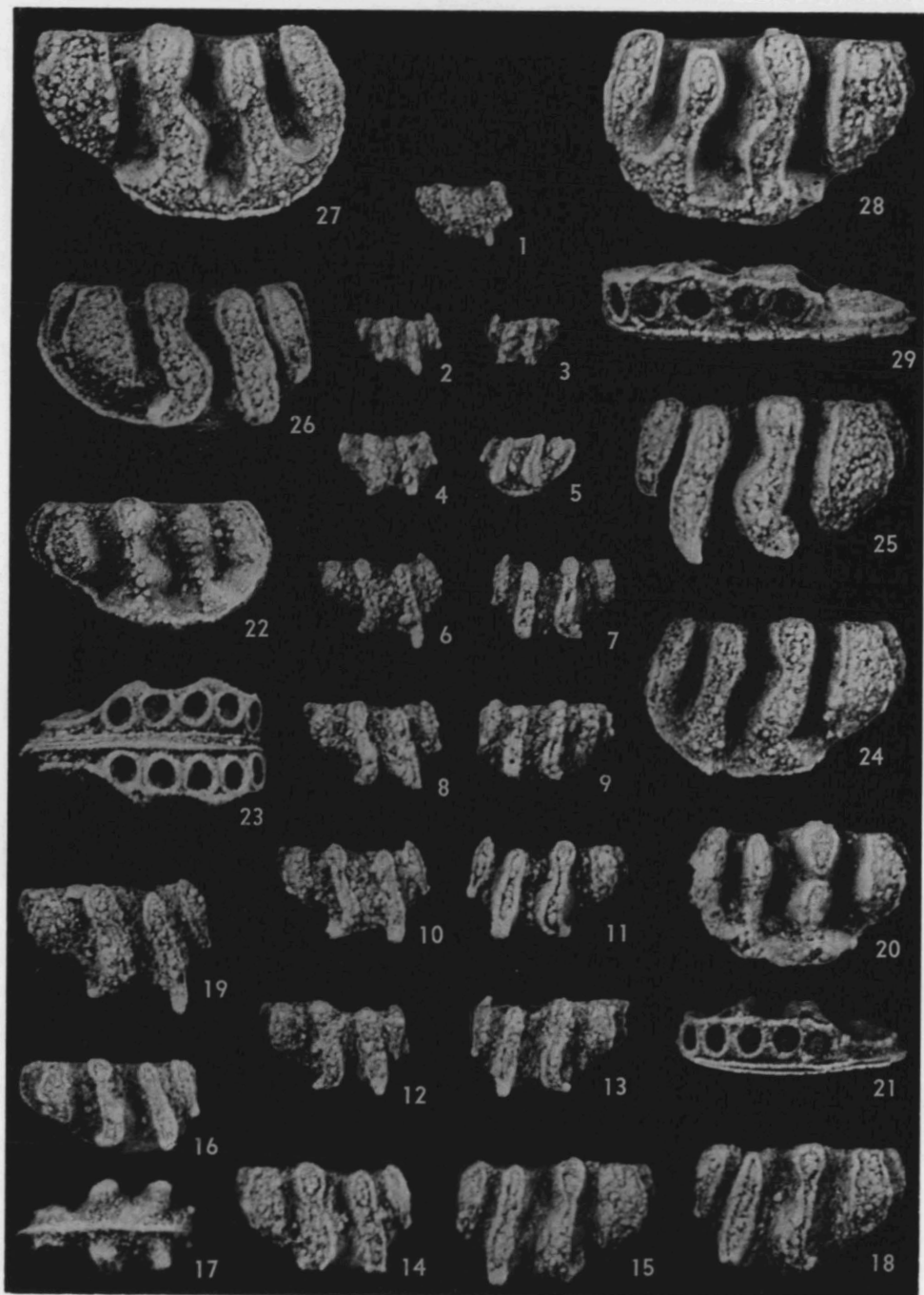
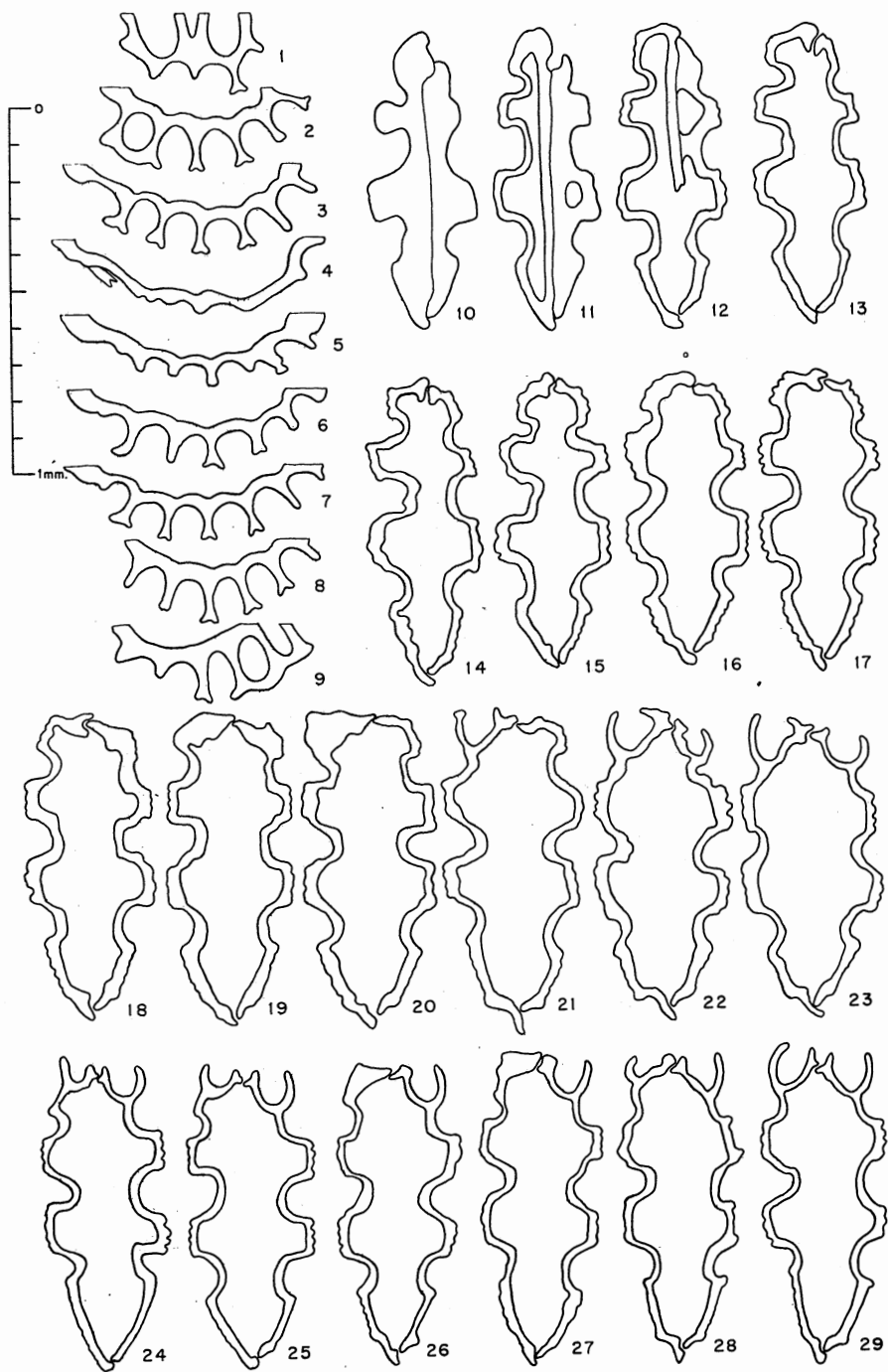


PLATE II



EXPLANATION OF PLATE II

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FIG. 1-9. A series of polished sagittal surfaces of the ventral part of an adult female carapace made from the right side to the left side. Surfaces spaced approximately 0.025 mm. apart. Dorsal part of same carapace shown as a series of polished frontal surfaces in Figures 10-23.

FIGS. 10-23. A series of polished frontal surfaces of the dorsal part of an adult female carapace made from dorsal to ventral. Surfaces spaced approximately 0.0185 mm. apart. Ventral part of same carapace shown as a series of polished sagittal surfaces in Figures 1-9.

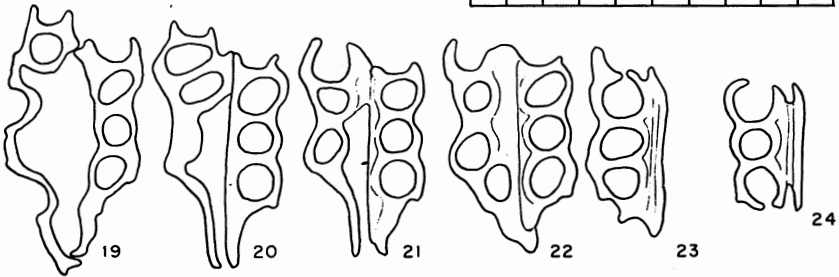
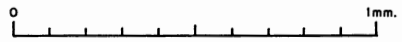
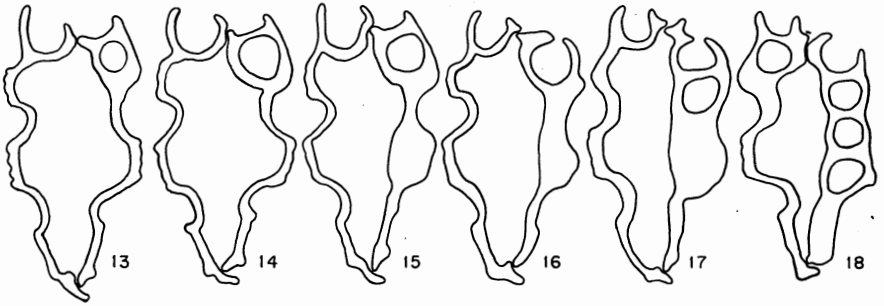
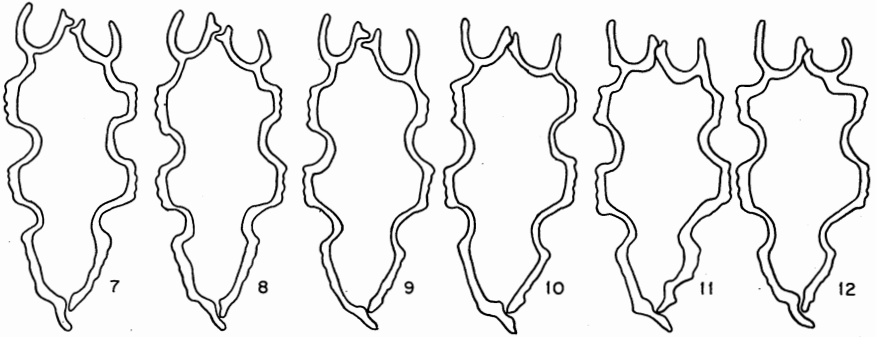
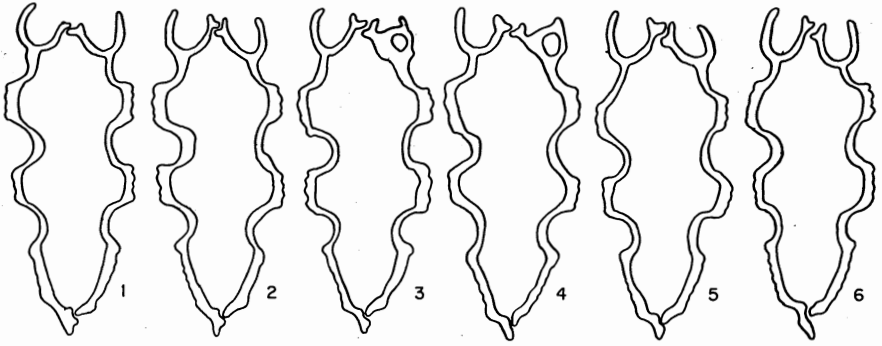
FIGS. 24-29. A series of polished frontal surfaces of the middle part of an adult female carapace made from dorsal to ventral. Surfaces spaced approximately 0.01 mm. apart. Ventral part of same carapace shown as a series of polished frontal surfaces on Plate III.

EXPLANATION OF PLATE III

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FIGS. 1-24. A series of polished frontal surfaces of the ventral part of an adult female carapace made from dorsal to ventral. Surfaces spaced approximately 0.01 mm. apart. Middle part of same carapace shown as a series of polished frontal surfaces on Plate II, Figures 24-29.

PLATE III



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