# PHYLOGENY OF THE DEVONIAN OSTRACOD GENUS *CTENOLOCULINA* BASSLER

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ABSTRACT—Quantitative phyletics, adapted as a computer procedure, is used to analyze the ostracod genus *Ctenoloculina*. On the basis of measured and descriptive data for twelve species, an evolutionary tree is constructed. This tree is compared against the known stratigraphic and geographic distribution of the species.

## INTRODUCTION

RECENT ADVANCES in computer programs now permit employment of all characters, impartially, in comparing related species. Within a genus, it is further possible to arrange the species in a phylogenetic tree which incorporates all available data on morphological characters. Since the computer performs the necessary mathematical operations in seconds, the micropaleontologist can modify the quantitative phyletics at any time by adding additional characters into the program without long and tedious "hand" computations. Certain ostracods are well suited to such phyletic treatment.

Recent ostracod taxonomy is based largely on the structure of the appendages of these microcrustaceans. Since these parts are composed of chitin, preservation in the fossil record is rare. Therefore, a different scheme must be used to differentiate fossil species. The problem becomes one of choosing characters which reflect actual extraspecific differences and not intraspecific variations.

Classification of the order Palaeocopida, . . . "is based primarily on dimorphism, relationship of valves along the free margin, and muscle scars . . ." (*Treatise on Invertebrate Paleontology,* 1961, p. Q111). A common characteristic of many families in the order is the high degree of surface ornamentation, such as costae, papillae, spines, knobs, and frills. Since all palaeocopid families are restricted to the Paleozoic, a direct comparison between extinct and living forms may be invalid. However, one area of comparison may be sexual dimorphism. Dimorphism in certain living species is manifest in the posterior portion of female cara-

paces as a swelling to accommodate reproductive organs. Various fossil forms have been termed dimorphic because of different ornamentation or because the female dimorph has posterior inflations (kloedenellids), enlargement of velate structure (sigmoopsids), or incurved velate structures or loculi (hollinids). Nomenclature used follows that in the *Treatise on Invertebrate Paleontology* (1961).

The genus *Ctenoloculina* Bassler (1941) offers an excellent opportunity to study the relationships between external and internal morphology. Recognizing this, Kesling (1952a) reconstructed the probable soft-part orientation for the type species, *Ctenoloculina cicatricosa* (Warthin). He noted that the species is unusual in that carapace configurations must be accounted for in the reconstruction of the location of organs and appendages (see Kesling, 1952a, figs. 4,5). Also, each species of *Ctenoloculina* is different on the basis of external morphology. Whether or not these features reflect internal differences is a measure of the accuracy of the taxonomic method used.

This paper is an attempt to utilize the computer program created by Kluge & Farris (1969) to construct, on the basis of external morphologic differences, an evolutionary tree for the ctenoloculine species as described in paleontologic literature.

## ACKNOWLEDGMENTS

### SCOPE OF STUDY

Eighteen species of the genus *Ctenoloculina* Bassler (1941) are currently recognized in literature. Their systematic descriptions are presented in Appendix A.

Six species were deleted from the analysis: *Ctenoloculina cristata, C. punctocarinata, C. elongata, C. kelletae, C. snajdri,* and *C. scalae.*

*Ctenoloculina cristata* is known from one poorly preserved specimen. Bassler (1941) created the species and figured the only known specimen at the same time he erected the genus. Because the holotype does not seemingly bear any resemblance to species subsequently included as ctenoloculines, the species was not included in this study. *Ctenoloculina punctocarinata* Swartz & Swain (1941) and *C. elongata* Stewart (1950) were not utilized due to insufficient specimens. The author visited the type localities of both species during the summer of 1970. Careful collecting at these and numerous other sites failed to produce any specimens of either species.

Three of the seven European species could not be included; the only known specimens of *Ctenoloculina kelletae* Pokorný (1950), *C. snajdri* Přibyl (1955), and *C. scalae* Adamczak (1968) were holotypes and allotypes and were not available for study.

The twelve species used and the number of valves of each dimorph are listed in table 1. The specimens from North America used in this study are catalogued and deposited in the collections of the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan. Those specimens from Europe utilized were on loan from the Geologiska Institutionen, Stockholm, Sweden. Localities from which specimens were obtained are listed in Appendix B.

### STATISTICAL TREATMENT

*Collection of material.*—Initially, it was believed that 120 specimens per species, representing 30 left valves and 30 right valves per dimorph, was most desirable. Such a sample size would be large enough to permit accurate representation of population parameters, yet small enough to be stored on two cardboard slides. During the collecting and cleaning process, it became evident that this number of specimens could not be obtained for all species. Only one species was represented by 120 well-preserved valves; two species had only four valves each (table 1). Therefore, the mean value of a measurement as determined here may not reflect the true mean of the population. However, it is hoped that the randomness of field sampling produced specimens reasonably representative of the species to which they were assigned.

As specimens were collected, they were mounted on cardboard slides according to dimorph as established by Warthin (1934) and according to species. As noted, single valves were utilized whenever possible.

*Measurements.* — Several linear measurements were recorded from each specimen using a Gaertner Traveling Micrometer. Of these, the three determined to be most useful were length, height, and width. Kesling (1952a) and others noted that as ostracods molt there is an incremental increase of the volume contained within the carapace. Length, height, and width reflect this incremental growth. To distinguish immature instars from the adults of other species, only those suites of specimens containing some adult females were studied. Because size of carapace is such a significant factor, the most accurate method available for obtaining the three measurements was utilized. In text-figure 1a, the directions of length and height measurements are shown for a single valve. Length was measured parallel to the hinge line from the most anterior extent of the contact margin to the most posterior extent of the margin, and height was measured perpendicular to the hinge line from the hinge line to the most ventral extent of the contact margin. I believe this is the most accurate method because it closely reflects the internal volume and disregards commonly fragile and ornamental extensions of the carapace which are subject to corrosion. Width was measured from the plane of the contact margin to the approximate center of the median sulcus, S2; this is the greatest width exclusive of lobe protrusions.

Two angles were measured on each specimen, using a Zeiss Petrographic Microscope with a rotating stage and a low power ocular lens. The first angle was the anterior cardinal angle (text-fig. 1a). The second angle was that
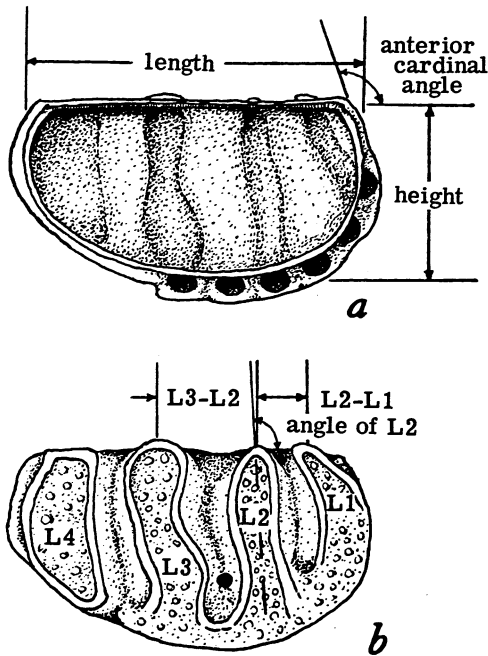
TEXT-FIG. 1—*Ctenoloculina cicatricosa* (Warthin), show-
ing locations and orientation of several measure-
ments. *a,* internal view of left valve of adult fe-
male. *b,* lateral view of right valve of adult female;
the black spot between L2 and L3 represents ap-
proximate location of the width measurement taken
from the outer surface of the valve to the plane of
the contact margin. (After Kesling, 1952a, figs. 1,4).

TABLE 1—NUMBER OF SPECIMENS OF EACH SPECIES
USED IN THIS STUDY

| *Ctenoloculina* species | Female valves Left | Right | Male valves Left | Right |
|---|---|---|---|---|
| C. acanthina Kesling | 8 | 12 | 3 | 0 |
| C. beckeri Adamczak | 7* | | 5* | |
| C. cicatricosa (Warthin) | 30 | 30 | 19 | 9 |
| C. eurybathrota Kesling | 27 | 22 | 6 | 2 |
| C. exocha Kesling & Peterson | 1 | 2 | 1 | 0 |
| C. latisulcata Adamczak | 4* | | 11* | |
| C. myurilobata Kesling | 30 | 30 | 0 | 1 |
| C. platyca Kesling & Peterson | 2 | 0 | 0 | 0 |
| C. platyzanclota Kesling | 30 | 20 | 0 | 0 |
| C. skalyensis Adamczak | 3* | | 3* | |
| C. thliberilobata Kesling | 30 | 30 | 30 | 30 |
| C. vulgaris Adamczak | 2* | | 2* | |

* Species represented only by complete carapaces. Meas-
urements made to correspond to those of left valves.

crete integers. The length/total, height/total,
and width/total values were plotted on three
separate histograms for all left and right valves
of males and females for all species used in the
study. In each case, a definite binomial distri-
bution of values was noted and this was coded
0 for the lower value ratio and 1 for the upper
value. A similar procedure was followed with
the angular measurements. The range of integer
values for the cardinal angle and the L2 angle
was 0 to 2 on both distribution histograms.
The data means for each species are recorded
in table 2.

When the coding of variables was initiated,
characters were chosen which might reflect in-
ternal differences. These characters had several
different states and a hierarchal coding scheme
was used with 0 as the presupposed primitive
state and N-1 as the most advanced state where
N equals the total number of different states
for that variable. This procedure was followed
in coding each of the sixteen descriptive vari-
ables for each specimen. The means for each
variable were calculated using the General Data
Description Program and are tabulated for
each species in table 3.

*Statistical procedure.*—In recent years, nu-
merical taxonomy has been offered as a more
precise method to replace the classical evolu-
tionary taxonomy. Conversely, numerical tax-
onomy has been criticized for disregarding
evolutionary relationships in the groups being
studied. Kluge & Farris (1969) made a study
of anuran frog families and used a computer
program after the method of Wagner (1961)
to incorporate "the precision of numerical tech-
niques and the power of evolutionary inference"
(Kluge & Farris, 1969, p. 1). This taxonomic
procedure was termed quantitative phyletics. A
goal of this method is to eliminate a research-
er's personal bias in the selection of characters

made by the hinge line and a line which bi-
sects L2 (text-fig. 1b).

In addition to the measurements, sixteen
other variables were recorded for each specimen.

*Coding.*—The five measurements and six-
teen variables from each specimen were tabu-
lated on punch cards. Three variables were
created from the length, height, and width of
each specimen. These values were calculated
and punched out using the Transformation
Program, BMD9S, available from the Statisti-
cal Research Laboratory at The University of
Michigan. Briefly, the three variables were cal-
culated as follows: (1) the length, height, and
width for a specimen were summed; (2) this
total was then divided into each of the three
measurements; and (3) the percentages were
punched out on the card. For species repre-
sented by more than eight valves per dimorph,
another Statistical Lab Program, General Data
Description, BMDiD, was used to calculate
the mean for all measured, descriptive, and cal-
culated variables. For those species represented
by seven or less valves per dimorph, a desk
calculator was used to calculate mean values.

For measured and calculated variables, a
following method was used to code them as dis-

TABLE 2—MEAN MEASUREMENTS AND CODING OF SPECIES USED IN THE STUDY

| Species | Valve | L (mm) | H (mm) | W (mm) | %L | Code (L) | %H | Code (M) | %W | Code (N) | Ant. card. angle (o) | Code (O, P) | Ang. of L2 (o) | Code (Q, R) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C. acanthina | L | 0.8742 | 0.4730 | 0.1444 | 58.6 | 0 | 31.7 | 0 | 9.7 | 1 | 100.1 | 1 | 75.4 | 1 |
| | R | 0.8907 | 0.4681 | 0.1319 | 59.8 | | 31.4 | | 8.8 | | 101.7 | 1 | 76.6 | 2 |
| C. beckeri | L | 0.8606 | 0.4939 | 0.1124 | 58.7 | 0 | 33.8 | 1 | 7.7 | 0 | 119.0 | 2 | 73.2 | 1 |
| | R | * | * | * | * | | * | | * | | 114.7 | 2 | 76.7 | 2 |
| C. cicatricosa | L | 1.2200 | 0.6426 | 0.2234 | 58.5 | 0 | 30.8 | 0 | 10.7 | 1 | 106.3 | 1 | 74.5 | 1 |
| | R | 1.1950 | 0.6228 | 0.2130 | 58.8 | | 30.7 | | 10.5 | | 114.1 | 2 | 76.6 | 2 |
| C. eurybathrota | L | 0.8942 | 0.4693 | 0.1289 | 59.9 | 1 | 31.4 | 0 | 8.6 | 0 | 99.9 | 1 | 73.3 | 1 |
| | R | 0.9177 | 0.4785 | 0.1270 | 60.3 | | 31.4 | | 8.3 | | 102.3 | 1 | 76.1 | 2 |
| C. exocha | L | 0.9120 | 0.4590 | 0.1550 | 59.8 | 1 | 30.1 | 0 | 10.2 | 1 | 106.2 | 1 | 69.8 | 1 |
| | R | 0.8275 | 0.4545 | 0.1360 | 58.3 | | 31.4 | | 9.5 | | 102.9 | 1 | 74.9 | 1 |
| C. latisulcata | L | 1.2210 | 0.6827 | 0.1325 | 59.7 | 1 | 33.7 | 1 | 6.6 | 0 | 106.6 | 1 | 72.3 | 1 |
| | R | * | * | * | * | | * | | * | | 101.6 | 1 | 81.2 | 2 |
| C. myurilobata | L | 1.0710 | 0.5615 | 0.1848 | 58.9 | 0 | 31.9 | 0 | 10.2 | 1 | 99.5 | 1 | 79.2 | 2 |
| | R | 0.9844 | 0.5147 | 0.1765 | 58.7 | | 30.8 | | 10.5 | | 104.7 | 1 | 80.3 | 2 |
| C. platyca | L | 0.9460 | 0.4795 | 0.1295 | 60.8 | 1 | 30.9 | 0 | 8.3 | 0 | 83.2 | 0 | 74.2 | 1 |
| | R | * | * | * | * | | * | | * | | * | 0† | * | 1† |
| C. platyzanclota | L | 0.9697 | 0.4919 | 0.1545 | 60.0 | 1 | 30.4 | 0 | 9.6 | 1 | 99.7 | 1 | 72.2 | 1 |
| | R | 0.9935 | 0.5206 | 0.1622 | 59.2 | | 31.1 | | 9.7 | | 97.7 | 1 | 75.3 | 1 |
| C. skalyensis | L | 1.1300 | 0.6503 | 0.1466 | 58.7 | 0 | 33.6 | 1 | 7.7 | 0 | 111.0 | 2 | 66.6 | 0 |
| | R | * | * | * | * | | * | | * | | 102.4 | 1 | 71.8 | 1 |
| C. thliberilobata | L | 1.3770 | 0.6820 | 0.2325 | 60.1 | 1 | 29.8 | 0 | 10.1 | 1 | 102.3 | 1 | 74.8 | 1 |
| | R | 1.3090 | 0.6802 | 0.1950 | 59.9 | | 31.1 | | 8.9 | | 113.7 | 2 | 77.1 | 2 |
| C. vulgaris | L | 0.9940 | 0.5585 | 0.1465 | 58.5 | 0 | 33.0 | 1 | 8.5 | 0 | 112.6 | 2 | 62.5 | 0 |
| | R | * | * | * | * | | * | | * | | 106.7 | 1 | 66.1 | 0 |

* No measurements for right valve.
† Inferred code state.

to be used to infer relationships between groups of organisms.

The technique used involves an algorithm which finds the smallest differences between two coded character groups. These groups shall be herein termed OTU's—Operational Taxonomic Units (after Sokal & Sneath, 1963). This difference is set forth by Kluge & Farris (1969, p. 6) in their equation:

$$D(A,B) = \sum_i |X(A,i) - X(B,i)|$$

where $X(A,i)$ is the state of character i in OTU A, and $D(A,B)$ equals the sum of the differences in states between OTU A and OTU B. For clarification, it is necessary to list the Wagner method as described by Kluge & Farris (1969, p. 6,7):

(1) Choose an ancestor OTU. Go to 2.

(2) Find the OTU that has the smallest difference, as defined in equation (1). Connect it to the ancestor to form an interval. Go to 3.

(3) Find the unplaced OTU A, that differs least from the ancestor. Go to 4.

(4) Find the interval from which the OTU identified in 3 differs least. The differ-

ence, $D(A, INT(B))$, between OTU A and interval B, is computed as follows: INT(B) is a connection between OTU B and OTU B's most recent ancestor on the existing tree. Let this most recent ancestor be denoted ANC(B). Then $D(A, INT(B)) = (D(A,B) + D(A,ANC(B)) - D(B,ANC(B)))/2.$ Go to 5.

(5) Attach OTU A to the interval found in 4, denoted B. To do this construct an intermediate, Y, and insert it into the tree. The insertion is shown in text-figure 2. For each character, i, $X(Y, i)$ is computed as the median of $X(A, i)$, $X(B, i)$, and $X(ANC(B), i)$. Go to 6.

(6) If any OTU's remain unplaced, go to 3. Otherwise, stop.

The program used in this study, constructed by Kluge & Farris, is a refined version of the one used in their study of anurans. Hereafter, the program will be referred to as the Advanced Sequenced Wagner Program. The method has considerable merit because:

(1) it does not assume that character states are irreversible;

TABLE 3—CODES OF DESCRIPTIVE VARIABLES FOR CTENOLOCULINE SPECIES

| Species | Male spurs (Codes not used) | | | Lobe heights | | | Lobe elevations | | | | Sulci | | L4 | Lobe Conn. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L1 | L2 | L3 | L1 (A) | L2 (B) | L3 (C) | L1 (D) | L2 (E) | L3 (F) | L4 (G) | S1 (H) | S2 (I) | (J) | (K) |
| C. acanthina | 2 | 5 | 5 | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 0 |
| C. beckeri | 1 | 2 | 5 | 2 | 0 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 0 |
| C. cicatricosa | 1 | 2 | 5 | 2 | 0 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 2 |
| C. eurybathrota | 1 | 4 | 5 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 2 | 0 |
| C. exocha | 1 | 2 | 5 | 3 | 2 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 |
| C. latisulcata | 1 | 2 | 5 | 2 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 |
| C. myurilobata | 2 | 4 | 5 | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 0 |
| C. platyca | *– | – | – | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 1 | 2 |
| C. platyzanclota | *– | – | – | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 2 | 0 |
| C. skalyensis | 1 | 4 | 6 | 2 | 0 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 0 | 0 |
| C. thliberilobata | 1 | 5 | 5 | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 1 | 1 | 2 | 2 |
| C. vulgaris | 1 | 2 | 6 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 |

* Males not known for species.

(2) it allows for both convergence and divergence in an evolutionary tree;

(3) it allows variable selection of an ancestor state; and

(4) its computer utilization allows for inclusion of more OTU's and coded cases than could ever be realistically handled otherwise.

Following the program format, the data, representing the means for all variables (table 4), was recorded on computer cards. There were eighteen coded cases with a range of two to four character states for each case. The number of states, when summed, was 24. This number will be used later in estimating procedure validity.

Given an ancestor state specified by the computer user, the data is operated upon by the algorithm. The computer output is in the form of a listing of the intervals on the tree which is being constructed. The length of the interval is given as the sum of character-state changes across the interval. Also, the end points of the interval in terms of OTU's, real or hypothetical, are given. For each hypothetical intermediate, the character state of each coded variable is given.

The first attempt at defining a tree involved the choice of a hypothetical ancestor with all 0 states. This was the most logical choice, as the coding had been done with 0 being the primitive state for each coded character. The total length, which equaled the sum of all intervals on the tree, was 57 units.

We may use a mathematical equation to interpret the value of a tree with this length. This equation defines C, the consistency index, as the ratio of the total number of changes in character states (R) to the length of the pro-
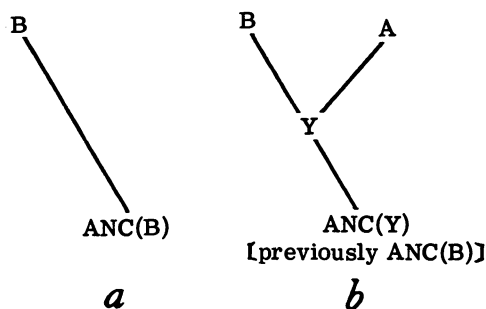


TEXT-FIG. 2—Insertion of a new OTU and intermediate onto a phylogenetic tree. a, before insertion of A; the tree has one interval, B. b, after insertion of A; the tree shows three intervals: B, A, and Y. (After Kluge & Farris, 1969).

posed tree (L). Ideally, C should equal unity. This equation is as follows:

$$C = R/L$$

For this initial tree, C = 0.421 which is considerably less than unity. Therefore, it would be logical to suppose a rather large divergence between the constructed tree and the true evolutionary pattern. The divergence may be due to ancestor selection.

If we were to find the earliest stratigraphic appearance of the genus and designate that species as the ancestor state, we would arrive at a different tree such as shown in text-figure 3. Ctenoloculina exocha Kesling & Peterson has the earliest known stratigraphic occurrence of species used in the study. The tree derived has a total length of 41 units. This gives a consistency index equal to 0.586. This, too, is considerably less than unity.

Subsequently, when each of the other species in the study was tried as the ancestor state, its C value was smaller than the C value

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TABLE 4—CODES OF VARIABLES FOR OPERATIONAL TAXONOMIC UNITS. Variables are listed A–R in table 5.

| OTU | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C. exocha | 3 | 2 | 3 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| Hypothetical I | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| C. platyca | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 2 | 1 | 0 | 0 |
| C. platyzanclota | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 |
| Hypothetical II | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 |
| Hypothetical III | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 |
| C. acanthina | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 |
| C. myurilobata | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 2 | 2 | 0 | 0 | 1 |
| Hypothetical IV | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 1 |
| C. cicatricosa | 2 | 0 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 2 | 1 | 2 | 1 | 2 | 0 | 0 | 1 |
| C. beckeri | 2 | 0 | 2 | 1 | 2 | 2 | 0 | 0 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 0 | 0 |
| C. thliberilobata | 2 | 1 | 2 | 1 | 2 | 2 | 0 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 2 | 1 | 0 | 1 |
| C. eurybathrota | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 1 |
| Hypothetical V | 2 | 0 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 |
| C. latisulcata | 2 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 |
| Hypothetical VI | 2 | 0 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 |
| C. skalyensis | 2 | 0 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 |
| C. vulgaris | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 |
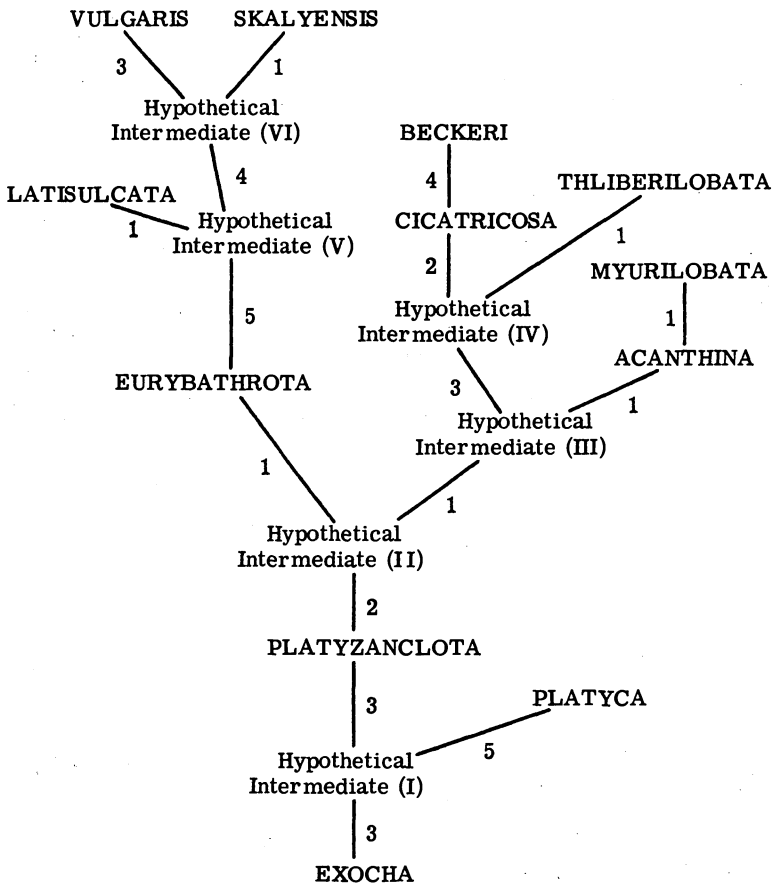


TEXT-FIG. 3—Tree constructed from the output of the Advanced Wagner Computer Program of the species of the ostracod genus *Ctenoloculina*. The numbers represent the sum of character-state changes between OTU's.

TABLE 5—CODING OF VARIABLE CHARACTER STATES

| VARIABLE | CODE |
|---|---|
| A—Lobe height—L1<br>B—Lobe height—L2<br>C—Lobe height—L3 | 0—Does not extend to hinge line<br>1—Even with hinge line<br>2—Slightly above hinge line<br>3—Strong projection above hinge line |
| D—Lobe elevation—L1<br>E—Lobe elevation—L2<br>F—Lobe elevation—L3<br>G—Lobe elevation—L4 | 0—Only slightly raised above carapace outer surface<br>1—Moderately raised<br>2—Strongly raised |
| H—Sulcus curvature—S1<br>I—Sulcus curvature—S2 | 0—Straight or slightly curved<br>1—Strongly geniculate |
| J—Shape of L4 | 0—D-shape, sharp ventral point directed to anterior<br>1—As in "O", with conspicuous posterodorsal incurvature of<br>lobe rim<br>2—D-shape nearly gone, rounding of points creates oval shape |
| K—L2 and L3 connection to frill in female | 0—No connection<br>1—Thin line connection<br>2—Connection as wide as ornamented lobe areas |
| L—Left valve anterior cardinal angle<br>M—Right valve anterior cardinal angle | 0—Less than 95°<br>1—95° to 110°<br>2—Greater than 110° |
| N—Left valve L2 angle<br>O—Right valve L2 angle | 0—Less than 70°<br>1—70° to 76°<br>2—Greater than 76° |
| P—Length % of total | 0—Less than 59%<br>1—Greater than 59% |
| Q—Height % of total | 0—Less than 32.5%<br>1—Greater than 32.5% |
| R—Width % of total | 0—Less than 9.2%<br>1—Greater than 9.2% |

for *Ctenoloculina exocha* as ancestor. The closest C value was that for *C. platyca,* which occurs in the same formation as *C. exocha.* On this basis, the tree with ancestor equal to *C. exocha* appears to be the best fit for this data.

*Ctenoloculina exocha,* as ancestor, poses an interesting problem concerning the evolution of characters. We note in table 4 that the character states of *C. exocha* are, for the most part, the most advanced states in the manner of the original coding procedure. In viewing the tree as constructed, each OTU appears to be more primitive in many character states than its closest ancestor. This may seem to imply that the evolutionary pattern of the genus has been one of degeneration. This is not necessarily the case. The change from complicated to uncomplicated structures is known in the fossil record. The classic example is that of the change from many toes to a single toe in horse evolution. We may then conclude that, according to this computer fit, the species have evolved to states of lower external complexity (text-fig. 5).

Another method of testing the usefulness of the tree is to compare it with the known stratigraphic occurrence of the species in the study (text-fig. 3). It must be recognized that the ranges of each species are by no means completely known. However, chronologic succession is a desirable end product in a true evolutionary pattern. Comparison of the chronostratigraphic succession (text-fig. 4) to the evolutionary tree (text-fig. 3) discloses the first major discrepancy: *Ctenoloculina platyzanclota* appears as the ancestor for all species except *C. exocha* and *C. platyca. C. platyzanclota* gives rise to a Hypothetical Intermediate (III) which in turn has a branch including one species which occurs below *C. platyzanclota* in stratigraphic sequence. This discrepancy may not be as significant as it appears. The known time range of *C. platyzanclota* is rather small as is its known geographic extent. Further field work may uncover older occurrences of the species. It is quite possible, then, that *C. platyzanclota* is the ancestor to the species in the tree as drawn in text-figure 3. A similar argument may be used to explain *C. eurybathrota* as an intermediate between *C. platyzanclota* and the European species.

Comparison of text-figures 3 and 4 also focuses attention on the geographic factor. In two instances, we have North American species giving rise to European species, either directly as with *Ctenoloculina cicatricosa* to *C. beckeri* or indirectly through intermediates as with *C. eurybathrota* to *C. latisulcata, C. skalyensis,* and *C. vulgaris.* Ostracods are generally vagrant
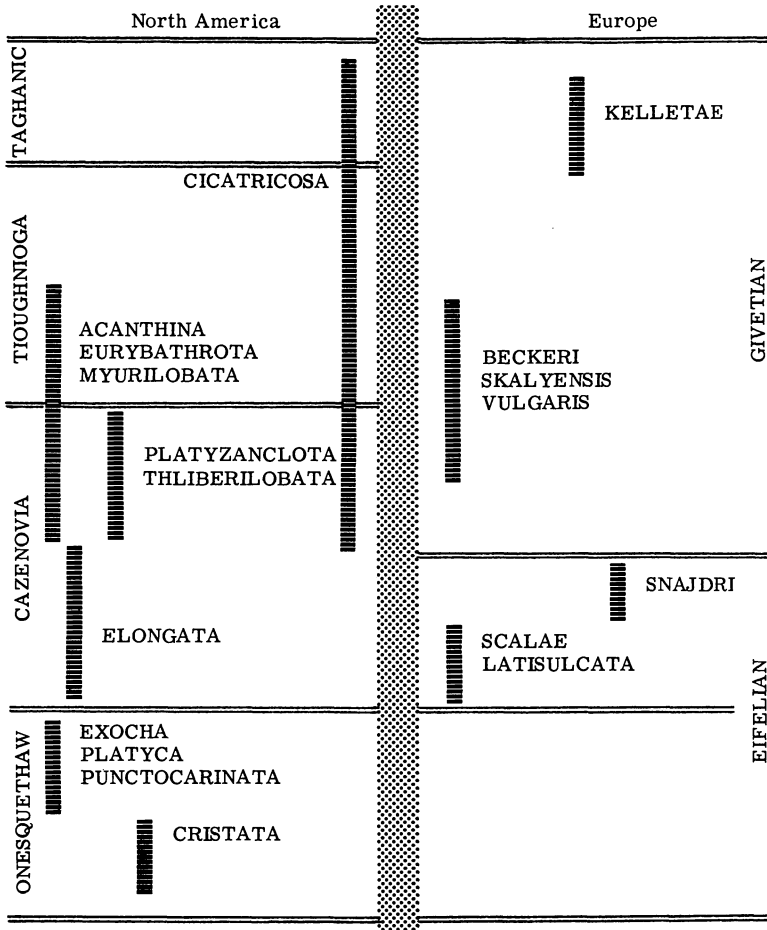
TEXT-FIG. 4—Diagram showing approximate stratigraphic ranges in North America and Europe of the known species of the genus *Ctenoloculina*.

benthonic in nature. Close relationships between ostracods found on two continents, now widely separated, are neither inconsistent nor improbable.

From the new concepts of global tectonics and continental drift, Bird & Dewey (1970) proposed a mechanism for the creation and

deformation of Appalachia. They said that the collision of two irregular continental masses could have caused the pulsation of uplifts as seen in the Appalachian through the Paleozoic. It is not my intent to discuss the mechanics of this model but to offer it as a possible explanation for the geographic distribution of the cten-

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EXPLANATION OF PLATE 1

All figures × 35. Specimens coated with ammonium chloride.

FIGS. 1–4—*Ctenoloculina acanthina* Kesling. *1,2,* hypotype UMMP 58401; adult female right valve. *1,* lateral view, note characteristic large papillae; *2,* internal view. *3,* hypotype UMMP 58402; adult female left valve, lateral view. *4,* topotype UMMP 58398; adult male right valve, lateral view.

5–8—*Ctenoloculina beckeri* Adamczak. *5,6,* unnumbered paratype, female carapace. *5,* right lateral view; *6,* left lateral view. *7,8,* unnumbered paratype, male carapace. *7,* right lateral view; *8,* left lateral view. Specimens on loan from the Geologiska Institutionen, Stockholm, Sweden.

9–13—*Ctenoloculina cicatricosa* (Warthin). *9,* topotype UMMP 58417; adult male right valve, lateral view. *10,* hypotype UMMP 58421; adult male left valve, lateral view. *11,* hypotype UMMP 58161; adult female right valve, lateral view. *12,13,* hypotype UMMP 58134, adult female left valve. *12,* interior view; *13,* lateral view.

14–16—*Ctenoloculina eurybathrota* Kesling. *14,15,* hypotype UMMP 58470, adult female right valve. *14,* lateral view; *15,* interior view. *16,* hypotype UMMP 58448; adult female left valve, lateral view.
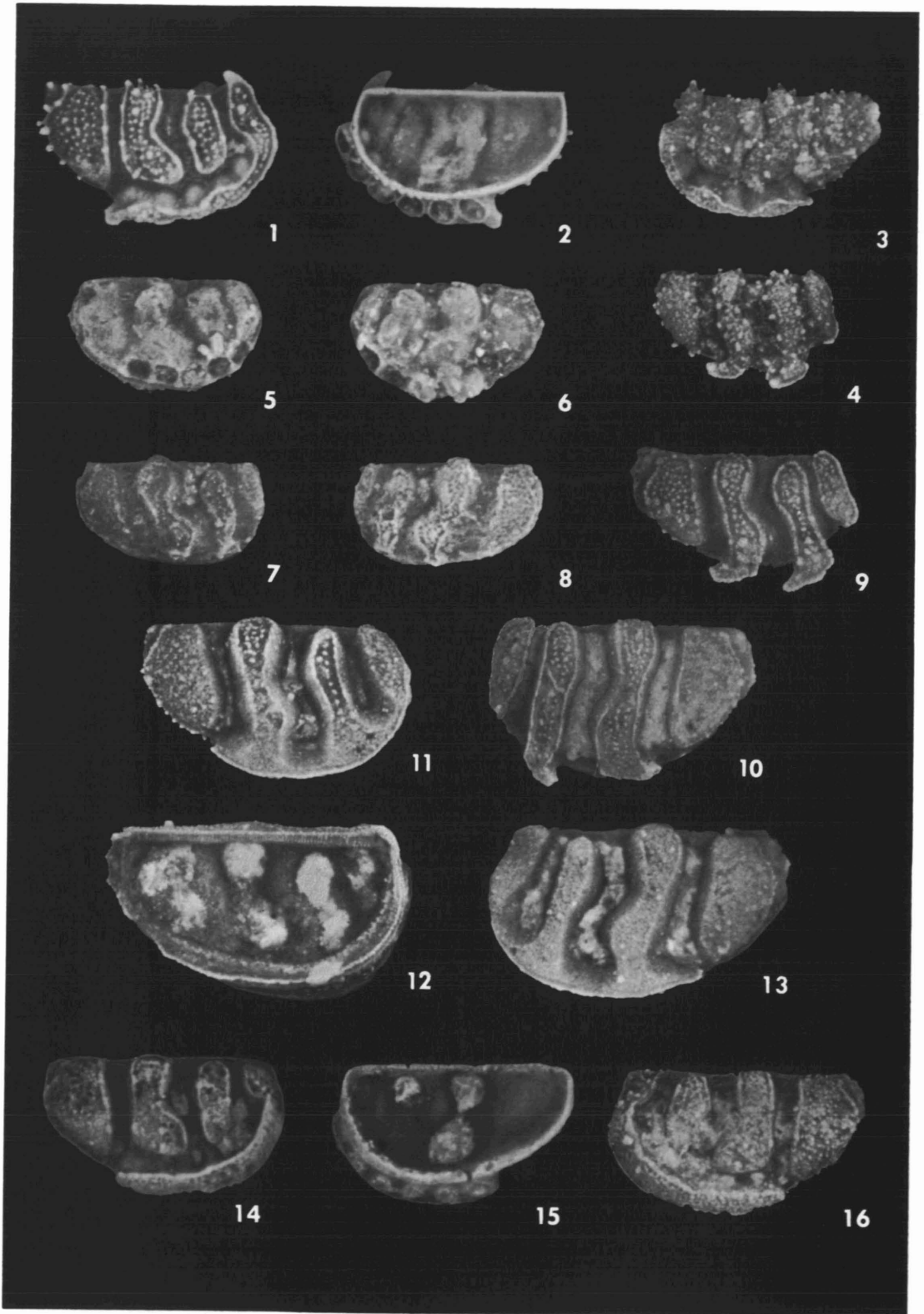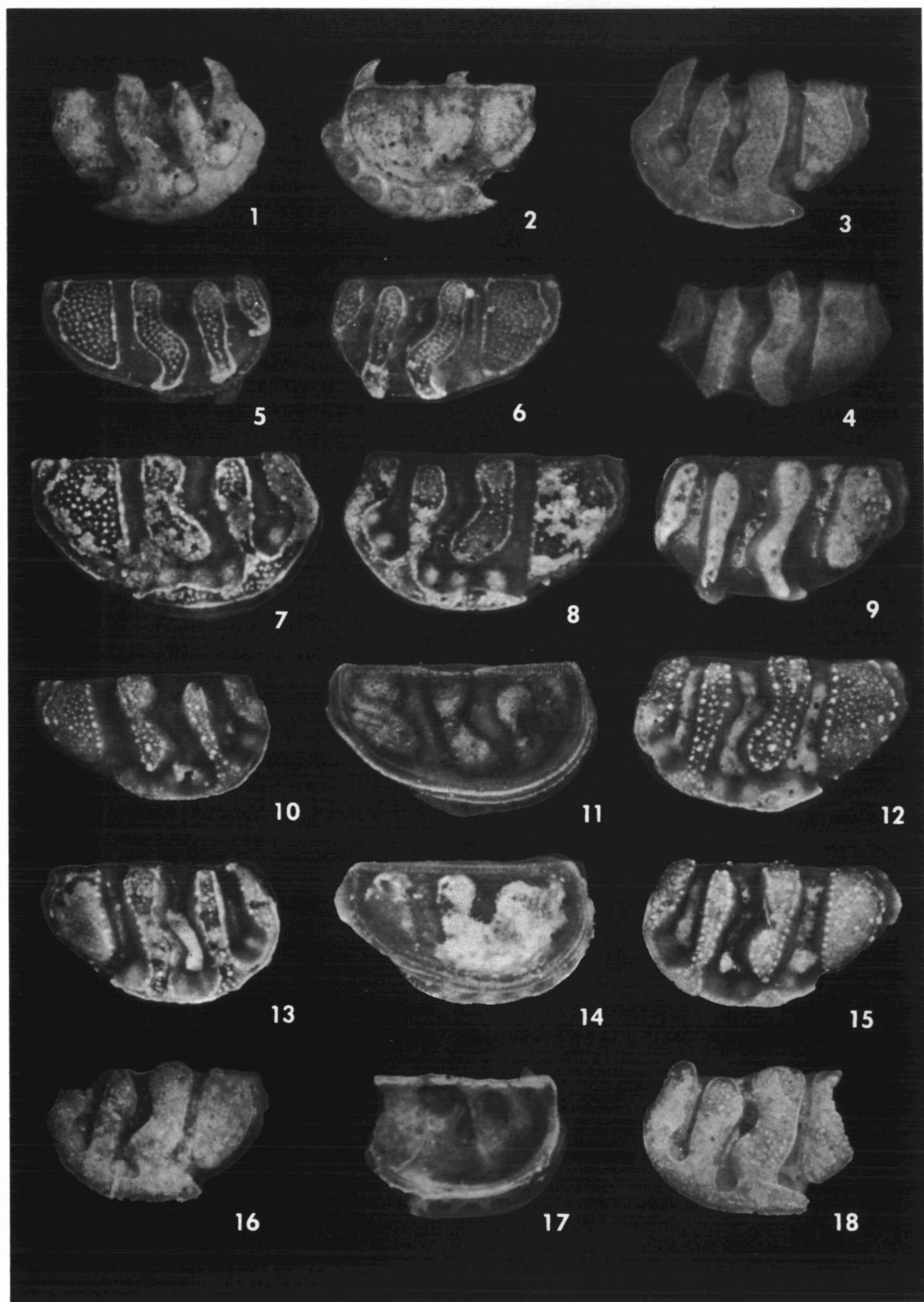
PLATE 1

PLATE 2

oloculines which were most likely shallow-water marine creatures. Two continental masses in close proximity could have afforded a means to disperse these animals in a relatively short time, resulting in the close evolutionary relationships shown in the tree (text-fig. 5).

## CONCLUSION

The tree created with the Advanced Sequenced Wagner Program appears, at this time, to be the best approximation of the true evolutionary pattern of the genus *Ctenoloculina*. The inclusion of hypothetical intermediates in the tree offers an opportunity to speculate upon the positions of those species which were not used in the study and also upon the nature of species which may yet be discovered. Although the consistency index value of 0.586 falls well below the ideal index value of 1.0, the constructed tree generally overlaps the known time-stratigraphic occurrence of individual species. Furthermore, characters show a general decrease in complexity from the ancestral state. Perhaps when we understand how external changes reflect internal changes, we may refine our data to produce a tree with a C value close to unity; its structure may not differ significantly from the one created here.
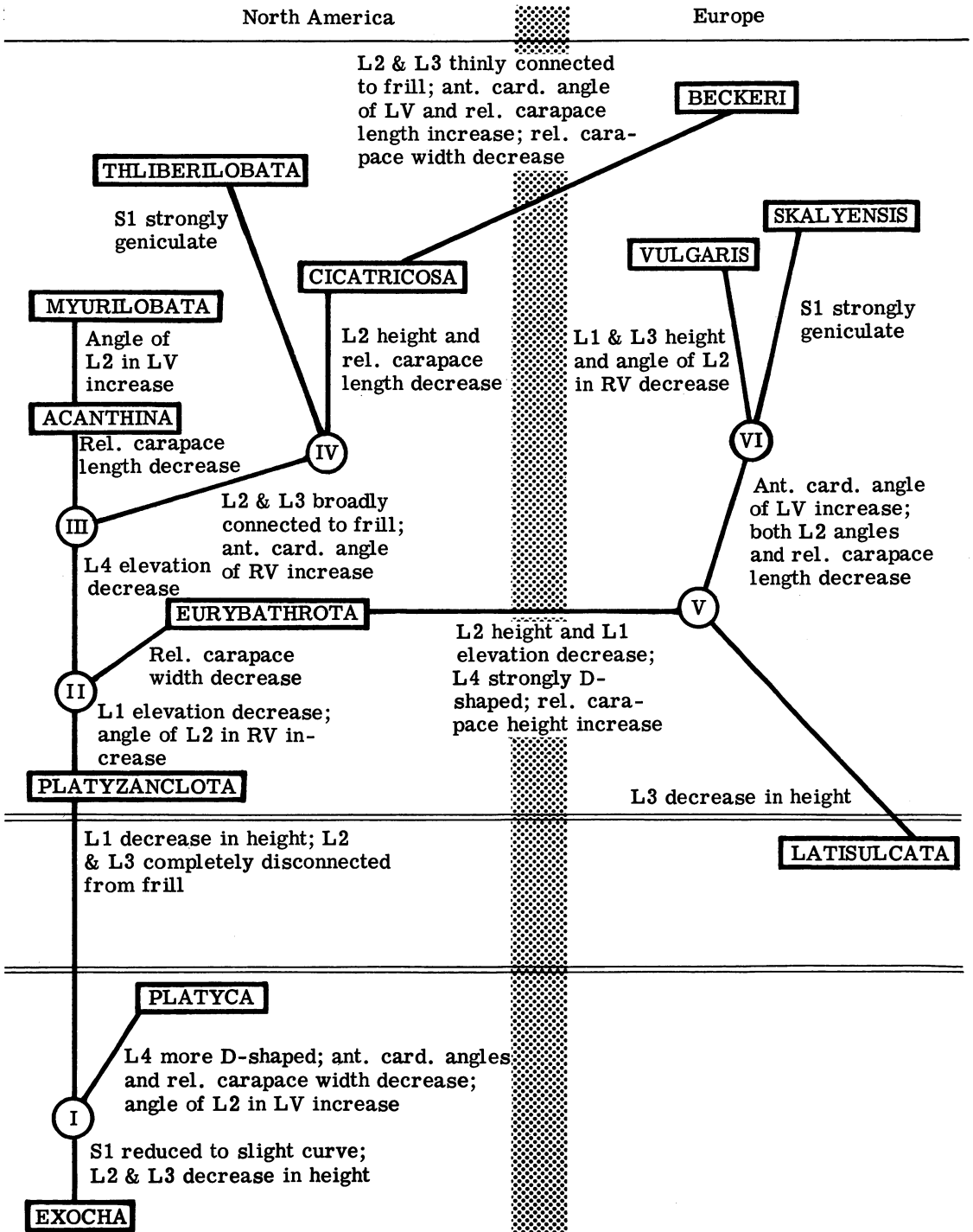
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North America | Europe

L2 & L3 thinly connected to frill; ant. card. angle of LV and rel. carapace length increase; rel. carapace width decrease

BECKERI

THLIBERILOBATA

S1 strongly geniculate

SKALYENSIS

VULGARIS

MYURILOBATA

CICATRICOSA

Angle of L2 in LV increase

L2 height and rel. carapace length decrease

L1 & L3 height and angle of L2 in RV decrease

S1 strongly geniculate

ACANTHINA

Rel. carapace length decrease

IV

VI

III

L2 & L3 broadly connected to frill; ant. card. angle of RV increase

Ant. card. angle of LV increase; both L2 angles and rel. carapace length decrease

L4 elevation decrease

EURYBATHROTA

V

Rel. carapace width decrease

L2 height and L1 elevation decrease; L4 strongly D-shaped; rel. carapace height increase

II

L1 elevation decrease; angle of L2 in RV increase

PLATYZANCLOTA

L3 decrease in height

LATISULCATA

L1 decrease in height; L2 & L3 completely disconnected from frill

PLATYCA

L4 more D-shaped; ant. card. angles and rel. carapace width decrease; angle of L2 in LV increase

I

S1 reduced to slight curve; L2 & L3 decrease in height

EXOCHA

Text-fig. 5—Final phylogenetic tree for *Ctenoloculina,* with species shown in their approximate stratigraphic positions. The inferred evolutionary changes from each OTU to its descendant(s) are listed.

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MANUSCRIPT SUBMITTED MARCH 15, 1971.

## APPENDIX A

SYSTEMATIC DESCRIPTIONS

Phylum ARTHROPODA
Class CRUSTACEA
Subclass OSTRACODA
Order PALAEOCOPIDA
Superfamily HOLLINACEA
Family HOLLINIDAE Swartz 1936
Genus CTENOLOCULINA Bassler

*Type species.*—*Tetradella cicatricosa* Warthin, 1934, p. 209, pl. 1, figs. 4–6, by subsequent designation of Bassler (1941).

*Original description.*—Bassler (1941, p. 22, 23) described the genus very briefly:

> *Tetradella*-like shells with valves crossed transversely by four flat-topped finely reticulated ridges separated by narrow furrows and with the free margins surrounded by a false border, which in the female is swollen to form 4 to 6 loculi or brood chambers. Right valve grooved on free margin to receive edge of the left.

CTENOLOCULINA CICATRICOSA (Warthin)

Text-fig. 1; pl. 1, figs. 9–13

*Tetradella cicatricosa* Warthin, 1934, p. 209, pl. 1, figs. 4–6.

*Tetradella cicatricosa* Bassler & Kellett, 1934, p. 479.

*Tetradella cicatricosa* Stewart, 1936, p. 748, pl. 100, figs. 23,24.

*Tetradella cicatricosa* Warthin, 1937, Card 54.

*Ctenoloculina cicatricosa* Bassler, 1941, p. 22,23.

*Ctenoloculina cicatricosa* Shimer & Shrock, 1944, p. 667, pl. 281, figs. 36,37.

*Ctenoloculina cicatricosa* Stewart & Hendrix, 1945, p. 102, pl. 11, fig. 11.

*Ctenoloculina acanthophora* Swartz & Oriel, 1948, p. 553, pl. 79, figs. 8–14.

*Ctenoloculina cicatricosa* Kesling, 1951, pl. 13, figs. 1a,b, 2.

*Ctenoloculina cicatricosa* Kesling & McMillan, 1951, p. 49,50; pl. 4, figs. 9,10.

*Ctenoloculina acanthophora* Moore, Lalicker, & Fischer, 1952, p. 530, fig. 8.

*Tetradella cicatricosa* Moore, Lalicker, & Fischer, 1952, p. 531, fig. 12 a,b.

*Ctenoloculina cicatricosa* Kesling, 1952a, p. 247–290, pls. 1–3.

*Ctenoloculina cicatricosa* Kesling & Weiss, 1953, p. 43,44; pl. 2, figs. 9–14; pl. 3, fig. 1.

*Ctenoloculina cicatricosa* Weiss, 1954, p. 24,25; pl. 7, figs. 1–10.

*Ctenoloculina levis* Weiss, 1954, p. 28,29; pl. 8, figs. 7–14.

*Ctenoloculina acanthophora* Smith, M., 1956, p. 1–8, 1 plate, 1 chart.

*Ctenoloculina levis* Smith, J., 1959, p. 32,33; pl. 9, figs. 21–24; pl. 10, fig. 7.

*Ctenoloculina cicatricosa* Melik, 1966, p. 215–217, pl. 1, figs. 9-11; pl. 7, figs. 15–24; pl. 17, figs. 8-11; pl. 19, figs. 8,9.

not *Tetradella cicatricosa* Coryell & Malkin, 1936, p. 3, fig. 9.

*Remarks.* — As Kesling (1952a, p. 249) noted, the specimens illustrated by Swartz & Oriel (1948, pl. 79, figs. 8–14) are very highly corroded. Since the morphological features described are similar to the type species, it may be assumed that the specimens are probably highly corroded carapaces of *Ctenoloculina cicatricosa* (Warthin). A similar assumption may be made in the case of *Ctenoloculina levis* Weiss, 1954. The holotype, a female, illustrated by Weiss (1954, pl. 8, fig. 7) has loculi which are without the typical outer frill wall covering. Ornamentation is nearly lacking in the holotype as well as in the paratypes. Here, as with the specimens of Swartz & Oriel, corrosion of the carapace

may be the differentiating factor. The distinctive connection of the ventral portion of L3 with L2 (Weiss, 1954, p. 29) may be no more than erosion of the lobes until they become confluent in S2. The specimens figured by Weiss (1954, pl. 8, figs. 7–14) and those by Smith (1959, pl. 9, figs. 21–24; pl. 10, fig. 7) were obtained from the Petoskey Formation of northern lower Michigan. The only *Ctenoloculina* species to be reported from the Petoskey Formation is the type species (Weiss, 1954). On the basis of morphologic similarity with the type species and the possibility of corrosion, the specimens designated by Weiss as *C. levis* are probably *C. cicatricosa* (Warthin).

As pointed out by Weiss (1954, p. 25), the specimens figured by Coryell & Malkin (1936) are most likely specimens of *Ctenoloculina eurybathrota* Kesling.

*Occurrence.*—*Ctenoloculina cicatricosa* (Warthin) has been described from the following Devonian formations: the Rockport Quarry Limestone, the Four Mile Dam Formation, the Potter Farm Formation, the Beebe School Formation, the Norway Point Formation, and the Petoskey Formation, all from the Traverse Group of Michigan; the Hungry Hollow Formation of Ontario; and the Silica Formation of Ohio (Weiss, 1954); the Bell Shale, basal formation of the Traverse Group of Michigan (Kesling & McMillan, 1951); the Olentangy Shale of Ohio (Stewart & Hendrix, 1945); and the Ferron Point Formation of the Traverse Group of Michigan (Kesling, 1952a).

In the course of this investigation, the species was also discovered in the Silica Formation at Martin-Marietta Quarry, Washtenaw County, Michigan. In addition, the specimens assigned to *Ctenoloculina acanthophora* by Swartz & Oriel (1948) are found in the Windom Beds of New York.

*Types.*—Topotypes, UMMP 27811–27816, 58404 – 58419; hypotypes, UMMP 58113 – 58172, 58420–58425.

## CTENOLOCULINA ACANTHINA Kesling
### Pl. 1, figs. 1–4

*Ctenoloculina acanthina* Kesling, 1953, p. 206,207; pl. 2, figs. 1–13.
*Ctenoloculina acanthina* Weiss, 1954, p. 26, pl. 7, figs. 13–16.

*Remarks.*—This species bears a close resemblance to *Ctenoloculina eurybathrota* Kesling. The general outline, lobation, and size are very similar. The main point of difference is the ornamentation from which the species name is derived. The low distinct knobs on the rims and lobes of *Ctenoloculina acanthina* serve to separate them from *C. eurybathrota*.

*Occurrence.*—This distinctive little species was first described from the Arkona Shale of Ontario (Kesling, 1953). Other Devonian strata in which it has been found are the Ferron Point Formation of the Traverse Group of Michigan (Weiss, 1954) and the Widder Formation of Ontario.

*Types.*—Paratypes, UMMP 28943, 28944; topotypes, UMMP 58383–58398; hypotypes, UMMP 58399–58403.

## CTENOLOCULINA BECKERI Adamczak
### Pl. 1, figs. 5–8

*Ctenoloculina* cf. *cicatricosa* (Warthin) Becker, 1964, p. 69, pl. 11, fig. 3.
*Ctenoloculina* n. sp. A. aff. *cicatricosa* (Warthin), Becker, 1964, p. 69,70; pl. 2, figs. 3,4.
*Ctenoloculina* sp. B, Becker, 1964, p. 70, pl. 11, fig. 6.
*Ctenoloculina beckeri* Adamczak, 1968, p. 70,71, fig. 46; pl. 26, figs. 1–4.

*Remarks.*—This species is characterized by great variation in the shape and size of the lobes. Such variability is common among the ctenoloculines, as seen in *Ctenoloculina myurilobata* and *Ctenoloculina thliberilobata*.

*Occurrence.*—This species has been found in the Skały beds: Skały, Holy Cross Mountains in Poland (Adamczak, 1968); Nohn beds, Ahdorf beds, Rodert beds, and Cürten beds of the Eifel Mountains in Western Germany (Becker, 1964).

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EXPLANATION OF PLATE 3
All figures × 35. Specimens coated with ammonium chloride.

FIGS. *1–3*—*Ctenoloculina platyzanclota* Kesling. *1*, topotype UMMP 58567; adult female right valve, lateral view. *2,3*, topotype UMMP 58586, adult female left valve. *2*, interior view; *3*, lateral view.
   *4–7*—*Ctenoloculina skalyensis* Adamczak. *4,5*, unnumbered paratype, female carapace; *4*, right lateral view; *5*, left lateral view. *6,7*, unnumbered paratype, male carapace; *6*, right lateral view; *7*, left lateral view. Specimens on loan from the Geologiska Institutionen, Stockholm, Sweden.
   *8–12*—*Ctenoloculina thliberilobata* Kesling. *8*, topotype UMMP 58112; adult male right valve, lateral view. *9*, topotype UMMP 58034; adult female right valve, lateral view. *10,11*, topotype UMMP 57995, adult female left valve. *10*, interior view, note posterior ornamentation beyond the contact margin; *11*, lateral view. *12*, topotype UMMP 58056; adult male left valve, lateral view.
   *13–16*—*Ctenoloculina vulgaris* Adamczak. *13,14*, unnumbered paratype, female carapace. *13*, right lateral view; *14*, left lateral view. *15,16*, unnumbered paratype, male carapace. *15*, left lateral view; *16*, right lateral view. Specimens on loan from the Geologiska Institutionen, Stockholm, Sweden.
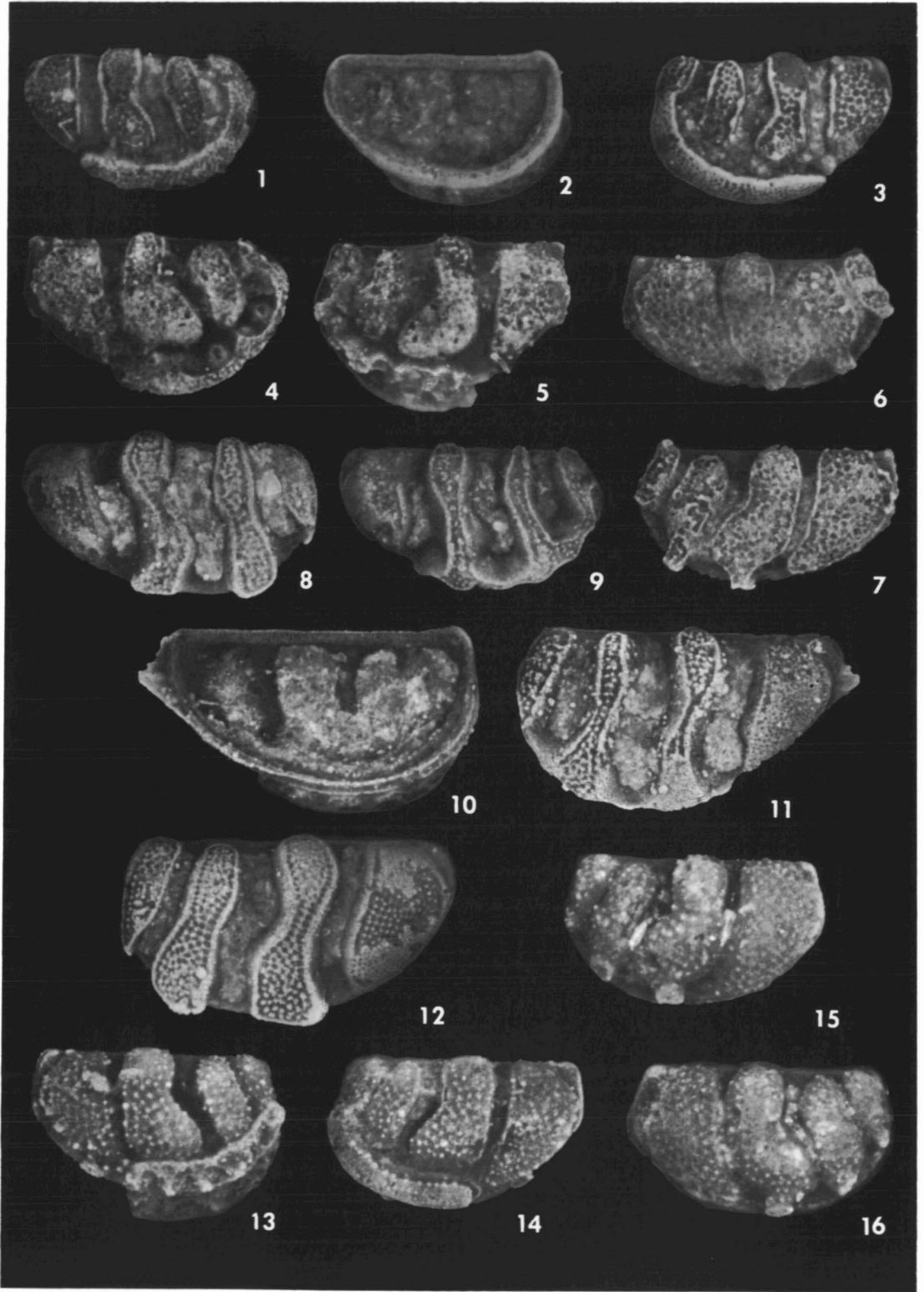
PLATE 3
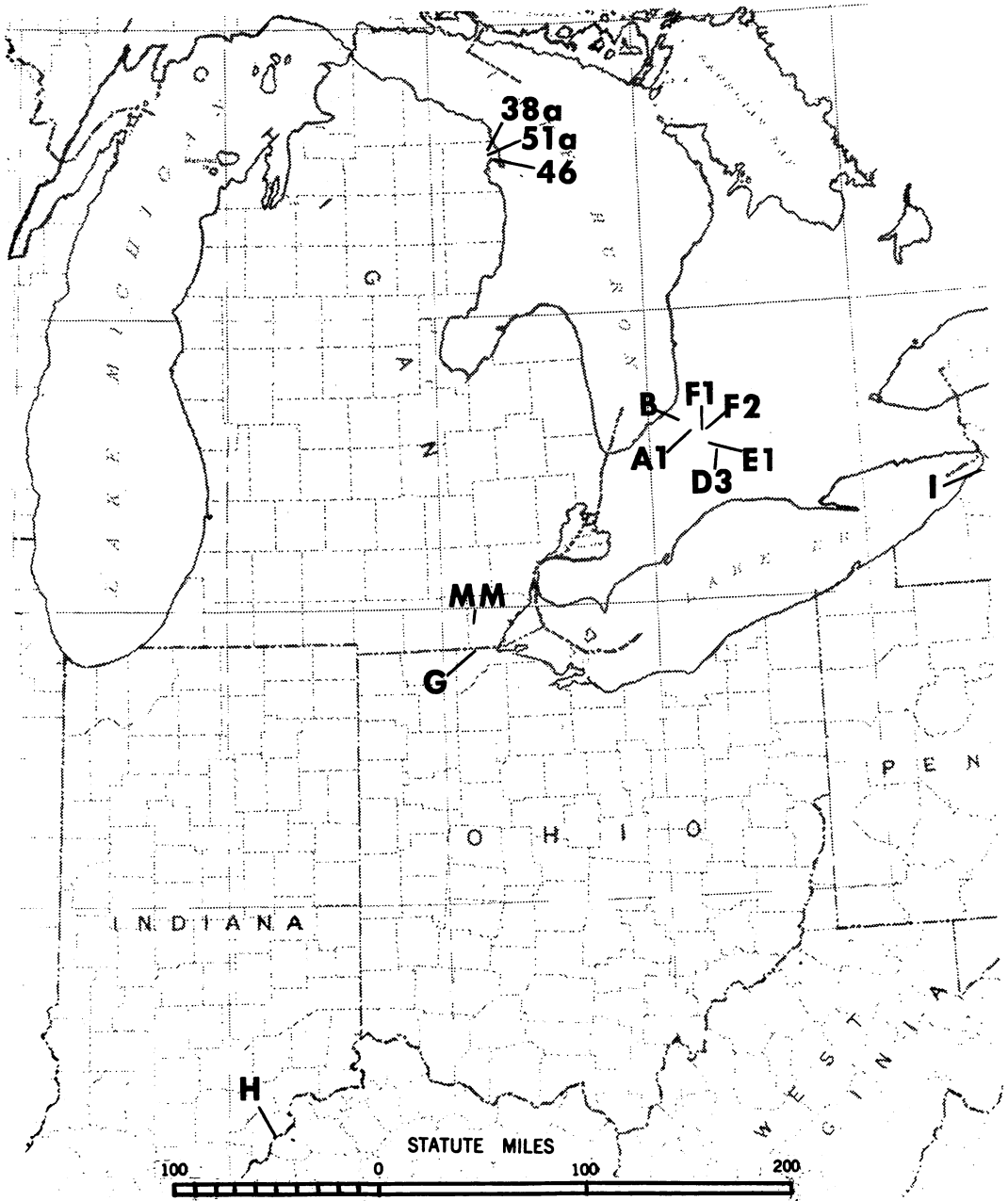
TEXT-FIG. 6—Map of localities in North America yielding specimens of *Ctenoloculina* used in this study.

*Types.*—Unnumbered paratypes of the species on loan from the Geologiska Institutionen, Stockholm, Sweden.

CTENOLOCULINA CRISTATA Bassler

*Ctenoloculina cristata* Bassler, 1941, p. 23, pl. 1, fig. 4.

*Remarks.*—Upon examination of the specimen figured by Bassler, it is most evident that the distinct quadrilobate form of the genus is lacking. The sharp crestlike line dividing the "anterior" lobes is unique to this species. It is interesting to note that the species included by Bassler at the time of erection of the genus bears little or no resemblance to the species now referred to as *Ctenoloculina*. Hence, as noted in the text of this paper, this species has been deleted from the study.

*Occurrence.*—The only noted occurrence of this species is in the Camden Chert of Tennessee.

## CTENOLOCULINA ELONGATA Stewart

*Ctenoloculina elongata* Stewart, 1950, p. 659,660; pl. 85, figs. 22,23.

*Remarks.*—Stewart figured two male valves when describing this species; the female is still unknown. The species is very similar to the type species, but as Stewart pointed out, the dorsal and ventral extensions of the L1, L2, and L3 are extreme compared to *Ctenoloculina cicatricosa.*

*C. elongata* bears some resemblance to *Ctenoloculina platyca* Kesling & Peterson but differs in lobe width. *C. elongata* has sulci twice as wide as the lobes, whereas *C. platyca* has lobes and sulci of approximate equal width.

*Occurrence.*—This species was identified from the Third Bone Bed, Delaware Formation of Ohio, locality 8 (Stewart, 1950). This is the only known occurrence.

## CTENOLOCULINA EURYBATHROTA Kesling
Pl. 1, figs. 14–16

*Tetradella cicatricosa* Coryell & Malkin, 1936, p. 3, fig. 9.
*Ctenoloculina eurybathrota* Kesling, 1952b, p. 46–48, pl. 1, figs. 1–9.
*Ctenoloculina eurybathrota* Kesling & Tabor, 1953, p. 94, pl. 1, figs. 1,2.
*Ctenoloculina eurybathrota* Kesling, 1953, p. 207,208; pl. 2, figs. 17–19.
*Ctenoloculina eurybathrota* Weiss, 1954, p. 26,27; pl. 8, figs. 1–6.

*Remarks.*—This species is one of two North American forms in which the ventral portions of L2 and L3 terminate above the frill and are completely surrounded by a ridge. The other species, *Ctenoloculina platyzanclota* Kesling, differs in having a frill covered by low papillae.

The ostracods identified as *Tetradella cicatricosa* by Coryell & Malkin (1936) are, as pointed out by Weiss (1954), most likely *Ctenoloculina eurybathrota* Kesling, specimens of which are common in the Arkona Shale.

*Occurrence.*—*Ctenoloculina eurybathrota* has been described from the Bell Shale, Rockport Quarry Limestone, Ferron Point Formation, and Genshaw Formation of the Traverse Group of Michigan (Weiss, 1954); the Arkona Shale (Kesling, 1953); and the Hungry Hollow Formation (Coryell & Malkin, 1936). This paper records the first known appearance of the species in the Kashong Shale of the lower Moscowville Formation and in the "*Pleurodictyum* beds," Wanakah Shale, of the Ludlowville Formation, both of which are in the Hamilton Group of New York State.

*Types.*—Topotypes, UMMP 58426–58429; hypotypes, UMMP 58430–58482.

## CTENOLOCULINA EXOCHA Kesling & Peterson
Pl. 2, figs. 1–4

*Ctenoloculina exocha* Kesling & Peterson, 1958, p. 138, pl. 2, figs. 8–13, 17–19.

*Remarks.*—The high dorsal extensions of L1, L2, and L3 and the wide ornamented frill combine to make this species, as its name implies, the most exotic of the ctenoloculines.

*Occurrence.* — This species was described from the Jeffersonville Limestone at the Falls of the Ohio (Kesling & Peterson, 1958).

*Types.*—Holotype, UMMP 34644; allotype, UMMP 34645; paratypes, UMMP 34646, 34647; topotype, UMMP 58483.

## CTENOLOCULINA KELLETAE Pokorný

*Ctenoloculina kelletae* Pokorný, 1950, p. 597–599, pl. 1, figs. 6,7.

*Remarks.*—Pokorný (1950) illustrates both a male and a female of this species. The full carapace of the former shows excessive wear as the lobes lack the papillose ornamentation indicative of the genus. The right valve of the female, shown from the interior, is also corroded. This species resembles *Ctenoloculina skalyensis* Adamczak. The shape and relative size of lobes are similar and the spurs on the L2 and L3 of the males are similar.

*Occurrence.*—This species has only been recorded from the type locality at Čelechovice, Czechoslovakia, in the Upper Middle Devonian Red Coral Limestone.

## CTENOLOCULINA LATISULCATA Adamczak
Pl. 2, figs. 5–8

*Ctenoloculina latisulcata* Adamczak, 1968, p. 65,66, fig. 43; pl. 22, figs. 2–4.

*Remarks.*—*Ctenoloculina latisulcata* bears a marked resemblance to the North American species *Ctenoloculina myurilobata* Kesling and *Ctenoloculina cicatricosa* (Warthin). As in the type species, the lobes and sulci are of equal to subequal width. The L2 has a fairly straight posterior border and L3 has a strong anterior curve in the ventral portion as in *C. myurilobata.*

*Occurrence.* — This species occurs in the Lower Middle Devonian Grzegorzowice beds in the Holy Cross Mountains of Central Europe.

*Types.*—Unnumbered paratypes of the species on loan from the Geologiska Institutionen, Stockholm, Sweden.

## CTENOLOCULINA MYURILOBATA Kesling
Pl. 2, figs. 9–15

*Ctenoloculina myurilobata* Kesling, 1952b, p. 48, pl. 1, figs. 10–15.
*Ctenoloculina myurilobata* Weiss, 1954, p. 27,28, pl. 7, fig. 12.

*Ctenoloculina myurilobata* Melik, 1966, p. 217, pl. 17,
fig. 7; pl. 18, figs. 11,12; pl. 19, figs. 5–7.

*Remarks.*—This species is very closely re-
lated to the type species. However, its lobes are
only half as wide as the sulci; whereas, in the
type, lobes and sulci are of equal width. Also
*Ctenoloculina myurilobata* has a very straight
posterior border and a high variability in the
constricted ventral portion of L3.

*Occurrence.*—*C. myurilobata* was identified
from the Ferron Point Formation of the Trav-
erse Group of Michigan (Kesling, 1952b) and
has been found in the Arkona Shale (Weiss,
1954). This paper notes the occurrence of the
species in the Widder Formation of Ontario and
in the Wanakah Shale member of the Ludlow-
ville Formation of New York State.

*Types.*—Hypotypes, UMMP 58484-58544.

CTENOLOCULINA PLATYCA Kesling & Peterson
Pl. 2, figs. 16–18

*Ctenoloculina platyca* Kesling & Peterson, 1958, p. 138,
pl. 2, figs. 14–16, 20–22.

*Remarks.*—This species, designated in the
same paper with *Ctenoloculina exocha* Kesling
& Peterson, bears a close affinity to *Ctenoloc-
lina elongata* Stewart. The angularity of the
lobes in this species is similar to that of *C.
elongata.* The width of the lobes is the main
differentiating factor between the two species.
The lobes are half the width of the sulci in *C.
elongata,* whereas the lobes and sulci are of
equal to subequal width in *Ctenoloculina pla-
tyca.*

*Occurrence.*—This species occurs in the Jef-
fersonville Limestone at the Falls of the Ohio
(Kesling & Peterson, 1958).

*Types.* — Holotype, UMMP 34648; para-
type, UMMP 34649.

CTENOLOCULINA PLATYZANCLOTA Kesling
Pl. 3, figs. 1–3

*Ctenoloculina platyzanclota* Kesling, 1953, p. 208,209;
pl. 2, figs. 20–24.
*Ctenoloculina platyzanclota* Weiss, 1954, p. 27, pl. 7,
fig. 11.

*Remarks.*—Males of *Ctenoloculina platy-
zanclota* have not been identified. At the time
of erection of the species, Kesling (1953) offered
an explanation that since the females of *Cten-
oloculina eurybathrota* and *C. platyzanclota*
were similar, the males of the species may close-
ly resemble each other. Two dissimilarities be-
tween females may be noted. *C. platyzanclota*
has a frill covered by low fused papillae, where-
as *C. eurybathrota* has papillae widely spaced
as on the lobes. Also, L2 of *C. platyzanclota* is
ventrally acuminate, while on *C. eurybathrota,*
L2 is blunt ventrally.

*Occurrence.*—This species has been noted in

the Arkona Shale (Kesling, 1953; Weiss, 1954).
This paper first records the occurrence in the
Ferron Point Formation of the Traverse Group
of Michigan.

*Types.* — Holotype, UMMP 28953; para-
type, UMMP 28954; topotypes, UMMP 58545-
58592.

CTENOLOCULINA PUNCTOCARINATA
Swartz & Swain

*Ctenoloculina punctocarinata* Swartz & Swain, 1941,
p. 427, pl. 2, figs. 1a–c.

*Remarks.*—This species, as described by
Swartz & Swain, closely resembles *Ctenolocu-
lina exocha* Kesling & Peterson (1958). As re-
ported in Swartz & Swain (1941), the species
is very rare. In the summer of 1970 this author
visited all but one of the localities mentioned
by Swartz & Swain and failed to find any speci-
mens in over one hundred pounds of material.

*Occurrence.* — *Ctenoloculina punctocarinata*
was described from the Onondaga Formation in
Pennsylvania and West Virginia (Swartz &
Swain, 1941). No other occurrence has been
noted.

CTENOLOCULINA SCALAE Adamczak

*Ctenoloculina scalae* Adamczak, 1968, p. 66,67, fig. 9A;
pl. 26, fig. 5.

*Remarks.*—This species was described on
the basis of one left valve of a carapace. The
specimen, as illustrated, shows what appears to
be considerable corrosion. The ornamentation
differs from that of the type species. The loculi
appear to be more broadly separated than in
other ctenoloculines. The lobes are broadly con-
fluent unlike other *Ctenoloculina* species in the
same formation.

*Occurrence.*—This species has been found
in the Grzegorzowice beds, Grzegorzowice, Po-
land.

CTENOLOCULINA SKALYENSIS Adamczak
Pl. 3, figs. 4–7

*Ctenoloculina skalyensis* Adamczak, 1968, p. 69,70, fig.
45; pl. 22, fig. 1; pl. 25, figs. 1–5; pl. 26, fig. 4.

*Remarks.*—*Ctenoloculina skalyensis* shows
one particular characteristic common to the
species of the genus: intraspecific variation in
L2 and L3 in the confluence with the frill or
"adventral structure" (Adamczak, 1968, p. 11).
As Adamczak points out, (1968, p. 70), this
species closely resembles *Ctenoloculina latisul-
cata* Adamczak, except for the L3 adventral
confluence. It also bears some resemblance to
*Ctenoloculina eurybathrota* Kesling in the shape
of L2 above the frill.

*Occurrence.*—This species has been described

from the Lower Middle Devonian Skały beds at Skały and Sniadka, Poland.

*Types.*—Unnumbered paratypes of the species on loan from Geologiska Institutionen, Stockholm, Sweden.

### CTENOLOCULINA SNAJDRI Přibyl

*Ctenoloculina snajdri* Přibyl, 1955, v. 21, p. 270, pl. 1, figs. 12,13; pl. 3, figs. 7,8.

*Remarks.*—The most obvious feature of the specimens illustrated by Přibyl (1955) is the apparent corrosion of the carapace. Ornamentation is nearly lacking as is the definite frill structure characteristic of the genus.

*Occurrence.*—This species has been described by Přibyl (1955) in two Middle Devonian formations in Czechoslovakia: the upper part of the Hluboceopy Limestone and the Chotec Limestone.

### CTENOLOCULINA THLIBERILOBATA Kesling
Pl. 3, figs. 8–12

*Ctenoloculina thliberilobata* Kesling, 1953, p. 204–206, pl. 1, figs. 4–13; pl. 2, figs. 14–16.
*Ctenoloculina thliberilobata* Weiss, 1954, p. 26, pl. 7, figs. 13–16.

*Remarks.* — *Ctenoloculina thliberilobata* is the largest of the ctenoloculine species. Lengths in excess of 1.30 mm and heights greater than 0.65 mm are not uncommon (see table 2). This species is strongly characterized by a high variability in the form of the ornamentation areas on L2 and L3. Similar variability is seen in *Ctenoloculina myurilobata* and *Ctenoloculina skalyensis.*

*Occurrence.*—This species has been reported in the following Middle Devonian formations: the Arkona Shale of Ontario (Kesling, 1953) and the Alpena Limestone of the Traverse Group of Michigan (Weiss, 1954).

*Types.*—Topotypes, UMMP 57993–58112.

### CTENOLOCULINA VULGARIS Adamczak
Pl. 3, figs. 13–16

*Ctenoloculina vulgaris* Adamczak, 1968, p. 67,68, figs. 9B,17,23,44; pl. 21, figs. 1–3; pl. 23, figs. 1,2; pl. 24, figs. 1–5.

*Remarks.*—*Ctenoloculina vulgaris* closely resembles the North American species *Ctenoloculina eurybathrota* Kesling and *Ctenoloculina platyzanclota* Kesling, particularly in the general shape of the lobes and in the separation of L2 and L3 from the frill.

*Occurrence.*—This species has been described from the Middle Devonian Skały beds at Sniadka, Poland.

*Types.*—Unnumbered paratypes of the species on loan from the Geologiska Institutionen, Stockholm, Sweden.

### APPENDIX B

#### LOCALITIES
#### NORTH AMERICA

The locality number system is the one used by the Michigan Geological Survey and the Museum of Paleontology, The University of Michigan. The convention for Ontario follows that of Weiss (1954).

##### INDIANA

H.  Exposure along the Falls of the Ohio River, at Jeffersonville, Clark County. Jeffersonville Limestone. Sample obtained from R. V. Kesling. Collected by R. S. Bassler in the early 1930's.

##### MICHIGAN

38a. Abandoned quarry of Kelley's Island Lime and Transport Company, Rockport, Alpena County, sec. 6, T 32 N, R 9 E. 12 feet below contact with Rockport Quarry Limestone. Bell Shale. Collected by G. M. Ehlers, R. V. Kesling, and M. Weiss in 1952.

46.  Shale bank on south side of Thunder Bay River on Potter Farm about one mile downstream from Four Mile Dam, Alpena County, sec. 18, T 31 N, R 8 E. Norway Point Formation. Collected by G. M. Ehlers, R. V. Kesling, and M. Weiss in 1952.

51a. Abandoned shale pit of Alpena Portland Cement Company about 8 miles northeast of Alpena, Alpena County, SE¼ sec. 18, T 32 N, R 9 E. Upper part of Ferron Point Formation. Collected by G. M. Ehlers, R. V. Kesling, and M. Weiss in 1952.

MM. Shale pile beside the abandoned Martin-Marietta Quarry located on the south side of Arkona Road, ¼ mile past the C & O Railroad crossing, 2 miles from Milan, Augusta Township, Washtenaw County, Silica Formation. Collected by Mrs. Ruth B. Chilman in 1970.

##### NEW YORK

I.  Shale, Wanakah member. Ludlowville Formation (*Pleurodictyum* beds). Bay View Creek, Bay View, Erie County. Collected by George McIntosh in 1970.

##### OHIO

G.  Quarry of the Medusa Portland Cement Company, 1½ miles southwest of Sylvania, Lucas County, NE¼ sec. 18, Sylvania Township. Silica Formation. Units 9 and 11 (Ehlers, Stumm, & Kesling, 1951, p. 18–20). Collected by Mrs. Ruth B. Chilman in 1969.

## ONTARIO

A1. Shale, light gray, highly fossiliferous. Shale weathers to clay. Brick and tile yard, about ½ mile north of Thedford, Lambton County, Bosanquet Township, about ⅛ mile east of north-south road. Arkona Shale. Obtained from R. V. Kesling. Collected by Mr. and Mrs. E. P. Wright in 1952.

B. Small exposure containing numerous specimens of brachiopod *Spinocyrtina* sp., one mile west and ½ mile north of Ravenswood, Lambton County. Ipperwash Limestone. Collected by E. C. Stumm in 1952.

D3. Shale, light gray, weathering easily to clay. Sample from a layer 4 feet below the Encrinal limestone. Hungry Hollow locality on the Ausable River, about 2 miles east and ¾ mile north of Arkona, Lambton County. Arkona Shale. Collected by Wm. W. Collier in 1970.

E1. Shale, light gray. Sample from a layer 14 feet below the Encrinal limestone. Near junction of Rock Glen and the Ausable River, on the east bank of the river, Middlesex County, West Williams Township, about 1 mile northeast of Arkona. Arkona Shale. Obtained from R. V. Kesling. Collected by Mr. and Mrs. E. P. Wright in 1952.

F1. Shale, light gray in outcrop, extremely weathered and winnowed, abundant shell hash residue. Widder Formation type locality (Shimer & Grabau, 1902). A low swale, inundated during heavy rains, 1 mile east of Thedford, along Highway 82. Collected by Wm. W. Collier in 1970.

F2. Shale, light gray, fossiliferous. Abandoned Jim Bell's Quarry, north of intersection of Ridge Road and Canadian National Railways line, 1 mile northeast of Thedford. Widder Formation. Obtained from Mrs. Ruth B. Chilman.

### EUROPE

#### POLAND

The specimens obtained from F. Adamczak were collected by him in the Lgsogóry Region in the Holy Cross Mountains in southern Poland. The four localities are listed here in order of their stratigraphic exposures:

Wydryszów
Grzegorzowice
Skały
Sniadka