THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

ARTHROPODA

ARTICLE 4

Pages 1-26, Plates 1-4, Figures 1-8

POSTGLACIAL (HOLOCENE) OSTRACODES FROM LAKE ERIE

By Richard H. Benson and Harold C. Macdonald

University of Kansas Publications

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By RICHARD H. BENSON and HAROLD C. MACDONALD
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ABSTRACT

Ten cores, collected by personnel on C. M. S. *Porte Dauphine* from the central and eastern basins of Lake Erie, were examined for ostracodes at the University of Kansas. The cores varied in length from several inches to 35 feet. The ostracodes present suggest changes in the lake's thermal history from colder to warmer conditions and differential rates of sedimentation. Analyses of valve shapes and muscle-scar patterns of the predominantly cypridacean Ostracoda indicate the presence of eleven species. One cold-water species appears to be nearing extinction.

The species discussed include four new species, *Candona faba, C. novacandata, C. subtriangulata* and *Limnocythere friabilis;* and seven previously described species which include, *Candona candata,* KAUFMANN, *C. crogmaniana* TURNER, *C. nyensis* GUTENTAG & BENSON, *Physocypria pustulosa* (SHARPE), *Cypridopsis vidua* MÜLLER, *Cytherissa lacustris* (SARS), and *Limnocythere verrucosa* HOFF.

The ostracodes were found in abundance throughout most of the length of the cores, generally in a ratio of 20 to 1 compared with the occurrence of pelecypod and gastropod shells. One ostracode species, previously described from Pleistocene periglacial lakes and ponds of Kansas, was found to diminish in abundance from the bottom to the top of the cores. This decrease in population seems to indicate a progressive warming. The initial stages of lake formation are not indicated and are believed to be recorded in the strata beneath the sediments studied.

The shorter cores obtained from the southern edge of the lake contain relic, shallow, cold-water sediments. The longest core (35 feet), obtained from the deepest part of the lake off Long Point, seems to have penetrated sediments representing only later stages of lake formation. Longer cores from this area should contain ostracode faunas representing the early stages of lake formation.

An aid to the identification of fresh-water ostracodes has been developed through the utilization of the dorsal body scars. These scars are generally as well preserved as the adductor muscle scars and are believed to have important taxonomic significance.

The gradual transition of one species of *Candona* to another form has been traced through a continuous sedimentary record, and the evolutionary trends within the carapace shapes are believed to be indicative of an orthogenetic descent.

INTRODUCTION

The use of microfossils for determining stratigraphic relationships within marine sediments is well known. The index species of Foraminifera in Cenozoic marine strata and ostracodes in Paleozoic marine strata have proven to be dependable for correlation as long as brackish- or fresh-water environments were not introduced during the history of the area concerned. Biostratigraphy in fresh-water strata has always included more difficulties because proven index-fossils are less abundant. In the interpretation of the history of continental phases of sedimentation such as are represented in Lake Erie, stratigraphers necessarily rely less on paleontology and more on physical methods, because of the paucity of tested index-fossils.

The valves of ostracodes are usually abundant in lake sediments; however, not many species have been recognized or described from the Late Pleistocene or Holocene deposits of North America. Accordingly, their usefulness as guide-fossils for those interested in the stratigraphy of lake deposits has been impaired. Phylogenetic trends of modern genera are not known in sufficient detail to show the development of any living species. This apparent void in ancestry stems from the inability to recognize minor morphologic differentiation in the comparatively simple, unornamented cypridacean carapace. Recent successful attempts to use internal muscle-scar patterns to separate and classify forms have encouraged us to attempt development of the ostracodes as indicators of some phases of the history of the Great Lakes. We have examined the dorsal body scars above the adductor and antennal muscle-scar patterns and now believe these can be incorporated with the more conventional taxonomic characters to identify and relate some lower taxa of cypridacean ostracodes.

The availability of cores from Lake Erie containing abundant ostracodes provided an opportunity to study a continuous fossil record formed during a great climatic and physiographic change. It was hoped that the Holocene history of Lake Erie had encouraged selection of several identifiable assemblages to mark stages in its formation or to force the morphologically identifiable adaptation of a sequence of chronospecies. The time interval represented by the cores could not represent more than 6,000 to 8,000 years, but the changes and perhaps the environmental pressures had been extreme. It therefore seemed theoretically possible that ecologic and stratigraphic indicator species and the record of interspecific evolution could exist in these cores. Certainly significant shifts in the populations of pre-existing species should be indicated.

The ostracodes were present in great abundance at many levels in the cores. The sieved and washed residues were composed of from 30 to 80 percent ostracode carapaces. They were rare or absent only in the coarser sands which were probably deposited near shore where waves created an unstable and undesirable environment. If ostracodes had been abundant the abrasiveness of the shifting sands would have destroyed much of the fossil record.

Using conventional taxonomic methods, cypridacean species are notably wide ranging geographically. At least three species found in the Great Lakes have also been reported from northern Europe. Locally, most of the species reported from Lake Michigan were found to be present also in Lake Erie.

This apparent tendency for fresh-water ostracode species to be so cosmopolitan did not encourage us to believe any general or world-wide evolutionary trend would be discovered, but as the formation of large inland lakes was rare in the early Neogene, perhaps such large new habitats as the Great Lakes would provide special circumstances analogous to those formed by newly risen oceanic islands.

In summary, large populations of a little known group of fossils present in a continuous sequence and representing life during a time of severe to relaxed environmental stress, together with the need for stratigraphic markers in a new area, provided the stimulus for this study.

PREVIOUS STUDIES

In 1933 FURTOS described 13 species of ostracodes from Lake Erie collected in plankton nets. She considered certain species characteristic of weedy inlets, others of "stony bars and rock pools," and others of a mud-bottom found at a depth of 25 feet or more. Most of the forms examined in the present study are generally characteristic of much deeper water in Lake Erie than those described by FURTOS.

A history of studies of American fresh-water ostracodes up to about 1940 was presented by HOFF (1942), and a summary of literature on Pleistocene and Recent fresh-water ostracodes was compiled by STAPLIN (1953) in an important but yet unpublished doctoral thesis. STAPLIN states that a few Pleistocene species (since found in the sediments of Lake Erie) are apparently valuable as temperature indicators.

GUTENTAG & BENSON (1962) described a Pleistocene fauna from the High Plains of western Kansas. They have used one apparently cold-water species (also present in Lake Erie sediments) to discriminate Pleistocene from Pliocene sediments.

KESLING (1951) presented a thorough study of adductor, mandibular and antennal muscles and a short discussion of their muscle scars in his morphological and ontogenetic researches on *Cypridopsis vidua,* but the dorsal body scars were not considered. The systematic importance of adductor muscle-scar patterns on the family level was suggested by POKORNÝ (1958). SWAIN (1961) presented the most comprehensive modern summary of fresh-water cypridacean ostracodes from the paleontological point of view.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to Professor GEORGE B. LANGFORD, Director, Great Lakes Institute, who was instrumental in arranging financial support by the Great Lakes Institute to make possible participation by the junior author in one of the voyages on Lake Erie to obtain cores.

We would like especially to thank Dr. R. E. DEANE, Director of Research, Great Lakes Institute, for sending the initial core to the University of Kansas, and C. F. M. LEWIS, a graduate student associated with the Institute, for his assistance while on board the *Porte Dauphine*.

Appreciation is also expressed to ROGER L. KAESLER and ROSALIE F. MADDOCKS, graduate students at the University of Kansas, who were particularly helpful during this study.

DESCRIPTION OF STUDY AREA

Lake Erie, one of the five Great Lakes, is approximately 250 miles long and has a maximum width of nearly 60 miles. The major part of the lake is less than 30 meters in depth, but its maximum depth in the eastern basin is about 64 meters. The basement rocks out of which the several basins of Lake Erie have been formed are Devonian in age, consisting of shales, limestone, and sandstone (FISH, 1929).

Ten cores ranging in length from several inches to 35 feet were recovered from the central and eastern basins of Lake Erie (Fig. 1). The longest core (station 3) was obtained from the deepest part of the lake (200 feet) in the eastern basin just east of the peninsula of Long Point on the north shore, where the sediments are generally a soft, gray, silty clay. Shorter cores were recovered in shallower (57 to 90 feet) parts of the lake nearer the shore and in the open but shallow central region. These bottom areas were covered with sediments consisting of compact clays and coarse sands.

The areal distribution of the lithofacies of Lake

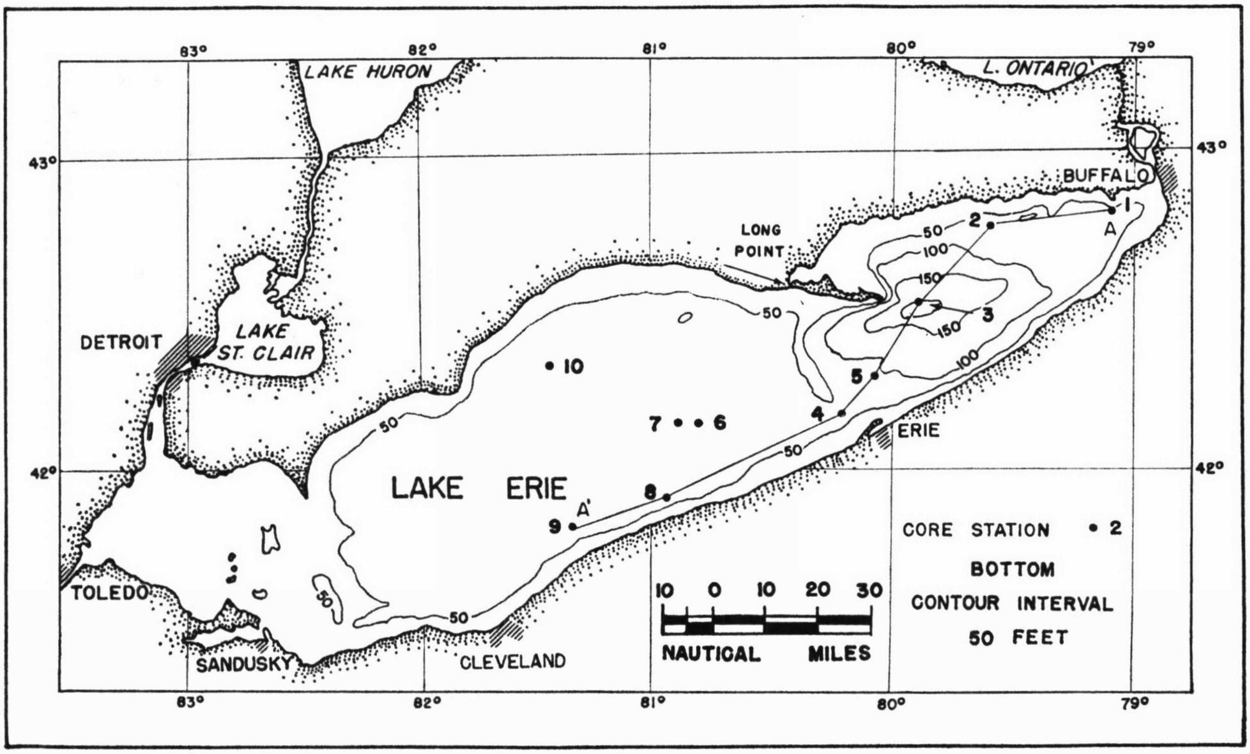


FIG. 1. Index map of core-collecting stations in Lake Erie showing the bottom topography (after HOUGH, 1958), and the traverse of the biozonal profile as shown in Figure 5.

Erie's eastern and central basins has been classified (C. F. M. LEWIS, personal communication) as follows:

Eastern basin: sands or silty sands paralleling the northern shoreline in a band 5-10 miles wide; a deep basin containing laminated silty clay and clay; and extensively rippled sands along the southern shore in a belt 10-15 miles wide.

Central basin: a belt along the eroded north shore, 5-15 miles wide, containing very firm gray clay; a depositional medial belt extending east-west, 10-12 miles wide, containing compact gray clays overlain by tens of feet of soft silty clay; a southern shore zone containing sandier sediments than those of the northern and medial belts commonly alternating with layers of fine silt and clay.

FIELD METHODS

Collection of 2-inch cores from the various stations in the central and eastern basins of Lake Erie was accomplished with the help of the technical staff of the research vessel *Porte Dauphine* during August, 1961. The cores were recovered from the lake bottom by the "Toronto piston corer," which is a modification of the Kullenberg piston corer.

The entire gravity corer stem, composed of 5-foot lengths of 2-inch ID, AX Diamond drill casings, was forced into the sediment by 800 pounds of weights. The recovered corer stem was broken down into 5-foot segments aboard the research vessel, the cores extruded and given a superficial examination for color and sediment consistency. Each segment of core (or a portion thereof) was separately packed in a partitioned core box. Particular precautions were taken when packing the cores for transport to avoid any possible mixing or contamination. The original orientation of the cores was marked, and measurements taken to check for later shrinkage. The measured sections of the cores were recorded, and the positions and lengths were also marked on the core boxes.

A period of about two weeks elapsed from the time of recovery of the cores and time of opening the core boxes at the University of Kansas. Shrinkage due to loss of water content or compaction due to transport was noted at this time.

LABORATORY WORK

The cores were split or divided into two parts (depending on the consistency of the sediments) along their longitudinal axes. In the nine cores taken in shallow water a 4-inch sample was taken from the bottom, middle, and top of one of the halves of the 5-foot sections, thus leaving half of the original core intact for later processing or restudy. In the one 35-foot core taken in the deepest part of the lake, a 4-inch sample was extracted for analysis from each foot of the total length of the core.

Each sample was soaked individually in a solution of water and commercial water softener for 48 hours and then held at a temperature just below boiling for approximately 15 minutes (boiling of the sample was found to cause breakage of the more fragile specimens). The sample was then carefully processed through a series of 20-40-80 mesh screens. All sieve fractions were examined individually and picked for ostracodes while still wet. Drying of the sieve fractions was found to cause many of the more fragile specimens to adhere to the drying container, and numerous specimens were broken in attempting to remove them for examination. With few exceptions, all of the specimens were picked from each sample and retained on conventional micropaleontological slides. In some of the samples the ostracodes exceeded 700-900 in number and a random sample of about 350 specimens was picked for examination. After all, or the desired number, of specimens from each sample were picked, the remaining sediment was oven-dried and retained for future reference.

A preliminary examination of the variance of the muscle-scar patterns revealed consistencies which proved taxonomically useful. Three of the most stratigraphically abundant species were statistically analysed by graphically comparing carapace length and height ratio with the ontogenetic development of the muscle-scar patterns (Figs. 6, 7, 8). For each of the three species, 300 valves were selected and measured. All ontogenetic stages were considered, instar stages determined, and the morphological features analyzed. Dorsal body scars were given particular emphasis, and their significance is described later in this report.

IDENTIFICATION

In the past, features used by paleontologists for classification of fresh-water cypridacean ostracodes have included such criteria as general shape and outline of the carapace, type of valve overlap, ornamentation (sulci, lobes, reticulations), configuration of the duplicature (list, selvage, flange), type of normal- and radial-pore canals, and arrangement of the adductor, antennal, and mandibular muscle scars. The morphology of the hinge is usually not sufficiently variable to be used taxonomically.

Generally, the most reliable features of fresh-water ostracodes for generic classification have been the adductor, antennal, and mandibular muscle scars (Plate 4). A separate group of scars, referred to here as the dorsal body scars, has been poorly understood and generally ignored by ostracode workers. Examination of the specimens collected from Lake Erie revealed that these scars were generally as well preserved as the adductor muscle scars. We believe these dorsal body scars have important taxonomic significance.

The dorsal body scars represent points of attachment (bosses) of the flexor and extensor muscles of the basal podomere of each cephalic appendage. KESLING (1951), in his morphological examination of a fresh-water species, mapped the dorsal muscles, but did not correlate the dorsal muscles with the dorsal body scars.

For the purpose of clarification and discussion in the present study, the dorsal body scars have been divided into two groups (Fig. 2), termed major and minor dorsal body scars. The minor dorsal body scars

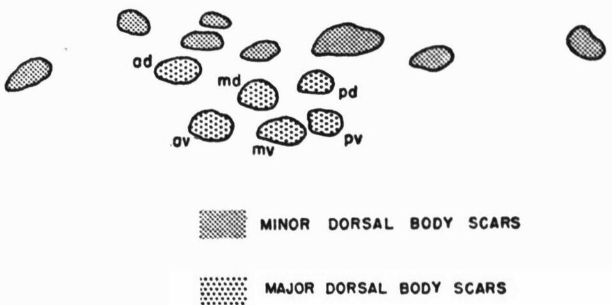


FIG. 2. Diagram of the dorsalbody scars showing the distribution of the major and minor scar groups. The major scars include anterodorsal (ad), mid-dorsal (md), posterodorsal (pd), anteroventral (av), midventral (mv), and posteroventral (pv) scars. The distribution of the individual minor scars seems to be less taxonomically significant than that of the major scars.

of the candonid species examined remain relatively unchanged in their distribution, number, and pattern within a species; however, the major dorsal body scars change significantly between species. The minor scars of candonid species such as *Candona subtriangulata* consists of seven to eight individual scars (Plate 4). The major dorsal body scars of this species are composed of six scars, including two longitudinal rows of three scars each. They are here designated accord-

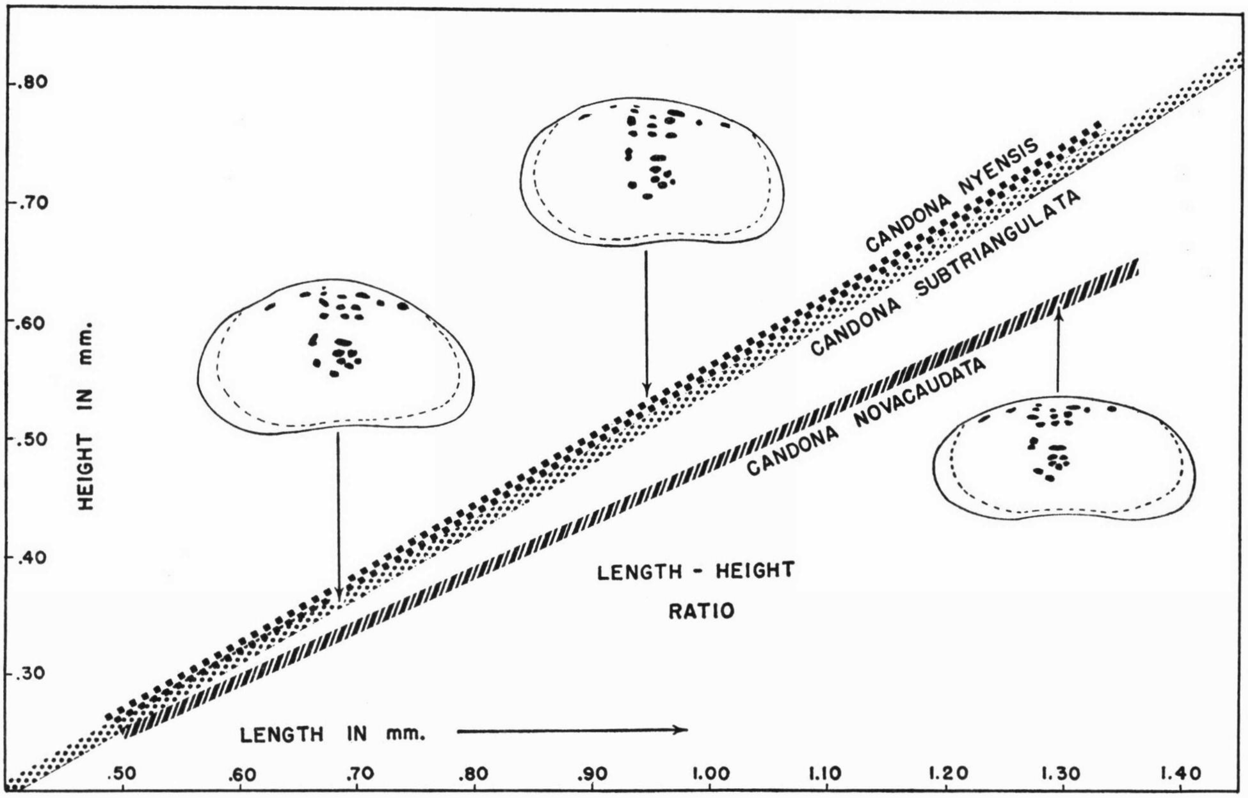


FIG. 3. The length-height ratios of the carapaces of three species of *Candona* showing the coincidence and divergence of this parameter compared to the differences in carapace shape and muscle scar distribution throughout the ontogeny of their instar development.

ing to their position on the carapace; anterodorsal (ad), mid-dorsal (md), posterodorsal (pd), anteroventral (av), mid-ventral (mv), and posteroventral (pv).

The variation in the relative position and orientation of these major scars provides an important aid to specific identification. The differences in shape between male and female specimens of a single species exhibiting dimorphism, which usually makes identification difficult, can now be more accurately resolved. Early instar stages (not possessing the taxonomically important adult characteristics) of one species can be distinguished from similarly shaped carapaces of another species on the basis of the configuration of the dorsal body scars.

The carapace length-height ratios of three species of *Candona* are illustrated in Figure 3, and though the plots of two species have a similar distribution, their instar stages can be separated into their respective species by utilizing the dorsal body scars. The ontogenetic and dorsal body-scar development of three species of *Candona* are illustrated in Figures 6, 7 and 8, and discussed in more detail under the systematic taxonomy.

Analysis of the dorsal body scars was accomplished through the use of a projection apparatus that was modified from a photomicrographic camera especially for study of the internal features of the more transparent carapaces.

STRATIGRAPHIC PALEONTOLOGY

When the Great Lakes were formed with the retreat and melting of the last Wisconsinan glacier, a large new aquatic habitat was formed for the ostracode populations that had been previously forced to retreat southward. Only the hardiest forms could have endured the severe pressures of restricted space, forced immigration, and increased competition. The presence of large-scale unoccupied environments provided new and comparatively limitless opportunities for the invasion, expansion, and proliferation of the ostracode species. Similar circumstances in the formation of other continental lakes such as in Lake Baikal in the U.S.S.R. and in the lakes of the East Africa rift valleys (SYLVESTER-BRADLEY, 1960) have provided evolutionary explosions among the endemic populations of fish, gastropods, shrimp and other invertebrates. These inhabitants have undergone distinct phases of multiple branching orthogenesis or cladogenetic evolution much in the same fashion as that caused by the formation and subsequent invasion of volcanic archipelagos in isolated regions. The stratigraphic record of the early phases of such areas, if found, would contain the history of the physiographic and climatic succession of the invading faunas, as well as the eruption of latent species characteristics previously held in check. Not until a competitive equilibrium had been established through successional stages toward complete occupancy of the area would stability be forced on the newly diversified morphology. As SYLVESTER-BRADLEY (1960) has pointed out, the fossil record of such evolutionary explosions can be recognized to have occurred repeatedly in many stratigraphically important groups. This "adaptive radiation" and subsequent selection is typical of the patterns of biologic readjustment that take place after major geologic events.

Recognition of cladogenesis in its earlier stages is difficult because the initial morphologic differences in a divergent population are slight. The systematic study of such groups as the mammals and the ammonites in their early development is characterized by problems of horizontal and vertical classification on every taxonomic level. Where isolation has been effected by a geographic barrier, small differences in morphology are more likely to be accepted as taxonomically diagnostic of separate species. However, if no such obvious separation has occurred, as is typical of selection forced by ecologic differences in a geographically continuous region, the same, perhaps subtle, morpholic changes might not be acceptable as evidence of speciation. Only through study of a population over a period of time such as recorded in a sedimentary sequence can cladogenesis be demonstrated, and then only rarely.

Such may be the case for the ostracodes of the present study, wherein morphologic instability and variance is recognizable in some species, and the populations undergo periods of considerable fluctuation and eventual transition. In the evolution of *Candona caudata* to *C. novacaudata,* one form seems clearly to

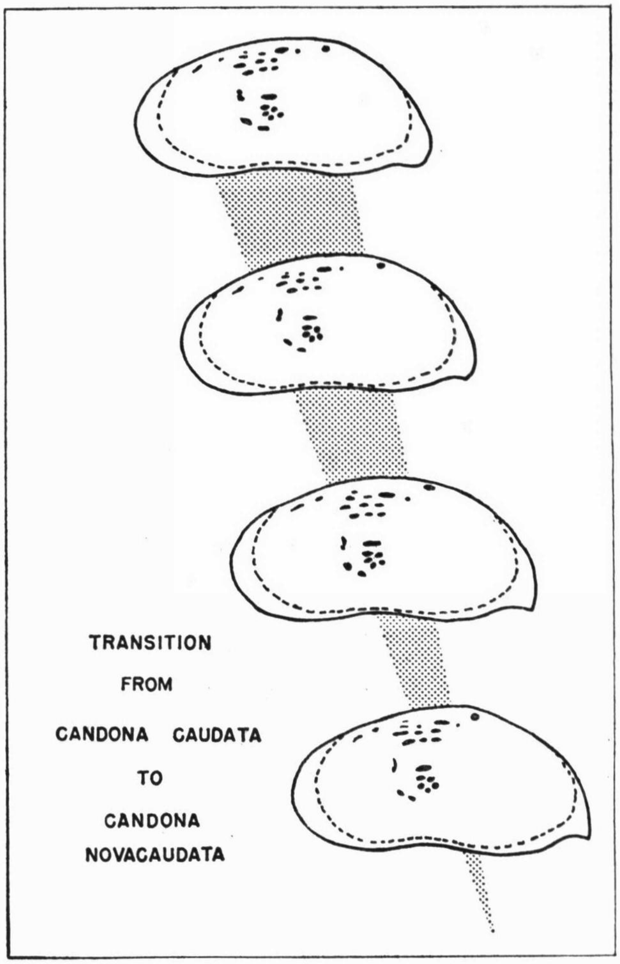


FIG. 4. Evolution in the shape of the carapace showing gradual changes from *Candona caudata* to *C. novacaudata* and their muscle-scar patterns.

replace the other through gradual transition upward through the sedimentary record (Fig. 4). The descent seems to be orthogenetic and the sedimentary record continuous, at least in the deep-water (64 meters) core, in which no breaks in sedimentation are apparent.

In the bottom of the 35-foot long core *Candona caudata* is characterized by a decidedly pointed, hooked posterior and a relatively shorter, higher carapace, many females and few males. Specimens of *C. caudata* outnumber the specimens of *C. novacaudata* in a ratio of about 4:1. In the upper layers of deep basin sediment represented in this core, the relative proportion of *C. caudata* to *C. novacaudata* is reversed, and the proportion of males increases. Intermediate between these extremes a gradual replacement of one form by the other is recorded in an ap-

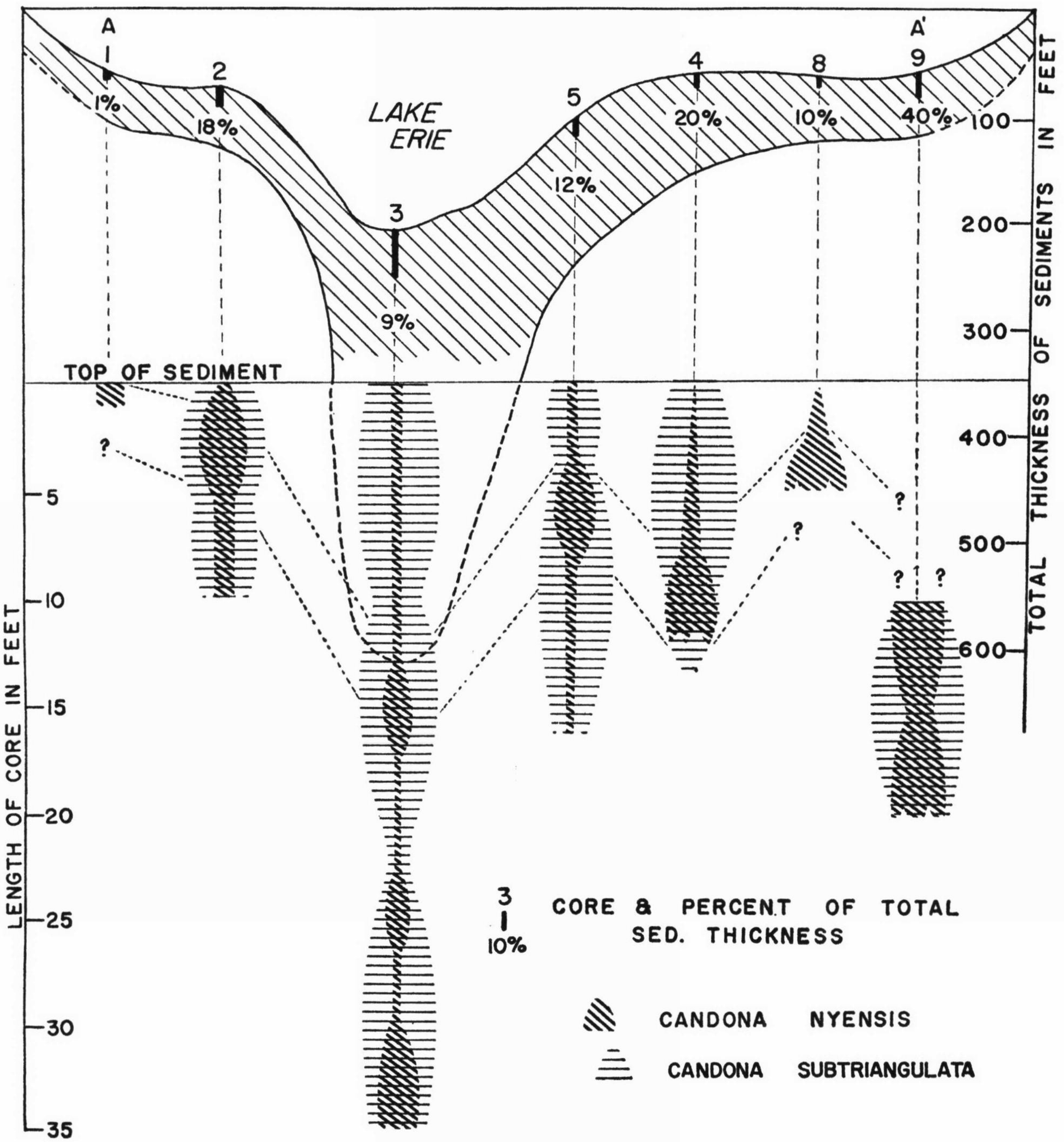


FIG. 5. A biozonal cross-section of the sediments in Lake Erie penetrated by cores along the traverse A-A′ as indicated on Figure 1. This diagram shows the relative distribution of two ostracode species and a possible correlation of the fluctuations in size of their relative populations.

parent orthogenetic descent. Detailed statistical examination of longer cores may reveal that the replacement is much more erratic than seems at present, reflecting cycles or irregularities in the environmental pressures. As yet vertical fluctuations in fossil populations attributable to seasonal changes have not been noticed.

Breaks in sedimentation in the cores obtained in shallower water are noticeable, not only in the sudden change of sediment character, but also in the rapid increase or decrease in abundance of ostracode carapaces. It is evident that the benthonic ostracode population depended in large part on the stability of the bottom, and that rapid changes in effective wave base or rates of sedimentation affected the size of the living population as well as diluted or concentrated their paleontologic record. Thus far, changes in morphology within a shallow-water species are not as noticeable as in deeper water inhabitants, although some stages of development of *Candona subtriangulata* and *C. nyensis* can be correlated between the two areas. Perhaps the shallow-water species are more eurythermal, and selection has not occurred within the short time represented. Longer cores in shallow water penetrating the record of earlier stages of lake formation will be likely to reveal attempted invasions and successions of pond and small lake forms which will be stratigraphically meaningful.

Candona nyensis has been described from Pleistocene sediments of Kansas (GUTENTAG & BENSON, 1962) and Illinois and appears to be nearing extinction toward the tops of the cores taken from Lake Erie. The population distribution of this species indicates changes in the lake's thermal history from colder to warmer conditions. Figure 5 shows an attempted correlation between the population maxima of *C. nyensis* in various areas of the lake sampled, and either the slow rate of permanent deposition in the shallower waters or a termination in sedimentation of fines that include the more recent ostracode valves, representing a relic sediment. An increase in general population level as a function of the forms becoming acclimatized to some overall changes in environment is also probably reflected. The relative abundance of populations of *C. nyensis* and *C. subtriangulata* throughout the period of transition between predominance of one and absolute dominance of the other, may be significant in denoting contemporaneity of sections of several of the cores. It was not possible, however, to find such an ideal relationship in all of the cores. A certain amount of interpolation was necessary when considering the total record of the two species. The differential effects of possible competition of these two forms in shallow- versus deep-water habitats cannot be ignored, but because no way is available to judge this factor, it cannot be evaluated.

In general, *Candona subtriangulata* appears to be a more widespread form in the Great Lakes than *C. nyensis,* because it is found in Pleistocene sediments of Lake Michigan, and is abundant also in the cores from Lake Erie. Even though it is found in colder water, *C. subtriangulata* apparently favors relatively warmer waters, as it replaces *C. nyensis* toward the tops of the cores.

The 35-foot long core contained 9 of the 11 species found in the other cores, though the total number of specimens per sample was considerably less than those of the shorter cores. Of the nine species contained in this core, only *Candona subtriangulata* tends to stabilize in relative population numbers, and this occurs in the upper 15 feet of the core.

The assemblage of different species contained in this core is probably to some extent a reflection of a stable environment caused by the greater depth of water, although the varied species representation may in some case be indicative of thanatocoensis.

Some of the species found in the cores of Lake Erie have been previously described from other areas and ecologically evaluated. *Candona subtriangulata* has been discussed by STAPLIN (1953) in his unpublished thesis, and he states that this species is associated with cold-water stenothermic species, such as *C. nyensis,* which has also been described in Pleistocene sediments of Kansas. *C. caudata* has been found by HOFF (1942) in ditches, stripland ponds, and an oxbow lake. European specimens are described from canals and lakes. *Cytherissa lacustris* is usually associated with *C. subtriangulata,* and *C. nyensis* is commonly found in the muddy bottoms of large lakes of northern Europe, particularly Sweden. *C. crogmaniana,* found only in the bottom half of the 35-foot long core, has been found in anaerobic water at the bottom of Lake Mendota, Wisconsin, and in saline late Tertiary deposits of the central plains (FRYE & HIBBARD, 1941). This form has also been described by FURTOS (1933) from temporary ponds and by HOFF (1942) from the edge of a permanent oxbow lake.

Shore samples collected along the edges of Lake Erie contained numerous specimens of *Cypridopsis vidua,* but this species was not present in the core samples. Two species of the genus *Limnocythere* found throughout most of the cores of Lake Erie have been previously described from Pleistocene lake deposits, and one of these species has also been described from permanent lakes in Illinois.

CONCLUSIONS

From study of the ostracodes found in the ten cores from Lake Erie certain conclusions can be drawn as follow.

1. The composition of the ostracode assemblage has changed in the later history of the lake represented in the cores. These cores penetrated, with one exception, 9 to 40 percent of the total thickness of the sedimentary record. One species usually associated with Pleistocene strata in other areas has been progressively displaced as a predominant form. Fluctuations in its relative abundance with another characteristic form can be seen in most of the cores. These fluctuations can be correlated from the deepest part of the lake, where the longest core penetrated only a small percentage of the sedimentary record, to the shallower areas where recent times of nondeposition are locally indicated. The paleontological record has been concentrated in these areas of nondeposition.

2. The very large populations of fossil ostracodes, along with the formation of new habitats in large lakes, suggest the possibility of conditions favoring explosive evolution. Because only the later part of the history of the populations has been studied, the results are inconclusive, but so far indicate that orthogenesis is occurring in at least one species and considerable morphologic instability is suggested in at least one other. Longer cores may reveal more indigenous variation existing in the descendants of the original invaders, but within the tolerances of paleontologic techniques developed for this study it seems to be confined to the subspecific level.

3. The time and the magnitude of changes involved in the history of Lake Erie represented in the cores has not allowed for the developmnt of striking index fossils among the ostracodes which might serve as horizon markers in the conventional stratigraphic sense. Rather, this study points to the need for further examination of the more subtle trends in variation of older forms, possible gradual evolution and adaptation of new forms, and invasion of species from adjacent aquatic areas undergoing progressive climatic succession.

4. The utilization of dorsal body scars is believed to have taxonomic significance. The differences in shape between male and female of one species exhibiting dimorphism can be correlated, and instars of one species can be distinguished from those of similarly shaped species on the basis of dorsal body scar configuration. The variation in the relative position and orientation of these scars has provided an important aid to the identification of cypridacean Ostracoda.

SYSTEMATIC PALEONTOLOGY

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYPRIDACEA Baird, 1845
Family CANDONIDAE Kaufmann, 1900
Genus CANDONA Baird, 1846

Candona BAIRD, 1846, p. 152; BRADY, 1868, p. 381; BRADY & NORMAN, 1889, p. 98; KAUFMANN, 1900, p. 379; MÜLLER, 1900, p. 15; KLIE, 1938, p. 25; SWAIN, 1947, p. 520; TRIEBEL, 1949, p. 205; SWAIN, 1955, p. 607; LUTTIG, 1955, p. 151; WAGNER, 1957, p. 18; GUTENTAG & BENSON, 1962, p. 32.

Eucandona DADAY, 1900, p. 242; SWAIN, 1961, p. Q234.

Type-species. Cypris candida MÜLLER, 1776.

Diagnosis. Differs from other genera of the family by its elongate subreniform carapace and characteristic adductor muscle-scar pattern, consisting of a circular group of five scars surmounted by a larger, more elongate cap scar. *?Permian, Triassic-Recent.*

Description. In lateral view, carapace of both sexes elongate, medium-sized, subreniform. Greatest height posterior to middle. Dorsal margin strongly arched to nearly straight. Ventral margin sinuate and extremities rounded, with anterior generally narrower than posterior. Left valve slightly larger and overlapping right. Surface smooth or finely punctate. Inner lamellae broadest anteriorly, with simple, widely spaced radial-pore canals.

Adductor muscle-scars composed of a compact group of five surmounted by a larger and more elongate cap scar. The dorsal body scars are composed of two groups; a minor group of 7 to 8 scars and a major group of six scars arranged in two longitudinal rows of three scars each.

Occurrence. The members of this genus are considered to be creepers and burrowers which live in a variety of environments.

CANDONA CAUDATA Kaufmann, 1900

Pl. 1, Figs. 1, 3, 4

Candona caudata KAUFMANN, 1900, p. 365-368, pl. 24, figs. 16-20, pl. 26, figs. 17-23; SARS, 1925, p. 76-77, pl. 35; KLIE, 1938, p.

68, figs. 223-225; HOFF, 1942, p. 80-82, pl. 3, figs. 33-35; SWAIN, 1955, p. 608-609, pl. 59, fig. 5; GUTENTAG & BENSON, 1962, p. 33, text-fig. 8A-B, pl. 2, fig. 11.

Candona elongata G. W. MÜLLER, 1912 (*non* HERRICK, 1879), p. 140.

Diagnosis. Differentiated from other species of *Candona* by the pointed and hook-shaped posteroventral angle of the female left valve, the elongate carapace, and small posteroventral extension of the right valve. *Pleistocene-Recent; Holarctic, N.Am.-Eu.*

Description of adult female. Carapace elongate reniform in lateral view. Greatest height posteromedially and less than half the length. Dorsal margins of both valves arched, right valve slightly sinuate anterodorsally; ventral margin sinuate below adductor muscle-scar group; a second sinuation immediately anterior to posteroventral extension; anterior margin somewhat narrowly rounded, posterior flatly convex; posteroventer of left valve pointed and hook-shaped, forming a posteroventral extension with slight curvature toward right valve. Surface smooth, translucent with scattered normal-pore canals. Only individual valves were available for study; however, relative shape and hinge projections indicate the left valve overlaps the right.

Hingement adont; slight groove on left valve receives bladelike edge of right. Duplicature widest anteriorly, vestibule widest anteriorly and in area of posteroventral extension; line of concrescence removed from anterior, posterior, and ventral margins. Radial-pore canals numerous, short, and closely spaced, not visible in area of sinuate ventral infolding of the valves.

Adult male. Not previously described. Carapace elongate reniform in lateral view. Slightly greater in height and length and more inflated than female. Ventral margin deeply sinuate with sharp angulation on both valves immediately anterior to ventral sinuation; anterior margin evenly rounded with sharp angulation formed at anteroventer of left valve, not so conspicuous on right valve; dorsal margin smoothly arched. Gonad traces generally evident.

Muscle scars. Adductor muscle-scar pattern generally a compact group of five scars: an anterior row of three scars and a posterior row of two scars, surmounted by a single cap scar. Two mandibular scars are located anteroventral to this group. A single antennal muscle scar is located anterior to the cap scar and usually attains the shape of a figure eight in the adult forms.

The major dorsal body scars have a parallel arrangement with the antero-, the mid-, and the postero-dorsal scars generally parallel to the antero-, the mid-, and the postero-ventral scars. Spacing between the major dorsal body scars is essentially equal with the exception of the position of the anterodorsal scar, which is offset to the anterior.

TABLE 1. *Measurements of Representative Specimens of Candona caudata*

Length	*Height*	*Valve*	*Sex*
1.33 mm	0.65 mm	Left	Male
1.32	0.63	Right	"
1.20	0.57	Left	"
1.10	0.54	Right	Female
1.16	0.54	Left	"
1.10	0.53	"	"
0.66	0.39	"	Instar
0.71	0.33	Right	"

Occurrence. This species was found with few exceptions only in the 35-foot core of station 3, and was most abundant in the bottom half of this core. This form has been found by HOFF (1942) in ditches, strip-land ponds, and an oxbow lake. European specimens are described from canals and lakes. This form was commonly associated with *Candona nyensis, C. crogmaniana* and *C. subtriangulata* in the Lake Erie sediments.

Remarks. This species is distinguished from *Candona novacaudata* BENSON & MACDONALD, n. sp., *C. eriensis* FURTOS, 1933, and *C. sigmoides* SHARPE, 1897, by the pointed and hook-shaped posteroventral extension. The 35-foot core from station 3 contained several "dwarfed" specimens of this species, possessing all of the mature characteristics but smaller in height and length from typical specimens. The height-length ratio was the same as that of typical adult specimens.

The males of *Candona caudata* KAUFMANN, 1900, and *C. novacaudata* are similar and the apparent differences extant between these two species is distinguishable only in the female.

CANDONA CROGMANIANA (Turner), 1894

Pl. 1, Fig. 2

Candona crogmaniana TURNER, 1894, p. 20-21, pl. 8, figs. 24-33; FURTOS, 1933, p. 476, pl. 8, figs. 1-3, pl. 9, figs. 17-18, pl. 11, figs. 9-10; HOFF, 1942, p. 79-80, pl. 3, figs. 31-32; GUTENTAG & BENSON, 1962, p. 35, text-fig. 9A-B, pl. 2, fig. 10.

Candona crogmani TURNER, 1895, p. 300-301, pl. 71, figs. 24-33, pl. 81, figs. 4-5; SHARPE, 1918, p. 824, figs. 1295a-c.

Diagnosis. The subtriangular shape of the female carapace and flatly arched dorsal margin with the truncate posterior and sharp posteroventral angle distinguish this species from other species of the genus

Candona. Late Triassic-Recent; Nearctic, north-central U.S.

Description of adult female. Carapace thin, elongate in lateral view. Greatest height in the posterior third, almost half the length. Anterior broadly rounded; ascending slope of dorsal margin flatly convex and extending to point of greatest height, anterodorsal margin of right valve slightly sinuate, right valve more flatly convex along dorsal margin than that of left. Posterior margin truncate about 60 degrees from a straight line drawn parallel to the venter, posteroventral angle acute and narrowly rounded; ventral margin sinuate beneath the adductor muscle-scar group. Surface smooth, translucent, with scattered normal-pore canals. Only individual valves were available for study; however, relative shape and hinge projections of left valves indicate overlapping of this valve on the right.

Hingement adont; slight groove on left valve receives bladelike edge of right. Line of concrescence very slightly removed from anterior, ventral, and poseroventral margins; radial-pore canals short, widely and regularly spaced, few in number, and not visible in ventral marginal area of infolding; duplicature widest anteriorly, vestibule present along the anterior, ventral, and posterior margins.

Muscle scars. Not enough specimens were present in the samples for proper analysis of the dorsal body scars; however, a general analysis is as follows: adductor muscle scars typically candonid, consisting of a compact group of five located immediately ventral to a slightly larger cap scar. Two mandibular scars are anteroventral to the adductor scars. A single antennal scar is located directly anterior to the cap scar.

The major dorsal body scars are equally spaced with the exception of the anterodorsal scar, which is greatly offset anterodorsally. The antero-, the mid-, and the postero-ventral scars form a conspicuous arc that is concave dorsally.

TABLE 2. *Measurements of Representative Specimens of Candona crogmaniana*

Length	*Height*	*Valve*	*Sex*
1.16 mm	0.60 mm	Left	Female
1.21	0.61	Right	"
1.20	0.61	Left	"
1.14	0.58	Right	"

Occurrence. This form was found only in the lower 15 feet of the 35-foot core of station 3. This species has been described from shallow temporary ponds (TURNER, 1895), from an oxbow lake (HOFF, 1942), anaerobic waters of a deep lake, Tertiary deposits of the Central Plains (FRYE & HIBBARD, 1941), and Pleistocene deposits of Lake Michigan and Kansas.

Remarks. No males or instar stages attributed to this species were found in the samples taken from Lake Erie. This species appears to be related to *Candona subtriangulata* BENSON & MACDONALD, n. sp.

CANDONA FABA Benson & MacDonald, n.sp.

Pl. 1, Figs. 5, 6

Diagnosis. Differentiated from other similar species of *Candona* by its elongate reniform outline, flattened anterodorsal and posterodorsal margins, and more narrowly rounded posterior on right valve of female. *Postglacial-Recent.*

Description of adult female. Carapace elongate-reniform in lateral view. Greatest height in posterior third. Anterior flange broadly rounded, slightly higher than posterior on the right valve; dorsal margin flatly convex, becoming slightly truncate along posterodorsal and anterodorsal margins of the right valve, less conspicuously so on the left valve; posterior smoothly rounded, descending from flattened posterodorsum to bluntly obtuse posteroventer; ventral margin slightly sinuate below adductor muscle-scar pattern. Surface smooth, translucent, with scattered normal-pore canals. No whole specimens were available for study; however, general valve outline indicated left overlapping right.

Hinge adont; composed of sharp dorsal flange in left valve overlapping that of right. Line of concrescence slightly removed from anterior, posterior, and ventral margins. Radial-pore canals short and closely spaced. Duplicature simple, widest anteriorly; vestibule present along anterior, ventral, and posterior margins and of equal width along anterior and posteroventer.

Adult male. Similar to female in most respects, except that the male is slightly longer and higher; posterior more broadly rounded, larger than anterior; dorsal margin flatly convex. Gonad traces were not evident on the specimens examined, and sex was determined by valve shape.

Muscle scars. The adductor muscle-scar pattern is typically candonid, composed of a compact group of five scars overlain by a larger elongate cap scar. Two mandibular scars are located anteroventrally to the adductor scars; the dorsal-most scar tends to be longitudinally oriented. One single antennal scar is located immediately anterior to the cap scar.

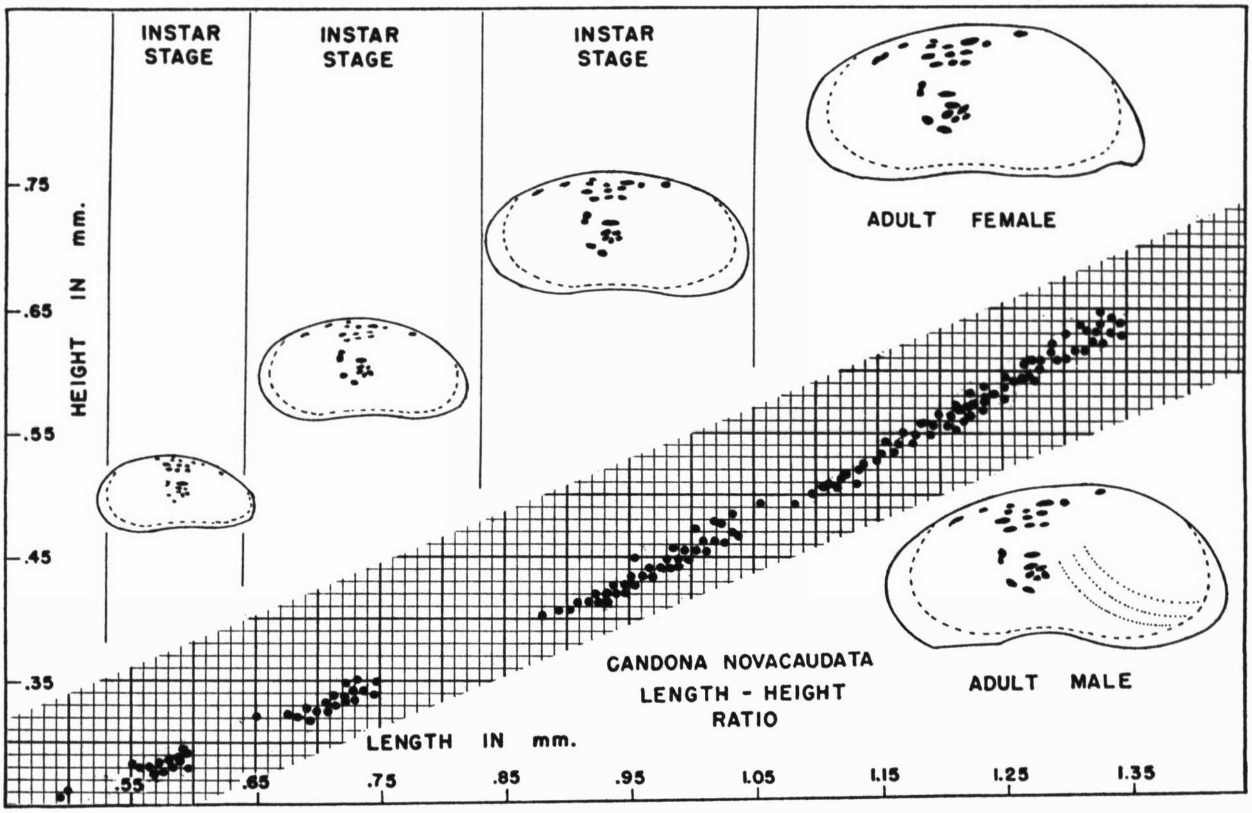


FIG. 6. Allometric diagram of the latter ontogenetic stages of *Candona novacaudata* showing the constancy of muscle scar morphology with different instars and sexual dimorphism.

The antero-, mid-, and posteroventral dorsal body scars are equally spaced and parallel to the equally spaced postero- and middorsal scars. The anterodorsal scar is slightly offset dorsally and conspicuously oriented at an angle of about 60-80 degrees from a straight line drawn parallel to the venter.

TABLE 3. *Measurements of Representative Specimens of Candona faba*

Length	*Height*	*Valve*	*Sex*
1.18 mm	0.60 mm	Right	Male
1.12	0.56	Left	"
1.08	0.56	Right	"
1.10	0.56	"	Female
0.92	0.48	"	"
0.84	0.44	Left	"
0.83	0.40	Right	"
0.74	0.34	"	Instar
0.75	0.37	Left	"

Occurrence. This species was found only in the lower 15 feet of the 35-foot core of station 3, and usually associated with *Candona crogmaniana*, *C. subtriangulata*, and *C. nyensis*. This form is probably related to *C. novacaudata* or *C. subtriangulata*.

Remarks. This species is similar to *Candona exilis* as illustrated by FURTOS (1933), but *C. faba* is larger and has extremities which are not equally well-rounded. HOFF in 1942 described *Candona simpsoni* as having a similar shape, but the form is poorly illustrated and differs from the type as illustrated by SHARPE in 1897. WINKLER (1960) described *Candona poseyensis* and his illustrations are very similar to *C. faba*. WINKLER named this form after one described by STAPLIN (1953), but their illustrations of the two forms appear to differ considerably. WINKLER also failed to designate whether the type of *C. poseyensis* was his illustrated forms or STAPLIN's

CANDONA NOVACAUDATA Benson & MacDonald, n.sp.

Pl. 2, Figs. 1-4

Diagnosis. The female is differentiated from other species of *Candona* by the blunt, noselike, posteroventral extension of the left valve, smaller extension in the posteroventer of the right valve, its elongate carapace and association with abundant males. *Post-Glacial-Recent.*

Description of adult female. Carapace elongate reniform in lateral view. Greatest height in posterior third. Dorsal margins of both valves arched, right valve slightly sinuate anterodorsally, posterior broadly arched, anterior margin evenly rounded, posteroventer of left valve blunt noselike extension of flange with slight curvature toward right valve. Ventral margin slightly sinuate below adductor muscle-scar group with second sinuation immediately anterior to posteroventral extension. Surface of valves smooth, translucent, normal-pore canals scattered. Narrow and elliptical in dorsal outline, greatest width posterior to middle, width slightly greater than one-third length, both extremities narrowly terminated, left valve overlaps right.

Hinge adont; slight groove on left valve receiving bladelike edge of right valve. Duplicature simple, widest anteriorly, vestibule widest anteriorly and in area of posteroventral extension; line of concrescence removed from anterior, posterior, and ventral margins; radial-pore canals short, numerous, and closely spaced, not visible in area of infolding of valves.

Adult male. Carapace elongate reniform in lateral view; slightly greater in height and length and more inflated than female; ventral margin deeply sinuate with sharp angulation on both valves immediately anterior to ventral sinuation. Anterior margin evenly rounded, with definite angulation formed at anteroventer of left valve. Ventral margin very flatly convex between ventral sinuation and anteroventral angle; dorsal margin smoothly arched. Gonad traces generally evident.

Muscle scars. Adductor muscle-scar pattern typically candonid, consisting of a compact group of five scars with a single cap scar. Two mandibular scars are located anterior to the cap scar and usually attain the shape of a figure eight in the adult forms. The major dorsal body scars have a parallel arrangement, with the antero-, mid- and posterodorsal scars generally parallel to the antero-, mid-, and posteroventral scars. Spacing between the dorsal body scars is essentially equal, with the exception of the anterodorsal scar, which is offset to the anterior. The ontogenetic development and consistency of the dorsal body scars is illustrated in Figure 6.

Occurrence. This species was found in core samples from all of the stations, but was particularly abundant in the cores recovered from waters with depths less than 30 meters.

Remarks. This species is distinguished from *Candona caudata* and the female of *C. eriensis* Furtos, 1933, by the blunt noselike posteroventral extension of the left valve and its much larger size. The male of *C. eriensis* Furtos, 1933, is similar in outline to the male of *C. novacaudata* Benson & MacDonald, n. sp., but is much smaller in size. The female of *C. sigmoides* Sharpe, 1897, is somewhat similar in outline, but the male from which Sharpe originally described this species is quite different in shape. *C. caudata* as illustrated by Sars (1925) is somewhat similar to *E. novacaudata,* but lacks the presence of abundant males.

Table 4. *Measurements of Representative Specimens of Candona novacaudata*

Length	*Height*	*Valve*	*Sex*
1.33 mm	0.65 mm	Left	Male
1.30	0.62	Right	"
1.33	0.67	Left	"
1.30	0.66	"	"
1.29	0.64	Right	"
1.28	0.63	Left	"
1.32	0.63	Right	"
1.19	0.58	Left	Female
1.18	0.55	Right	"
1.22	0.58	"	"
1.17	0.55	Left	"
1.25	0.59	"	"
1.16	0.54	Right	"
0.93	0.40	Left	Instar
1.01	0.48	"	"
1.00	0.45	Right	"

CANDONA NYENSIS Gutentag & Benson, 1962

Pl. 1, Figs. 7-10

Candona nyensis Gutentag & Benson, 1962, p. 37, text-fig. 10A-D, pl. 2, fig. 1-3.

Candona sp. aff. *Cypris pubera* O. F. Müller, Swain, 1947, pl. 76, fig. 14-16.

Diagnosis. The truncate posterior of the left valve and bluntly rounded posterior of the right valve of the adult female distinguish this species from other similar species of *Candona. Pleistocene-Recent; Nearctic, north-central U.S.*

Description of adult female. Carapace thin, subreniform in lateral view. Greatest height posterior to middle. Dorsal margin broadly arched, slightly sinuate on anterodorsally right valve; anterior margin narrowly rounded; posterior margin of left valve extremely truncate, about 80 degrees from the horizontal producing bluntly obtuse posteroventral and posterodorsal angles, posterior margin of right valve broadly arched, forming blunt posteroventer; ventral margin sinuate below adductor muscle-scar group. Surface smooth, translucent, and with scattered normal-pore canals. Elliptical in dorsal outline, anterior more narrowly terminated than posterior. Greatest width posterior to middle. Left valve overlaps right.

Hinge adont; composed of thin flange and grooved selvage on left valve, which engages flange on right valve. Line of concrescence submarginal in anterior,

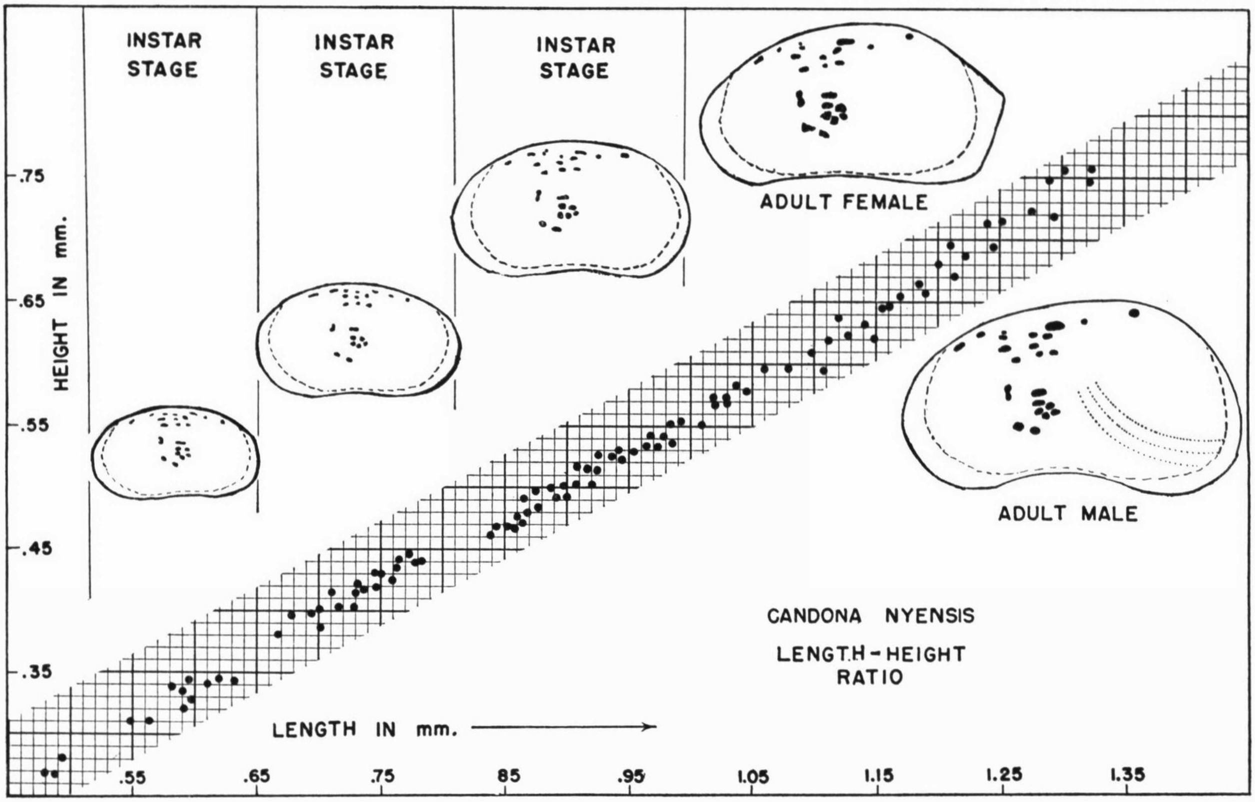


FIG. 7. Allometric diagram of the latter ontogenetic stages of *Candona nyensis* showing the constancy of muscle-scar morphology with different instars and sexual dimorphism.

posterior, and ventral margins; radial-pore canals short, numerous, closely spaced; duplicature widest anteriorly; vestibule widest anteriorly, near posterior of left valve, and also near angular posteroventer of the right valve.

Adult male. Carapace as seen in lateral view slightly longer and higher than that of female. Dorsal margin broadly arched, slightly sinuate on right valve anterodorsally; posteroventer bluntly rounded; anterior evenly rounded, anteroventer sharply obtuse on right valve, evenly rounded on left; ventral margin deeply sinuate with greatest concavity below adductor muscle-scar group. Gonad traces generally evident.

Muscle scars. The complete ontogenetic development can be seen in Figure 7. The adductor muscle scar pattern is typically candonid and consists of a compact group of five scars located immediately ventral to a somewhat larger cap scar. Two mandibular scars are present anteroventral to the adductor group. A single antennal scar is immediately anterior to the cap scar.

The mid-dorsal, posterodorsal, midventral, and posteroventral major dorsal body scars are essentially equally spaced laterally, and the anterodorsal and anteroventral scars are offset to the anterior. The anterodorsal and posterodorsal scars are offset dorsally from the lateral row that is composed of the anteroventral, midventral, and posteroventral scars.

TABLE 5. *Measurements of Representative Specimens of Candona nyensis*

Length	*Height*	*Valve*	*Sex*
1.29 mm	0.75 mm	Right	Male
1.32	0.77	Left	"
1.30	0.72	"	"
1.23	0.71	"	"
1.02	0.57	Right	Female
1.11	0.59	Left	"
1.15	0.62	"	"
1.20	0.63	"	"
1.00	0.57	Right	"
1.07	0.60	"	"
0.62	0.34	Left	Instar
0.69	0.39	Right	"
0.50	0.29	Left	"

Occurrence. This species was most abundant in the lowest part of the Lake Erie cores and appears to become extinct toward the tops of the cores. STAPlin (1953) reported this form to be extremely abundant in Pleistocene strata in Illinois but it has not been found in Recent lakes of the same area. Gutentag & Benson (1962) use the presence of this species to indicate the transition from Pliocene to Pleistocene sediments in southwest Kansas. They consider *Candona nyensis* restricted to the Pleistocene. In the Lake Erie sediments *C. nyensis* was generally associated with *C. novacaudata*, n.sp., and *C. subtriangulata*, n. sp.

Remarks. Swain (1947) illustrated this species as *Candona* sp. aff. *Cypris pubera* from Lake St. John, Colorado. Staplin (1953, p. 162-166) described this form as "*Candona swaini.*"

CANDONA SUBTRIANGULATA Benson & MacDonald, n.sp.

Pl. 2, Figs. 6-8

Diagnosis. The subtriangular shape, truncate posterodorsum, bluntly rounded posteroventer, and high posterodorsal margin distinguish this species from other species of the genus *Candona*. *Pleistocene-Recent; Nearctic.*

Description of adult female. Carapace thin, subtriangular in lateral view. Greatest height in posterior third, exceeding half of length. Anterior margin broadly rounded; ascending slope of dorsal margin flatly convex and extending to point of greatest height, dorsal margin slightly sinuate anterodorsally, sinuation more pronounced in right valve; posterior truncate at about 50 degrees from a straight line drawn parallel to the venter, passing ventrally into bluntly rounded posteroventer; ventral margin sinuate below adductor muscle-scar group. Surface smooth with scattered normal-pore canals. Narrow and elongate in dorsal view; anterior and posterior bluntly terminated. Posterior slightly wider than anterior.

Hingement adont; slight groove on left valve accommodating bladelike edge of right valve. Line of concrescence slightly removed from anterior, ventral, and posteroventral margins. Radial-pore canals of posteroventral margin widely and regularly spaced; radial-pore canals of anterior margin more closely spaced and almost double the number per unit area as compared with posteroventral margin; not always visible in ventral area of infolding. Duplicature simple, widest anteriorly. Vestibule widest anteriorly and at posteroventer.

Adult male. Carapace subtriangular in lateral view; greatest height near posterior third, greater than half of length, higher and longer than female. Anterior extremity somewhat broadly rounded, equal to posterior; dorsal margin as in female, sinuation of anterodorsal margin very pronounced on right valve; ventral margin deeply sinuate below adductor muscle-scar group; posterior flatly convex, forming bluntly obtuse posteroventer; anteroventral margin flat, forming pronounced angle with sinuate venter.

Muscle scars. The adductor muscle-scar pattern is typically candonid and generally consists of a compact group of five scars located immediately below a larger and more elongate cap scar. Two mandibular scars are anteroventral to the adductor scars; a single antennal scar is located directly anterior to the cap scar.

The equally spaced mid-dorsal and posterodorsal major dorsal body scars are parallel to the anteroventral, midventral, and posteroventral scars. In most adult forms the ventral scars form a slight arc concave toward the dorsum. The anterodorsal scar is located anterodorsally to the mid-dorsal scar.

Complete ontogenetic development and comparative dorsal body scars are illustrated in Figure 9.

Table 6. *Measurements of Representative Specimens of Candona subtriangulata*

Length	*Height*	*Valve*	*Sex*
1.05 mm	0.57 mm	Left	Male
1.39	0.78	"	"
1.28	0.72	"	"
1.12	0.60	Right	"
1.30	0.71	"	"
1.42	0.81	Left	"
1.26	0.68	Right	Female
1.18	0.64	"	"
1.23	0.64	"	"
1.28	0.71	Left	"
1.25	0.69	"	"
1.21	0.69	"	"
0.48	0.26	Right	Instar
0.39	0.22	Left	"
0.50	0.27	Right	"

Occurrence. Staplin (1953) in his unpublished doctoral thesis described this form from Pleistocene sediments of Lake Michigan. This form was generally abundant in all of the Lake Erie cores, being associated with *Candona nyensis*, *C. caudata*, and *C. novacaudata.*

Remarks. Staplin (1952, p. 121-126) called this form "*Candona houghi.*" *C. subtriangulata* differs from the type-species in having a narrow posterior and a broadly rounded anterior. This form is probably related to and is somewhat similar in shape to *C. crogmaniana* Sharpe, 1897, but *C. subtriangulata* has a more broadly rounded posteroventer, and the position of greatest height is nearer the middle of the carapace.

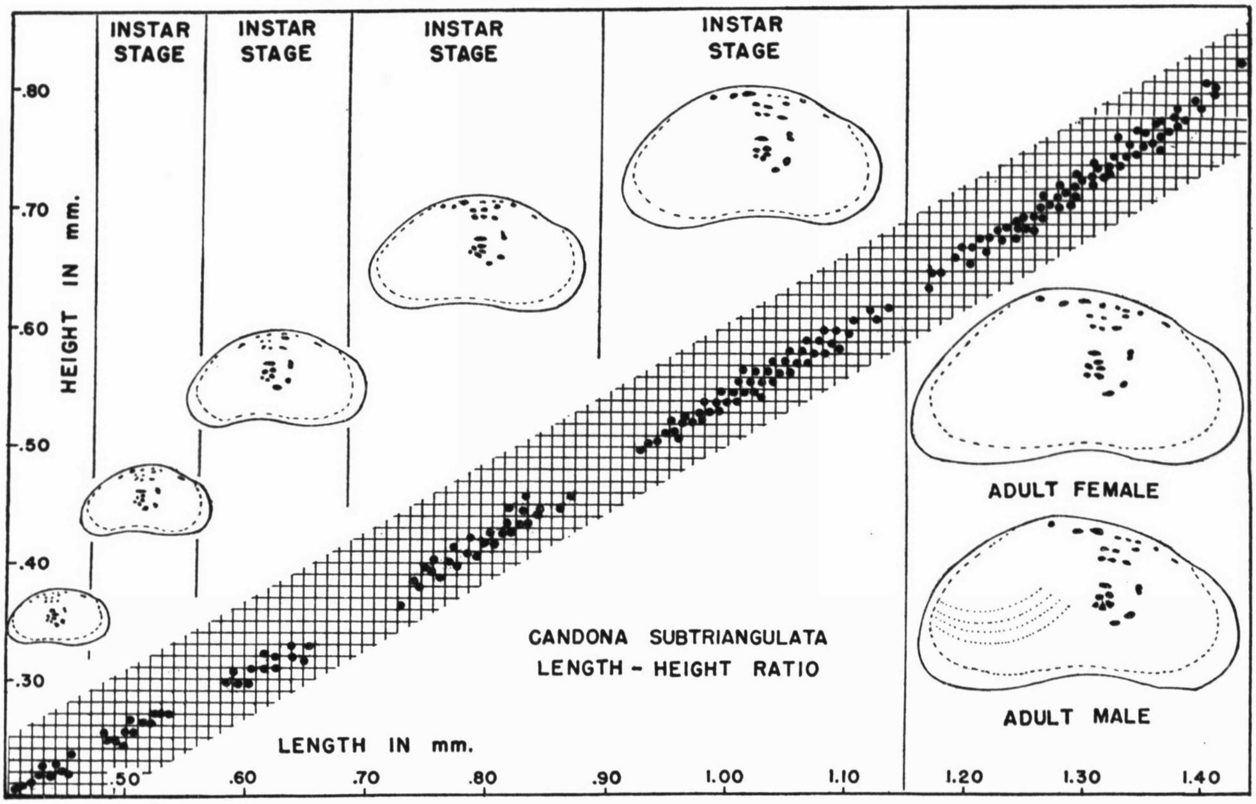


FIG. 8. Allometric diagram of the latter ontogenetic stages of *Candona subtriangulata* showing the constancy of muscle-scar morphology with different instars and sexual dimorphism.

Family CYCLOCYPRIDIDAE Kaufmann, 1900

Genus PHYSOCYPRIA Vavra, 1898

Physocypria VAVRA, 1898, p. 7; POKORNÝ, 1958, p. 234; SWAIN, 1961, p. Q234.

Type-species. Physocypria bullata VAVRA, 1898, p. 7.

Diagnosis. Differentiated from other similar genera by the subovate to subtriangular shape, the serrate or spinose free margins, and the overlapping of valves along the dorsal and ventral margins. *Pleistocene-Recent.*

Description. Carapace subovate to subtriangular in lateral view. Dorsal margin strongly arched, ventral margin slightly sinuate. Greatest height posteromedially. Valves very unequal, with either right or left valve overlapping dorsally or ventrally. Anterior marginal area narrower than posterior with free margins of left or right valves serrate or spinose. Duplicature narrow, widest in anterior.

Remarks. Cypria and *Physocypria* are differentiated on the basis of tubercles along the free margins. These tubercles are extremely variable, and the separation of these two genera is doubtful.

PHYSOCYPRIA PUSTULOSA (Sharpe), 1897

Pl. 2, Figs. 9, 10

Cypria pustulosa SHARPE, 1897, p. 461-462, pl. 48, figs. 6-10.

Cypris (Physocypria) pustulosa SHARPE, 1918, p. 821, figs. 1287a-e.

Physocypria pustulosa (Sharpe), G. W. MÜLLER, 1912, p. 134; FURTOS, 1933, p. 470, pl. 16, figs. 10-12; HOFF, 1942, p. 121-125, pl. 7, fig. 98; SWAIN, 1955, p. 610, pl. 60, figs. 5a-b; SWAIN, 1961, p. Q234, fig. Q168,1a-b.

Physocypria globula FURTOS, 1933, p. 468-469, pl. 16, figs. 1-9.

Diagnosis. This species differs from other physocyprid species by its small delicate carapace, ovate shape, minute tubercles, and the bulging dorsal and ventral margins of the left valves. *Pleistocene-Recent; Nearctic, Alaska to Texas.*

Description. Carapace small, delicate, ovate to subcircular in lateral view. Greatest height immediately posterior to middle of left valve and in middle of right valve. Terminal margins broadly rounded; ventral margin slightly convex on adult forms and flattened on immature forms; dorsal margin broadly convex. Surface smooth, translucent, with scattered normal-pore canals. Anterior and posterior margins of right valves contain minute tubercles, which are variable in size and number. Left valve larger than right, overlapping right valve along free margins. Suboval in dorsal view, narrowly blunt posterior. Anterior narrowly pointed with greatest width posterior to middle.

Hinge adont; consisting of narrow flange groove on right valve engaging selvage of left. Dorsal and ventral margins infolded, reflecting external bulging; line of concrescence slightly removed from anterior, posterior, and ventral outer margins; radial-pore canals closely spaced in anterior. Vestibule narrow, widest in anterior.

Muscle scars. Adductor muscle-scar pattern consists of a central group of six scars; one larger cap scar located dorsal to the other five, which consist of an anterior row of three scars and a posterior row of two scars; the two ventral scars of this group are smaller than the other three. Two mandibular scars are located anteroventrally and a single antennal scar anterodorsally to the adductor group.

The dorsal body scars of this species differ considerably from the candonid types previously described in this study. No other species for comparison of *Physocypria* were present in the specimens examined from Lake Erie; however the dorsal body scars consist of seven scars: a rectangular group of five scars located posteriorly to a lateral line of two scars (pl. 2, fig. 9-10).

Occurrence. This species was found in samples from all of the core stations but was most abundant in the cores taken from shallower water. It was found in association with *Limnocythere verrucosa* HOFF, 1942, and *L. friabilis* BENSON & MACDONALD, n. sp. In North America this form has been reported from San Antonio Bay by SWAIN (1955) to Alaska by DOBBIN (1941).

Remarks. This species has great variation, and HOFF in 1942 attempted to subdivide it into groups, but found most of the characters transitional between forms.

TABLE 7. *Measurements of Representative Specimens of Physocypria pustulosa*

Length	*Height*	*Valve*
0.50 mm	0.40 mm	Left
0.54	0.40	"
0.53	0.40	"
0.46	0.31	Right
0.54	0.36	"
0.50	0.40	Left
0.52	0.37	Right
0.52	0.36	"
0.44	0.29	"
0.54	0.41	Left

Family CYPRIDIDAE Baird, 1845
Subfamily CYPRIDOPSINAE Kaufmann, 1900
Genus CYPRIDOPSIS Brady, 1868

Cypridopsis BRADY, 1868a, p. 117; KESLING, 1951, p. 1-2; SWAIN, 1961, p. Q230; GUTENTAG & BENSON, 1962, p. 25.
Pionocypris BRADY & NORMAN, 1896, p. 725.
Proteocypris BRADY, 1905, p. 335.
Pionocypris and *Cypridopsis*, SARS, 1925, p. 135, 142.
Type-species. Cypris vidua O. F. MÜLLER, 1776, p. 199.

Diagnosis. The distinctive subtriangular shape, tumid dorsal appearance, and small size differentiate *Cypridopsis* from other genera of the subfamily Cypridopsinae. *?Perm., U.Cret.-Rec.*

Description. Carapace reniform, subtriangular, and short in lateral view. Inflated in dorsal view, thickest postmedially, and moderately convex. Dorsal margin strongly arched, angulated medially, and somewhat truncate on either side of the position of greatest height. Ventral margin sinuate. Right valve slightly larger than left; one valve sometimes contains minor tubercles.

Occurrence. This genus has been described from localities throughout the world. It is usually found living as a swimmer amongst vegetation.

EXPLANATION OF PLATE 1
CANDONA
(All illustrated forms are from Lake Erie)

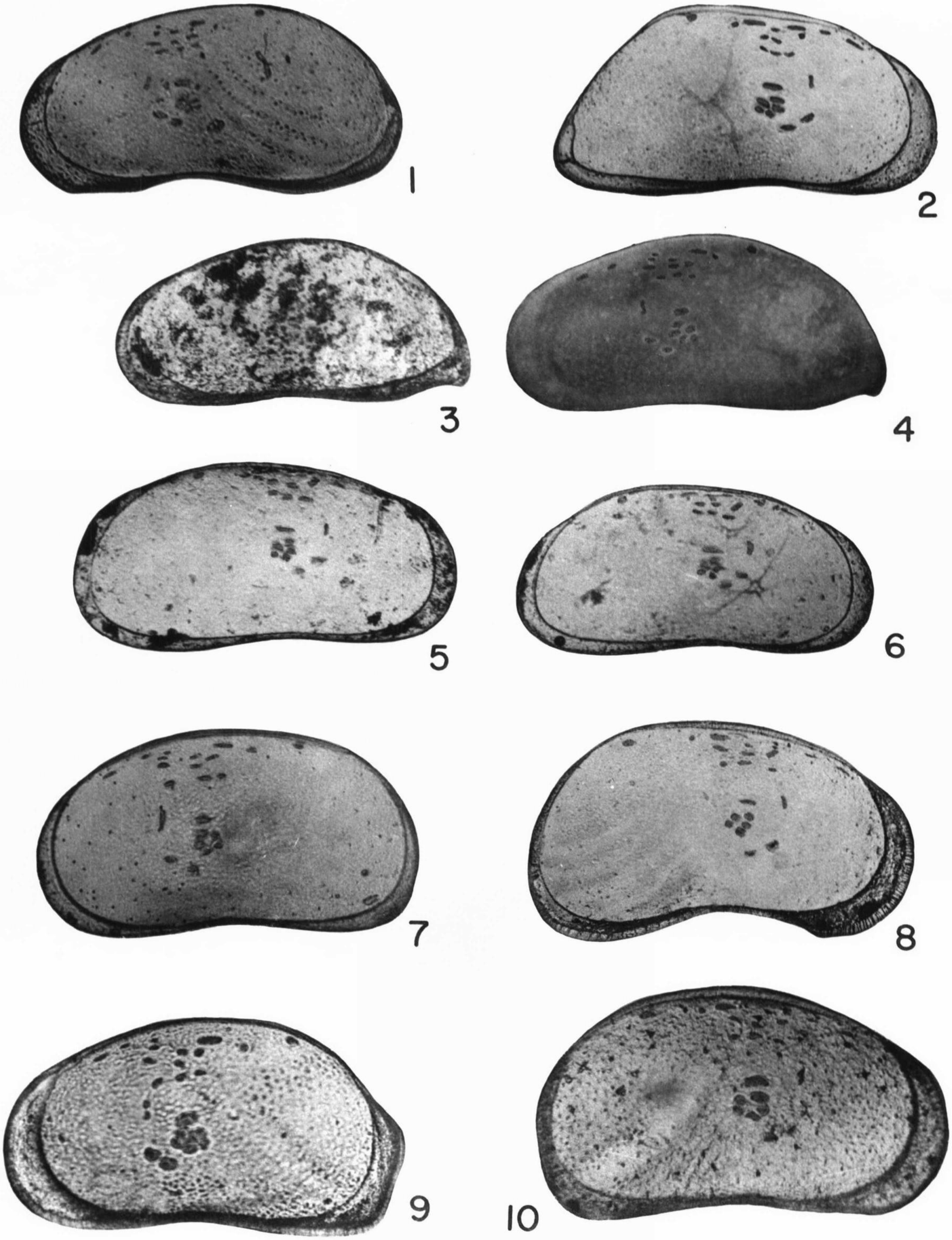
FIGURE PAGE

1,3,4.—*Candona caudata* KAUFMANN, 1900; *1*, exterior lateral view of left valve of adult male, ×45; *3*, exterior lateral view of left valve of adult female, ×50; *4*, exterior lateral view of left valve of adult female, ×50 12

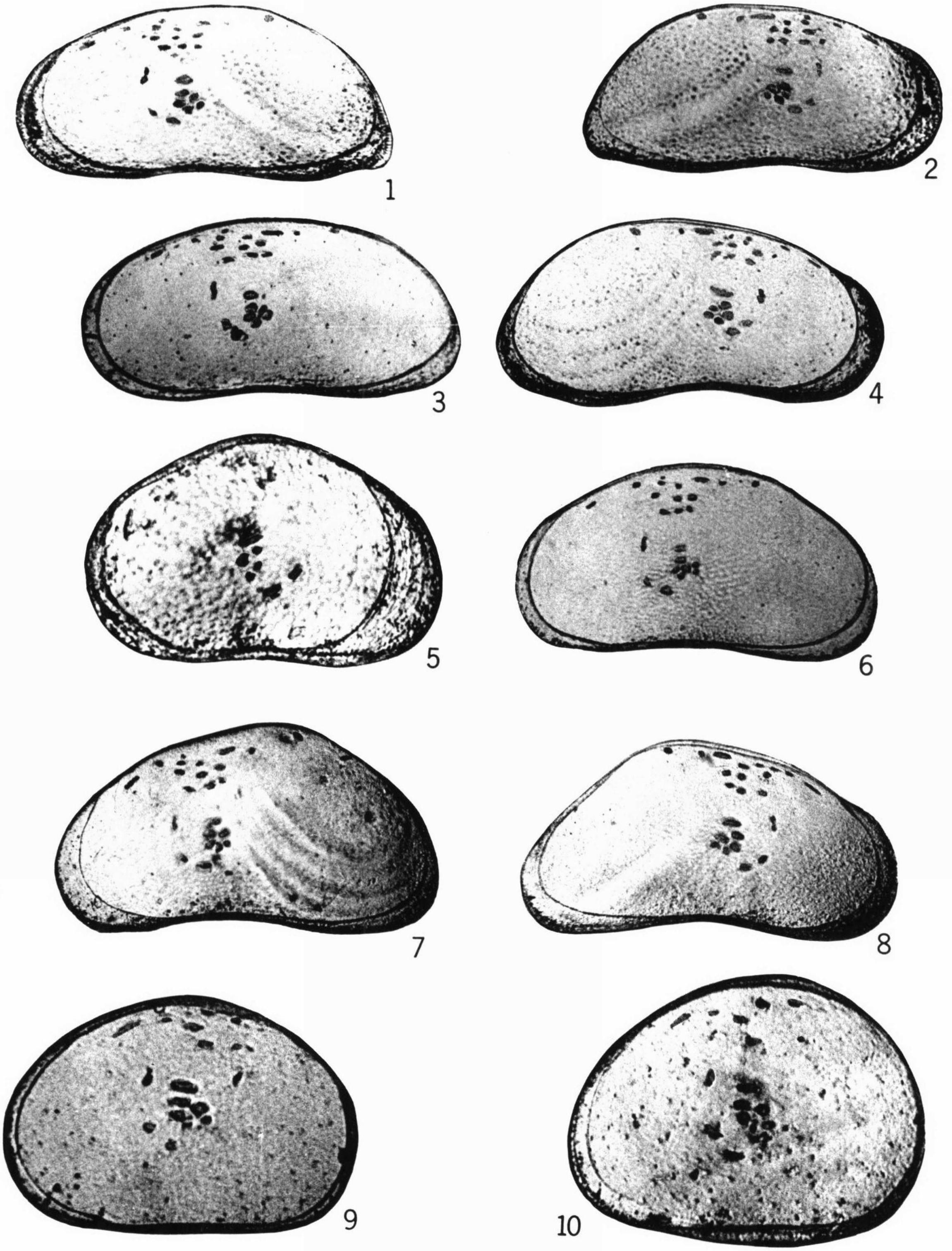
2.—*Candona crogmaniana* TURNER, 1894; exterior lateral view of right valve of adult female, ×50 13

5,6.—*Candona faba* BENSON & MACDONALD, n.sp.; *5*, exterior lateral view of right valve of adult male; *6*, exterior lateral view of right valve of adult female; both ×55 14

7-10.—*Candona nyensis* GUTENTAG & BENSON, 1962; *7*, exterior lateral view of left valve of late instar, ×60; *8*, exterior lateral view of right valve of adult male, ×45; *9*, exterior lateral view of left valve of adult female, ×55; *10*, exterior lateral view of right valve of adult female, ×55 16



BENSON & MAC DONALD — Postglacial Ostracodes from Lake Erie



Benson & Mac Donald — Postglacial Ostracodes from Lake Erie

CYPRIDOPSIS VIDUA (O. F. Müller), 1776

Pl. 2, Fig. 5

Cypris vidua O. F. MÜLLER, 1776, p. 199.

Cypridopsis vidua (O. F. Müller), BRADY, 1868a, p. 117; TURNER, 1892, p. 73; SHARPE, 1918, p. 807, fig. 1253; HOFF, 1942, p. 151-153, pl. 8, figs. 115-117; KESLING, 1951, p. 2-116, plates; SWAIN, 1955, p. 606-607, pl. 60, figs. 6a-c; GUTENTAG & BENSON, 1962, p. 26, text-fig. 6, pl. 1, fig. 10.

Cypridopsis vidua obesa FURTOS, 1933 (*non* BRADY & NORMAN, 1870, p. 15), p. 431.

Cypridopsis pustulosa FURTOS, 1933, p. 431-432, pl. 6, figs. 5-9.

Diagnosis. The small size, subtriangular appearance in lateral view, tumid appearance in dorsal view, and the obtusely angled dorsal margin differentiate this species from other species of *Cypridopsis*. *?Permian, Upper Cretaceous-Recent; World-wide distribution.*

Description of adult female. Carapace subtriangular in lateral view. Greatest height about two-thirds of length and located above adductor muscle-scar pattern. Both extremities broadly rounded with anterior slightly narrower than posterior, dorsal margin sharply arched forming blunt obtuse angle at point of greatest height, ventral margin slightly sinuate directly below adductor muscle-scar group. Surface sometimes smooth, generally marked by minute pits. Left valve overlaps right anteriorly, posteriorly, and ventrally. In dorsal view, carapace tumid, anterior bluntly pointed, posterior bluntly rounded, greatest width slightly more than height, hinge line slightly curved.

Hingement formed by selvage projection of left valve engaging flange groove of right; areas of greatest height of left and right valves have minute "teeth." Line of concrescence slightly removed from anterior, posterior, and ventral margins, forming a very narrow band containing widely spaced radial-pore canals. Duplicature prominent and complex, widest in anterior and posteroventer. Duplicature generally folded at anteroventer, area of ventral sinuation and posteroventer producing a shallow vestibule at these points. Slight selvagelike ridge produced in area of ventral sinuation.

Muscle scars. The adductor muscle-scar pattern usually consists of a group of six scars: an anterior row of three scars and a posterior row of two scars; the two ventral scars of this group are considerably smaller than the other three; these five occur immediately below a larger cap scar. Two mandibular scars are located anteroventrally and a single antennal scar located immediately anterior to the cap scar.

The dorsal body scars of this group differ considerably from other species of this study. However, no other species of *Cypridopsis* were present among the specimens studied, and a contrast within the genus was not accomplished. The dorsal body scars are about eight in number, forming a V-shaped pattern, with the apex of the V immediately above the adductor body scar group.

TABLE 8. *Measurements of Some Representative Specimens of Cypridopsis vidua*

Length	*Height*	*Valve*
0.60 mm	0.38 mm	Right
0.60	0.39	"
0.59	0.40	Left
0.46	0.26	Right
0.64	0.42	Left
0.61	0.41	Right
0.61	0.40	Left
0.63	0.41	Right

Occurrence. This species is very abundant and widely distributed in Europe and America. HOFF (1942) reported this form common throughout the Holarctic region. STAPLIN (1953) and GUTENTAG & BENSON (1962) report it to be common in Pleistocene shallow water sediments. This species was found only along the shallow inlets along the shore of Lake Erie.

EXPLANATION OF PLATE 2

CANDONA, CYPRIDOPSIS, PHYSOCYPRIA

(All illustrated forms are from Lake Erie)

FIGURE — PAGE

1-4.—*Candona novacaudata* BENSON & MACDONALD, n.sp.; *1*, exterior lateral view of left valve of adult female; ×45; *2*, exterior lateral view of right valve of adult female, ×45; *3*, exterior lateral view of left valve of late instar, ×60; *4*, exterior lateral view of right valve of adult male, ×45 15

5.—*Cypridopsis vidua* (O. F. MÜLLER), 1776, exterior lateral view of right valve, ×90 21

6-8.—*Candona subtriangulata* BENSON & MACDONALD, n.sp.; *6*, exterior lateral view of left valve of late instar, ×50; *7*, exterior lateral view of left valve of adult male, ×45; *8*, exterior lateral view of right valve of adult female, ×50 18

9,10.—*Physocypria pustulosa* (SHARPE), 1897; *9*, exterior lateral view of left valve of late instar, ×110; *10*, exterior lateral view of left valve, ×100 19

Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925
Subfamily NEOCYTHERIDEIDINAE Puri, 1957
Genus CYTHERISSA Sars, 1925

Cytherissa G. O. Sars, 1925, p. 152-153; Pokorný, 1958, p. 248; Swain, 1961, p. Q290.

Type-species. Cytherissa lacustris Sars, 1863, p. 30.

Diagnosis. Differentiated from other genera of the subfamily Neocytherideidinae by its clavate shape, roughly sculptured surface, and a lophodont hinge. *?Oligocene (Belgium), Recent of Europe and Asia, Pleistocene-Recent of N. America.*

Description. Carapace clavate, robust, with roughly sculptured surface. Valves subequal, with thickened marginal zone. Hinge lophodont, showing slight trace of anterior and posterior cardinal teeth. Marginal areas narrow, muscle scars as in *Cytheridea.*

Occurrence. This genus has been reported from glacial lakes of Scotland, Norway, Sweden and Siberia.

CYTHERISSA LACUSTRIS (G. O. Sars), 1863

Pl. 3, Figs. 7, 8

Cythere lacustris G. O. Sars, 1863, p. 30.

Cyprideis torosa Jones, 1856, p. 21, t. 2, figs. 1a-i.

Acanthopus resistana Vernet, 1878, p. 506, t. 17, figs. 1-13.

Cytheridea lacustris Brady, 1868b, p. 427, pl. 26, figs. 18-21, pl. 40, fig. 2; Brady, Crosskey & Robertson, 1874, p. 179-180, pl. 6, figs. 16-20.

Cytherissa lacustris G. O. Sars, 1925, p. 153-154, pl. 70; Bronstein, 1930, p. 129, t. 1, figs. 1-2, t. 2, figs. 1, 2, 9, t. 3, figs. 1, 2, 9, 11-17, t. 4, figs. 1-7.

Diagnosis. Distinguished from other cytherissid species by its clavate shape, stout carapace, single transverse furrow bounded by two obtuse protuberances, and reticulate surface. *Pleistocene-Recent; Holarctic.*

Description of adult female. Carapace clavate, stout. Broadly rounded in lateral view at anterior margin, posterior margin bluntly rounded and much narrower. Dorsal margin straight, except for slight anterodorsal swelling, ascending from posterior to anterodorsal swelling. Ventral margin sinuate below adductor muscle-scar group. Greatest height in anterior one-third, about three-fifths of length.

Surface uniformly reticulate, with slight transverse sulcus dorsal to adductor muscle scar depression, bounded by two obtuse protuberances; two minor protuberances generally located subcentrally, one just anterior to the location of adductor muscle-scar pattern and bounded anteriorly by mandibular muscle scars, the other immediately posterior to adductor muscle-scar pattern; normal-pore canals papillate, scattered.

Carapace ovate, tumid in dorsal view; sinuate in area of transverse furrow. Greatest width immediately posterior to transverse furrow; posterior extremities obtusely pointed, anterior extremities somewhat narrower.

Hinge lophodont, two weak anterior and posterior cardinal teeth and central dorsal groove of right valve engage cardinal sockets and central dorsal sharp flange of left valve. Duplicature fused, forming narrow marginal area containing 10 to 12 short, widely spaced radial-pore canals in anterior and 6 to 8 in posterior. Radial-pore canals not evident in area of ventral sinuation and valve infolding.

Muscle scars. Adductor muscle scars consist of a vertical row of four with the ventral three being essentially parallel to the dorsal margin; the fourth or uppermost scar of this group is offset at an angle. A single mandibular and an antennal scar are located anterior to the adductor scar group, a second mandibular scar is located anteroventral to the adductor group.

The dorsal body scars of this species differ considerably from the other species examined in this study. No comparative species of *Cytherissa* were available in the Lake Erie sediments; however, the scars consist of an S-shaped centrodorsal group of six scars, and a single scar located anterior to this group.

Table 9. *Measurements of Representative Specimens of Cytherissa lacustris*

Length	*Height*	*Valve*
0.70 mm	0.44 mm	Right
0.68	0.43	"
0.70	0.46	"
0.52	0.36	Left
0.52	0.37	Right
0.40	0.28	"
0.70	0.44	Left
0.84	0.50	"
0.84	0.51	Right

Occurrence. Cytherissa lacustris was found in most of the shallow water cores, but it was very sparse in the deep-water, 35-foot core. This species has been reported from large lakes of Sweden, where it is believed to crawl on the muddy bottoms. It has been found in Pleistocene sediments of Lake Michigan and lakes of northern Europe.

Remarks. Except for Staplin's (1953) having reported *Cytherissa lacustris* from Pleistocene sediments of Lake Michigan, it has never previously been reported from America. Instar stages show considerable shell sculpture in the form of many protuberances and much coarser reticulation than that of the adult. The male of this species was not found in the samples examined.

Family LIMNOCYTHERIDAE Klie, 1938
Genus LIMNOCYTHERE Brady, 1868

Limnocythere BRADY, 1868a, p. 121; KLIE, 1938, p. 150; SWAIN, 1955, p. 612; POKORNÝ, 1958, p. 242; SWAIN, 1961, p. Q309.
Limnicythere BRADY, 1868b, p. 419; SARS, 1928, p. 149; FURTOS, 1933, p. 422; DOBBIN, 1941, p. 185.
Type-species. Cythere inopinata BAIRD, 1843, p. 195.

Diagnosis. The subtriangular shape, tubercular or spinose ornamentation, delicate carapace, and straight dorsum differentiate this genus from other genera of the family Limnocytheridae. *Jurassic-Recent.*

Description. Carapace thin, subreniform to subrectangular. Dorsal margin straight to slightly arched. Anterior more broadly rounded than posterior, and ventral margin slightly sinuate. Marginal areas broad, with numerous straight radial-pore canals. Surface with reticulate, tuberculate, or spiny surface. Four adductor scars with crescentic antennal and oval mandibular scars in front. Surface reticulate, spinous, or tuberculate.

Occurrence. The habitat of members of this genus is usually the mud bottoms of lakes.

LIMNOCYTHERE VERRUCOSA Hoff, 1942
Pl. 3, Figs. 5, 6

Limnocythere verrucosa HOFF, 1942, p. 161-163, pl. 9, figs. 127-135.

Diagnosis. Differs from other similar species of *Limnocythere* by its subrectangular shape, finely reticulate surface, straight dorsum, subtruncate posterior, and peculiar inflated condition of the shell caused by the bulging nodes. *Pleistocene-Recent; Nearctic.*

Description of adult female. Carapace fragile, subrectangular in lateral view. Height slightly greater than one-half length. Dorsal margin straight except for small swelling at anterodorsal angle; anterior margin broadly rounded with wide hyaline flange; posterior margin truncate above and rounded below an obtuse angulation located midposteriorly, narrow hyaline flange follows rounded portion of the posterior decreasing in width and diminishing in area of ventral sinuation; ventral margin well sinuated, deepest posteroventral to adductor muscle scar group. Carapace finely reticulate; anterior half of each valve with two irregular, transverse sulci; posterior sulcus longest, extending to adductor muscle-scar pit. Three large nodes are located in anterior two-thirds of carapace, one anteroventral to anterior furrow, one posteroventral to posterior furrow, and one located near ventral margin just posteroventral to adductor muscle-scar pit. In anterior and posterior marginal zones ridges of reticulate surface superimposed on and strengthening radial-pore canals. Only individual valves were available for study, but general shape was indicative of a narrowly terminated anterior as compared with the broader posterior.

Hinge lophodont; two poorly defined cardinal sockets and projection of left valve engage two weak anterior and posterior cardinal teeth and flange groove of right. Duplicature fused, radial-pore canals simple, straight, and widely spaced. Raised nodes of interior muscle-scar pattern reflected in external ornamentation as large pits. These pits are always present for the adductor scars. Generally smaller pits are present for the antennal and dorsal scars, but never present for the mandibular scars.

Adult male. Carapace longer and not as high as female; nodes greatly reduced, carapace prominently inflated dorsal to ventral sinuation; posterodorsal and anterodorsal angles bluntly angulated.

Muscle scars. The adductor muscle-scar pattern is composed of a closely spaced vertical row of four, which are longitudinally elongate with their axes paralleling the dorsum; they are located subcentrally on the carapace in a large pit. The mandibular scars are located anteroventrally to the adductor group; the antennal scar is located immediately anterior to the lowermost adductor scar.

The dorsal body scars of this species consist of a pattern of eight; a straight line of three (parallel with dorsal margin) above the adductor group, an arc of three that is located middorsally and concave to the anterior, and two scars anterodorsal to the arc of three.

TABLE 10. *Measurements of Representative Specimens of Limnocythere verrucosa*

Length	*Height*	*Valve*	*Sex*
0.62 mm	0.31 mm	Left	Male
0.60	0.28	Right	"
0.54	0.29	Left	Female
0.54	0.28	Right	"
0.59	0.29	Left	"
0.46	0.24	"	Instar

Occurrence. Limnocythere verrucosa was not abundant in the samples taken from Lake Erie. About two specimens per sample of *L. verrucosa* generally were found. HOFF (1942) reported this form from a permanent lake in Illinois with abundant aquatic vegetation including algae. STAPLIN (1953) found this species in Pleistocene lake sediments containing moderate organic matter.

LIMNOCYTHERE FRIABILIS Benson & MacDonald, n.sp.

Pl. 3, Figs. 1-4

Diagnosis. This species is distinguished from other species of *Limnocythere* by its small size, subquadrate shape, delicate carapace, and the marginal zone traversed by ridges of the reticulate surface, which are superimposed on and strengthen the radial-pore canals, which are terminated in minor tubercles or spines. *Pleistocene-Recent; Nearctic.*

Description of adult female. Carapace small, fragile, subquadrate in lateral view. Greatest height exceeding half the length. Dorsal margin of right valve flatly convex, dorsal margin of left valve broadly convex. Ventral margin slightly sinuate on right valve, moderately sinuate on left valve. Anterior margin broadly rounded, posterior narrowly rounded. Distinctly flattened marginal zone, narrower in posterior. In anterior and posterior marginal zones ridges of reticulate surface superimposed to strengthen radial-pore canals, which are generally terminated by minute spines (10-14) on posterior. Two irregular furrows in anterior half are separated by a single prevalent node, posterior furrow largest, extending ventrally to adductor muscle-scar pit. In dorsal view carapace subelliptical, narrowly pointed anteriorly, narrowly rounded posteriorly; left valve extending slightly behind right; greatest width in posterior third, posterodorsally to ventral sinuation.

Surface finely reticulate, with several small pits in anterior half reflecting muscle-scar locations, one directly above the larger adductor muscle-scar pit, one anterodorsal to the adductor pit at location of antennal scar, and several surrounding the single node at locations of several dorsal body scars.

Hinge lophodont; two obscure cardinal sockets and curved dorsal bar of left valve engage two obscure cardinal teeth and central dorsal groove of right; duplicature fused, widest anteriorly; radial-pore canals simple, straight, and widely spaced, conspicuous in anterior but difficult to see in posterior because of valve curvature.

Adult male. Sexual dimorphism pronounced. Carapace longer and not as high as female, height less than half of length. Dorsal margin straight; anterior broadly rounded, posterior narrow and bluntly rounded. Surface finely reticulate. Both valves inflated greatly centroventrally immediately dorsal to ventral sinuation; posteroventral quarter of both valves depressed. Greatest width approximately in the middle.

Muscle scars. Adductor muscle-scar pattern consists of a vertical compact group of four elliptical scars oriented parallel to the dorsal margin. Two widely spaced mandibular scars are located anteroventrally to the adductor group; a single antennal scar is located immediately anterior to the uppermost adductor and accented on the exterior of the carapace by a small pit.

The dorsal body scars of this species differ from the other species of *Limnocythere* present in the Lake Erie sediments. Eleven scars are present: five larger scars located centrodorsally approximating the shape of the letter T, and six smaller scars located anteriorly to the larger scars.

Occurrence. Limnocythere friabilis was found at all core locations in Lake Erie but most prevalently in the shallow water cores and very sparsely in the deep water core of station 3. STAPLIN (1953) reported this form in the low-water stage of Lake Michigan Pleistocene sediments.

Remarks. This form is very similar to *Limnocythere staplini* GUTENTAG & BENSON, 1962, but *L. fria-*

EXPLANATION OF PLATE 3

LIMNOCYTHERE, CYTHERISSA

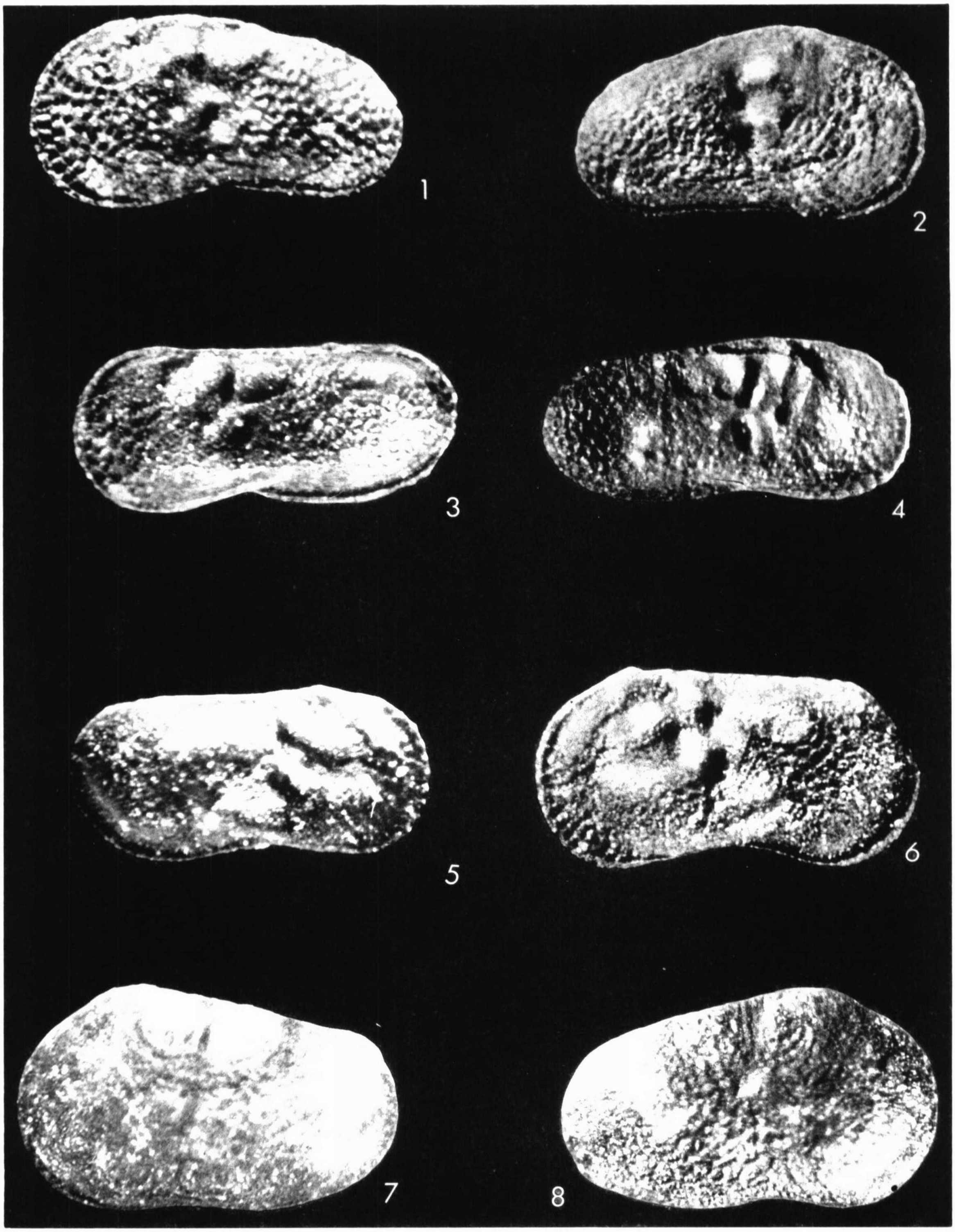
(All illustrated forms are from Lake Erie)

FIGURE PAGE

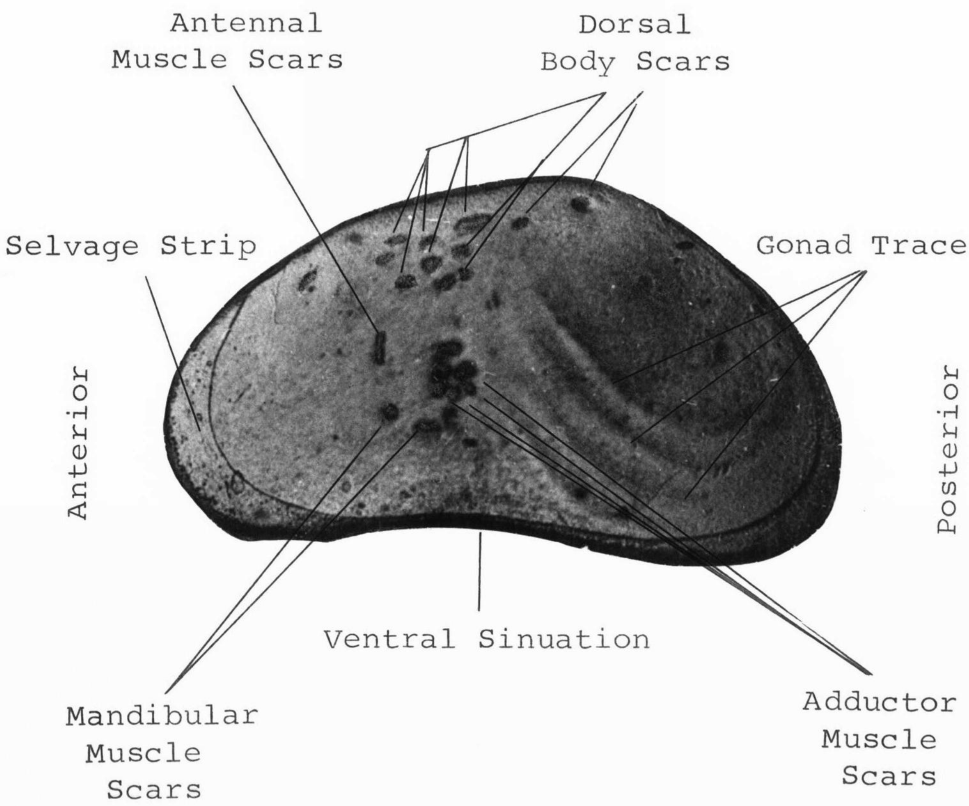
1-4.—Limnocythere friabilis BENSON & MACDONALD, n.sp.; *1*, exterior lateral view of left valve of female; *2*, exterior lateral view of right valve of female; *3*, exterior lateral view of left valve of male; *4*, exterior lateral view of right valve of male; all ×115 24

5,6.—Limnocythere verrucosa HOFF, 1942; *5*, exterior lateral view of right valve of male, ×95; *6*, exterior lateral view of left valve of female, ×110 23

7,8.—Cytherissa lacustris (G. O. SARS), 1863; *7*, exterior lateral view of left valve; *8*, exterior lateral view of right valve; both ×85 22



BENSON & MAC DONALD — Postglacial Ostracodes from Lake Erie



Taxonomically significant morphological features of *Candona subtriangulata*.

bilis has a smaller and more ornamented carapace and is distinctly flattened in the marginal zone. It has, in addition, marginal tubercles and spines and lacks the wide controventral sulcus of *L. staplini*. *L. glypta* DOBBIN, 1941, has somewhat similar carapace ornamentation, but it is larger and lacks the irregular furrows and narrow marginal zone of *friabilis*. *L. sanctipatricii* var. A as illustrated by SWAIN (1955) is very similar to the male of *L. friabilis*. This species is also similar to *L. reticulata* HOFF, 1942. STAPLIN (1953) described this species as "*L. chippewaensis*" (p. 245-248) in his unpublished doctoral thesis.

TABLE 11. *Measurements of Representative Specimens of Limnocythere friabilis*

Length	*Height*	*Valve*	*Sex*
0.50 mm	0.23 mm	Left	Male
0.50	0.22	Right	"
0.52	0.24	"	"
0.52	0.26	Left	"
0.51	0.28	Right	Female
0.44	0.23	"	"
0.48	0.26	"	"
0.46	0.24	Left	"
0.46	0.25	"	"
0.46	0.24	"	"
0.48	0.27	Right	"
0.50	0.28	Left	"

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